

Sea lice (*Lepeophtheirus salmonis*) infestations and the productivity of pink salmon (*Oncorhynchus gorbuscha*) in the Broughton Archipelago, British Columbia, Canada

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Abstract: The spread of salmon lice (*Lepeophtheirus salmonis*) from salmon farms may threaten some wild salmon populations. Infestations of wild juvenile pink salmon (*Oncorhynchus gorbuscha*) have been associated with high mortality and population decline. Using stock–recruit data for pink salmon from the central coast of British Columbia, we analyzed how fishing mortality and spatial covariation combine with louse infestation to affect pink salmon population dynamics. The results indicate substantial coherence in survival at nested spatial scales — large-scale regional covariation and smaller scale covariation within management areas. Populations exposed to salmon farms (those from the Broughton Archipelago) show a sharp decline in productivity during sea lice infestations relative to pre-infestation years. Unexposed populations (comprising four management areas) did not experience a change in productivity during infestation years and had similar productivity to exposed populations before infestations. Our results suggest that sea lice infestations may result in declines of pink salmon populations and that management and policy of salmon farms should consider protecting wild juvenile salmon from exposure to sea lice.

Résumé : La dispersion de poux du saumon (*Lepeophtheirus salmonis*) à partir des élevages de saumons peut menacer certaines populations sauvages de saumons. Des infestations chez de jeunes saumons roses (*Oncorhynchus gorbuscha*) sauvages ont été associées à de fortes mortalités et des déclinés de la population. À l'aide de données de stock-recrues de saumons roses de la côte centrale de la Colombie-Britannique, nous analysons de quelle manière la mortalité due à la pêche et la covariation spatiale se combinent à l'infestation de poux pour affecter la dynamique de population des saumons roses. Nos résultats indiquent une cohérence substantielle dans la survie à des échelles spatiales emboîtées — une covariation régionale à grande échelle et une covariation à plus petite échelle dans les aires de gestion. Les populations exposées aux élevages de saumons (celles de l'archipel de Broughton) subissent un net déclin de leur productivité durant les infestations de poux de mer par rapport aux années précédant l'infestation. Les populations non exposées (comprenant quatre aires de gestion) ne connaissent aucune modification de leur productivité durant les années d'infestation et ont une productivité semblable à celles des populations exposées avant les infestations. Nos résultats indiquent que les infestations de poux de mer peuvent causer des déclinés des populations de saumons roses; la gestion et la politique des élevages de saumons devraient viser à protéger les jeunes saumons sauvages d'une exposition aux poux de mer.

[Traduit par la Rédaction]

Introduction

The growth of aquaculture (Duarte et al. 2007; Food and Agricultural Organization of the United Nations 2007; Naylor et al. 2000) has led to the emergence of infectious diseases that affect both fisheries and aquaculture (Gaughan 2001; Murray and Peeler 2005; Costello 2009). One example is the salmon louse (*Lepeophtheirus salmonis*), a marine ectoparasitic copepod that is native to the northern hemisphere and has become a threat to wild and farmed salmonids in Europe and Canada (Johnson et al. 2004; Costello

2006; Krkošek 2010b). Sea lice are common on both wild and farmed adult salmon and feed on host surface tissues causing morbidity and mortality at high infection intensity (Costello 2006; Pike and Wadsworth 1999). Sea lice infestations of wild juvenile salmonids during early marine life have been associated with reduced survival of some wild salmon populations (Gargan et al. 2002; Skilbrei and Wennevik 2006; Krkošek et al. 2007a). However, fisheries data are notoriously noisy, multifactorial, and subject to spurious correlation, leading to continued debate on the effects of sea lice on wild salmon survival (Brooks and Jones 2008; Rid-

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dell et al. 2008). For example, the links between louse transmission and salmon population dynamics may be mediated by predation (Krkošek et al. 2010), fish size (Jones and Hargreaves 2009), farm management (Morton et al. 2005), and the duration of exposure (Krkošek 2010b). In this paper, we evaluate how fishing mortality and environmental covariation combine with louse infestation to affect the productivity of pink salmon populations in the Broughton Archipelago, British Columbia.

Sea lice and salmon have been intensively studied in the Broughton Archipelago, particularly for pink salmon (*Oncorhynchus gorbuscha*) (Krkošek 2010b). Like other Pacific salmon, pink salmon are anadromous and semelparous, but they are also relatively unique among salmonids in life history. Unlike other salmon species (except chum salmon, *Oncorhynchus keta*), juvenile pink salmon do not rear in fresh waters but instead migrate to sea after hatching and then occupy nearshore (often intertidal) marine waters during a several-month period of rapid growth. After one winter, during which they migrate offshore, pink salmon then return to their natal rivers to spawn, thereby creating a life cycle that is 2 years long. Thus, there are distinct odd and even year populations that do not interbreed but yet occupy the same rivers. In terms of sea lice, much research has been focused on pink salmon because their small size at ocean entry makes them more vulnerable to infestation than larger salmon smolts. In addition, because pink salmon have a short life cycle (2 years) as opposed to other species, stock–recruit data have become available to test hypotheses about productivity and infestations for this species sooner than the others. For more information on pink salmon see Heard (1991).

Salmon farming began in the Broughton Archipelago in 1987 and has since grown in terms of the number of farms and overall production. Sea lice infestations of juvenile pink and chum salmon were first reported in the Broughton Archipelago in 2001 (Morton and Williams 2003) and have since occurred repeatedly there (Morton et al. 2004; Krkošek et al. 2005, 2006) and elsewhere in British Columbia (BC) (Morton et al. 2008). We consider infestations of pink salmon as beginning in the Broughton Archipelago in 2001 because they are conspicuous in nature and are unlikely to have gone previously unnoticed given the local population of biologists, first nations, and fishermen. The cause of a rapid (as opposed to gradual) increase in sea lice abundance may be related to host density thresholds, which can underlie the outbreak, as well as the eradication, of parasites in host populations (Krkošek 2010a). After the 2001 infestation, local populations of pink salmon collapsed, which generated recommendations from the Canadian Pacific Fisheries Resource Conservation Council to follow the Broughton Archipelago to protect the juvenile salmon that were produced by the collapsed brood year (Pacific Fisheries Resource Conservation Council 2002). The recommendations were partially implemented by provincial regulators in spring 2003 that followed a primary migration corridor for juvenile pink salmon, which reduced sea lice abundance on juvenile salmon and improved the survival of that cohort (Morton et al. 2005; Beamish et al. 2006). However, infestations of juvenile pink salmon in the Broughton Archipelago occurred in 2001 (Morton and Williams 2003), 2002 (Morton et al. 2004), as well as 2004 and 2005 (Krkošek et al. 2006).

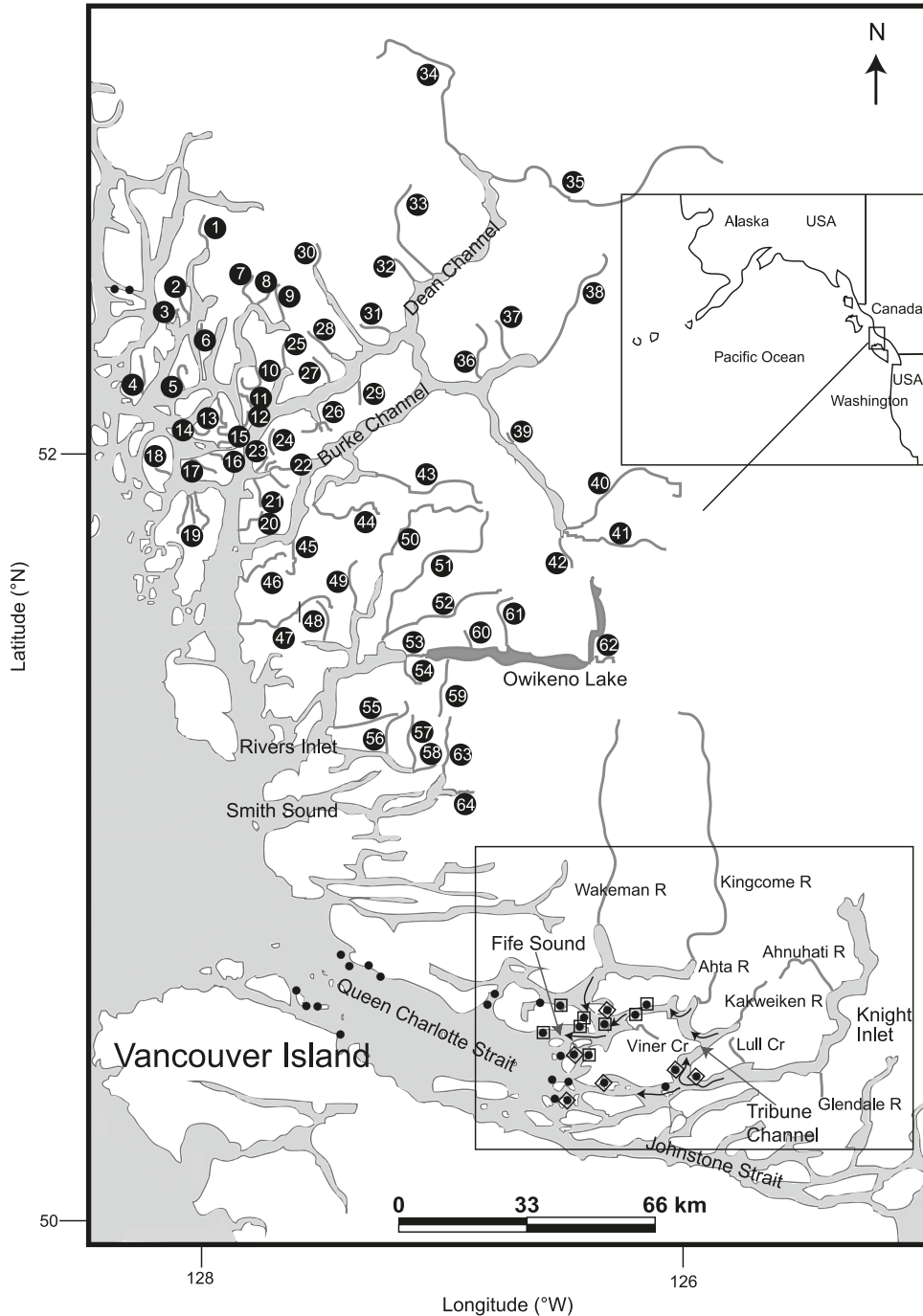
It is important to point out that sea lice are native to BC waters and have been present on wild salmon long before salmon farming began. In areas of BC without farms, the natural baseline estimates of louse infection of juvenile salmon during their first 3 months of marine life is approximately 5% (Krkošek 2010b; Krkošek et al. 2007b). Sea lice are rare on juvenile salmon during this time because the primary natural reservoir for lice, wild adult salmon, don't return to coastal waters on their spawning migration and overlap with wild juvenile salmon until summer when the juvenile salmon are larger and when transmission from wild adult to wild juvenile salmon occurs (Krkošek et al. 2007b; Krkošek 2010b). The working hypothesis is that transmission of sea lice from salmon farms to wild juvenile salmon can increase mortality of juvenile salmon via direct and indirect effects and thereby decrease productivity of wild salmon populations (Costello 2009; Krkošek 2010b). In this paper, we do not evaluate the effects of farms on sea lice transmission, as that has been done in numerous other works (Costello 2009; Krkošek 2010b). Rather, we test if the observed pattern of infestation is associated with expected declines in wild salmon productivity, while explicitly accounting for the potentially confounding effects of fishing mortality and spatial covariation inherent in pink salmon stock–recruit data.

Materials and methods

We used escapement data for pink salmon in one area exposed to salmon farms (the Broughton Archipelago) and a reference area not exposed to salmon farms (Fig. 1). The escapement data were described in two previous publications (Krkošek et al. 2007a; Ford and Myers 2008). Briefly, the data were collected primarily by stream walks and overhead flights by personnel at Fisheries and Oceans Canada. We screened the data, excluding populations with less than eight stock–recruit data pairs in the time series as well as rivers that experienced major changes in escapement methods or had enhancement projects. For example, the Klinaklini River in the Broughton Archipelago was excluded because escapement estimates changed from overhead flights to a fishwheel mark–recapture program. Exceptions include the Kakweiken River, which experienced a spawning channel that was largely unutilized by pink salmon, and the Glendale River, which also had a spawning channel constructed. For the Glendale River case, the spawning channel augmented production substantially, but we included this river nevertheless because of its numerical importance to the Broughton Archipelago stock complex. We compiled catch data from Fisheries and Oceans Canada for salmon management areas comprising the exposed (area 12) and unexposed populations (areas 7, 8, 9, 10). We assumed each population within an area experienced the same exploitation rate and modelled this with a random effect. For the 64 rivers in the unexposed area, there were 19 rivers in salmon management area 7, 28 rivers in area 8, 15 rivers in area 9, and 2 rivers in area 10 (Fig. 1). For these management areas comprising the unexposed populations, we also assumed each population within an area received the same exploitation rate.

The exposed and unexposed populations exist within a region of synchronous survival, suggesting shared environ-

Fig. 1. Map of the study area showing populations of pink salmon used in the analysis. There are populations from eight rivers categorized as exposed to salmon farms from the Broughton Archipelago (boxed region on the lower right). Unexposed populations are situated to the north and are identified by numbers 1–64. Populations are further grouped by Fisheries and Oceans Canada Management Areas 7 (rivers 1–19), 8 (rivers 20–47), 9 (rivers 48–62), 10 (rivers 63–64), and 12 (exposed populations). Salmon farms are identified by unnumbered small, black, filled circles. Squares and diamonds around farm symbols identify farms that were fallowed and held smolts, respectively, during the management intervention in 2003. Map was adapted from figure 1 in Krkošek et al. (2007a).



mental variation (Pyper et al. 2001). The populations also experience temporal autocorrelation, which can be accounted for in the Ricker model by parametric bootstrapping to obtain 95% confidence intervals on parameters (Dennis and Taper 1994). To account for the spatial and temporal correlation, we developed a mixed-model approach using

the Ricker model, allowing for spatial synchrony in survival at regional and management area levels. We applied the model following a matched case-control experimental design in epidemiology, where subjects experiencing common environmental conditions are divided into control (unexposed populations) and treatment (exposed populations) groups,

and inference is conducted on differences between groups (Rothman 1986; Krkošek et al. 2008). The structure of the analysis is also similar to BACI (before–after control–impact) and IVRS (impact vs. reference sites) analyses (Wiens and Parker 1995), except that there is spatial and temporal replication within exposed and unexposed groups both before and during infestations and that statistical inference was conducted by comparing parameter estimates from a hierarchical Ricker model using a bootstrapping algorithm to generate 95% confidence intervals.

To structure the data according to a matched case-control study design, we divided the stock and recruitment data pairs into six categories: exposed and unexposed populations prior to sea lice infestations (recruitment 1972–2001), exposed and unexposed populations during sea lice infestations (recruitment between 2002 and 2006, except 2004), and exposed and unexposed populations during a fallowing management action (recruitment in 2004) corresponding to a management intervention (the provincial government's Sea Lice Action Plan: www.agf.gov.bc.ca/ahc/fish_health/sealice_BA_monitoring.htm) that fallowed farms along a primary wild juvenile salmon migration route and left remaining farms carrying primarily smolts (which are low infection risk) during the outmigration period of juvenile salmon in 2003 (Tribune Channel and Fife Sound; Fig. 1), which is the same cohort that returned to spawn in 2004 (Morton et al. 2005; Krkošek 2010b). For that year, juvenile pink salmon in the Broughton Archipelago encountered primarily fallowed farms (Kingcome, Wakeman, and Tribune populations) or fallowed and smolt farms (Knight Inlet populations). Because pink salmon have a 2-year life cycle, there are odd and even year lineages that occupy each river. Despite occupying the same habitats, the lineages are temporally separated and exhibit different genetics, abundances, and population dynamics (Heard 1991; Quinn 2005). We therefore treated each lineage as a separate population, as is common practice in other analyses of pink salmon stock–recruit data (Pyper et al. 2001; Dorner et al. 2008).

Stock–recruit model

The model development begins by describing the calculations for stock and recruitment values and then by building a stock–recruit model based on the Ricker model (Ricker 1954). We then build upon the basic Ricker model by including terms for the spatial structure of synchrony in salmon survival as well as considering variation in population growth rates in relation to spatial and temporal exposure to sea lice infestation. First, we incorporate fishing mortality to build the stock–recruit relationship for each population by calculating recruitment R for population i in year t as

$$(1) \quad R_{i,t} = N_{i,t}(1 - \mu_{i,t})^{-1}$$

where $N_{i,t}$ is the spawning abundance of pink salmon (i.e., escapement estimate) from population i in year t and $\mu_{i,t}$ is the exploitation rate (catch divided by catch plus escapement) for population i in year t . The spawning stock abundance for population i producing the recruitment in year t is simply the escapement estimate for that population but lagged by 2 years to account for the 2-year life cycle of pink salmon.

To formulate the base model, we assume stochastic Ricker population dynamics for pink salmon, giving the stock–recruit relationship

$$(2) \quad R_{i,t} = N_{i,t-2} \exp(r - b_i N_{i,t-2} + \varepsilon_{i,t})$$

where r is the population growth rate, b_i determines density-dependent mortality and is related to the carrying capacity for population i , and $\varepsilon_{i,t}$ is a normally distributed random variable representing the influence of environmental stochasticity on pink salmon productivity. We do not consider measurement error in our modeling approach, but rather assume that it is small relative to the effects of environmental variation on salmon survival and that it contributes a small (but unknown) amount to the stochastic terms in the model. The process for fitting eq. 2 involves first transforming the model into its linear form

$$(3) \quad \ln(R_{i,t}/N_{i,t-2}) = r - b_i N_{i,t-2} + \varepsilon_{i,t}$$

which can be fit by simple linear regression (Dennis and Taper 1994; Hilborn and Walters 2001).

With eq. 3 as the base, we developed and compared more complex models that structure components of environmental stochasticity to be coherent among populations within management areas and within the entire study region, as well as variation among populations exposed and not exposed to salmon farms and sea lice infestation. We first extended eq. 3 to include variation among populations exposed and unexposed to salmon farms before and during sea lice infestations

$$(4) \quad \ln(R_{i,t}/N_{i,t-2}) = r_j - b_i N_{i,t-2} + \varepsilon_{i,t}$$

The index j corresponds to populations belonging to one of the six exposure categories — time periods before infestations, during infestations, and during the fallow treatment for populations exposed to salmon farms and populations not exposed to salmon farms (Fig. 1). Importantly, r_j are fixed effects in the following analysis as opposed to random effects, which we introduce next to account for the structure of variation (spatial coherence and among populations) in model parameters. We extended this model (eq. 4) by allowing for a spatially synchronous component in environmental stochasticity, as evidenced in Pyper et al. (2001), with a hierarchical or mixed modeling approach

$$(5) \quad \ln(R_{i,t}/N_{i,t-2}) = (r_j + \theta_t) - b_i N_{i,t-2} + \varepsilon_{i,t}$$

Here, θ_t is a normally distributed random variable with mean equal to zero and variance to be estimated. Equation 5 contains two components to environmental stochasticity — variation among years synchronously for all populations (captured by θ_t) and variation among populations that is independent among years (captured by $\varepsilon_{i,t}$).

However, coherence among populations in environmental stochasticity may also occur at smaller spatial scales, with nearby populations exhibiting greater covariation in survival than distant populations (Pyper et al. 2001). For example, populations aggregated at the scale of Fisheries and Oceans Canada management areas within our study system may exhibit different patterns in population dynamics among the management areas. To accommodate this possibility, we ex-

tended eq. 5 to include a second hierarchical term for management area nested within year

$$(6) \quad \ln(R_{i,t}/N_{i,t-2}) = (r_j + \theta_t + \theta_{t,a}) - b_i N_{i,t-2} + \varepsilon_{i,t}$$

The hierarchical random effect components in eq. 6, θ_t and $\theta_{t,a}$, operate by structuring variation such that there is a random normal deviate (with mean equal to zero) common to all populations in each year t , and then another random normal deviation that further partitions variation within each year to populations according to which management area, a , they belong.

Finally, we also considered populations to have intrinsic variation among each other in r , and therefore included a third hierarchical component in the full model

$$(7) \quad \ln(R_{i,t}/N_{i,t-2}) = (r_j + \theta_i + \theta_t + \theta_{t,a}) - b_i N_{i,t-2} + \varepsilon_{i,t}$$

Here, the hierarchical random effects structure variation in a way similar to eq. 6 except that each population i has a population growth rate determined by a further random normal deviation from the growth rate r_j . The remaining variation structure in the hierarchical components follows similarly from eq. 6. In each year, the growth rate for each population has further random deviation from r_j , first according to the deviate for that year common to all populations and then according to the deviate for each management area a .

To complete the hierarchical model development and application, we considered all possible combinations of the random effects components in the hierarchical models. That is, we considered random effects on population, year (eq. 5), area, population plus year, population plus area, area within year (eq. 6), and population plus area within year (eq. 7). Although not all model formulations are detailed by equations in the main text, they are tabulated in the Results. For each formulation of random effects, we compared two models: one that included and one that excluded the fixed effects that structure the population growth rate by time periods preceding and during sea lice infestation (i.e., r is common to all populations in all years or r is specific to population group-period j). All models were fit to the data using maximum likelihood methods in the hierarchical modeling package lme4 in R (www.r-project.org). For each formulation of the random effects components, we used a likelihood ratio test to evaluate if including r_j in the model significantly improved the fit over the model with r constrained to the same value for all groups j . For the full set of candidate models, we used Akaike's information criteria to identify which model had the greatest support from the data. This process provided inference on which random effects components were important for explaining the data and whether structuring r according to population group-periods improved the model fit. However, it did not provide a statistical comparison among population growth rates from the different population groups of exposure to farms and infestation. To make statistical comparisons among these parameter estimates, we developed a bootstrapping algorithm to construct 95% confidence intervals on r_j as per Dennis and Taper (1994) (described in the next section).

We further evaluated the quality of fit of the best-supported model by analyzing the residuals and time series of random effects for covariation. We tested for temporal

autocorrelation in the residuals, for both the entire data set as well as specifically for exposed populations, by using likelihood ratio tests to compare models for the mean of the residuals with and without a first-order autoregressive process (AR1). Similarly, we tested for temporal autocorrelation in the time series of random effects from the best-fit model by using likelihood ratio tests to compare models for the mean random effect with and without a first-order autoregressive process. Regardless of the significance of including the autoregressive process, we report the estimated correlation coefficient for each analysis. We also analyzed the residuals of the exposed populations for spatial covariation. To do this, we conducted pairwise Pearson correlation tests for each combination of exposed river pairs to evaluate covariation in residuals (positive or negative) for each possible pair of populations from rivers in the Broughton Archipelago. We also tested if there was significant correlation between the time series of exploitation estimates and time series of area-level random effects $\theta_{t,a}$ to evaluate if some of the area-level spatial covariation modeled in the data was due to assuming equal exploitation rates for each population within an area.

Growth rate comparisons

To statistically compare the estimates for r among exposed and unexposed populations during and before infestations, we used parametric bootstrapping to obtain 95% confidence intervals on r (Dennis and Taper 1994). However, the hierarchical structure of the data and models are more complex than analysis of individual time series as in Dennis and Taper (1994). We therefore modified the bootstrapping approach in a way that accounted for the hierarchical spatial structure in the data, exploitation, missing data values, and changes in productivity according to louse infestations. The bootstrapping algorithm forecasted recruitment values for each $N_{i,t}$ observation where there was a valid observed $N_{i,t}$ and $N_{i,t-2}$ data pair. The value of r used for each forecasted value corresponded to the estimate from unexposed and exposed populations before and during infestations. To include stochasticity in the simulation, we followed the same hierarchical structure in the hierarchical Ricker models that were fit to the stock-recruit data, of which eq. 6 was the best supported model (see Results).

To use eq. 6 in the bootstrap algorithm, we first drew a random deviate from θ_t for each year. Within each year we drew five random deviates — one for each management area in each year — which were then applied to each population in the respective management area. Finally, residual random environmental variation, represented by $\varepsilon_{i,t}$, was applied by drawing a random variable from $\varepsilon_{i,t}$ separately for each population in each year. With the stochastic components of eq. 6 generated appropriately, we then used the untransformed version of eq. 6

$$(8) \quad R_{i,t} = N_{i,t-2} \exp[(r_j + \theta_t + \theta_{t,a}) - b_i N_{i,t-2} + \varepsilon_{i,t}]$$

to simulate recruitment data for each $N_i(t)$ observation where there was a valid observed $N_{i,t}$ and $N_{i,t-2}$ data pair. We then fit the same model (eq. 6) to the simulated data in exactly the same manner as with the original data and recorded the values of r for each population group (before infestations, during infestations, and the fallow year for exposed and un-

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exposed populations). This bootstrap procedure was repeated 1000 times, generating six sets of 1000 estimates for r corresponding to unexposed and exposed populations preceding infestations, during infestations, and during the fallow. Each of the 95% confidence intervals on r then correspond to the 2.5 and 97.5 percentiles of the 1000 bootstrap estimates.

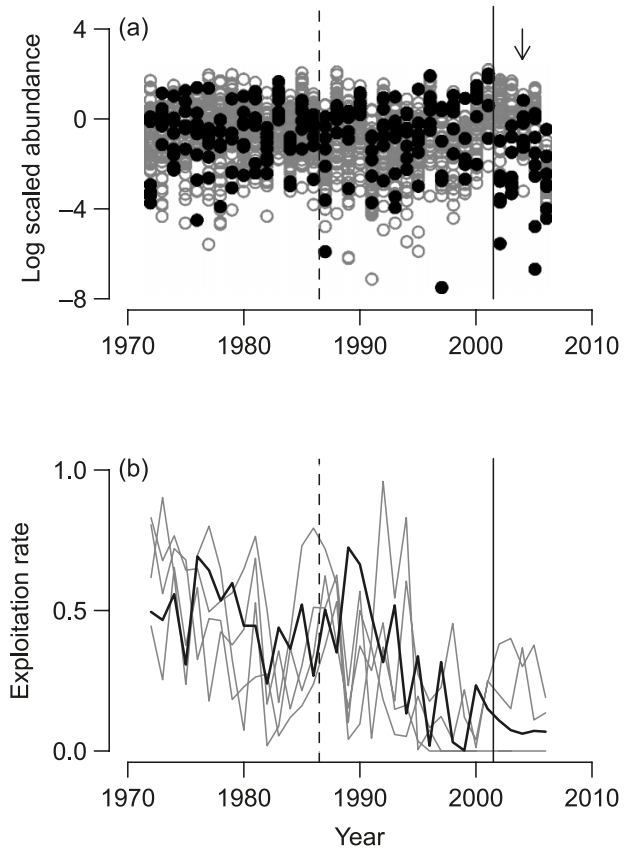
We also evaluated the potential effects of measurement error on uncertainty in the parameter estimates by repeating the above simulations under scenarios where the standard deviation of the residual error was divided between process error and measurement error. To evaluate the potential effects of measurement error, we assumed a log-normal distribution of uncertainty around the escapement estimates and then multiplied each escapement estimate by a random number drawn from the log-normal distribution to determine the number of spawners used in the forecast of recruits. The log-normal distribution had a mean of zero and a standard deviation that was a proportion of the residual error. We conducted four simulations, where measurement error had standard deviations that were 0%, 25%, 50%, and 75% of the standard deviation of the residual errors. The process error in these simulations had corresponding reductions in standard deviation such that 100%, 75%, 50%, and 25% of the standard deviation of the residual error was allocated to process error $\varepsilon_{i,t}$.

Results

The time series of escapement data for pink salmon in the study region indicates populations in the exposed area experienced a decline in abundance relative to populations from unexposed areas during the period of sea lice infestations (Fig. 2). During infestation years, escapement to the exposed populations declined (except for the fallow year) while at the same time there was a reduction in fishing mortality from rates commonly exceeding 50% to rates less than 10% (Fig. 2). Unexposed populations also experienced a decline in fishing mortality in recent years, with populations in management areas 9 and 10 (rivers 48–64 in Fig. 1) experiencing zero fishing mortality in recent years (Fig. 2). However, the majority of populations in the unexposed area were from management areas 7 and 8 (rivers 1–47), where exploitation rates remained between 10% and 40% during infestation years. Although exposed populations in the Broughton Archipelago experienced exploitation between 5% and 10% during infestation years, the targeted fisheries on these populations have been closed, and the estimated fishing mortality is mostly due to incidental mortality from fisheries targeting more southern populations as they migrate through Queen Charlotte Strait and Johnstone Strait (Fig. 1). Despite these changes in fishing mortality, exposed populations experienced a marked decline in survival during sea lice infestation years, whereas unexposed populations did not (Table 1; Fig. 2).

We fit and compared many variations of the Ricker model to the data (Table 2). The model formulations differed in two particular ways: (i) the structure of hierarchical random effects terms and (ii) whether the population growth rate was fixed to the same value for all populations or was structured by exposure to salmon farms and sea lice infestations. For each formulation of random effects, likelihood ratio

Fig. 2. Time series of scaled escapement estimates ($\ln(N_{i,t}/m_i)$, where m_i is the mean escapement for population i) and exploitation rates (proportion of returning salmon harvested by fisheries) for unexposed populations (grey points and lines) and exposed populations (black points and lines). Escapement data are given per river, whereas exploitation rates are given per management area. The vertical dotted line marks the onset of salmon aquaculture in the Broughton Archipelago, the vertical thin line marks the onset of sea lice infestations, and the arrow identifies the fallow treatment in the Broughton Archipelago.



tests indicated that structuring the population growth rate according to sea lice infestation and exposure to salmon farms significantly improved the fit of the model (Table 2). That is, the null hypothesis that the population growth rate was equal among populations exposed and not exposed to salmon farms before and during sea lice infestations was rejected. Among the various model formulations, likelihood values and Akaike's information criteria indicated that the model with hierarchical random effects for year and management area within year was best supported by the data. This suggests populations show spatial covariation in survival rates throughout the study area and also within management areas. The results also indicate there was no evidence for variation in average productivity among populations (θ_i) or areas (θ_a) (Table 2). The best model (eq. 6, Table 2) showed substantial variation in the components of stochasticity, with the standard deviation for regional coherence among years (the random effect on year) equal to 0.61, the standard deviation for coherence within management area (the random effect for area within year) equal to 0.50, and residual standard deviation equal to 1.12.

Table 1. Observations of log recruits per spawner ($\ln(R_t/N_{t-2})$) for pink salmon populations during sea lice infestation years and the fallow treatment (2004).

Population	2002	2003	2004	2005	2006
Ahta	-4.363	-3.088	3.459	1.129	-2.657
Kakweiken	-4.916	-1.679	2.520	0.646	-0.478
Kingcome	-3.680	-0.999	2.691	-1.864	-1.863
Wakeman	-1.879	1.097	0.927	-3.580	-1.484
Viner	-0.396	-2.020	1.632	-0.979	-2.953
Lull	-6.616	-5.234	4.345	3.626	-3.089
Ahnuhati	-4.000	0.478	2.885	0.059	-2.471
Glendale	-3.617	-2.044	3.656	0.396	-1.220
Average	-3.683	-1.686	2.764	-0.071	-2.027

Table 2. Results of fitting various formulations of the Ricker model.

Random effects	Lice	NLL	AIC	Δ AIC	χ^2	df	<i>p</i>
None	No	2866.8	5973.6	460.5			
	Yes	2820.3	5890.7	377.6	93	5	2.20×10^{-16}
<i>P</i>	No	2866.8	5975.6	462.5			
	Yes	2820.3	5892.7	379.6	93	5	2.20×10^{-16}
<i>Y</i>	No	2709.1	5660.3	147.2			
	Yes	2673.6	5599.2	86.1	71.1	5	5.97×10^{-14}
<i>A</i>	No	2866.8	5975.6	462.5			
	Yes	2820.3	5892.7	379.6	93	5	2.20×10^{-16}
<i>P + Y</i>	No	2709.1	5662.3	149.2			
	Yes	2673.6	5601.2	88.1	71.1	5	5.97×10^{-14}
<i>P + A</i>	No	2866.8	5977.6	464.5			
	Yes	2820.3	5894.7	381.6	93	5	2.20×10^{-16}
<i>Y A</i>	No	2646.6	5537.1	24			
	Yes	2629.6	5513.1	0	34	5	2.37×10^{-6}
<i>P + Y A</i>	No	2646.6	5539.1	26			
	Yes	2629.6	5515.1	2	34	5	2.37×10^{-6}

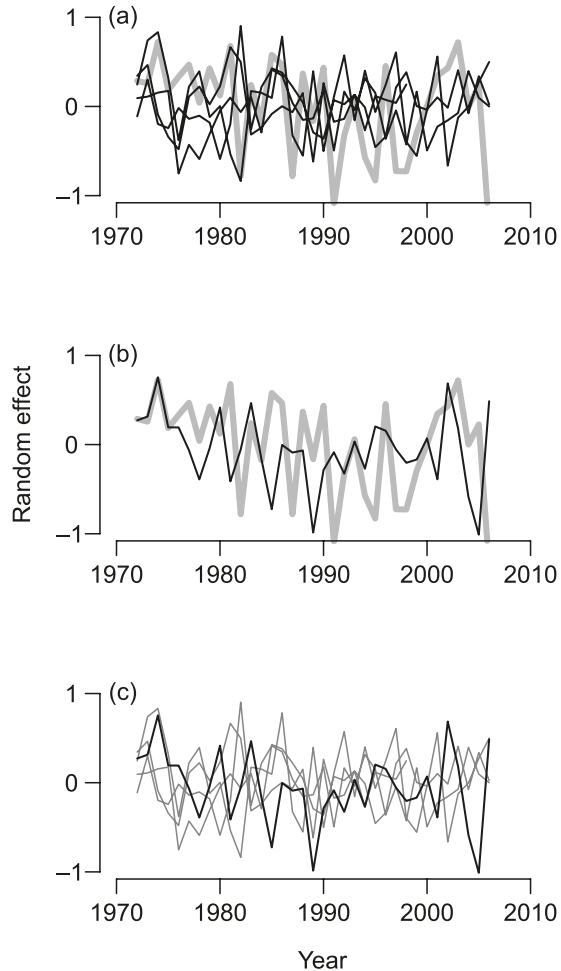
Note: Random effects indicates the nesting structure of random effects components in the hierarchical Ricker model, with *P* indicating population, *Y* indicating year, and *A* indicating area. For example, *P + Y|A* indicates that area was nested within year and that population was a separate random effect. The column Lice indicates if the population growth rate *r* was structured according to periods preceding infestation, during infestation, and during the fallow treatment for exposed and unexposed populations. A value of “no” in the Lice column corresponds to a null model formulation where *r* was a single parameter common to all population groups. For each formulation of random effects, we give the likelihood ratio statistic (χ^2) and associated degrees of freedom (df) and *p* value from the likelihood ratio test comparing models with and without *r* structured by infestation and exposure information. The likelihood ratio tests each had five degrees of freedom — the difference in the number of parameters between the candidate models. Other columns show the negative log-likelihood value (NLL) as well as the Akaike information criteria (AIC) and AIC differences (Δ AIC) for each model. The best-supported model is indicated in bold.

Analysis of the best-fit model indicated that the time series of random deviations for the year and area within year random effects showed substantial environmental stochasticity organized by regional and management area scales (Fig. 3). There was low-level, negative temporal autocorrelation in the residuals for the full data set but no systematic temporal autocorrelation in the random effects from the best-fit model (eq. 6), aside from weak temporal autocorrelation in the random effects for area 9 (Table 3). There was no temporal autocorrelation detectable in the residuals for the exposed populations (Table 3 and Fig. 4), but there was a small degree of spatial covariation evident among rivers in

the exposed region (Table 4). Of the 28 pairwise comparisons, nine showed significant correlation, of which six were negative correlations and three were positive correlations. Much of the spatial covariation is attributable to pink salmon from the Glendale River, which covaried significantly with four of the seven populations. Interestingly, the structure of covariation with the Glendale population involved positive correlation with rivers nearby, no correlation with rivers at intermediate distance, and negative correlation with more distant rivers within the Broughton Archipelago (Table 4 and Fig. 1). The time series of area-level random effects, $\theta_{t,a}$, were not significantly correlated with exploita-

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Fig. 3. Time series of hierarchical random effects components, θ , of the best-fit model (eq. 6). The random deviate common to all populations for each year θ_t is shown as the thick grey line in panels (a) and (b). The random deviates for each unexposed area $\theta_{t,a}$ (management areas 7, 8, 9, 10) within each year are shown as the four black lines in panel (a). The random deviates for the exposed area within each year $\theta_{t,e}$ are shown as the black line in panel (b). Panel (c) shows the time series of random deviates within each year $\theta_{t,a}$ for the exposed area (black line) relative to the random deviates within each year for the unexposed areas (grey lines).



tion rates for management areas 8, 9, and 12, but were significantly correlated for management areas 7 and 10 (Table 5). Introducing measurement error (ME) into the bootstrap procedure had small effects on the estimated 95% confidence intervals for the population growth rate of exposed populations during infestation years (0% ME: -1.72 to -0.32 ; 25% ME: -1.68 to -0.27 ; 50% ME: -1.73 to -0.30 ; 75% ME: -1.74 to -0.31).

Model selection statistics (Table 2) as well as estimates of the population growth rates (r ; Table 6 and Fig. 5) indicate that r was not equal among data groups. To statistically compare estimates of r among data groups, we turned to a parametric bootstrapping algorithm to construct 95% confidence intervals on r for stock–recruit data grouped by exposure to salmon farms and sea lice infestation. The results of the bootstrapping procedure indicate that exposed and unexposed populations did not differ in productivity preceding

sea lice infestations and that during sea lice infestations productivity of exposed populations declined significantly relative to pre-infestation years. In contrast, unexposed populations did not experience a change in productivity during sea lice infestations (Table 6, Fig. 5). During the fallow year, exposed populations experienced an increase in productivity, whereas unexposed populations did not change substantially (Table 6, Fig. 5), although there were few data and no temporal replication for the fallow treatment.

Discussion

Our analysis of stock–recruit data for pink salmon evaluated how the effects of fishing mortality and spatial hierarchies of environmental covariation combine with louse infestation to affect the productivity of pink salmon populations. Diagnostic analysis of the best-fit model indicates there was little covariation remaining in the random effects and residuals of the model and that measurement error likely has little effect on uncertainty in parameter estimates. Overall, the small amount of covariation in residuals and random effects is unlikely to affect the results, which indicate that there is substantial natural variation among and within pink salmon populations and that louse infestations can depress and extirpate pink salmon populations. These results are consistent with previous predictions of high mortality of pink salmon during infestations (Morton and Routledge 2005; Krkošek et al. 2006; Krkošek et al. 2010), analyses of population dynamics of pink salmon (Krkošek et al. 2007a) and coho salmon (Connors et al. 2010) in relation to sea lice infestations, and the global pattern of decline of wild salmon stocks exposed to industrial salmon aquaculture operations (Ford and Myers 2008).

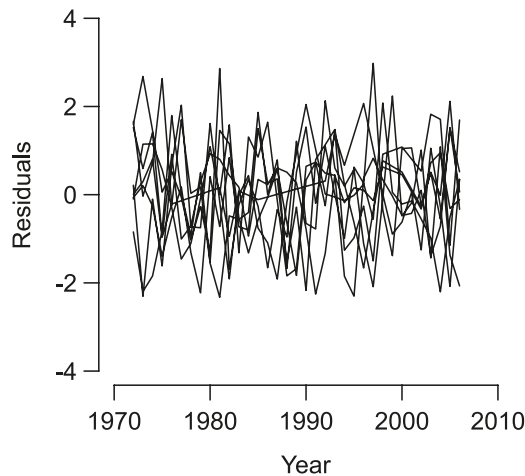
For pink salmon, spatial covariation in survival decays with distance between stocks, but can still persist at regional scales encompassing 500–1000 km (Pyper et al. 2001, 2005). The spatial scale that encompasses the pink salmon populations in our study (~ 500 km) indicates we should expect a small degree of regional coherence in survival rates as well as a larger degree of local coherence in survival rates, possibly due to local environmental conditions as well as fishing mortality. The model accommodated these two spatial scales of covariation in survival via a random effect on year for all stocks collectively and also separately for stocks within separate management areas. This also accounted for any synchronizing effect at the management area scale that could have been caused by the assumption of equal exploitation rates among populations within a management area. However, the analysis of random effects indicated two significant correlations (out of five possible) between area-level random effects and harvest rates, indicating our treatment of exploitation rates did not substantially confound natural coherence at the spatial scale of management units. The diagnostic analysis of the best-fit model found there was minimal spatial covariation among populations in the residuals, indicating our treatment of individual populations as independent samples was robust within the modeling framework. The hierarchical model was further able to differentiate natural regional variability from sea lice effects, such as in 2006 when there was a large negative random effect on all populations that contributed to the poor survival observed during sea lice infestation of exposed populations.

Table 3. Tests for temporal autocorrelation in residuals and random effects in the best-fit model (eq. 6).

	NLL (null)	NLL (alt.)	<i>L</i> ratio	<i>p</i>	Φ
Residuals (all)*	2457.19	2441.88	30.62	<0.0001	-0.14
Residuals (BA)	408.48	408.39	0.18	0.67	0.03
θ_t Year	29.83	29.82	0.01	0.91	0.02
$\theta_{t,a}$ Area 7	16.57	15.36	2.41	0.12	0.27
$\theta_{t,a}$ Area 8	17.38	17.28	0.19	0.66	-0.02
$\theta_{t,a}$ Area 9	14.70	12.81	3.78	0.05	0.36
$\theta_{t,a}$ Area 10	4.75	4.17	1.17	0.28	0.28
$\theta_{t,a}$ Area 12	17.19	17.11	0.15	0.70	-0.07

Note: Residuals are analyzed for the entire data set (all) as well as for the exposed populations in the Broughton Archipelago (BA), specifically. Time series for random effects occurred for an overall year effect (θ_t) as well as for each area ($\theta_{t,a}$: areas 7, 8, 9, 10, 12). Likelihood ratio tests were conducted by comparing models for the mean residual or random effect versus models for the mean residual or random effect with a first-order autoregressive process (see Materials and methods). Shown are the negative log-likelihood values (NLL) for null models (null; no temporal autocorrelation) and alternative models (alt.; first-order autoregressive process), the likelihood ratio test comparing null and alternative models (*L* ratio), corresponding *p* values, and the estimated coefficient for temporal autocorrelation (Φ). Significant effects (*p* = 0.05) for temporal autocorrelation are shown by an asterisk (*).

Fig. 4. Time series of residuals from the best-fit model (eq. 6) for populations from each river in the exposed region, the Broughton Archipelago.



There was, however, one interesting result from the analysis of the spatial covariation of residuals. Of the nine significant correlations of residuals among populations, four were associated with the Glendale River, which covaried with four of the seven other populations. Correlations with Glendale River were positive for nearby rivers and negative for more distant rivers. Because Glendale River has experienced major enhancement (via a spawning channel built in the 1990s) and is numerically dominant among populations in the Broughton Archipelago, this result has interesting implications. One interpretation is that enhancement in one large river may have positive effects on nearby rivers (possibly because of straying) and negative effects on more distant rivers (via competition) where straying rates are reduced but with which there is significant spatial overlap in juvenile salmon habitats. Because enhanced fish are not distinguished from native fish in rivers near Glendale River, it is not possible to evaluate if the positive correlation is indeed due to

straying nor is it possible to evaluate if native populations in nearby rivers (i.e., the subset of fish that are not strays from the spawning channel in Glendale) actually experience a decline in survival due to increased competition. Nevertheless these results are consistent with other findings that enhancement may have negative effects on nearby populations via competition (Hilborn and Eggers 2000), which has also been posited by other authors as an alternate hypothesis for declines in pink salmon populations in the Broughton Archipelago (Riddell et al. 2008). Our results indicate that effects of enhancement in Glendale River may indeed be a component of pink salmon population dynamics in the Broughton Archipelago, but such effects are in addition to — rather than in place of — the effects of louse infestation. During infestations, Glendale River populations followed the same pattern of decline as the other populations in the Broughton Archipelago (Krkošek et al. 2008).

By incorporating fishing mortality, we have better captured the impact of infestations on wild salmon productivity relative to previous estimates, which did not consider variation in harvest rates (Krkošek et al. 2007a). Fishing mortality is a potential confounding factor, since exploitation rates on pink salmon from the Broughton Archipelago have varied from 0.2% to 72% within the time series. The estimated impact of infestations in our analyses was a decline in the population growth rate of pink salmon by 2.15 from $r = 1.15$ prior to infestations to $r = -1.0$ during infestations, a magnitude that is 16% larger than that proposed by Krkošek et al. (2007a). In addition, the uncertainty in parameter estimates was robust to measurement error, as shown by the bootstrap procedure. However, future analyses might consider state–space models as a way of formally modeling both process and measurement error in one analysis. However, such analyses may not control for possible systematic bias in measurement error. For example, the exceptional high survival for the 2004 brood year (Beamish et al. 2006) may be partially due to increased search effort in spawner counts as motivated by population collapse in the previous 2 years. The current analysis indicates the size of the 95%

Table 4. Pairwise Pearson correlations for time series of residuals from the best-fit model (eq. 6) for each river in the Broughton Archipelago.

	AT	KK	KC	WM	VN	LL	AN	GD
AT	—	0.665	0.207	0.308	0.406	0.950	0.053	0.260
KK	-0.076	—	0.915	0.973	0.015*	0.708	0.019*	0.123
KC	-0.226	0.019	—	0.629	0.729	0.170	0.368	0.005*
WM	-0.183	-0.006	0.087	—	0.230	0.005*	0.725	0.035*
VN	0.186	-0.510*	-0.083	0.281	—	0.033*	0.002*	0.117
LL	-0.011	0.068	-0.253	-0.489*	-0.456*	—	0.675	0.022*
AN	-0.340	0.407*	-0.162	-0.064	-0.658*	0.078	—	0.013*
GD	-0.196	0.266	-0.476*	-0.369*	-0.344	0.397*	0.427*	—

Note: The p values for pairwise correlations are shown above the diagonal (upper right) and the correlation coefficients are shown below the diagonal (lower left). Significant ($p < 0.05$) data are indicated with an asterisk (*). River identities are Ahta (AT), Kakweiken (KK), Kingcome (KC), Wakeman (WM), Viner (VN), Lull (LL), Ahnuhati (AN), and Glendale (GD).

Table 5. Results of Pearson product moment correlation tests between time series of exploitation rates and area-level random effects $\theta_{t,a}$, for each management area.

Area	t	df	p	Correlation	95% CI
7	4.17	33	0.0002	0.59	(0.32 to 0.77)
8	0.63	33	0.53	0.11	(-0.23 to 0.42)
9	1.15	33	0.26	0.20	(-0.15 to 0.50)
10	2.10	28	0.04	0.37	(0.01 to 0.64)
12	-0.38	33	0.71	-0.07	(-0.39 to 0.27)

Note: Data shown include the test statistics (t statistic, degrees of freedom (df), p values) and estimated correlation with the 95% confidence interval (CI) for each management area.

confidence intervals on the estimates of the population growth rate is larger than that of Krkošek et al. (2007a), reflecting the increased difficulty in measuring the effects of sea lice infestation given the spatial hierarchical structure in survival combined with the relatively low level of temporal replication within the sea lice infestation category (4 years).

The change in productivity of pink salmon populations is from a recruits-per-spawner value of 3.16 prior to infestations compared with a recruits-per-spawner value of 0.37, which corresponds to a decline in survival by 90%. This change in survival is consistent with similar trends for declines in coho salmon productivity in the Broughton Archipelago associated with sea lice infestations (Connors et al. 2010), estimates of direct mortality of juvenile salmon during infestations (Morton and Routledge 2005; Krkošek et al. 2006) plus indirect effects via mortality from predators (Connors et al. 2008; Krkošek et al. 2010). However, it is important to point out, as others have (Brooks and Jones 2008), that experimental infection studies consistently show high survival of juvenile salmon and high mortality of lice, suggesting parasite rejection of juvenile salmon that are larger than 0.7 g (Jones et al. 2006, 2007; Jones and Hargreaves 2009). The differences in mortality suggested by field and experimental studies may be reconciled by the duration of exposure to sea lice, which can be 2–3 months in field conditions as opposed to less than 1 day in experimental studies (Krkošek et al. 2009), or may be due to increased predation risk of infected fish (Krkošek et al. 2010). The negative population growth rate for infested populations implies population decline (Dennis et al. 1991; Lande 1993) if the environmental conditions causing the decline are sus-

tained. However, we note that a new management system has been implemented in the Broughton Archipelago that combines following and chemical treatment to minimize the risk of sea lice transmission from farmed salmon to wild juvenile salmon. Evaluation of this management plan for reducing sea lice and halting the decline is an important area of current research (Morton et al. 2011).

One key assumption in the analysis is that sea lice infestations of juvenile wild pink salmon in the Broughton Archipelago began in 2001. Morton and Williams (2003) reported high levels of lice on juvenile wild pink salmon in the Broughton Archipelago in 2001, with prevalence of infection exceeding 98% and intensity of infection exceeding 12 lice per fish at locations exposed to farms. Infestations on this scale are highly conspicuous to casual observation from docks or boats without a need for collection and examination of fish to be noticed. Given the local population of biologists, fishermen, fish farmers, and First Nations peoples in the Broughton Archipelago, we consider it unlikely that infestations of this scale occurred without notice prior to 2001. The sudden emergence of infestations is a common characteristic of host–parasite ecology due to the effects of host-density thresholds, where parasite population dynamics can switch from endemic to outbreak conditions (Grenfell and Dobson 1995). Such effects have occurred for sea lice on salmon farms in other regions (New Brunswick, Canada) and are likely to occur in aquaculture–fishery interactions because of increases in aquaculture production, changes in abiotic factors that favour parasite population growth (e.g., warming), or increases in the abundance of sympatric wild host populations (Krkošek 2010a). Given gradual trends in ocean warming, increases in aquaculture production, and high return abundances of adult pink salmon in 2000, it may be that these factors combined to trigger outbreak conditions for sea lice. Nevertheless, the absence of sea lice data from years preceding 2001 means we are unable to test the assumption that infestations of sea lice began in the Broughton Archipelago in 2001.

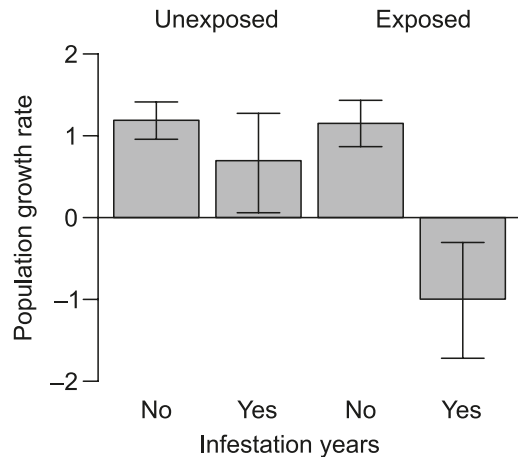
The productivity of fish stocks at low population size, also known as the maximum reproductive rate or the population growth rate, is fundamental to understanding the population biology of fish and informing fisheries management (Myers et al. 1995, 1999). The population growth rate for pink salmon populations not subjected to sea lice infesta-

Table 6. Population growth rates (r) with 95% confidence intervals (CI) for pink salmon populations exposed and unexposed to salmon farms before and during sea lice infestations.

	Before infestations	During infestations	Fallow
Exposed	1.15 ($n = 219$; CI: 0.87 to 1.43)	-1.00 ($n = 32$; CI: -1.72 to -0.32)	2.81 ($n = 8$; CI: 1.36 to 4.24)
Unexposed	1.19 ($n = 1259$; CI: 0.96 to 1.42)	0.70 ($n = 102$; CI: 0.08 to 1.31)	0.18 ($n = 25$; CI: -1.12 to 1.46)

Note: Data in parentheses are point estimates for r from analyzing the unscaled escapement data and the sample sizes (n), the number of stock–recruit data pairs in each category.

Fig. 5. Population growth rates ($\pm 95\%$ confidence intervals, CI) for pink salmon populations from exposed and unexposed regions prior to and during years when sea lice infestations were observed for exposed populations.



tions in our analysis was very near the expected value of $r = 1.2$ (standard deviation = 0.35) estimated for pink salmon in the large meta-analysis by Myers et al. (1999). Similarly, analyses of stock–recruit time series of pink salmon from numerous stocks from BC, Washington, and Alaska indicate good agreement between our estimates of natural productivity and those from the BC central coast as well as the spatial variation in population growth rates (Su et al. 2004; Dorner et al. 2008). This indicates that for populations not experiencing sea lice infestation, the productivity of pink salmon populations in the study region was characteristic of basic pink salmon biology elsewhere throughout their range. However, one departure from the other multistock analyses of pink salmon (e.g., Dorner et al. 2008) is that there was little indication for variation in average productivity among populations or areas (i.e., random effect on population or area). One explanation may be that other multistock analyses cover large spatial variation in stocks (from Washington through Alaska), which would imply greater variation among populations in average productivity due to habitat and climate variation. The populations we studied were at a spatial scale that is smaller than an individual stock in the other analyses, meaning that spatial variation in climate and habitat would be relatively low.

The years of infestations of juvenile wild pink salmon spanned 2001 to 2005 (Morton and Williams 2003; Morton et al. 2004; Krkošek et al. 2006) but also contained a management intervention in 2003 where farms on the migration routes were primarily fallowed or carried smolts (Morton et al. 2005). Sea lice abundances on juvenile wild salmon in the Broughton Archipelago in 2003 were markedly reduced

relative to infestation years (Morton et al. 2004, 2005; Jones and Hargreaves 2007). Our analysis here agrees with other analyses that the 2003 cohort that experienced the fallow treatment and returned to spawn in 2004 also experienced excellent marine survival (Beamish et al. 2006; Krkošek et al. 2007a). However, the increased productivity of this cohort (r estimated as 2.8) greatly exceeds natural rates (population growth rate is typically 1.2, as discussed above), which indicates other factors in the marine environment in addition to reductions in sea lice abundances likely contributed to the productivity of this cohort. However, we caution against overinterpretation of the effects of the fallowing intervention in this analysis, as it only occurred in one year and has not been replicated. Carefully controlled replication of fallowing and (or) chemical treatment is required before sufficient data are accumulated to evaluate the efficacy of management interventions to reduce sea lice and protect wild pink salmon in the Broughton Archipelago. Such a management system is now in place and is an important area of focus for current work (Morton et al. 2011).

Our study design, which compared exposed and unexposed populations before the infestations, during the infestations, and during the fallow, is related to a matched case-control statistical design used in epidemiology (Rothman 1986). The reasoning is that after conditioning on a shared environment, differences between subjects that received a treatment and subjects that did not are attributable to a treatment effect — sea lice infestation in our case. An unavoidable drawback of applying this approach to field data is that control (unexposed populations) and treatment (exposed populations) are not assigned randomly but are based on observations of proximity to salmon farms and sea lice infestations (Krkošek et al. 2008). Further, although the changes in louse abundance for the exposed group may resemble a “natural experiment”, this does not constitute an intentional manipulation to test a hypothesis, making results more difficult to interpret than their experimental counterparts (Lubchenco and Real 1991). For sea lice and salmon, alternate factors cannot be ruled out, but no confounding factors have been identified by regulatory agencies or scientists despite millions of dollars invested into several multiyear studies (Fraser et al. 2009). Nevertheless, a large-scale experiment where sea lice abundances are manipulated according to the scientific principles of randomization and replication would help determine causation between sea lice and salmon productivity. While our results indicate the spread of infection from salmon farms may threaten wild pink salmon populations in the Broughton Archipelago, further work is needed to expand the spatial and taxonomic sample size of studies on these effects. Nevertheless, our results suggest that sea lice infestation is likely a factor that influences the productivity of wild salmon.

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