

Coho salmon productivity in relation to salmon lice from infected prey and salmon farms

Brendan M. Connors^{1*}, Martin Krkošek^{2,3}, Jennifer Ford⁴ and Lawrence M. Dill¹

¹Earth to Ocean and Evolutionary and Behavioural Ecology Research Groups, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada; ²School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat St, Seattle, WA 98105, USA; ³Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand; and ⁴Oceans and Coastal Management Division, Bedford Institute of Oceanography, Fisheries and Oceans Canada, Dartmouth, NS B2Y 4A2, Canada

Summary

1. Pathogen transmission from open net-pen aquaculture facilities can depress sympatric wild fish populations. However, little is known about the effects of pathogen transmission from farmed fish on species interactions or other ecosystem components. Coho salmon *Oncorhynchus kisutch* smolts are susceptible hosts to the parasitic salmon louse *Lepeophtheirus salmonis* as well as a primary predator of juvenile pink *Oncorhynchus gorbuscha* salmon, a major host species for lice.

2. We used a hierarchical model of stock-recruit dynamics to compare coho salmon population dynamics across a region that varies in salmon louse infestation of juvenile coho and their pink salmon prey.

3. During a period of recurring salmon louse infestations in a region of open net-pen salmon farms, coho salmon productivity (recruits per spawner at low spawner abundance) was depressed approximately sevenfold relative to unexposed populations. Alternate hypotheses for the observed difference in productivity, such as declines in coho prey, perturbations to freshwater habitat or stochasticity, are unlikely to explain this pattern.

4. Lice parasitizing juvenile coho salmon were likely to be trophically transmitted during predation on parasitized juvenile pink salmon as well as directly transmitted from salmon farms.

5. *Synthesis and applications.* The finding that species interactions may cause the effects of pathogen transmission from farmed to wild fish to propagate up a marine food web has important conservation implications: (i) the management of salmon aquaculture should consider and account for species interactions and the potential for these interactions to intensify pathogen transmission from farmed to wild fish, (ii) the ecosystem impact of louse transmission from farmed to wild salmon has likely to have been previously underestimated and (iii) comprehensive monitoring of wild salmon and their population dynamics in areas of intensive salmon aquaculture should be a priority to determine if open net-pen salmon aquaculture is ecologically sustainable.

Key-words: aquaculture, Pacific salmon, parasite, predator–prey, trophic transmission

Introduction

As a result of the extensive marine migrations of anadromous salmonids, juveniles are spatially and temporally separated from adults during early marine life. This serves as an allopatric barrier to pathogen transmission between age classes until they occur in sympatry either in the outer coastal environment

or in the open ocean (Krkosek *et al.* 2007b; Gottesfeld *et al.* 2009). A consequence of migratory allopatry is that during the first few months of marine life, when they are most vulnerable, juvenile salmonids are not subject to some pathogens common to older and larger salmonids. Intensive open net-pen salmon aquaculture can undermine this natural barrier to transmission by providing a year-round host population in the nearshore marine environment whose pathogens can spill over to sympatric wild juvenile salmonids (Costello 2009). As global

*Correspondence author. E-mail: bconnors@sfu.ca

salmon aquaculture production continues to grow, many wild salmon populations in areas of intensive aquaculture are in decline as a result of pathogen transmission from farmed salmon to wild juvenile salmon as well as from competition and interbreeding (Ford & Myers 2008).

Pathogen transmission from farmed to wild salmon has been particularly well studied in the Broughton Archipelago of British Columbia, Canada, where salmon lice *Lepeophtheirus salmonis* Krøyer from salmon farms can infect out-migrating juvenile pink salmon *Oncorhynchus gorbuscha* (Krkosek, Lewis & Volpe 2005) and elevate their early marine mortality (Krkosek *et al.* 2006). Coincident with louse exposure, pink salmon populations in the Broughton Archipelago have sharply declined (Krkosek *et al.* 2007a). However, much debate surrounds the role that louse infection from salmon aquaculture has played in these declines (Costello 2009) as well as the broader consequences of louse transmission for the marine ecosystems in which it occurs.

Juvenile pink salmon are subject to intense predation from other larger juvenile salmonids, including coho salmon smolts *Oncorhynchus kisutch* Walbaum during the first few months of marine life. Unlike pink salmon, which head to sea immediately after emergence from the gravel, coho spend 1 year or more in freshwater before entering the marine environment. The larger size of coho at marine entry may buffer juvenile coho from the impact of louse infection early in marine life. In coastal marine environments, coho smolts can be a major predator of pink salmon (Parker 1968) and salmon lice have the potential to alter this natural predator–prey dynamic by increasing the susceptibility of pink salmon to predation (Krkosek *et al.* in press), and through the trophic transmission of lice during predation events (Connors, Krkosek & Dill 2008). This latter process increases infection on coho smolts two- to threefold in areas where they rear and interact with

infected juvenile pink salmon prey (Connors *et al.* 2010). Therefore, louse transmission from salmon farms may indirectly influence the health of sympatric coho salmon smolts via the accumulation of lice from the infected prey on coho. While the trophic accumulation of lice may undermine the protection from ectoparasites conferred by the larger body size of coho, the effect of salmon louse infestation on coho at the population level has not been evaluated.

Here, we examine time series data on coho salmon populations from the central coast of British Columbia (Fig. 1) that have varied in their exposure to salmon louse infestations associated with salmon aquaculture. We compared coho productivity (recruits per pawner at low spawner abundance) between populations exposed and unexposed to salmon farms, both before and during louse infestations. Our findings demonstrate that coho populations had depressed productivity when exposed to louse infestations associated with salmon farms, suggesting that parasite transmission from farmed to wild salmon can propagate up a salmonid food web with negative consequences for predatory salmon populations and the ecosystems in which they are embedded.

Materials and methods

We compiled Fisheries and Oceans Canada escapement data (number of adult spawners) for 53 watersheds in four management areas from 1975 to 2007 (Fig. 1; see Appendix S1, Supporting Information). All records of ‘none-observed’ and ‘adults present’ as well as watersheds subject to coho enhancement programmes (i.e. hatcheries) were removed. Because of temporal and spatial autocorrelation, commercial exploitation of coho ranging from 4% to 90% over the time series, and within- and among-year environmental stochasticity, we used a hierarchical model of stock–recruit dynamics with spatially covarying productivity. This allowed us to control for commercial exploitation, account for sources of environmental stochasticity, and

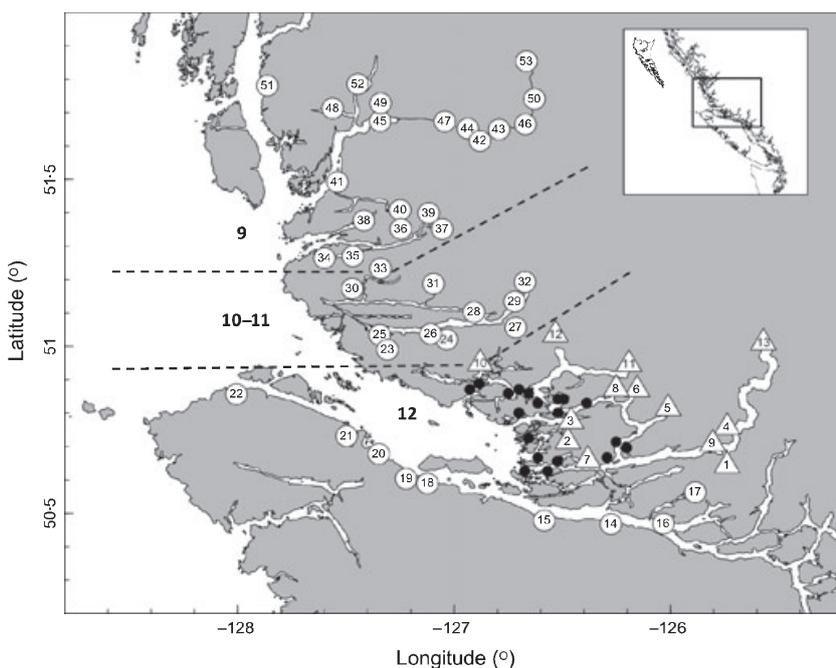


Fig. 1. Coho salmon populations (see Appendix S1, Supporting Information, for corresponding names) from the midcoast of British Columbia used to examine population dynamics in exposed (open triangles, 1–13) and unexposed (open circles, 14–53) populations before and during recurrent salmon louse infestations associated with salmon farms (solid black circles). Dashed lines separate Fisheries and Oceans Canada management areas. Locations of watersheds and farms are approximate and farms outside of the region associated with recurrent salmon louse infestations are not plotted.

test for an influence of recurrent louse infestations on coho population dynamics.

To incorporate commercial exploitation we obtained estimated exploitation rates for the populations in each year of the time series from Fisheries and Oceans Canada. These estimates are based on coded-wire tags placed in out-migrating smolts and recovered by fisheries as adults return to their natal watersheds (Simpson *et al.* 2004). Average exploitation based on estimates from three indicator streams (Quinsam, Big Qualicum and Black Creek), when available, was used from 1975 to 1998 for all populations. In 1998, coho fisheries became selective for hatchery fish and so only estimates from Black Creek (a wild indicator stock) were used subsequently. Big Qualicum exploitation estimates from 1986 to 1989 were excluded because of concerns with smolt quality (J. Irvine, Fisheries and Oceans Canada, pers. comm.).

With the escapement records and exploitation estimates we calculated recruitment for each population in each year:

$$R_{i,t} = N_{i,t}[1 - \mu_t]^{-1} \quad \text{eqn 1}$$

where R is the number of adult recruits, N is the coho escapement estimate and μ is the exploitation estimate for all populations in year t . The stock that produced the recruits in population i and year t is the escapement estimate for population i in year $t - 3$ assuming a 3-year life cycle for coho (Groot & Margolis 1991). We then assumed stochastic Ricker population dynamics (Ricker 1954) and incorporated recruitment from eqn. (1) to build the stock recruit relationship:

$$R_{i,t} = N_{i,t-3} \exp[r - b_i N_{i,t-3} + \varepsilon_{i,t}] \quad \text{eqn 2}$$

where r is productivity at low spawner abundance and b reflects density dependence in relation to the carrying capacity of population i . Eqn 2 can be log transformed to obtain the linear equation:

$$\ln[R_{i,t}/N_{i,t-3}] = r - b_i N_{i,t-3} + \varepsilon_{i,t} \quad \text{eqn 3}$$

whose parameters can be estimated using linear mixed effects models.

Salmon louse infestations on juvenile pink salmon have been documented in the Broughton Archipelago in the spring of 2001, 2002 and from 2004 to 2006 (Morton & Williams 2003; Morton *et al.* 2004; Krkosek, Lewis & Volpe 2005; Krkosek *et al.* 2006; Jones & Hargreaves 2007), which correspond to adult coho that returned to spawn in 2002, 2003 and from 2005 to 2007. Juvenile coho have been examined for lice in two of these years (spring of 2004 and 2005) and in both years infestations on coho were positively correlated with infestation on pinks (Connors *et al.* 2010). We extended eqn 3, which became the null model, to include variation in productivity among populations exposed and unexposed to salmon farms before and during salmon louse infestations:

$$\ln[R_{i,t}/N_{i,t-3}] = r_j - b_i N_{i,t-3} + \varepsilon_{i,t} \quad \text{eqn 4}$$

where j is one of six groups: exposed and unexposed populations in years preceding salmon louse infestations (1975–2000), during recurrent salmon louse infestations (2001–2002, 2004–2006) and during a non-random fallowing management action (i.e. emptying of salmon farms during the spring of 2003).

We also extended the null and stratified models (eqn 4) to include synchronous environmental variation at two spatial scales:

$$\ln[R_{i,t}/N_{i,t-3}] = (r_j + \theta_t + \theta_{t,a}) - b_i N_{i,t-3} + \varepsilon_{i,t} \quad \text{eqn 5}$$

resulting in three components of environmental stochasticity: variation among years synchronously for all populations (θ_t), variation among years synchronously for populations within each

Fisheries and Oceans management area nested within θ_t ($\theta_{t,a}$; Fig. 1) and variation within populations that is independent among years ($\varepsilon_{i,t}$). Each of these components was normally distributed random variables with a mean of zero and variance that is estimated. The null and stratified models as well as the components of environmental stochasticity were fit using maximum likelihood and compared using AIC (Burnham & Anderson 2002) and likelihood ratio tests (Hilborn & Mangel 1997) using R (R Development Core Team 2010). The best-fit model was validated graphically by plotting observed values vs. fitted values and residuals against fitted values and explanatory variables to verify homogeneity. A histogram of the residuals was generated to check for normality.

To statistically compare parameter estimates (i.e. productivity among exposed and unexposed populations before and during infestations), we constructed 95% confidence intervals for r_j by modifying the bootstrapping algorithm of Dennis & Taper (1994) to account for the hierarchical nature of the data, commercial exploitation and changes in productivity. In each iteration of the algorithm, we forecasted recruitment for each $N_{i,t}$ observation where there was a $N_{i,t}$ and $N_{i,t-3}$ data pair using the r_j corresponding to the estimate from exposed and unexposed populations before and during infestations. Stochasticity was included in the simulation by drawing a random deviate from θ_t for each year, $\theta_{t,a}$ for each management area in each year and $\varepsilon_{i,t}$ for each population within each year. Once these stochastic elements were generated, we used the untransformed version of eqn 5 to simulate recruitment data for each $N_{i,t}$ observation where there was a $N_{i,t}$ and $N_{i,t-3}$ data pair. The same model (i.e. eqn 5) was then fit to the simulated data, as described above with the original data set, 1000 times and at each iteration values of r were recorded for each population group (before infestations, during infestations, and the fallow year for exposed and unexposed populations). Confidence intervals were then calculated as the 2.5 and 97.5 percentiles of the 1000 bootstrap estimates of r .

To examine the likelihood that the observed difference in population growth rates between exposed and unexposed populations during salmon louse infestations was spurious, we built on an approach first described by Carpenter *et al.* (1989) to detect changes in a manipulated ecosystem relative to an undisturbed reference system when opportunities for randomization and replication are not available. This involved fitting eqn 5 retaining the same exposed/unexposed before/during infestation grouping structure (i.e. 2 years exposed to sea lice followed by a fallow year and then 3 exposed years with the remaining years of the time series as pre-exposed) in 1-year increments starting in 1975. At each of the 27 iterations we calculated the difference in r between 'exposed' and 'unexposed' populations during 'infestations'. This approach allowed us to compare the observed difference in productivity between exposed and unexposed populations during the true infestations to the difference we would expect to see based on chance alone given the natural variability in productivity among populations and years in the data set. A normal distribution was fit to the distribution of simulated differences in r and the probability of observing a difference as great as or greater than the one observed was calculated.

Results

Excluding populations with years without escapement estimates resulted in 636 stock-recruit data pairs (see Appendix S1, Supporting Information). The best-supported model included group-specific productivity and variation among

years synchronously for all populations and populations within each management area (Table 1). During recurrent salmon louse infestations exposed populations were characterized by generally negative survival (i.e. ln recruits per spawner; Table 2) and had significantly lower productivity than (i) unexposed populations during the recurrent infestations, and (ii) exposed and unexposed populations prior to salmon louse infestations (Fig. 2; Table S1, Supporting Information). Exposed and unexposed productivity during the fallow year was not significantly different from pre-salmon louse infestation productivity. However, given the paucity of stock recruit pairs for coho that went to sea during the fallow (i.e. 2003 and returned to spawn in 2004), our power to detect a difference was weak. The point estimates of productivity translate into approximately sevenfold decline in productivity for coho salmon populations in the exposed region relative to those not exposed to salmon aquaculture (i.e. e^r for exposed populations was ~ 0.75 recruits per spawner at low spawner abundance while for control populations it was ~ 5.75 recruits per spawner at low spawner abundance). The next best-supported model

Table 1. Relative fit of models predicting productivity of coho salmon populations

Model	Δ AIC	No. parameters
$S \sim P + D_i + \epsilon$	724.1	55
$S \sim P_m + D_i + \epsilon$	687.1	60
$S \sim P + D_i + (1 Y) + \epsilon$	34.7	56
$S \sim P_m + D_i + (1 Y) + \epsilon$	5.5	61
$S \sim P + D_i + (1 Y/A) + \epsilon$	28.4	56
$S \sim P_m + D_i + (1 Y/A) + \epsilon$	0	62

Models relate survival (S ; $\ln[\text{recruits}/\text{spawner}]$) to productivity of all populations (P) or populations within each louse exposure group (subscript m) while accounting for population specific (subscript i) density dependence (D) and residual variation (ϵ). Variation among years synchronously for all populations ($1|Y$) and variation among years synchronously for populations within each management area nested within year ($1|Y/A$) are also included. Δ AIC is the AIC difference between the model in question and the best-supported model in bold.

Table 2. Observed survival ($\ln[R_t/N_{t-3}]$) for exposed coho salmon populations in the Broughton Archipelago during salmon lice infestation years and the fallow treatment (i.e. the cohort that went to sea in 2003 and returned in 2004). Exposed watersheds without stock-recruit pairs from 2002 to 2007 (i.e. Ahta Valley, Embley, Gilford and Glendale) are not presented

Population	2002	2003	2004	2005	2006	2007
Ahnuhati	0.52	-0.90	-	-1.14	-1.18	-3.46
Ahta	-1.22	-2.69	-	1.45	0.34	-3.22
Kakweiken	1.30	-1.32	-	-3.3	0.36	0.24
Kingcome	-0.54	-	-	-0.24	-	-1.92
Klinaklini	0.77	0.17	-	-	-	-
Kwlate	-1.21	-0.70	-	1.68	-	-
Shoal Harbour	-	-1.57	-0.01	-	0.42	-
Viner	0.19	-1.64	3.41	-	-	-
Wakeman	-	-1.34	-	1.27	0.42	-3.74
Average	-0.03	-1.25	1.7	-0.05	0.07	-2.42

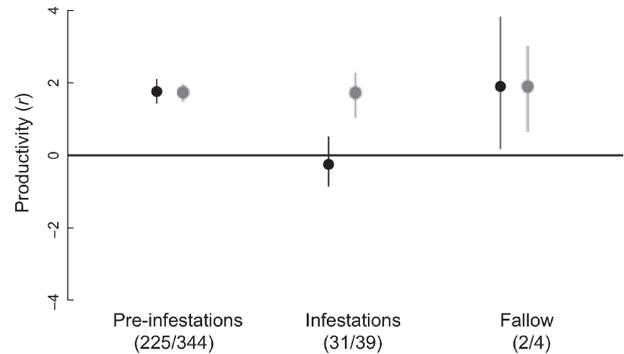


Fig. 2. Productivity ($\pm 95\%$ bootstrapped confidence intervals) of coho salmon populations from exposed (black circles) and unexposed regions (grey circles) prior to and during years when salmon lice epizootics were observed in exposed populations as well as during the fallow treatment year. Values given in parentheses below groups represent the number of stock recruit pairs used to estimate productivity for exposed and unexposed populations respectively.

(Δ AIC of 5.5; Table 1) did not include variation among years synchronously for populations within each management area. Productivity estimates based on the next best-supported model did not differ substantially from the best-supported model [i.e. Δ in productivity between control and exposed populations during louse infestations changes by 0.03 (from -1.99 to -1.96)].

The observed difference in productivity between exposed and control groups during louse infestations was unprecedented in the time series (see Fig. S3, Supporting Information). The probability of observing a difference in productivity as great as or greater than the one observed, given the distribution of differences in the rest of the time-series, was 0.000017 ($\mu = -0.12, \sigma = 0.45; Z\text{-score} = -4.14$).

Discussion

Our results indicate that relative to unexposed populations coho salmon productivity in an area of intensive salmon aquaculture was depressed approximately sevenfold during a period of salmon louse infestations. These declines are consistent with known louse exposure. Declines in productivity coincide with the first documented salmon louse epizootics in the Broughton Archipelago (Morton & Williams 2003). When farms were fallowed, lice abundance on out-migrating salmonids declined (Morton, Routledge & Williams 2005) and coho productivity appeared to rebound to pre-infestation levels, although we had low power to detect a difference if one did exist. Estimated productivity for populations in years and regions not exposed to lice are consistent with those estimated for salmonids elsewhere (Myers, Bowen & Barrowman 1999).

Coho from the unexposed rivers were unlikely to interact with farmed salmon and infected pink salmon during early marine life because of the assumed direction of their migration. However, some unexposed populations may pass by salmon farms at a considerable distance later in marine life, and are therefore only relatively unexposed compared with our exposed populations. Nonetheless, this would tend towards

conservative estimates of an influence of farms because our analysis would then be trying to detect a localized effect in addition to any broader effects.

Pink salmon populations in the Broughton Archipelago have also declined over the same time period (Krkosek *et al.* 2007a). As juvenile pink salmon can be an important early marine resource for coho smolts, declines in pink salmon could in theory contribute to, or even drive, the observed decline in coho productivity. However, evidence of a relationship between pink and coho salmon abundance in areas not exposed to aquaculture is equivocal (e.g. Briscoe *et al.* 2005; Beamish *et al.* 2008) suggesting that coho populations are not limited by the abundance of pink salmon fry during early marine life. We also cannot rule out the possibility that another factor specific to the Broughton Archipelago, such as a sudden coincident change in early marine productivity or degradation of freshwater habitat, drives both pink and coho productivity during exposed years. However, despite millions of dollars invested into government, industry and academic research programmes a non-lice factor has yet to be identified (Fraser *et al.* 2009).

Salmon louse transmission from farmed to wild pink salmon compromises the ability of juvenile pink salmon to escape predation, resulting in selective predation of infected pinks by coho (Krkosek *et al.* in press) and the accumulation of motile (pre-adult and adult) lice on coho from their prey (Connors, Krkosek & Dill 2008; Connors *et al.* 2010). Our findings suggest that coho populations are depressed, at least in part, because of this indirect transmission of lice from salmon aquaculture. While the direct transmission of infective stage lice from farmed salmon to sympatric coho salmon undoubtedly contributes to salmon louse abundance on coho, the indirect accumulation of motile stage lice as a result of consuming infected prey may increase motile louse on coho by two to three times (Connors *et al.* 2010). As motile stage sea lice are the most pathogenic to host fish (Costello 2006; Wagner, Fast & Johnson 2008), the role of trophic transmission in the observed declines in coho productivity may be considerable.

High abundance of motile stage lice can cause host morbidity, and mortality and louse burdens at lower levels can lead to changes in host physiology (reviewed by Wagner, Fast & Johnson 2008), which may underlie observed changes in host behaviour and fitness with infection (Wagner *et al.* 2003; Webster, Dill & Butterworth 2007; Krkosek *et al.* in press). Our understanding of the influence of salmon louse infection on coho smolts is limited to the latter's physiology, immunology and histopathology following a single exposure of infective stage sea lice (Johnson & Albright 1992; Fast *et al.* 2002) at abundances lower than those observed in the field (Connors *et al.* 2010). Small changes in early marine growth in coho can strongly influence early marine survival and resulting spawner abundance (Beamish, Mahnken & Neville 2004) suggesting that if sub-lethal exposure to lice during the critical early marine period reduces coho smolt growth there could be consequences for coho population dynamics. The lack of data on salmon louse-coho interactions under controlled condi-

tions precludes drawing definitive links between louse abundance in the field and coho health, and highlights the need for future work on coho-salmon louse interactions. Demonstrating causal linkages would require an ecosystem-scale experiment with randomization and replication of coho salmon populations exposed to manipulated abundances of sea lice on salmon farms. Such a study would be expensive, logistically difficult, socially contentious and may raise ethical issues. However, it is important to note a coordinated management plan has recently been implemented in the Broughton Archipelago, the success of which for salmon population dynamics has yet to be evaluated.

Pacific salmon link marine and terrestrial ecosystems, and can strongly influence the productivity of coastal environments (Gresh, Lichatowich & Schoonmaker 2000; Schindler *et al.* 2003). Our findings provide evidence to suggest that the transmission of salmon lice, directly and indirectly, from farmed salmon to coho salmon can depress coho salmon productivity. This may have important consequences for the structure and function of the coastal ecosystems in which farmed and wild salmon occur. That coho salmon populations are depressed in concert with louse exposure from salmon farms has a number of important implications for the management of intensive open net-pen aquaculture in regions with wild salmon populations. The transmission of parasites from farmed to wild fish does not occur in an ecological vacuum; rather, interactions among species may intensify or mitigate transmission and its consequences. We suggest there is an urgent need to consider the broader ecosystem consequences of pathogen transmission from farmed to wild salmon and to tailor monitoring and management accordingly. This should include monitoring the health of all salmonids during early marine life in areas of intensive salmon aquaculture in concert with management actions aimed at eliminating the transmission of lice from farmed to wild salmon. Only through monitoring and rigorous assessment of the health of salmon at both the individual and population levels can managers and conservationists begin to determine if wild and farmed salmon can co-exist in coastal marine environments.

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References

- Beamish, R.J., Mahnken, C. & Neville, C.M. (2004) Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Transactions of the American Fisheries Society*, **133**, 26–33.

- Beamish, R.J., Sweeting, R.M., Lange, K.L. & Neville, C.M. (2008) Changes in the population ecology of hatchery and wild coho salmon in the Strait of Georgia. *Transactions of the American Fisheries Society*, **137**, 503–520.
- Briscoe, R.J., Adkison, M.D., Wertheimer, A. & Taylor, S.G. (2005) Biophysical factors associated with the marine survival of Auke Creek, Alaska, coho salmon. *Transactions of the American Fisheries Society*, **134**, 817–828.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference*. Springer, New York, NY.
- Carpenter, S.R., Frost, T.M., Heisey, D. & Kratz, T.K. (1989) Randomized intervention analysis and the interpretation of whole-ecosystem experiments. *Ecology*, **70**, 1142–1152.
- Connors, B.M., Krkosek, M. & Dill, L.M. (2008) Sea lice escape predation on their host. *Biology Letters*, **4**, 455–457.
- Connors, B.M., Hargreaves, N.B., Jones, S.R.M. & Dill, L.M. (2010) Predation intensifies parasite exposure in a salmonid food chain. *Journal of Applied Ecology*, doi: 10.1111/j.1365-2664.2010.01887.x.
- Costello, M.J. (2006) Ecology of sea lice parasitic on farmed and wild fish. *Trends in Parasitology*, **22**, 475–483.
- 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. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **276**, 3385–3394.
- Dennis, B. & Taper, M.L. (1994) Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs*, **79**, 426–411.
- Fast, M.D., Ross, N.W., Mustafa, A., Sims, D.E., Johnson, S.C., Conboy, G.A., Speare, D.J., Johnson, G. & Burka, J.F. (2002) Susceptibility of rainbow trout *Oncorhynchus mykiss*, Atlantic salmon *Salmo salar* and coho salmon *Oncorhynchus kisutch* to experimental infection with sea lice *Lepeophtheirus salmonis*. *Diseases of Aquatic Organisms*, **52**, 57–68.
- Ford, J.S. & Myers, R.A. (2008) A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biology*, **6**, 411–417.
- Fraser, J., Burrige, C., Lornie, J., Maynard, J., Nyce, H., Ryan, T. & Woodward, J. (2009) *BC Pacific Salmon Forum Final Report and Recommendations to the Government of British Columbia*. Vancouver, pp. 1–96.
- Gottesfeld, A.S., Proctor, B., Rolston, L.D. & Carr-Harris, C. (2009) Sea lice, *Lepeophtheirus salmonis*, transfer between wild sympatric adult and juvenile salmon on the north coast of British Columbia, Canada. *Journal of Fish Diseases*, **32**, 45–57.
- Gresh, T., Lichatowich, J. & Schoonmaker, P. (2000) An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries*, **25**, 15–21.
- Groot, C. & Margolis, L. (1991) *Pacific Salmon Life Histories*. UBC Press, Vancouver, WA.
- Hilborn, R. & Mangel, M. (1997) *The Ecological Detective*. Princeton University Press, Princeton, NJ.
- Johnson, S.C. & Albright, L.J. (1992) Comparative susceptibility and histopathology of the response of naive Atlantic, chinook and coho salmon to experimental infections with *Lepeophtheirus salmonis* (Copepoda : Caligidae). *Diseases of Aquatic Organisms*, **14**, 179–193.
- Jones, S.R.M. & Hargreaves, N.B. (2007) The abundance and distribution of *Lepeophtheirus salmonis* (Copepoda : Caligidae) on pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon in coastal British Columbia. *Journal of Parasitology*, **93**, 1324–1331.
- Krkosek, M., Lewis, M.A. & Volpe, J.P. (2005) Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proceedings of the Royal Society of London B-Biological Sciences*, **272**, 689–696.
- Krkosek, M., Lewis, M.A., Morton, A., Frazer, L.N. & Volpe, J.P. (2006) Epizootics of wild fish induced by farm fish. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 15506–15510.
- Krkosek, M., Ford, J.S., Morton, A., Myers, R.A. & Lewis, M.A. (2007a) Declining wild salmon populations in relation to parasites from farmed salmon. *Science*, **318**, 1711–1713.
- Krkosek, M., Gottesfeld, A., Proctor, B., Rolston, D., Carr-Harris, C. & Lewis, M.A. (2007b) Effects of host migration, diversity and aquaculture on sea lice threats to Pacific salmon populations. *Proceedings of the Royal Society of London B-Biological Sciences*, **274**, 3141–3149.
- Krkosek, M., Connors, B.M., Ford, H., Peacock, S., Mages, P., Ford, J.S., Morton, A., Volpe, J.P., Dill, L.M. & Lewis, M.A. (in press). Fish farms, parasites and predators: implications for salmon population dynamics. *Ecological Applications*.
- Morton, A., Routledge, R.D. & Williams, R. (2005) Temporal patterns of sea louse infestation on wild Pacific salmon in relation to the fallowing of Atlantic salmon farms. *North American Journal of Fisheries Management*, **25**, 811–821.
- Morton, A.B. & Williams, R. (2003) First report of a sea louse, *Lepeophtheirus salmonis*, infestation on juvenile pink salmon, *Oncorhynchus gorbuscha*, in nearshore habitat. *Canadian Field-Naturalist*, **117**, 634–641.
- Morton, A., Routledge, R., Peet, C. & Ladwig, A. (2004) Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 147–157.
- Myers, R.A., Bowen, K.G. & Barrowman, N.J. (1999) Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 2404–2419.
- Parker, R.R. (1968) Marine mortality schedules of pink salmon of Bella Coola river central British Columbia. *Journal of the Fisheries Research Board of Canada*, **25**, 757–764.
- R Development Core Team. (2010) *R: A Language and Environment for Statistical Computing*. Vienna, Austria.
- Ricker, W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**, 559–623.
- Schindler, D.E., Scheuerell, M.D., Moore, J.W., Gende, S.M., Francis, T.B. & Palen, W.J. (2003) Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment*, **1**, 31–37.
- Simpson, K., Chamberlain, M., Fagan, F., Tanasichuck, R.W. & Dobson, D. (2004) Forecast for southern British Columbia coho salmon in 2004. *Fisheries and Oceans Canada Canadian Science Advisory Secretariat*, **135**.
- Wagner, G.N., Fast, M.D. & Johnson, S.C. (2008) Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. *Trends in Parasitology*, **24**, 176–183.
- Wagner, G.N., McKinley, R.S., Bjorn, P.A. & Finstad, B. (2003) Physiological impact of sea lice on swimming performance of Atlantic salmon. *Journal of Fish Biology*, **62**, 1000–1009.
- Webster, S.J., Dill, L.M. & Butterworth, K. (2007) The effect of sea lice infestation on the salinity preference and energetic expenditure of juvenile pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 672–680.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Coho salmon escapement data used in analysis.

Table S1. Productivity of coho salmon populations before and during louse infestations.

Fig. S1. Histogram of differences in productivity between exposed and control population if year louse infestations began is randomly assigned.

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