

Cessation of a salmon decline with control of parasites

STEPHANIE J. PEACOCK,^{1,2,6} MARTIN KRKOŠEK,^{3,4} STAN PROBOSZCZ,⁵ CRAIG ORR,⁵ AND MARK A. LEWIS^{1,2}

¹Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2G1 Canada

²Centre for Mathematical Biology, Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta T6G 2G1 Canada

³Department of Zoology, University of Otago, Dunedin, New Zealand

⁴Salmon Coast Field Station, Simoom Sound, British Columbia V0P 1S0 Canada

⁵Watershed Watch Salmon Society, Coquitlam, British Columbia V3K 3B7 Canada

Abstract. The resilience of coastal social–ecological systems may depend on adaptive responses to aquaculture disease outbreaks that can threaten wild and farm fish. A nine-year study of parasitic sea lice (*Lepeophtheirus salmonis*) and pink salmon (*Oncorhynchus gorbuscha*) from Pacific Canada indicates that adaptive changes in parasite management on salmon farms have yielded positive conservation outcomes. After four years of sea lice epizootics and wild salmon population decline, parasiticide application on salmon farms was adapted to the timing of wild salmon migrations. Winter treatment of farm fish with parasiticides, prior to the out-migration of wild juvenile salmon, has reduced epizootics of wild salmon without significantly increasing the annual number of treatments. Levels of parasites on wild juvenile salmon significantly influence the growth rate of affected salmon populations, suggesting that these changes in management have had positive outcomes for wild salmon populations. These adaptive changes have not occurred through formal adaptive management, but rather, through multi-stakeholder processes arising from a contentious scientific and public debate. Despite the apparent success of parasite control on salmon farms in the study region, there remain concerns about the long-term sustainability of this approach because of the unknown ecological effects of parasiticides and the potential for parasite resistance to chemical treatments.

Key words: adaptive management; aquaculture; host–parasite; *Lepeophtheirus salmonis*; migration; Pacific Canada; parasiticide; salmon; sea lice.

INTRODUCTION

The resilience of social–ecological systems depends on their adaptive capacity to respond to human and environmental change (Walker et al. 2004, Liu et al. 2007). In many coastal seas, there is a rapid transition towards aquaculture (Goldburg and Naylor 2005, Duarte et al. 2007), which has created new ecological feedbacks that affect marine fisheries (Naylor et al. 2000) and ecosystems (Diana 2009). Large quantities of domesticated marine animals are now traded globally and can outnumber local related wild taxa (FAO 2009). Meanwhile, infectious disease has challenged the sustainability of some coastal social–ecological systems; salmon diseases alone may cost aquaculture industries billions annually (Asche et al. 2009, Costello 2009), and may also affect ecosystems (Dann et al. 2000, Krkošek 2010a) and human health (Cabello 2006).

A key to resilient coastal social–ecological systems may be the adaptive change of aquaculture management in response to disease outbreaks in farm and wild fishes. Farm fish raised in sea cages are vulnerable to native

pathogens from wild populations (Saksida 2006). Wild fish populations are vulnerable to bio-amplification of native pathogens in farming regions (Krkošek et al. 2006), as well as the introduction of novel pathogens (Gaughan 2001). Precautionary regulatory approaches include protected areas (Bjørn et al. 2011), parasite limits on farm fish (Heuch et al. 2005), and integrated coastal planning (Gudjonsson and Scarnecchia 2009). However, empirical evaluations of adaptive farm management and the resultant conservation gains have been rare.

Host migration may drive the dynamics of infectious disease in coastal ecosystems that support wild and farm salmon populations (Krkošek et al. 2007b, 2009). For example, the large abundance of wild salmon in coastal seas of the north Pacific is seasonally ephemeral, limited to the spring out-migration of juveniles transiting to offshore waters and the summer and autumn return of adult salmon to freshwaters to spawn (Quinn 2005). Effective disease control may require breaking transmission cycles between wild and farm salmon by timing parasite control strategies relative to migration schedules of wild salmon populations.

Study system

Salmon lice (*Lepeophtheirus salmonis*) are directly transmitted parasites that reproduce sexually while

Manuscript received 30 March 2012; revised 19 September 2012; accepted 18 October 2012. Corresponding Editor: K. Stokesbury.

⁶ E-mail: stephanie.peacock@ualberta.ca

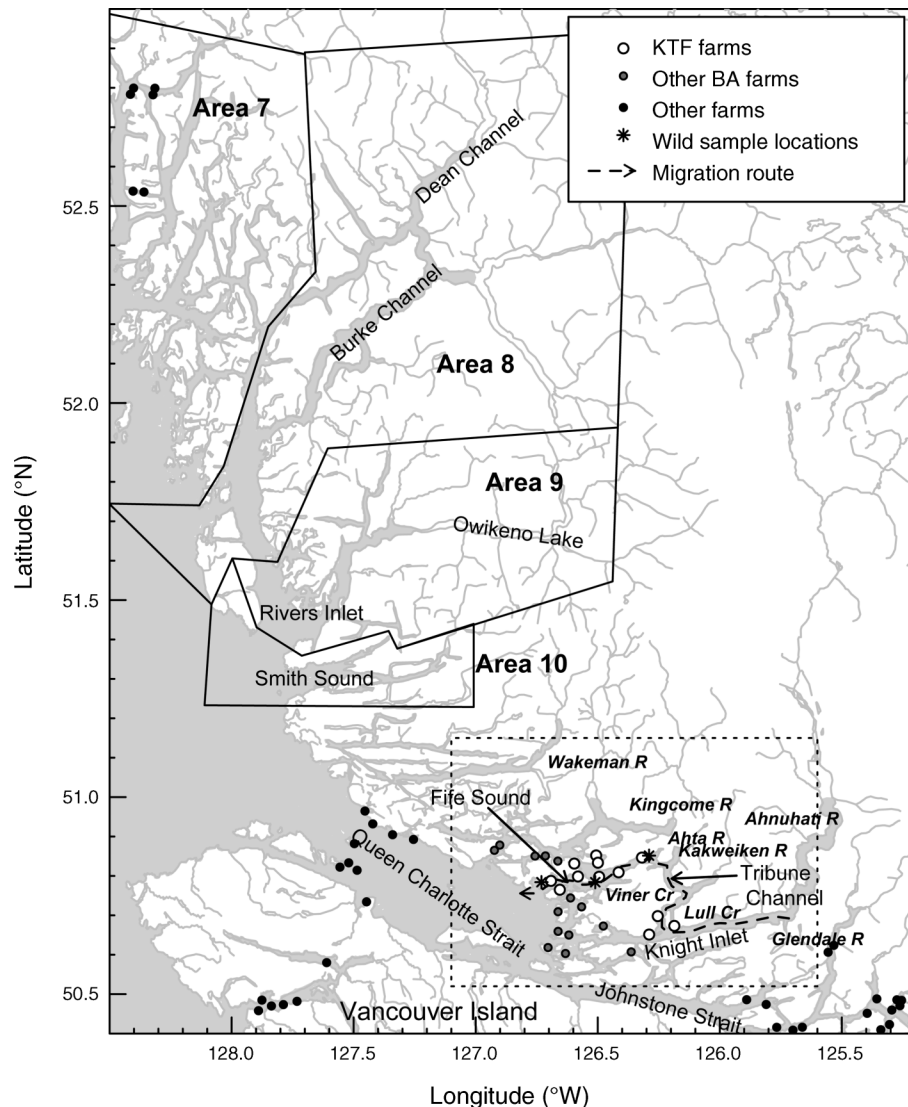


FIG. 1. Salmon populations on the coast of British Columbia, Canada, were categorized as unexposed (fishery management areas 7–10) or exposed to salmon farms (area 12, the Broughton Archipelago, with labeled rivers in the lower right). The focal study area is the Broughton Archipelago, outlined by the dotted box, and the Knight Inlet–Tribune Channel–Fife Sound (KTF) wild salmon migration corridor (dashed line). Salmon farm locations are shown by small black circles outside the Broughton Archipelago, while inside the Broughton Archipelago, small gray circles indicate those farms distant from the KTF migration corridor, and white circles indicate those farms on the KTF migration corridor. Stars (*) indicate the three weekly sample sites for wild juvenile salmon from 2001–2009.

attached to a host (Tully and Noland 2002, Costello 2006). Mated adult females extrude eggstrings from which free-swimming and non-feeding nauplii hatch, molt into copepodites, attach to a host fish, and then develop through a series of chalimus stages and then motile pre-adult and adult stages (Johnson and Albright 1991). The motile stages are mobile over the surface of their host and can also move among host fish (Ritchie 1997, Connors et al. 2008, 2010). Lice feed on host surface tissues, causing morbidity and mortality at high infection intensities (Pike and Wadsworth 2000; see Plate 1), as well as sublethal effects on physiology

(Nendick et al. 2011) and behavior (Krkošek et al. 2011a).

Management, policy, and science

Optimization of parasite management on salmon farms on the Pacific coast of Canada has involved formal policy development and management changes. In the Broughton Archipelago (Fig. 1), outbreaks of sea lice on wild juvenile pink salmon in 2001 and 2002 and accompanying population collapse of pink salmon (*Oncorhynchus gorbuscha*) stocks (PFRCC 2002, Morton and Williams 2003, Morton et al. 2004) triggered

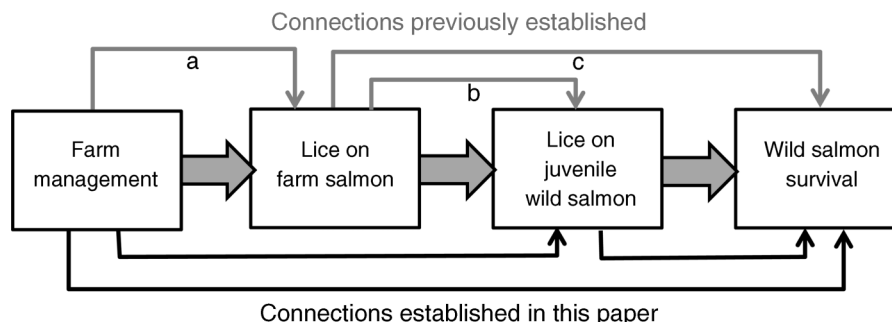


FIG. 2. This study addresses unanswered questions about the efficacy of sea louse (*Lepeophtheirus salmonis*) management on salmon farms in reducing wild juvenile-salmon epizootics and increasing wild salmon survival (black arrows, bottom). Connections previously established (gray arrows, top) include (a) the effect of treatments on sea lice abundance on farm salmon (Revie et al. 2003, Krkošek et al. 2010), (b) the transmission of lice from farm to wild salmon (Bjørn et al. 2001, Gargan et al. 2003, Morton et al. 2004, Krkošek et al. 2006, Marty et al. 2010), and (c) the effect of sea lice abundance on farm salmon on wild salmonid survival (Gargan et al. 2003, Krkošek et al. 2011b).

media attention, policy development, management changes, and scientific investigation (Krkošek 2010a).

Government regulators initiated guidelines for systematic monthly monitoring of sea lice on farms in 2003, and added that treatment with a parasiticide (emamectin benzoate, "SLICE"; Intervet/Schering-Plough Animal Health, Boxmeer, The Netherlands) or harvest of a farm should occur if the average abundance of motile-stage lice exceeds three lice per farm fish during the months March–June, when most juvenile wild salmon migrate through the area. During the remainder of the year, it was initially suggested farms treat or harvest if lice levels exceeded six motile lice per farm fish, but in 2006, this was changed to an increased monitoring frequency of twice per month and optional harvest or treatment at the discretion of the farming company (management strategy available online).⁷

Accompanying the implementation of these policies were scientific studies of sea lice transmission from farm Atlantic salmon (*Salmo salar*) to out-migrating juvenile wild salmon (*Oncorhynchus* spp.) (e.g., Krkošek et al. 2005a, 2006). Although it is now widely accepted that sea lice transmission from farm to wild salmonids does occur in British Columbia (Marty et al. 2010, Krkošek et al. 2011b), Norway (Bjørn et al. 2001), Ireland (Gargan et al. 2003), and Scotland (Butler and Watt 2003), the subsequent effects on wild salmon populations in Canada in particular have been hotly debated (Krkošek et al. 2007a, 2011b, Brooks and Jones 2008, Marty et al. 2010). Multiple sources of mortality, various spatial scales of synchrony in salmon population dynamics, environmental stochasticity, and observation error in both salmon and sea lice data have made even correlative studies subject to criticism. The gradual changes in management of sea lice on salmon farms in the Broughton Archipelago have further complicated

any potential relationship between salmon farms and wild salmon productivity.

Although there is no consensus on the population-level effects of sea lice on wild salmon, the scientific debate has brought attention to the potential for negative effects, and thus motivated the aforementioned management and policy changes. These changes did not result from systematic evaluation of conservation gains from various management scenarios in a controlled and replicated way, as in formal adaptive management (Walters 1997), but continue to evolve from multi-stakeholder processes and contentious scientific and public debate, and thus, we have termed them adaptive changes in management.

Here, we examine the links between adaptive changes in management of sea lice on salmon farms, observed infections on wild juvenile salmon, and wild salmon population dynamics (Fig. 2). In particular, we elucidate connections that have not yet been made between adaptive changes in management and parasites on wild juvenile salmon, and the sea lice observed on wild juvenile salmon and wild salmon population productivity. Drawing on data from a nine-year study of parasitic sea lice (*L. salmonis*) and pink salmon (*O. gorbuscha*) from Pacific Canada, our results indicate positive conservation outcomes due to adaptive changes in management of parasites in salmon aquaculture facilities. These results provide an example of how management of sea lice on farm salmon can be improved, with relevance to management of sea lice on farm salmon in Canada, Europe, and other areas of the world where the expansion of aquaculture has been accompanied by environmental concerns of parasite transmission to wild salmonids (e.g., Bjørn et al. 2001, Butler and Watt 2003, Gargan et al. 2003).

METHODS

Farm data

The farm data consist of monthly estimates of farm Atlantic salmon (*S. salar*) abundance and average

⁷ www.agf.gov.bc.ca/ahc/fish_health/sealice_MS.htm

number of adult female sea lice (*L. salmonis*) per farm salmon per farm in the Broughton Archipelago, British Columbia, Canada (Fig. 1), from 2001 to 2009, reported in Marty et al. (2010). We focused our analysis on farms located on the Knight Inlet–Tribune Channel–Fife Sound (KTF) corridor of the Broughton Archipelago in order to compare the farm data with field monitoring programs of juvenile salmon that migrate through that corridor (Fig. 1). The total louse population per farm and per region was estimated by multiplying the average number of lice per farm salmon by the number of salmon per farm, and then summing over farms (Orr 2007, Marty et al. 2010). The data also include records of in-feed parasiticide treatments with emamectin benzoate. We categorized advance, or “winter” treatments as those that occurred in January through March or October through December, prior to juvenile salmon migrations, which typically occur March through June (Morton et al. 2004, Krkošek et al. 2006, Jones and Hargreaves 2007, Krkošek 2010a).

Weekly louse monitoring of wild fish

We assembled data from a long-term monitoring program that sampled juvenile pink salmon for sea lice at weekly intervals during March through June between 2001 and 2009 at three sites in the Broughton Archipelago (Fig. 1). Data collection involved searching nearshore waters (~2–5 m from shore) visually for schools of juvenile salmon in the surface 0.3–2 m, depending on visibility. Once spotted, salmon were collected by dip net (45 cm diameter with 5-mm knotless mesh on a 2.45-m pole from a 7.5-m boat) between 2001 and 2003 (Morton and Williams 2003, Morton et al. 2004, Krkošek et al. 2005b). For 2004 through 2009, juvenile salmon were collected from the same sites using a beach seine net, whose dimensions varied among years ranging from the smallest dimensions of 15.2 m long by 1.8 m deep with 6-mm knotless mesh (2004–2007) to a larger net that was 40 m long by 2.5 m deep with 6-mm knotless mesh (2008–2009).

Upon collection, juvenile salmon were transferred into seawater-filled buckets either directly from the dip net (2001 through 2003) or from the bunt of the purse seine net using smaller dip nets (10–15 cm square on a 30-cm handle with 2-mm knotless mesh) during 2004 through 2009. From 2001 through 2004, juvenile salmon were placed individually from the buckets into individual sample bags, placed on ice, and then frozen for subsequent laboratory analysis. Frozen samples were analyzed under a dissecting microscope at 30× magnification, and species and stages of lice were identified according to Johnson and Albright (1991). From 2005 through 2009, juvenile salmon were analyzed nonlethally on site, using a 16× magnification hand lens to visually assay individual fish in zip-locked plastic bags (Krkošek et al. 2005b; see Plate 1). Pink and chum (*Oncorhynchus keta*) salmon were collected; however, only data of lice on pink salmon are presented here. We report the lice

per wild juvenile pink salmon as the sum of all attached stages of *L. salmonis*.

Intensive louse surveys of wild fish

To provide a more detailed analysis of changes in sea lice transmission dynamics in relation to management changes, we also assembled data from an intensive sampling program that studied sea lice infections on juvenile salmon as they migrated through the KTF corridor. These data consisted of ~100 juvenile pink (*O. gorbuscha*) salmon, collected at 1–3 km intervals along the length of the corridor (Fig. 1). Salmon were caught by beach seine and nonlethally assayed for lice as described in the previous section and in Krkošek et al. (2005b). At each sample location in weekly and intensive surveys of wild fish, temperature and salinity were recorded using a thermometer and a salinity refractometer. We contrasted average numbers of sea lice on pink salmon from 2009 with data from 2004 that were previously published by Krkošek et al. (2006).

Salmon spawner–recruit data

We obtained estimates of pink salmon spawner abundance for populations near active salmon farms in the Broughton Archipelago (fishery management area 12) and reference populations not exposed to salmon farms (areas 7–10; Fig. 1) from the Pacific salmon escapement database (Fisheries and Oceans Canada 2011). These data contained spawner abundance estimates (with missing values) for 277 rivers, each with independent even- and odd-year populations, spanning 60 years from 1950 to 2010. Fisheries and Oceans Canada (DFO) personnel generated the spawner abundance estimates via analyses of data from stream walks and overhead flights, also conducted by DFO personnel.

To calculate recruitment, we added the estimated abundance of pink salmon caught in fisheries (i.e., catch) to spawner abundance enumerated in rivers (i.e., escapement). We obtained raw catch data or estimates of exploitation rates of pink salmon from DFO stock assessment biologists for each year in each DFO management area that contained rivers in our study area (fishery management areas numbers 7, 8, 9, 10, 12; 12 includes the Broughton Archipelago). For areas 7–10, catch was assumed to consist of local populations within the management areas. For these areas, exploitation rates were calculated as $\mu_{i,t} = C_{a,t}[C_{a,t} + E_{a,t}]^{-1}$, where $C_{a,t}$ is the catch for area a in year t , and $E_{a,t}$ is the estimated total escapement for the area, expanded from counts of spawner abundance using the P_{\max} technique (Appendix A). For area 12, exploitation rates were provided directly by DFO, and also accounted for fisheries targeting primarily nonlocal populations who are fished in area 12 on their migration to rivers further south (e.g., the Fraser River). We assumed that returns to each river in a management area experienced the same exploitation rate in a given year. Recruitment, $R_{i,t}$, to river i in year t was calculated as $R_{i,t} = N_{i,t}[1 - \mu_{i,t}]^{-1}$,

where $N_{i,t}$ is the spawner abundance of pink salmon from river i in year t , and $\mu_{i,t}$ is the exploitation rate for river i in year t .

We structured the escapement data into odd- and even-year populations for each river, which is standard practice for pink salmon due to their two-year life cycle and intrinsic differences between odd- and even-year lineages (Pyper et al. 2001, Dorner et al. 2008). We then screened the data, keeping only populations for which there were at least 20 spawner–recruit data pairs. We further kept only the eight rivers for the Broughton Archipelago region that were used in previous analysis of the area (Fig. 1; Krkošek et al. 2007a, Krkošek and Hilborn 2011). This reduced the data set to 179 populations of odd- or even-year lineages of pink salmon, yielding 2385 spawner–recruit pairs distributed over 99 rivers from 1962 to 2010 (Appendix C: Table C1).

Analysis

Estimates of the mean abundance of *L. salmonis* per wild juvenile pink salmon per year were calculated from the weekly monitoring data via a generalized linear mixed-effects model (GLMM), with fixed effects for year and random effects for sample site and week. The data were highly over-dispersed, and found to be best represented by a zero-inflated negative binomial distribution. This model was fitted using the package glmmADMB (Bolker et al. 2012), using the software R (R Development Core Team 2012).

We investigated several relationships linking the effect of changes in management (e.g., timing of parasiticide treatments) to wild salmon population growth rates (Fig. 2). First, the trends over time in the total number of parasiticide treatments and proportion of those treatments occurring in winter (January–March or October–December, prior to the juvenile salmon out-migration) in the KTF corridor and the Broughton Archipelago were quantified using regression analysis. The yearly estimates of average lice per wild juvenile salmon from the aforementioned GLMM were then related to the total lice on farm salmon, and to the management changes, quantified as the total number of treatments, number of winter treatments, and proportion of total treatments occurring during winter on farms in the Broughton Archipelago. We then analyzed the survival of pink salmon populations in the Broughton Archipelago in relation to the average number of lice per wild juvenile salmon, on the premise that the latter was related to both farm lice and adaptive changes in management and provides a covariate that more closely captures the actual effect on wild salmon survival. Previous studies have related wild salmon survival to lice on farm salmon (Marty et al. 2010, Krkošek et al. 2011b), which is a less direct approach to determine the population-level effect of sea lice.

For this population-level analysis, we applied a hierarchical Ricker model to the pink salmon spawn-

er–recruit data. The data were spatially structured, first by populations exposed to salmon farms (Broughton Archipelago) and reference regions where populations were unexposed to salmon farms (Fig. 1). The unexposed region was further partitioned into four fishery management areas used for reporting of catch by the DFO. Exposed populations all existed within management area 12.

The model allowed for several levels of synchrony in salmon survival by treating year and management area within year as random and nested random effects, respectively. Density dependent mortality was treated as a fixed factor per population (i.e., different for even- and odd-year populations within the same river). The growth rate was treated as a fixed factor, and the average lice per wild juvenile salmon (as estimated from the GLMM) was included as a covariate. The full model was

$$R_{i,t} = N_{i,t-2} \exp[r - b_i N_{i,t-2} - c W_{a,t-1} + \theta_t + \theta_{a,t} + \varepsilon_{i,t}] \quad (1)$$

where $R_{i,t}$ is recruitment of population i in year t , and $N_{i,t}$ is the abundance of spawners of population i in year $t - 2$. Here, t is lagged two years to account for the two-year life cycle of pink salmon. The growth rate, r , was the same for the entire region, but the density dependence parameter, b_i , was different for each population as it relates to the habitat characteristics unique to each river and density-dependent competitive interactions within populations.

To test for an effect of sea lice infestations on survival, we included the average lice per wild juvenile salmon the previous year, $W_{a,t-1}$, as a covariate. We assumed the lice per wild juvenile salmon to be zero for reference regions, as louse abundance on juvenile pink salmon in nearshore waters is extremely low in the absence of salmon farms (Gottesfeld et al. 2009). Any sea lice on juvenile salmon in reference regions are likely originating from returning adult salmon (Gottesfeld et al. 2009), and transmission occurs further offshore and later in the season when juvenile pink salmon are less vulnerable to the effects of infection. For return years 2002–2010 in the Broughton Archipelago, $W_{a,t-1}$ was taken as the mean louse abundance per wild juvenile salmon, estimated from the GLMM for 2001–2009. Data describing louse abundances on farm and wild salmon from the onset of salmon farming in the Broughton Archipelago to the first reported infestation in 2001 (Morton and Williams 2003) were not available, but it is reasonable to assume that sea lice abundances were not epizootic during this period as outbreaks were not reported on salmon farms (Marty et al. 2010) or noticed on wild juvenile salmon (Morton and Williams 2003). However, to address this uncertainty, we treated $W_{a,t-1}$ as missing data for return years 1991 to 2001. Prior to 1991, we assumed $W_{a,t-1} = 0$ for the Broughton Archipelago, as salmon farming production was low (Pearsall 2008). The strength of the relationship between pink salmon survival and lice on wild juvenile salmon



PLATE 1. Sea lice (*L. salmonis*) feed on the skin, mucous, and blood of salmon, leading to lesions and scarring. Even low louse burdens may lead to elevated levels of mortality for juvenile pink salmon such as this. Photo credit: S. Proboszcz.

was controlled by the parameter c . The estimated percentage mortality of pink salmon due to sea lice on wild juvenile salmon is therefore equal to $1 - \exp(-cW_{a,t-1})$ (Krkošek et al. 2011b).

Environmental stochasticity was represented by spatially coherent variation among all populations (θ , a random normal variable for year with mean zero and variance to be estimated), spatially coherent variation for populations within a management area ($\theta_{a,t}$, a random normal variable for areas within years that has a mean of zero and variance to be estimated), and random annual variation that is independent among populations ($\epsilon_{i,t}$, also a random normal variable for each river in each year that has mean of zero and variance to be estimated). The random effect of area within year is also needed to accommodate the nonindependence of survival observations among rivers within a management area in a given year, due to the assumption that rivers within an area experience the same harvest rate. For this analysis, we ignored measurement error associated with the observation of spawners.

As is common in the application of the Ricker model to data, Eq. 1 was fit in its linear form as follows:

$$\ln[R_{i,t}/N_{i,t-2}] = r - b_i N_{i,t-2} - cW_{a,t-1} + \theta_t + \theta_{a,t} + \epsilon_{i,t} \quad (2)$$

using the lme4 package in R (Bates et al. 2011). Confidence intervals on model parameters were calculated via parametric bootstrapping as described in Krkošek et al. (2007a) and Krkošek and Hilborn (2011).

RESULTS

The total number of lice on farm salmon has been steadily declining over the last decade, with no corresponding declines in farm salmon production (Fig. 3a, b). The dynamics of lice on farm salmon in the KTF corridor of the Broughton Archipelago (Fig. 1) are characterized by large fluctuations in abundance that have a clear annual cycle (Fig. 3b). Louse abundances on farm fish increase during winter, and sometimes spring months, until parasiticide treatments appear to reduce sea lice to lower levels during spring and summer months. During autumn months, the cycle of louse population growth, treatment, and decline appears to begin anew. Farms were largely compliant with the regulatory guidelines of treatment (or harvest) when the abundance of motile-stage lice exceeded three lice per farm fish during the wild juvenile salmon out-migration season (March–June; Table 1). During the remaining months of the year, the abundance of lice that triggered treatment declined from 2004 onwards (Table 1). The total number of treatments in the KTF corridor and the

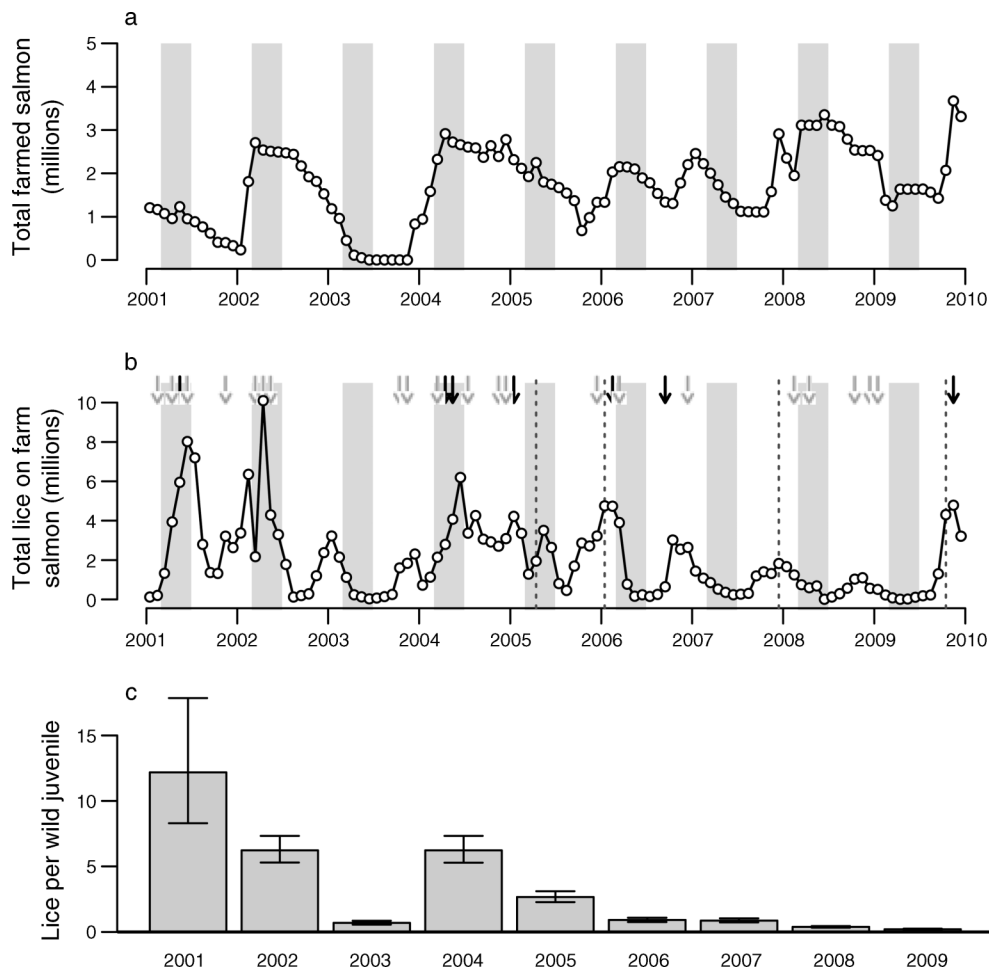


FIG. 3. (a) Total number of farm salmon in their second year of production, (b) total number of gravid *L. salmonis* on farm salmon, and (c) mean abundance ($\pm 95\%$ CI) of *L. salmonis* (all stages) per juvenile salmon in Tribune Channel and Fife Sound. Light gray vertical bars in panels (a) and (b) represent the time period of the juvenile salmon out-migration (March–June), and the vertical dotted lines in panel (b) indicate the occurrence of at least three parasiticide treatments of a salmon farm in that month, while gray and black arrows indicate one or two treatments in that month, respectively.

Broughton Archipelago have not increased significantly over time (linear regression; for KTF, $df = 7$, $F_{1,7} = 0.374$, $P = 0.560$; for Broughton Archipelago, $df = 7$, $F_{1,7} = 0.806$, $P = 0.399$; Appendix C: Table C3). However, the proportion of these treatments occurring in winter, preceding the juvenile salmon out-migration, has increased over time in both the KTF corridor (logistic regression, $df = 7$, $\exp(\beta) = 1.198$, $z = 1.807$, $P = 0.071$) and across the Broughton Archipelago ($df = 7$, $\exp(\beta) = 1.123$, $z = 1.790$, $P = 0.074$; Table 2, and Appendix C: Table C3).

The data set on weekly monitoring of lice on juvenile salmon comprised 19 113 lice on 7907 pink salmon sampled over nine years (Table 3). There were substantial interannual variations in louse abundance on wild juvenile salmon, as well as farm salmon (Table 3, Fig. 3b, c). The period 2001–2005 was characterized by relatively high sea louse abundance on wild juvenile

pink salmon, with the exception of 2003, when the fallowing management intervention was implemented by provincial regulators and farming companies (Morton et al. 2005). The period of high louse abundance on wild juvenile salmon corresponded to years when louse abundance on farm salmon was also high during the out-migration season (Fig. 3b, c). The fallow year (2003), showed a declining trend in louse abundance on farm fish in the early part of the migration season, which was not associated with parasiticide treatment, but rather a management intervention implemented by provincial regulators that fallowed most of the farms along the KTF corridor.

At a coarse scale, interannual patterns in the average abundance of lice on wild juvenile pink salmon in the KTF corridor are related to the total annual number of gravid lice on farm fish in the corridor during the out-migration season (Fig. 4a). In 2006 and later years,

TABLE 1. Mean abundance of motile-stage sea lice *Lepeophtheirus salmonis* per farm fish the month prior to treatment with parasiticide in the Knight Inlet–Tribune Channel–Fife Sound (KTF) migration corridor and the entire Broughton Archipelago, British Columbia, Canada (see Fig. 1), in 2001–2009.

Area and year	Motile-stage <i>L. salmonis</i> /farm fish			
	March–June		July–February	
	Mean	SE	Mean	SE
KTF corridor				
2001†	3.61	0.62	16.74	3.49
2002†	5.55	0.12
2003‡	3.09	1.59
2004	2.85	0.86	6.47	...
2005	2.55	0.90	3.10	0.94
2006	4.52	0.52	2.41	0.59
2007	2.38	...
2008	1.92	0.34	1.63	0.44
2009	1.04	0.52
Broughton				
2001†	3.39	0.4	16.74	3.02
2002†	7.68	1.01
2003‡	12.28	2.20	4.04	1.04
2004	6.44	1.18	12.25	2.62
2005	2.66	0.44	5.36	1.18
2006	2.63	0.58	4.78	0.97
2007	4.98	1.96
2008	1.92	0.25	2.13	0.42
2009	1.23	...	1.86	0.51

Note: Ellipses (...) indicate that no data were available (i.e. no farms were treated during that period, or only one farm was treated and so the standard error could not be calculated).

† Years 2001 and 2002 did not yet have systematic monitoring programs implemented, and there are numerous instances of missing data (Marty et al. 2010).

‡ The year 2003 corresponds to the fallowing intervention.

treatment of farm fish with parasiticide occurred more frequently prior to the juvenile salmon out-migration season (Table 2), and louse abundance on wild juvenile salmon shows a corresponding decline (Table 3, Fig. 4b). In particular, 2006 appears to be a turning point in management actions on the migration corridor and sea lice abundance on wild juvenile salmon in the migration corridor (Figs. 3 and 4). The proportion of total treatments occurring in winter had a greater effect on the average lice per wild juvenile salmon ($R^2 = 0.777$, $P = 0.002$, AIC = 8.0), than did the total number of treatments ($R^2 = 0.000$, $P = 0.981$, AIC = 21.5; Table 4).

Intensive louse surveys of wild juvenile salmon in 2004 and 2009 involved 6384 and 9482 pink salmon, respectively. These samples were separate and in addition to the weekly monitoring of lice on wild salmon. The 2004 data consisted of three replicate surveys, and the 2009 data consisted of five replicate surveys of the KTF corridor (Krkošek et al. 2006). The spatial survey data indicated major declines in the magnitude of transmission from farm salmon to wild juvenile salmon in 2009 relative to 2004 (Fig. 5). Focusing on two surveys in May, the peak of the mean number of motile lice per wild juvenile salmon was nearly 20 times lower in 2009 than 2004 (1.55 motiles/

fish vs. 0.08 motiles/fish; Fig. 5i, l). Further, the peaks in infection of wild juvenile salmon after they migrate past salmon farms that characterize the 2004 data (Krkošek et al. 2005a, 2006) were not apparent in 2009. These changes are consistent with changes between 2004 and 2009 in the abundance of farm fish and gravid lice per farm fish in farms on the migration route (Fig. 3b). The decline in abundance and spatial pattern of sea lice infection in 2009 was common to all replicate surveys (Appendix B: Fig. B1). Differences in salinity between years, while known to affect louse survival (Pike and Wadsworth 2000), were unlikely to have confounded our results. A paired t test on salinities in 2004 and 2009, paired by month and distance along the migration route, suggested no significant difference between years ($t = 0.047$, $df = 14$, $P = 0.963$; Appendix B: Fig. B2). Ranges in temperature and salinity were similar between 2004 and 2009 (Table 5).

There were significant declines in the survival of pink salmon populations with sea lice infestations in juveniles (Fig. 6). Including the covariate of average lice per wild juvenile salmon improved the fit of the model (likelihood ratio test, $\chi^2 = 12.128$, $df = 1$, $P < 0.001$). The growth rate for pink salmon over all areas was $r = 1.088$ (95% CI = 0.873, 1.302) and the parameter for the effect of lice on survival was significantly different from zero ($c = 0.190$, 95% CI = 0.087, 0.299), indicating a reduction in survival with increasing abundance of sea lice on wild

TABLE 2. Number of treatments with emamectin benzoate ("SLICE") on farms along the Knight Inlet–Tribune Channel–Fife Sound (KTF) migration corridor and the entire Broughton Archipelago (Fig. 1) in 2001–2009.

Area and year	Number of treatments		Proportion in winter
	Total	Winter	
KTF corridor			
2001†	6	2	0.33
2002†	3	0	0.00
2003‡	2	2	1.00
2004	7	1	0.14
2005	6	3	0.50
2006	9	8	0.89
2007	1	1	1.00
2008	6	5	0.83
2009	7	7	1.00
Broughton			
2001†	8	2	0.25
2002†	7	3	0.43
2003‡	7	7	1.00
2004	19	8	0.42
2005	17	11	0.65
2006	16	12	0.75
2007	4	4	1.00
2008	11	10	0.91
2009	17	16	0.94

Note: Winter treatments are those occurring in January–March or October–December, in advance of a juvenile salmon out-migration.

† Years 2001 and 2002 did not yet have systematic monitoring programs implemented, and there are numerous instances of missing data (Marty et al. 2010).

‡ The year 2003 corresponds to the fallowing intervention.

TABLE 3. Summary of annual characteristics of lice on wild and farm fish in the Knight Inlet–Tribune Channel–Fife Sound (KTF) corridor of the Broughton Archipelago between 2001 and 2009.

Year	Farm salmon		Juvenile pink salmon	
	Lice (millions)†	Winter treatments‡	Lice (millions)§	<i>n</i>
2001	19.2	no	12.17 (8.30, 17.85)	268
2002	19.9	no	6.23 (5.30, 7.33)	490
2003	1.5	yes¶	0.69 (0.56, 0.86)	367
2004	15.2	no	6.23 (5.28, 7.34)	546
2005	9.4	yes	2.66 (2.28, 3.10)	1892
2006	5.1	yes	0.91 (0.76, 1.08)	726
2007	2.0	yes	0.87 (0.73, 1.04)	1000
2008	2.0	yes	0.39 (0.34, 0.45)	2075
2009	0.2	yes	0.20 (0.16, 0.26)	543

† Farm salmon lice were the total number of female lice (millions) on farm salmon in the KTF corridor during the out-migration season (1 March–30 June) of each year.

‡ Winter treatments indicates whether the proportion of parasiticide treatments occurring in winter (January–March or October–December) was ≥ 0.50 (yes or no).

§ The mean louse abundance (all stages) on wild juvenile pink salmon (95% confidence intervals in parentheses) as estimated by the generalized linear model, and number of juvenile pink salmon sampled each year (*n*).

¶ The fallowing management intervention took place in 2003.

juvenile salmon. The estimated percentage mortality of pink salmon in the Broughton due to sea lice infestations ranged from 90.1% for returns in 2002, to 3.8% for returns in 2010, and showed a declining trend between 2002 and 2010 (Fig. 6b). Population-specific density-dependence parameters can be found in Appendix C: Table C1.

DISCUSSION

The spread of infection from domesticated animals can threaten wildlife (Krkošek et al. 2007a, Pedersen et al. 2007) and create situations of high management urgency and uncertainty (Haydon et al. 2002, Krkošek 2010a). For salmon and sea lice in the Broughton Archipelago, we found that infections of wild juvenile salmon increased with sea lice abundance on farm salmon. Intensive spatial surveys of sea lice on wild juvenile salmon showed low infection levels on juvenile salmon prior to migration past salmon farms, suggesting that sea lice transferred from farm salmon to wild salmon. Management actions, such as fallowing farms along the migration routes of juvenile salmon and winter treatments with parasiticide, lowered the abundance of sea lice on farm salmon, and therefore reduced infection of wild salmon. Finally, there was a strong negative relationship between pink salmon survival and sea lice infection of juveniles, implicating that efforts by the salmon farming industry to reduce sea lice levels during the wild salmon out-migration have positive implications for wild salmon survival and productivity.

Lepeophtheirus salmonis epizootics of wild juvenile salmon in the Broughton Archipelago were first observed in 2001 (Morton and Williams 2003). Earlier, lice were noted on salmon farms in the area, but outbreaks were not sufficiently widespread to require regular monitoring and treatment (Marty et al. 2010). The sudden nature of sea lice epidemics suggests a

critical host density threshold in the region, above which sea lice population growth will occur exponentially if left untreated, was exceeded (Frazer et al. 2012), and is consistent with louse outbreaks elsewhere (Jansen et al.

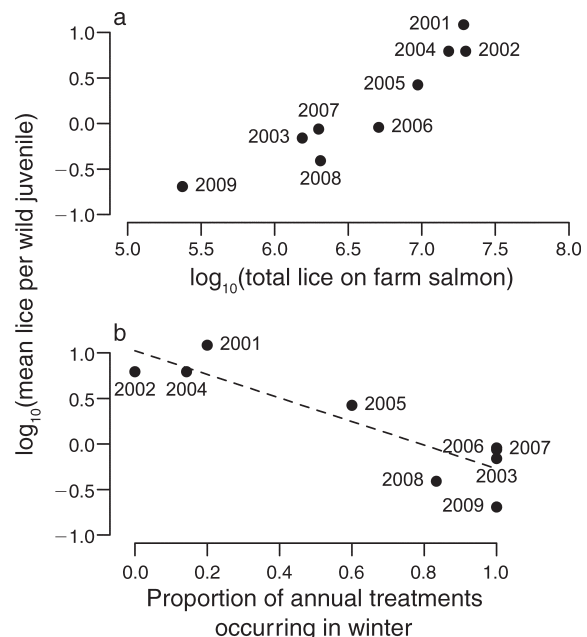


FIG. 4. (a) Relationship between the estimated mean number of *L. salmonis* per juvenile pink salmon per year and the total abundance of female *L. salmonis* on farm salmon in the Knight Inlet–Tribune Channel–Fife Sound migration corridor during the out-migration (1 March–30 June) each year, and (b) the proportion of all treatments of farm salmon with parasiticide that occurred in advance of the juvenile salmon out-migration each year (i.e., winter treatments). The dashed line in panel (b) is the linear regression of $\log_{10}(\text{mean } L. \text{ salmonis per juvenile pink salmon})$ over the proportion of winter treatments (Table 4).

TABLE 4. Linear regression shows that the sole best predictor of $\log_{10}(\text{mean lice per wild juvenile salmon})$ is the proportion of total treatments that occurred in winter in the KTF corridor, before the juvenile wild salmon migration (Model 3; in boldface type).

Model and predictor	Estimate	SE†	<i>t</i>	<i>P</i>	<i>R</i> ²	AIC‡	ΔAIC
1) Total number of treatments	−0.002	0.0873	−0.024	0.981	0.00	21.5	13.5
2) Number of winter treatments	−0.141	0.0618	−2.281	0.057	0.43	16.5	8.5
3) Proportion total treatments in winter	−1.353	0.2741	−4.936	0.002	0.78	8.0	0
4) Total number of treatments + proportion in winter	−0.021	0.0439	−0.473	0.653	0.78	9.7	1.7
	−1.365	0.2919	−4.678	0.003			

† Standard error on the parameter estimate.

‡ Akaike's information criterion.

2012) and epidemiological theory (Krkošek 2010b). The absence of lice data on wild juvenile salmon prior to 2001 necessitates making assumptions on lice abundance during the 1990s, when farms were present, but outbreaks were not reported. In our analysis, we assume these abundances on wild juvenile salmon were at roughly natural levels due to host density thresholds not being exceeded. The effects of lice on salmon survival during the 1990s are therefore absorbed into the estimation of the population growth rate, which would include louse-induced host mortality at natural louse levels. After outbreaks began, it took two years for

louse monitoring in the Broughton Archipelago to become systematic (in 2003; Jones et al. 2006, Marty et al. 2010), and our results indicate it took another three years before treatment became adjusted to the out-migration of wild juvenile salmon.

In the midst of the outbreaks in the early 2000s, a fallowing management intervention closed most farms on the migration route (Morton et al. 2005). This was implemented by provincial regulators, partially in response to the population collapse in the preceding year (PFRCC 2002). The fallowing management intervention reduced infection rates on wild juvenile salmon

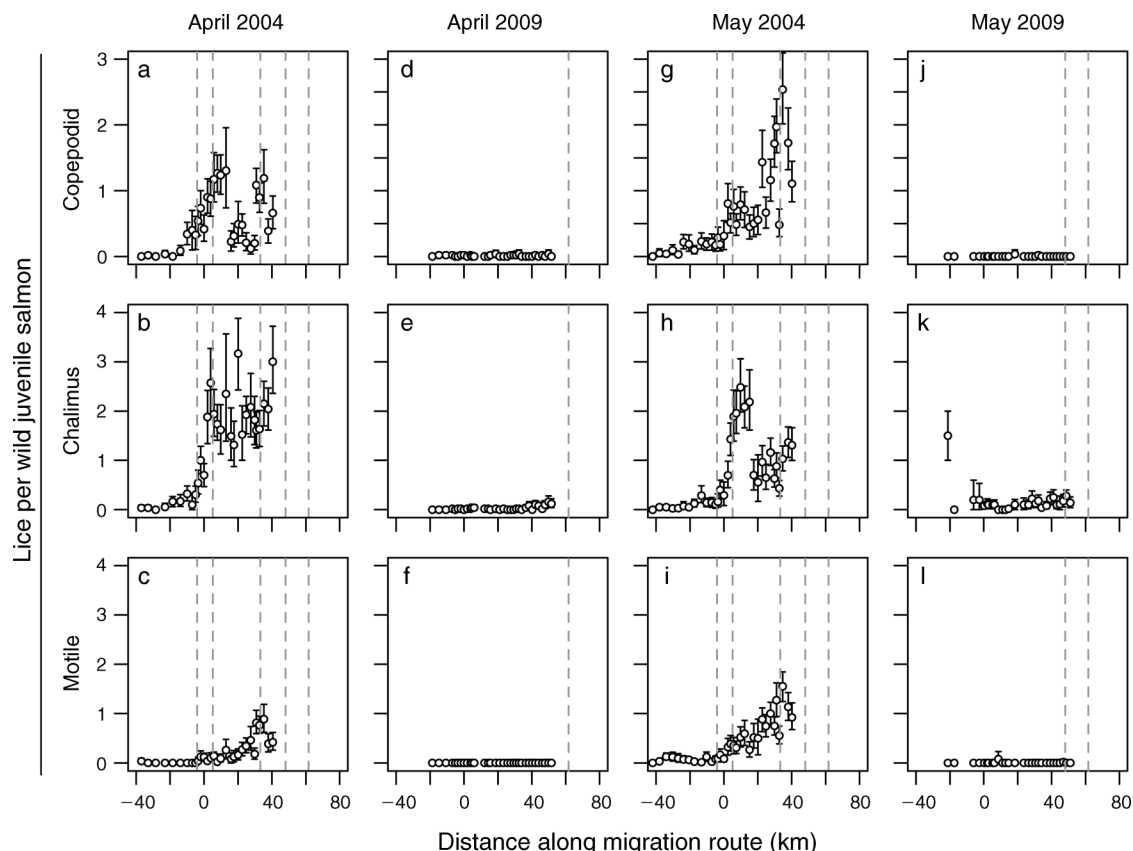


FIG. 5. Spatial distributions of the mean number of *L. salmonis* developmental stages on wild juvenile pink salmon in April and May of 2004 and 2009 along the Knight Inlet–Tribune Channel–Fife Sound migration corridor (direction of fish migration is from left to right within each panel). The top, middle, and bottom rows of the panels show the mean abundance of parasitic copepodid, chalimus, and motile stages per fish, respectively (with 95% bootstrapped CI). Vertical dashed lines indicate the locations of the active salmon farms in each year.

TABLE 5. Mean and range in temperature (°C) and salinity (parts per thousand) recorded at sample sites during the intensive louse surveys in 2004 and 2009 (n = sample size).

Year	Temperature (°C)			Salinity (ppt)		
	Mean	Range	n	Mean	Range	n
2004	10.39	8.0–15.0	117	26.47	10–33	117
2009	10.86	6.5–17.0	126	26.53	10–35	203

(Morton et al. 2005) and improved survival of the affected pink salmon cohorts (Beamish et al. 2006). Another study comparing parasite loads and marine survival between fallow and active migration routes in the same year reached similar conclusions (Morton et al. 2010). While fallowing is an effective management tool for controlling outbreaks, it is less economical for farms to be fallowed on an annual basis because salmon production cycles usually exceed one year.

Reliance on parasiticide use in sea cage salmon aquaculture therefore appears to be inevitable if current aquaculture production cycles continue and overall production exceeds regional host density thresholds below which outbreaks do not occur (Frazer et al. 2012). However, in a regime of parasite population growth in the Broughton Archipelago, we found that meeting conservation objectives for wild salmon did not involve a significant increase in the number of parasiticide treatments over previous management, but rather, a change in the timing of treatment in advance of wild salmon migration schedules. These winter treatments were not due to compliance of management with policy, as they occurred during months when regulatory policy did not necessitate management intervention, only increased monitoring frequency when sea lice abundances reach three motiles per farm salmon.

The changes in parasite management we have documented occurred during a period of intensive scientific study (PFRCC 2002, Krkošek 2010a). During this period, many multi-stakeholder processes connected research scientists with fisheries managers, aquaculture veterinarians, policy representatives, conservation organizations, First Nations, eco-tourism operators, commercial-fishing interests, and other groups. Examples include the Broughton Archipelago Monitoring Program (available online),⁸ the British Columbia Pacific Salmon Forum (PSF 2009), and Simon Fraser University's Speaking for the Salmon Series (Gallaughier and Wood 2004, Routledge et al. 2007). These processes may have been vital in exchanging and interpreting scientific information that aided a response from management during a period of high scientific progress and uncertainty.

Nevertheless, progress on science, management, and policy of salmon aquaculture and sea lice is constantly challenged by the correlative nature of analyses such as

ours. The interannual changes in louse abundance on wild and farm salmon, as well as salmon population growth rates, are consistent with a process of disease outbreaks and subsequent control. However, these linkages are not the product of formal scientific principles of replication and randomization, possible in a controlled setting, but rather correlations within components of a dynamic social–ecological system. It is therefore possible that our results are the product of other unknown processes that were spatially and temporally correlated with sea lice and salmon management and population dynamics, although no such alternative process has yet been identified. Despite such uncertainty, we found effective advance louse manage-

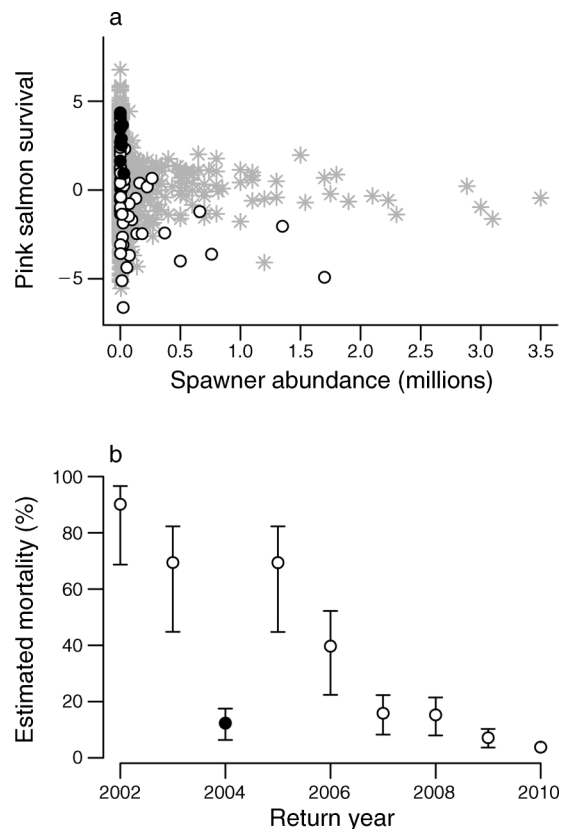


FIG. 6. (a) Pink salmon survival [$\log(R_{i,t}/N_{i,t})$, where $R_{i,t}$ are recruits and $N_{i,t}$ are spawners] for reference populations and the Broughton Archipelago prior to the onset of sea lice infestations (gray stars [*]), and during sea lice infestations in the Broughton Archipelago (2002 to present [open circles]). (b) The mortality of Broughton populations due to sea lice infestations of juvenile salmon [$1 - \exp(-cW_{a,t-1})$], where c is the louse parameter from a modified Ricker model fit to the data in panel (a) and $W_{a,t-1}$ is the average louse abundance on wild salmon in area a and return year $t - 1$. Prior to 2001 (return year 2002), there are no data on sea lice abundances on juvenile salmon, and mortality due to infestations was assumed to be negligible. Error bars indicate the range of mortality arising from a 95% bootstrapped CI on the parameter c . Solid circles in both panels (a) and (b) correspond to salmon that migrated through the Broughton Archipelago during the fallowing intervention of 2003.

⁸ www.bamp.ca

ment on farms has appeared to yield positive conservation benefits.

Another limitation of our analysis is the use of the Knight Inlet–Tribune Channel–Fife Sound migration corridor as an indicator of how sea lice abundance has changed among years in relation to farm management and influenced productivity of exposed pink salmon populations. It is our understanding, based on 10 years of fieldwork in the Broughton Archipelago, that the migration route we studied is the primary corridor through which the main biomass of juvenile salmon transits from rivers in the Broughton Archipelago to Queen Charlotte Strait. This also accords with traditional knowledge of local residents and aboriginals in the area, but is nevertheless an untested assumption and alternate migration routes are possible (e.g., directly to the mouth of Knight Inlet; Fig. 1). The locations of the various rivers in relation to the salmon farms will introduce some variability among populations in their exposure levels, and we have not directly accounted for such effects except for the area within year random effect in the spawner–recruit model.

Estimates of lice on wild juvenile pink salmon from weekly monitoring of three sites in the Broughton Archipelago are challenged by changing methodologies in sample collection and analysis throughout the study period. Juvenile salmon were collected by dip net (2001–2003) and beach seine (2004–2009), and each method has potential biases. Dipnetting may select for weaker fish that are slower to evade the net, but reduces the time fish spend in the net. Beach seining reduces selection bias (although fitter fish may be able to escape the net in suboptimal conditions), but increases the time spent in the net when lice and scales may be rubbed off (Morton et al. 2004). We assume the potential errors associated with each of these methods are small relative to the yearly differences in infection pressure, as there is no abrupt change in infection intensity with the change in collection methods. Similarly, switching from lethal examination in a laboratory under a microscope (2001–2004) to visual assays of live salmon using a hand lens in the field (2005–2009) may have confounded results as visual assays of live salmon have been shown to slightly underestimate the abundance of copepodite and chalimus stages (Krkošek et al. 2005b). However, these errors are again likely small relative to annual changes in infection intensity. Indeed, when we analyzed the counts of motile lice only, which are enumerated equally well on live and euthanized salmon (Krkošek et al. 2005b), the annual trends are the same and our results are unchanged.

Clearly, the magnitude and uncertainty of the linkages between lice on farms, lice on wild juvenile salmon, and salmon population growth are sensitive to assumptions of various plausible migration routes (Marty et al. 2010, Krkošek et al. 2011b). In this paper we have applied similar methodologies that previously documented epizootics and population decline of wild pink salmon

populations in the Broughton Archipelago (Krkošek et al. 2005a, 2006, 2007a, Krkošek and Hilborn 2011) to new data from the area in more recent years, and uncovered a significant negative relationship between lice on juvenile salmon and salmon survival. Together with the relationship between lice on juvenile salmon and management of lice on salmon farms, these results suggest that recent adaptive changes in parasite management have had positive effects for conservation of pink salmon in the Broughton Archipelago.

The changes in parasite management on salmon farms in the Broughton Archipelago are not an example of formal adaptive management (Walters 1997). These were not experimental changes that were planned according to a quantitative framework designed to systematically evaluate management effectiveness, but nor were they strictly trial and error. Rather, our results are likely the product of a contentious and productive scientific debate with continuing disagreement, multi-stakeholder involvement, and management responses. These processes may have nevertheless led to adaptive change in a social–ecological system, with at least temporary conservation gains. It is not clear if adaptive changes in management and policy in social–ecological systems are more commonly attributable to formal adaptive management or the more contentious multi-stakeholder process that has occurred for sea lice and salmon in the Broughton Archipelago. We suspect the latter, and there has been increasing interest in alternative views of adaptive management that regard conservation as a social process, where alternative objectives and perceptions must be considered (e.g., Cundill et al. 2012).

Sea lice outbreaks and concerns of transmission to wild salmonids are not new issues unique to the Broughton Archipelago. Concerns of declines of wild salmon and trout in Europe (e.g., Bjørn et al. 2001, Butler and Watt 2003, Gargan et al. 2003) and elsewhere (Ford and Myers 2008) have spurred coordinated area management and strategic delousing treatments of farm salmon in these areas. Winter treatment of farm salmon prior to wild salmon migrations and before warming temperatures spur sea lice population growth has been recommended in Europe and eastern Canada for almost a decade (Costello 2004). Some of these changes to sea lice management have been met with success, decreasing the infection pressure and numbers of sea lice on wild salmonids (e.g., Bjørn et al. 2011, Heuch et al. 2009), although connections from management changes to the productivity of wild fish populations have rarely been made.

The long-term sustainability of social–ecological systems that depend on wild and farm salmon remains to be resolved. In the Broughton Archipelago, current louse management could be undermined by parasite evolution of resistance to chemical treatments, as has occurred or is occurring elsewhere (Lees et al. 2008, Westcott et al. 2010). In addition, there is little known of

potential impacts of parasiticide use on other ecosystem components or processes (Burridge et al. 2010). Beyond sea lice, other infectious diseases, such as infectious salmon anemia (Olivier 2002), or ecological effects of farming nonnative species (Volpe et al. 2001) may be of concern. Coordinated fallowing of farms after harvest may help break the cycle of infection for sea lice and other pathogens (Costello 2004). As global aquaculture growth continues (FAO 2009), adaptive changes in disease management may be fundamental to resilience of social–ecological systems dependent on both wild and farm fish.

ACKNOWLEDGMENTS

We thank two anonymous referees whose comments greatly improved the manuscript. We are grateful to those at DFO who generated and shared escapement and catch data, A. Morton for providing the weekly monitoring data, and the many individuals who contributed to the sea lice fieldwork: E. Nelson, J. Volpe, S. Rogers, A. Park, D. Stabel, H. Ford, A. Yeomans-Routledge, M. Paleczny, G. Garramone, and S. Durkee. We are also grateful to A. Ibell and L. Rogers for assembling and preparing the database. This work was supported by funding from the University of Otago, the British Columbia Pacific Salmon Forum, National Geographic Society, the David Suzuki Foundation, Watershed Watch Salmon Society, the Wilderness Tourism Association of British Columbia, the Living Oceans Society, the Canadian Sablefish Association, Finest at Sea, the Mathematics of Information Technology and Complex Systems National Centre of Excellence of Canada, scholarships from the Natural Sciences and Engineering Research Council of Canada (to M. Krkošek and S. J. Peacock), Alberta Innovates (to S. J. Peacock), and NSERC Discovery and Accelerator Grants and a Canada Research Chair (M. A. Lewis). M. A. Lewis also gratefully acknowledges a Research Fellowship from the Oxford Centre for Collaborative and Applied Mathematics, supported by Award Number KUK-CI013-04 made by King Abdullah University of Science and Technology (KAUST).

LITERATURE CITED

- Asche, F., H. Hansen, R. Tveteras, and S. Tveteras. 2009. The salmon disease crisis in Chile. *Marine Resource Economics* 24:405–411.
- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.999375-38. R Foundation for Statistical Computing, Vienna, Austria. <http://CRAN.R-project.org/package=lme4>
- Beamish, R. J., S. Jones, C. E. Neville, R. Sweeting, G. Karreman, S. Saksida, and E. Gorden. 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 Journal of Marine Science* 63:1326–1337.
- Bjørn, P. A., B. Finstad, and R. Kristoffersen. 2001. Salmon lice infection of wild sea trout and arctic char in marine and freshwaters: the effects of salmon farms. *Aquaculture Research* 32:947–962.
- Bjørn, P. A., R. Sivertsgard, B. Finstad, R. Nilsen, R. M. Serrallinares, and R. Kristoffersen. 2011. Area protection may reduce salmon louse infection risk to wild salmonids. *Aquaculture Environment Interactions* 1:233–244.
- Bolker, B., H. Skaug, D. Fournier, A. Nielsen, and A. Magnusson. 2012. glmmADMB: generalized linear mixed models using AD model builder. R package version 0.7.2.7/r189. R Foundation for Statistical Computing, Vienna, Austria. <http://R-Forge.R-project.org/projects/glmmadmb/>
- Brooks, K., and S. Jones. 2008. Perspectives on pink salmon and sea lice: scientific evidence fails to support the extinction hypothesis. *Reviews in Fisheries Science* 16:403–412.
- Burridge, L., J. S. Weis, F. Cabello, J. Pizarro, and K. Bostick. 2010. Chemical use in salmon aquaculture: A review of current practices and possible environmental effects. *Aquaculture* 306:7–23.
- Butler, J. R. A., and J. Watt. 2003. Assessing and managing the impacts of marine salmon farms on wild Atlantic salmon in western Scotland: identifying priority rivers for conservation. Pages 93–118 in D. Mills, editor. *Salmon at the edge*. Blackwell Science, Oxford, UK.
- Cabello, F. C. 2006. Heavy use of prophylactic antibiotics in aquaculture: a growing problem for human and animal health and for the environment. *Environmental Microbiology* 8:1137–1144.
- Connors, B. M., M. Krkošek, and L. M. Dill. 2008. Sea lice escape predation on their host. *Biology Letters* 4:455–457.
- Connors, B., M. Krkošek, J. S. Ford, and L. M. Dill. 2010. Coho salmon productivity in relation to salmon lice from infected prey and salmon farms. *Journal of Applied Ecology* 47:1372–1377.
- Connors, B. M., C. Lagasse, and L. M. Dill. 2011. What's love got to do with it? Ontogenetic drivers of dispersal in a marine ectoparasite. *Behavioral Ecology* 22:588–593.
- Costello, M. J. 2004. A checklist of best practice for sea lice control on salmon farms. *Caligus* 8:18.
- Costello, M. J. 2006. Ecology of sea lice parasitic on farmed and wild fish. *Trends in Parasitology* 22:475–483.
- Costello, M. J. 2009. The global economic cost of sea lice to the salmonid farming industry. *Journal of Fish Diseases* 32:115–118.
- Cundill, G., G. S. Cumming, D. Biggs, and C. Fabricius. 2012. Soft systems thinking and social learning for adaptive management. *Conservation Biology* 26:13–20.
- Dann, P., F. I. Norman, J. M. Cullen, F. J. Neira, and A. Chiaradia. 2000. Mortality and breeding failure of little penguins, *Eudyptula minor*, in Victoria, 1995–96, following a widespread mortality of pilchard, *Sardinops sagax*. *Marine and Freshwater Research* 51:355–362.
- Diana, J. S. 2009. Aquaculture production and biodiversity conservation. *Bioscience* 59:27–38.
- Dorner, B., R. M. Peterman, and S. L. Haeseker. 2008. Historical trends in productivity of 120 Pacific pink, chum, and sockeye salmon stocks reconstructed by using a Kalman filter. *Canadian Journal of Fisheries and Aquatic Sciences* 65:1842–1866.
- Duarte, C. M., N. Marbá, and M. Holmer. 2007. Rapid domestication of marine species. *Science* 316:382–383.
- FAO [Food and Agricultural Organization of the United Nations]. 2009. State of the world's fisheries and aquaculture. FAO, Rome, Italy.
- Fisheries and Oceans Canada. 2011. NuSEDS V2.0 Regional adult salmon escapement database pink: 1950–2010. Fisheries and Oceans Canada, Ottawa, Ontario, Canada. <http://www.pac.dfo-mpo.gc.ca/gis-sig/maps-cartes-eng.htm>
- Ford, J., and R. Myers. 2008. A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biology* 6(2):e33.
- Frazer, L. N., A. Morton, and M. Krkošek. 2012. Critical thresholds in sea lice epidemics: Evidence, sensitivity, and subcritical estimation. *Proceedings of the Royal Society B* 279:1950–1958.
- Gallaugh, P., and L. Wood. 2004. Conveners' report from the scientists' roundtable on sea lice and salmon in the Broughton Archipelago area of British Columbia. Simon Fraser University Speaking for the Salmon Series, Vancouver, British Columbia, Canada.
- Gargan, P., O. Tully, and W. Poole. 2003. Relationship between sea lice infestations, sea lice productions and sea trout survival in Ireland, 1992–2001. Pages 119–135 in D.

- Mills, editor. Salmon at the edge. Blackwell Science, Oxford, UK.
- Gaughan, D. J. 2001. Disease-translocation across geographic boundaries must be recognized as a risk even in the absence of disease identification: the case with Australian Sardinops. *Reviews in Fish Biology and Fisheries* 11:113–123.
- Goldburg, R., and R. Naylor. 2005. Future seascapes, fishing, and fish farming. *Frontiers in Ecology and the Environment* 3:21–28.
- Gottesfeld, A. S., B. Proctor, L. D. Rolston, and C. Carr-Harris. 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.
- Gudjonsson, S., and D. L. Scarnecchia. 2009. “Even the evil need a place to live”: wild salmon, salmon farming, and zoning of the Icelandic coastline. *Fisheries* 34:477–486.
- Haydon, D. T., M. K. Laurenson, and C. Sillero-Zubiri. 2002. Integrating epidemiology into population viability analysis: Managing the risk posed by rabies and canine distemper to the Ethiopian wolf. *Conservation Biology* 16:1372–1385.
- Heuch, P. A., P. A. Bjørn, B. Finstad, J. C. Holst, L. Asplin, and F. Nilsen. 2005. A review of the Norwegian ‘National Action Plan against Salmon Lice on Salmonids’: The effect on wild salmonids. *Aquaculture* 246:79–92.
- Heuch, P. A., R. S. Olsen, R. Malkenes, C. Revie, G. Gettinby, M. Baillie, F. Lees, and B. Finstad. 2009. Temporal and spatial variations in lice numbers on salmon farms in the Hardanger fjord 2004–06. *Journal of Fish Diseases* 32:89–100.
- Jansen, P. A., A. B. Kristoffersen, H. Viljugrein, D. Jimenez, M. Aldrin, and A. Stien. 2012. Sea lice as a density-dependent constraint to salmonid farming. *Proceedings of the Royal Society B* 279:2330–2338.
- Johnson, S. C., and L. J. Albright. 1991. The developmental stages of *Lepeophtheirus salmonis* (Kroyer, 1837) (Copepoda, Caligidae). *Canadian Journal of Zoology* 69:929–950.
- Jones, S. R. M., and N. B. Hargreaves. 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.
- Jones, S. R. M., G. Prosperi-Porta, E. Kim, P. Callow, and N. B. Hargreaves. 2006. The occurrence of *Lepeophtheirus salmonis* and *Caligus clemensi* (Copepoda: Caligidae) on three-spine stickleback *Gasterosteus aculeatus* in coastal British Columbia. *Journal of Parasitology* 92:473–480.
- Krkošek, M. 2010a. Sea lice and salmon in Pacific Canada: ecology and policy. *Frontiers in Ecology and the Environment* 86:201–209.
- Krkošek, M. 2010b. Host density thresholds and disease control for fisheries and aquaculture. *Aquaculture Environment Interactions* 1:21–32.
- Krkošek, M., A. Bateman, S. Probsch, and C. Orr. 2010. Dynamics of outbreak and control of salmon lice on two salmon farms in the Broughton Archipelago, British Columbia. *Aquaculture Environment Interactions* 1:137–146.
- Krkošek, M., B. Connors, P. Mages, S. Peacock, H. Ford, J. S. Ford, A. Morton, J. P. Volpe, R. Hilborn, L. M. Dill, and M. A. Lewis. 2011a. Fish farms, parasites, and predators: Implications for salmon population dynamics. *Ecological Applications* 21:897–914.
- Krkošek, M., B. M. Connors, A. Morton, M. A. Lewis, L. M. Dill, and R. Hilborn. 2011b. Effects of parasites from salmon farms on productivity of wild salmon. *Proceedings of the National Academy of Sciences USA* 108:14700–14704.
- Krkošek, M., J. S. Ford, A. Morton, S. Lele, R. A. Myers, and M. A. Lewis. 2007a. Declining wild salmon populations in relation to parasites from farm salmon. *Science* 318:1772–1775.
- Krkošek, M., A. Gottesfeld, B. Proctor, D. Rolston, C. Carr-Harris, and M. A. Lewis. 2007b. Effects of host migration, diversity, and aquaculture on sea lice threats to Pacific salmon populations. *Proceedings of the Royal Society B* 274:3141–3149.
- Krkošek, M., and R. Hilborn. 2011. Sea lice (*Lepeophtheirus salmonis*) infestations and the productivity of pink salmon (*Oncorhynchus gorbuscha*) in the Broughton Archipelago, British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 68:17–29.
- Krkošek, M., M. A. Lewis, A. Morton, L. N. Frazer, and J. P. Volpe. 2006. Epizootics of wild fish induced by farm fish. *Proceedings of the National Academy of Sciences USA* 103:15506–15510.
- Krkošek, M., M. A. Lewis, and J. P. Volpe. 2005a. Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proceedings of the Royal Society B* 272:689–696.
- Krkošek, M., A. Morton, and J. P. Volpe. 2005b. Nonlethal assessment of juvenile pink and chum salmon for parasitic sea lice infections and fish health. *Transactions of the American Fisheries Society* 134:711–716.
- Krkošek, M., A. Morton, J. P. Volpe, and M. A. Lewis. 2009. Sea lice and salmon population dynamics: effects of exposure time for migratory fish. *Proceedings of the Royal Society B* 276:2819–2828.
- Lees, F., M. Baillie, G. Gettinby, and C. W. Revie. 2008. The efficacy of emamectin benzoate against infestations of *Lepeophtheirus salmonis* on farmed Atlantic salmon (*Salmo salar* L) in Scotland, 2002–2006. *PLoS ONE* 3.
- Liu, J. G., et al. 2007. Complexity of coupled human and natural systems. *Science* 317:1513–1516.
- Marty, G., S. Saksida, and T. J. Quinn. 2010. Relationship of farm salmon, sea lice, and wild salmon populations. *Proceedings of the National Academy of Sciences USA* 107:22599–22604.
- Morton, A., A. McConnell, R. Routledge, and M. Krkošek. 2010. Sea lice dispersion and salmon survival in relation to salmon farm activity in the Broughton Archipelago. *ICES Journal of Marine Science* 68:144–156.
- Morton, A., R. Routledge, C. Peet, and A. Ladwig. 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.
- Morton, A., R. D. Routledge, and R. Williams. 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., and R. Williams. 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.
- Naylor, R. L., R. J. Goldberg, J. H. Primavera, N. Kautsky, M. C. M. Beveridge, J. Clay, C. Folke, J. Lubchenco, H. Mooney, and M. Troell. 2000. Effect of aquaculture on world fish supplies. *Nature* 405:1017–1024.
- Nendick, L., M. Sackville, S. Tang, C. J. Brauner, and A. P. Farrell. 2011. Sea lice infection of juvenile pink salmon (*Oncorhynchus gorbuscha*): effects on swimming performance and postexercise ion balance. *Canadian Journal of Fisheries and Aquatic Sciences* 68:241–249.
- Olivier, G. 2002. Disease interactions between wild and cultured fish: Perspectives from the American Northeast (Atlantic Provinces). *Bulletin of the European Association of Fish Pathologists* 22:103–109.
- Orr, C. 2007. Estimated sea louse egg production from Marine Harvest Canada farmed Atlantic salmon in the Broughton Archipelago, British Columbia, 2003–2004. *North American Journal of Fisheries Management* 27:187–197.

- Pearsall, I. A. 2008. Broughton Archipelago: a state of knowledge. Pacific Salmon Forum. Pearsall Ecological Consulting, Nanaimo, British Columbia, Canada. <http://www.11bc.leg.bc.ca/public/PubDocs/bcdocs/438283/BroughtonStateofKnowledgeReport.pdf>
- Pedersen, A. B., K. E. Jones, C. L. Nunn, and S. Altizer. 2007. Infectious diseases and extinction risk in wild mammals. *Conservation Biology* 21:1269–1279.
- PFRCC [Pacific Fisheries Resource Conservation Council]. 2002. 2002 Advisory: the protection of Broughton Archipelago pink salmon stocks. PFRCC, Vancouver, British Columbia, Canada.
- Pike, A. W., and S. L. Wadsworth. 2000. Sealice on salmonids: Their biology and control. *Advances in Parasitology* 44:233–337.
- PSF. 2009. Pacific salmon forum final report and recommendations to the Government of British Columbia. Pacific Salmon Forum, Victoria, British Columbia, Canada.
- Pyper, B. J., F. J. Mueter, R. M. Peterman, D. J. Blackbourn, and C. C. Wood. 2001. Spatial covariation in survival rates of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:1501–1515.
- Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Washington, USA.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Revie, C. W., L. M. Dill, B. Finstad, and C. D. Todd. 2009. Salmon Aquaculture Dialogue Working Group report on sea lice. World Wildlife Fund, Washington, D.C., USA.
- Revie, C. W., G. Gettinby, J. W. Treasurer, and C. Wallace. 2003. Identifying epidemiological factors affecting sea lice *Lepeophtheirus salmonis* abundance on Scottish salmon farms using general linear models. *Diseases of Aquatic Organisms* 57:85–95.
- Ritchie, G. 1997. The host transfer ability of *Lepeophtheirus salmonis* (Copepoda: Caligidae) from farmed Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases* 20:153–157.
- Routledge, R. D., P. Gallagher, and C. Orr. 2007. Conveners' report on the summit of scientists on aquaculture and the protection of Wild Salmon, Alert Bay. Simon Fraser University Speaking for the Salmon Series, Vancouver, British Columbia, Canada.
- Saksida, S. M. 2006. Infectious haematopoietic necrosis epidemic (2001 to 2003) in farmed Atlantic salmon *Salmo salar* in British Columbia. *Diseases of Aquatic Organisms* 72:213–223.
- Tully, O., and D. Noland. 2002. A review of the population biology and host–parasite interactions of the sea louse *Lepeophtheirus salmonis* (Copepoda: Caligidae). *Parasitology* 124:165–182.
- Volpe, J. P., B. R. Anholt, and B. W. Glickman. 2001. Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 58:197–207.
- Walker, B., C. S. Hollin, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society* 9:5.
- Walters, C. J. 1997. Challenges in adaptive management of riparian and coastal ecosystems. *Conservation Ecology* 1:1.
- Westcott, J. D., C. W. Revie, B. L. Griffin, and K. L. Hammell. 2010. Evidence of sea lice *Lepeophtheirus salmonis* tolerance to emamectin benzoate in New Brunswick Canada. Sea lice 2010: Eighth international sea lice conference. Victoria, British Columbia, Canada.

SUPPLEMENTAL MATERIAL

Appendix A

Description of the P_{\max} technique used to calculate exploitation rates from catch and spawner abundance data ([Ecological Archives A023-028-A1](#)).

Appendix B

Supplemental figures showing details of louse abundance and salinity for spatially intensive surveys in the Broughton Archipelago, British Columbia, Canada, in 2009 ([Ecological Archives A023-028-A2](#)).

Appendix C

Supplemental tables describing the pink salmon spawning rivers included in the analysis and results from the analysis of parasiticide treatments on farm salmon ([Ecological Archives A023-028-A3](#)).

Supplement

Details of the analysis of pink salmon population data, including spawner and catch data and R code for compiling spawner–recruit pairs and fitting the Ricker model ([Ecological Archives A023-028-S1](#)).