

Effects of parasites from salmon farms on productivity of wild salmon

Martin Krkošek^{a,b,1}, Brendan M. Connors^{b,c}, Alexandra Morton^{b,d}, Mark A. Lewis^e, Lawrence M. Dill^f, and Ray Hilborn^f

^aDepartment of Zoology, University of Otago, Dunedin, New Zealand, 9016; ^bSalmon Coast Field Station, Simoom Sound, BC, Canada V0P 1S0; ^cEarth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6; ^dRaincoast Research Society, Simoom Sound, BC, Canada V0P 1S0; ^eCentre for Mathematical Biology, Department of Mathematical and Statistical Sciences, Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2G1; and ^fSchool of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105

Edited by William C. Clark, Harvard University, Cambridge, MA, and approved July 27, 2011 (received for review February 2, 2011)

The ecological risks of salmon aquaculture have motivated changes to management and policy designed to protect wild salmon populations and habitats in several countries. In Canada, much attention has focused on outbreaks of parasitic copepods, sea lice (*Lepeophtheirus salmonis*), on farmed and wild salmon in the Broughton Archipelago, British Columbia. Several recent studies have reached contradictory conclusions on whether the spread of lice from salmon farms affects the productivity of sympatric wild salmon populations. We analyzed recently available sea lice data on farms and spawner–recruit data for pink (*Oncorhynchus gorbuscha*) and coho (*Oncorhynchus kisutch*) salmon populations in the Broughton Archipelago and nearby regions where farms are not present. Our results show that sea lice abundance on farms is negatively associated with productivity of both pink and coho salmon in the Broughton Archipelago. These results reconcile the contradictory findings of previous studies and suggest that management and policy measures designed to protect wild salmon from sea lice should yield conservation and fishery benefits.

The spread of pathogens from salmon aquaculture operations is among the more prominent threats to salmon fisheries and conservation in Canada and Europe (1, 2). In particular, research has focused on the spillover and spillback of salmon lice (*Lepeophtheirus salmonis*), a native parasitic copepod, between wild and farmed salmon (3, 4). In the Broughton Archipelago, British Columbia, Canada (Fig. 1), salmon farms have been associated with louse infestations of wild juvenile Pacific salmon (5–8), elevated mortality in experiments (6, 9, 10), and decline of local stocks (11, 12). These relationships have been subject to contentious debate in Canada (13–20) and Europe (21). However, countries such as Norway, Iceland, and Canada have responded to disease and escape (22) risks by establishing protected areas where salmon farming is restricted (23–25).

Farmed salmon are raised in net pens that are commonly situated on the migration routes of wild salmon (2, 23). Salmon lice can spread among wild and farmed salmon via the free-swimming larval copepodite (3) as well as through the dispersal of motile preadult and adult lice in their search for mates (26) or evasion of predators (27). Once attached to a fish, lice feed upon host surface tissues, which can cause morbidity and mortality, as they develop from copepodid to chalimus and then motile stages (28). Transmission of lice from farms to wild juvenile salmon is thought to occur primarily through copepodites (6), but predation on infected prey also intensifies exposure of larger predatory salmonids to motile stages (27, 29). Populations of pink salmon (*Oncorhynchus gorbuscha*) and one of their major predators during the juvenile phase, coho salmon (*Oncorhynchus kisutch*), have shown depressed productivity [defined as the natural logarithm of recruits per spawner, $\ln(R/S)$] during infestations associated with farmed salmon (11, 12).

However, recent work focusing on a single pink salmon stock complex concluded that salmon farms do not affect the productivity of wild salmon (15). The study further advised against management and policy such as coordinated fallowing or closed containment technology that could reduce disease risk for wild

salmon (15). These conclusions and policy recommendations are based on a statistically nonsignificant result of a correlation test between pink salmon spawner–recruit data and *L. salmonis* abundance on salmon farms in the Broughton Archipelago. Here, we reanalyze the data in ref. 15, using a multistock model that assimilates data over broader temporal and spatial scales, and arrive at the opposite conclusion: Local declines in pink salmon, as well as coho salmon, are correlated with *L. salmonis* abundance on salmon farms, consistent with previous work (11, 12).

Results

Model selection statistics supported inclusion of the regional sea lice abundance estimates reported in ref. 15 as a predictor of survival for both pink and coho salmon from the Broughton Archipelago (Table S1). This result was consistent for all formulations of random effects in the model and for lice estimates for both March and April reported in ref. 15 (Table S1). For both April and March data, as well as for both pink and coho, model selection statistics suggest the best model included random effects for year and management area within year (Table S1). Inclusion of a random effect on population did not improve the fit of the model to the data (Table S1). These results for pink salmon are based on the same spawner–recruit data for the Broughton Archipelago and sea lice abundance estimates originally reported in ref. 15 (Dataset S1).

Using the best-supported model from Table S1 we then analyzed the spawner–recruit data for the control populations and the southeastern populations of the Broughton Archipelago (excluding the Embly River) under the four scenarios of infection risk (Data section in Methods, Figs. S1–S4). The four scenarios of infection risk differed among each other in some years such as 2000 and 2004 (Table 1). In 2000, the data indicate that two outbreaks occurred, both in the northwestern region of the Broughton Archipelago (15). Statistical support for any particular infection scenario was largely equivocal for pink salmon with only weak evidence that the regional estimate of lice from ref. 15 was less supported than estimates taken over the southeastern farms only (Table 2). For coho there was greater support for the regional estimate of lice than for estimates taken over southeastern farms only.

Given the different levels of support for the four infection scenarios (Table 2), we estimated the louse-induced mortality of pink and coho salmon for each scenario. There was substantial variation in the magnitude of estimated louse effect, c , among scenarios (Table 2). The estimated mortality of wild salmon due

Author contributions: M.K., B.M.C., A.M., M.A.L., L.M.D., and R.H. designed research; M.K. and B.M.C. performed research; M.K. contributed new reagents/analytic tools; M.K. and B.M.C. analyzed data; and M.K., B.M.C., A.M., M.A.L., L.M.D., and R.H. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: martin.krkošek@otago.ac.nz.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1101845108/-DCSupplemental.

Table 3. Results of power analysis for each infection scenario showing the proportion of simulations that yielded Δ AIC scores exceeding 4 and 8 between models with and without lice as a covariate for the multistock model (MS) and the linear regression of single-stock (SS) aggregated data as in ref. 15

Model	MS, Δ AIC > 8	MS, Δ AIC > 4	SS, Δ AIC > 8	SS, Δ AIC > 4	SS, $P < 0.05$
All stocks	0.22	0.48	0.07	0.22	0.27
Scenario 1	0.24	0.52	0.05	0.17	0.25
Scenario 2	0.60	0.83	0.07	0.23	0.30
Scenario 3	0.50	0.78	0.08	0.25	0.29
Scenario 4	0.55	0.78	0.07	0.22	0.31

The "All stocks" scenario is an assessment of methods in ref. 15, which includes all Broughton Archipelago populations and the regional louse estimates for April reported in ref. 15. Also shown is the proportion of simulations that yielded a P value < 0.05 in the linear regression test used in ref. 15.

ref. 15 and similarly for the four infection scenarios, whereas the multistock model yielded a higher percentage of simulations (up to 80% in the infection scenarios) where the Δ AIC value exceeded 4. For a level of statistical evidence for louse effects at Δ AIC = 8, the approach in ref. 15 was particularly weak compared with the multistock model approach (Table 3). The estimated statistical power of the linear regression test used in ref. 15 was $\sim 30\%$ (Table 3).

Discussion

Several recent studies have reached contradictory conclusions on the effects of sea lice from salmon farms on the productivity and conservation of wild Pacific salmon stocks (1, 11, 12, 15, 30, 31). Our reanalysis of the data in ref. 15 does not support their conclusion that sea lice from salmon farms do not affect wild salmon populations. Their conclusion (15) was based on a statistically nonsignificant correlation between survival of a pink salmon stock complex and sea lice abundance on farms. By placing their model (15) in a hierarchical multistock framework, spawner–recruit data at the river level can be accommodated, including spatial and temporal controls. The difference between our results and those of ref. 15 arises because the multistock model assimilates data over control populations as well as years before aquaculture began, which contribute to estimates of nonlouse parameters, thereby providing better estimates of the effects of lice on survival. Indeed, our power analysis indicated that the methods used in ref. 15 risk a 70% chance of committing a type II error (false negative).

Our results show that survival is negatively correlated with abundance of lice on salmon farms, for both pink and coho salmon. This is consistent with previous analyses of spawner–recruit data for both species that used a multistock approach that used a fixed factor to group years when infestations of wild juvenile salmon were observed relative to years before infestations were observed (11, 12). Our results here, which instead treat abundance of lice on farmed salmon as a time-varying covariate, indicate a direct link between survival and louse abundance on farms. However, this approach also reveals that the magnitude of the estimated effect of lice is sensitive to assumptions on the spatial distribution of lice among farms and the migration routes of wild juvenile salmon. Further work is needed on juvenile salmon migration routes and timing to quantitatively link farm location, louse abundance, and salmon survival.

An important uncertainty in the data is the lack of sea lice records from salmon farms during the 1990s when farm production was growing and lice were considered to have been present but no outbreaks or parasiticide treatments were documented (15). In addition, there are no data on sea lice numbers on wild juvenile salmon before 2001. In our analysis we have dealt with the absence of louse records from farms in the 1990s by treating them as missing data, removing spawner–recruit

observations in the Broughton Archipelago during the 1990s from the analysis. This assumption differs from previous analyses that assumed sea lice infestations of wild juvenile salmon did not occur before 2001. If lice were present but at a regionally negligible abundance before 2000, then there would likely be little change to the results. However, if lice were in fact abundant and infestations of wild juvenile salmon occurred in the 1990s, the estimated effect of lice on wild salmon survival would likely be diminished due to high salmon returns in those years.

A plausible explanation for an apparent emergence of louse epizootics of wild juvenile salmon starting in 2001 comes from the epidemiological concept of a host density threshold (32, 33), below which lice would persist at low levels and above which systematic regional outbreaks would occur (32). An abrupt transition from endemic to epidemic dynamics of lice has occurred elsewhere, in New Brunswick, Canada (34). For the Broughton Archipelago, lice were present in the 1990s but any outbreaks and treatment were undocumented and there was no need to monitor lice. Farm production in the Broughton Archipelago increased gradually during the 1990s until it plateaued in 2002 (15). Toward the end of this growth period, during 2000–2001, infestations on farms spread from rare isolated events to systematic regional outbreaks that required monitoring and frequent treatment with parasiticides (15). Also during that time, the first infestations of wild juvenile salmon, which are conspicuous events, were observed and reported (5, 35). This situation suggests that the critical host density for lice in the Broughton Archipelago was exceeded near the year 2001.

Other studies have also suggested that lice from farms do not affect the survival of wild salmon in the Broughton Archipelago (30, 31). Beamish et al. (31) interpreted one observation of exceptionally high survival of pink salmon as evidence that lice do not affect survival of wild salmon. However, the cohort studied in ref. 31 was not subjected to major sea lice infestation but rather to a management intervention that fallowed farms along a primary migration route and reduced sea lice abundance on wild juvenile salmon 10-fold relative to other observed infestations (36). Other extrapolations of laboratory studies suggesting louse-induced mortality of wild salmon is negligible (30) ignore the three orders of magnitude difference in infection period between laboratory studies (minutes or hours) and field conditions (months) (37), sublethal effects of infection on predation risk (10), and other indirect effects of lice that could affect survival such as reduced body growth (38). Sublethal effects, particularly on body growth, as well as trophic transmission of motile lice may be important for explaining elevated mortality of coho, which are larger and presumably more robust to infection than pink salmon (27, 29, 38).

Medical analysis in ref. 15 was claimed to support the conclusion that lice from salmon farms do not affect wild salmon populations. This consisted mainly of the argument that Koch's

postulates have not been fulfilled for sea lice and juvenile pink salmon, based on results from some of our previous studies that were not testing Koch's postulates (6, 9, 37). We (M.K., B.M.C., A.M., and L.M.D.) have conducted experiments on the effects of motile lice on the behavior of previously uninfected juvenile salmon (10, 26). Many of our trials and pilot studies have failed or ended due to morbidity or death whereas uninfected fish survived and appeared healthy. Koch's postulates have been fulfilled, although not reported as such. In addition, we note that sea lice (27), as well as other parasites (39), can leave dead hosts, and so Koch's postulates cannot be universally applied. The other component of the medical analysis in ref. 15 was an extrapolation from one other laboratory study, discussed above, suggesting that juvenile pink salmon with >0.7 g body weight are not killed by lice (30). Such extrapolation is flawed as explained above and also ignores that farms commonly expose pink salmon to sea lice at sizes <0.7 g (30).

Our analysis of the spawner–recruit data and sea lice abundance estimates assumes that infection and mortality occur as linear processes. However, density dependence is common during transmission (40), and density dependence may further mediate compensatory or depensatory predation that can affect dynamics of parasites and prey in complex ways (10). The multistock model we applied to the sea lice and spawner–recruit data does not address these nonlinear processes, although future analyses may shed light on these interactions. However, such analyses must first reduce the uncertainties in the connections among farm locations, salmon migration routes, and infection risk, which our assessment of infection scenarios suggests affect the estimated effects of lice on survival. In addition, we note that although we focused on estimating the effects of lice on salmon survival, many other factors affect the population dynamics of Pacific salmon (41–43). Our use of a multistock mixed-effects model helps control for these other factors by assimilating information across spatially covarying exposed and unexposed populations.

Some previous results have discounted a need for aquaculture management and policy that could protect wild salmon from sea lice (15). Currently, a moratorium on aquaculture development exists on the (mostly) undeveloped central coast of British Columbia, and there is a coordinated area management plan in the Broughton Archipelago (and many areas of Europe) that combines fallowing and parasiticides to constrain lice numbers. Such management changes may also be of value in other regions of British Columbia where infestations of wild juvenile salmon have also occurred (7, 44) and to control other diseases within and between farms (45–47). Although our results identify a negative association between louse abundance on farms and productivity of wild salmon in the Broughton Archipelago that is supported by underlying mechanisms of transmission and mortality (6, 10, 35), it is possible that other unknown factors that are spatially and temporally correlated with lice on farms may underlie our results. Nevertheless, our results indicate that the management and policy recommendations in ref. 15 are not supported, nor is their suggestion that lice may provide a food provision for juvenile salmon that improves productivity. Rather, initiatives that protect wild salmon from lice should yield fishery and conservation benefits.

Methods

Data. The spawner–recruitment data span 1970–2009 for populations of pink salmon and coho salmon in the Central Coast and Broughton Archipelago region of British Columbia. For pink salmon there are 104 populations not exposed to salmon farms and 17 populations exposed to salmon farms. For coho salmon, there are 40 unexposed and 13 exposed populations. The pink salmon data have been described in refs. 12 and 15, whereas the coho salmon data have been described in ref. 11. Rivers for exposed populations are shown in Fig. 1 and the data are further detailed in *SI Methods*.

We used monthly estimates of adult female *L. salmonis* abundance on salmon farms in the Broughton Archipelago (2000–2008) from ref. 15 to construct indexes of louse exposure that wild juvenile salmon may experience during their seaward migration. First, we used the estimates for regional total lice on farms in the Broughton Archipelago for March and April exactly as provided by ref. 15 to test whether their nonsignificant result was robust under the multistock modeling framework (described below). We then considered plausible migration routes for juvenile salmon on the basis of our 25 y of collective field experience during 2001–2011 studying juvenile salmon in the Broughton Archipelago (Fig. 1). Migration routes and the treatment of missing data from farms in 2000–2002 resulted in four infection scenarios: (i) regional estimates exactly as reported for April in ref. 15, (ii) sum of lice on southeastern farms only with missing lice estimates filled in as zero, (iii) sum of lice on southeastern farms only with missing lice estimates filled in for all stocked farms, and (iv) sum of lice on southeastern farms only with missing louse estimates filled in for farms in their second year of production only. Details of the four infection scenarios are in *SI Methods*.

Model. The model is a multistock version of the Ricker model (48). The simplest form of the model is

$$\ln[R_{i,t}/S_{i,t}] = r - b_i S_{i,t} - cL_{t+\tau} + \varepsilon_{i,t}, \quad [1]$$

where $S_{i,t}$ is the spawners in population i in year t , $R_{i,t}$ is adult recruitment produced by spawners in population i in year t , r is the population growth rate, b_i is density-dependent mortality for population i , and $\varepsilon_{i,t}$ is a random normal variable for environmental variability that is independent among years and populations. The variable $L_{t+\tau}$ is the regional abundance of adult female lice on farms in year $t + \tau$, where τ is the age of seawater entry of juvenile salmon (1 for pinks, 2 for coho). We used the estimates of L under the four scenarios described above and set $L = 0$ for unexposed populations and for years before farming began in the Broughton Archipelago. For years when farms exist but no lice data exist (1990–1999), L was treated as missing data.

We considered several variations of Eq. 1 as candidate models, each of which included random effects to account for spatial variation and covariation in survival (11, 12, 49). In particular, we considered random effects for year, fisheries management area, and population, each additive to the population growth rate and normally distributed with mean of zero and variance to be estimated. Random effects for year account for spatial synchrony in survival among all populations whereas random effects for area account for spatial synchrony within areas. Random effects on area within year allowed for nested spatial scales of synchrony. Random effects on population allowed for intrinsic variation among populations in productivity. The formulations of random effects in the multistock model that we considered are detailed in *SI Methods*. Analyses were implemented in the statistical programming language R (www.r-project.org), using the *lmer* function in the *lme4* package for mixed-effects modeling and the *mcmc* function (which uses locally uniform priors) to calculate 95% credible intervals on the louse parameter c .

Data Analysis. The analysis began by fitting Eq. 1 for all formulations of random effects for population, year, and area (*SI Methods*) to the full spawner–recruit datasets for pink salmon (brood years 1970–2007) and coho salmon (brood years 1972–2006). For each formulation of random effects, we fitted and compared models with and without sea lice on farms as a covariate. This was done twice, once each for the regional sea lice estimates reported in ref. 15 for March and April. Then, using the best supported model we reanalyzed the spawner–recruit data (brood years 1970–2007) according to the infection scenarios described in *Sea Lice Data* to compare which infection scenario was best supported by the spawner–recruit data as well as to evaluate the sensitivity of the estimates of the louse-associated mortality parameter c to assumptions on infection scenarios. This latter scenario excluded the Embly River to focus on the remaining populations in the southeastern unit of the Broughton Archipelago that share the infection scenarios (reference populations north of the Broughton Archipelago were still included). For each infection scenario, we provide estimates of the mortality in each cohort of pink salmon and coho salmon that is estimated to be due to sea lice from salmon farms.

Power Analysis. Using the model that was most supported on the basis of AIC scores, we then conducted a power analysis to investigate the ability of the multistock model to detect an effect of lice on survival of pink salmon. This was compared with the approach used in ref. 15 that yielded a statistically

nonsignificant result. To make inference from the two approaches comparable (the multistock model uses AIC values whereas ref. 15 used the P values from linear regression of survival vs. louse abundance), we evaluated the linear regression results by the AIC difference between linear regression models with and without lice as a covariate. The analysis was done by first stochastically simulating recruitment values using the best-supported model with spawner and lice data as input. Then the multistock model was fitted to the simulated data, and the linear regression was fitted to aggregated simulated data for Broughton populations only for recruitment years 2001–2009 exactly as was done in ref. 15. The simulation was conducted 1,000 times and we recorded the frequency of Δ AIC scores exceeding 4 and 8,

which could be considered moderate and strong levels of statistical evidence (50). In addition to the AIC differences, we also computed the P values from the linear regression approach in ref. 15 to calculate the power of their test (proportion of simulations that yielded $P < 0.05$).

ACKNOWLEDGMENTS. We are grateful for discussions with Carl Walters that improved the manuscript. This work was supported by a Mathematics of Information Technology and Complex Systems fellowship (to B.M.C.) (with industrial partner Watershed Watch Salmon Society and Save our Salmon Society) and a Natural Sciences and Engineering Research Council Discovery Grant and Canada Research Chair (to M.A.L.).

- Krkošek M, et al. (2007) Declining wild salmon populations in relation to parasites from farm salmon. *Science* 318:1772–1775.
- Costello MJ (2009) How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proc Biol Sci* 276: 3385–3394.
- Costello MJ (2006) Ecology of sea lice parasitic on farmed and wild fish. *Trends Parasitol* 22:475–483.
- Hilborn R (2006) Salmon-farming impacts on wild salmon. *Proc Natl Acad Sci USA* 103: 15506–15510.
- Morton AB, Williams R (2003) First report of a sea louse, *Lepeophtheirus salmonis*, infestation on juvenile pink salmon, *Oncorhynchus gorbuscha*, in nearshore habitat. *Can Field Nat* 117:634–641.
- Krkošek M, Lewis MA, Morton A, Frazer LN, Volpe JP (2006) Epizootics of wild fish induced by farm fish. *Proc Natl Acad Sci USA* 103:15506–15510.
- Price MHH, Morton A, Reynolds JD (2010) Evidence of farm-induced parasite infestations on wild juvenile salmon in multiple regions of coastal British Columbia, Canada. *Can J Fish Aquat Sci* 67:1925–1932.
- Price MHH, et al. (2011) Sea louse infestation of juvenile sockeye salmon in relation to marine salmon farms on Canada's west coast. *PLoS ONE* 6:e16851.
- Morton A, Routledge R (2005) Mortality rates for juvenile pink *Oncorhynchus gorbuscha* and chum *O. keta* salmon infested with sea lice *Lepeophtheirus salmonis* in the Broughton Archipelago. *Alaska Fish Res Bull* 11:146–152.
- Krkošek M, et al. (2011) Fish farms, parasites, and predators: Implications for salmon population dynamics. *Ecol Appl* 21:897–914.
- Connors B, Krkošek M, Ford JS, Dill LM (2010) Coho salmon productivity in relation to salmon lice from infested prey and salmon farms. *J Appl Ecol* 47:1372–1377.
- Krkošek M, Hilborn R (2011) Sea lice (*Lepeophtheirus salmonis*) infestations and the productivity of pink salmon (*Oncorhynchus gorbuscha*) in the Broughton Archipelago, British Columbia, Canada. *Can J Fish Aquat Sci* 68:17–29.
- Krkošek M, Ford JS, Morton A, Lele S, Lewis MA (2008) Response to comment on "Declining wild salmon populations in relation to parasites from farm salmon". *Science* 322:1790.
- Riddell BE, Beamish RJ, Richards LR, Candy JR (2008) Comment on "Declining wild salmon populations in relation to parasites from farm salmon". *Science* 322:1790.
- Marty GD, Saksida SM, Quinn TJ, 2nd (2010) Relationship of farm salmon, sea lice, and wild salmon populations. *Proc Natl Acad Sci USA* 107:22599–22604.
- Beamish RJ, et al. (2007) A proposed life history strategy for the salmon louse, *Lepeophtheirus salmonis* in the subarctic Pacific. *Aquaculture* 264:428–440.
- Dill LM, Connors B, Losos C, Mages P (2008) Comment on Beamish et al. "A proposed life history strategy for the salmon louse, *Lepeophtheirus salmonis* in the subarctic Pacific. *Aquaculture* 266:154–155.
- Brooks KM, Jones SRM (2008) Perspectives on pink salmon and sea lice: Scientific evidence fails to support the extinction hypothesis. *Rev Fish Sci* 16:403–412.
- Krkošek M, Ford JS, Lele S, Lewis MA (2008) Sea lice and pink salmon declines: A response to Brooks and Jones (2008). *Rev Fish Sci* 16:413–436.
- Frazer LN (2008) Sea-cage aquaculture, sea lice, and declines of wild fish. *Conserv Biol* 23:599–607.
- McVicar AH (2004) Management actions in relation to the controversy about salmon lice infections in fish farms as a hazard to wild salmonid populations. *Aquacult Res* 35: 751–758.
- Naylor R, et al. (2005) Fugitive salmon: Assessing the risks of escaped fish from net-pen aquaculture. *Bioscience* 55:427–437.
- Krkošek M (2010) Sea lice and salmon in Pacific Canada: Ecology and policy. *Front Ecol Environ* 86:201–209.
- Gudjonsson S, Scarnechia DL (2009) "Even the evil need a place to live": Wild salmon, salmon farming, and zoning of the Icelandic coastline. *Fisheries* 34:477–486.
- Paisley LG, et al. (2010) An overview of aquaculture in the Nordic countries. *J World Aquacult Soc* 41:1–17.
- Connors BM, Lagasse C, Dill LM (2011) What's love got to do with it? Ontogenetic drivers of dispersal in a marine ectoparasite. *Behav Ecol* 22:588–593.
- Connors BM, Krkošek M, Dill LM (2008) Sea lice escape predation on their host. *Biol Lett* 4:455–457.
- Pike AW, Wadsworth SL (1999) Sealice on salmonids: Their biology and control. *Adv Parasitol* 44:233–337.
- Connors BM, Hargreaves B, Jones SRM, Dill LM (2010) Predation intensifies parasite exposure in a salmonid food chain. *J Appl Ecol* 47:1365–1371.
- Jones SRM, Hargreaves NB (2009) Infection threshold to estimate *Lepeophtheirus salmonis*-associated mortality among juvenile pink salmon. *Dis Aquat Organ* 84: 131–137.
- Beamish RJ, et al. (2006) Exceptional marine survival of pink salmon that entered the marine environment in 2003 suggests that farmed Atlantic salmon and Pacific salmon can coexist successfully in a marine ecosystem on the Pacific coast of Canada. *ICES J Mar Sci* 63:1326–1337.
- Krkošek M (2010) Host density thresholds and disease control for fisheries and aquaculture. *Aquacult Environ Interact* 1:21–32.
- Lloyd-Smith JO, et al. (2005) Should we expect population thresholds for wildlife disease? *Trends Ecol Evol* 20:511–519.
- Hogans WE (1995) *Infection Dynamics of Sea Lice, Lepeophtheirus salmonis (Copepoda: Caligidae) Parasitic on Atlantic Salmon (Salmo salar) Cultured in Marine Waters of the Lower Bay of Fundy (Canadian Technical Report of Fisheries and Aquatic Sciences No. 2067)* (Fisheries and Oceans Canada, Ottawa, ON, Canada).
- 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. *Can J Fish Aquat Sci* 61:147–157.
- Morton A, Routledge RD, Williams R (2005) Temporal patterns of sea louse infestation on wild Pacific salmon in relation to the following of Atlantic salmon farms. *N Am J Fish Manage* 25:811–821.
- Krkošek M, Morton A, Volpe JP, Lewis MA (2009) Sea lice and salmon population dynamics: Effects of exposure time for migratory fish. *Proc Biol Sci* 276:2819–2828.
- Beamish RJ, Mahnken C, Neville CM (2004) Evidence that reduced early marine growth is associated with lower marine survival of Coho salmon. *Trans Am Fish Soc* 133:26–33.
- Nagel L, Zanuttig M, Forbes MR (2011) Escape of parasitic water mites from dragonfly predators attacking their damselfly hosts. *Can J Zool* 89:213–218.
- Grenfell BT, Dobson AP (1995) *Ecology of Infectious Diseases in Natural Populations* (Cambridge Univ Press, Cambridge, UK).
- Mueter FJ, Peterman RM, Pyper BJ (2002) Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can J Fish Aquat Sci* 59:456–463.
- Peterman RM (1977) Simple mechanism that causes collapsing stability regions in exploited salmonid populations. *J Fish Res Board Can* 34:1130–1142.
- Quinn TP (2005) *The Behavior and Ecology of Pacific Salmon and Trout* (Univ of Washington Press, Seattle).
- Morton AM, Routledge R, Krkošek M (2008) Sea lice infestation of wild juvenile salmon and herring associated with fish farms off the east central coast of Vancouver Island, BC. *N Am J Fish Manage* 28:523–532.
- Werkman M, Green DM, Murray AG, Turnbull JF (2011) The effectiveness of following strategies in disease control in salmon aquaculture assessed with an SIS model. *Prev Vet Med* 98:64–73.
- Murray AG, et al. (2010) Epidemiological investigation into the re-emergence and control of an outbreak of infectious salmon anaemia in the Shetland Islands, Scotland. *Dis Aquat Organ* 91:189–200.
- Olivares J, Marshall SH (2010) Determination of minimal concentration of *Piscirickettsia salmonis* in water columns to establish a fallowing period in salmon farms. *J Fish Dis* 33:261–266.
- Ricker WE (1954) Stock and recruitment. *J Fish Res Board Can* 11:559–623.
- Pyper BJ, Mueter FJ, Peterman RM, Blackburn DJ, Wood CC (2001) Spatial covariation in survival rates of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*). *Can J Fish Aquat Sci* 58:1501–1515.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference* (Springer, New York).