

Sea lice dispersion and salmon survival in relation to salmon farm activity in the Broughton Archipelago

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The risk of salmon lice (*Lepeophtheirus salmonis*) transmission to wild juvenile Pacific salmon has spurred management change to reduce lice on salmon farms. We studied the abundance of planktonic lice preceding the juvenile salmon outmigration as well as the abundance of lice on juvenile pink (*Oncorhynchus gorboscha*) and chum (*Oncorhynchus keta*) salmon in two distinct migration routes, one containing only fallow farms and the other active farms that applied a parasiticide. Results indicate that fallowing reduces the abundance and flattens the spatial distribution of lice relative to that expected in areas without farms. Active farms remained the primary source of lice, but transmission was reduced 100-fold relative to previous epizootics in the study area. On the migration route containing active farms, ~50% of the juvenile salmon showed evidence of louse damage to surface tissues and the estimated direct louse-induced mortality was <10%, not including indirect effects of infection on predation risk or competition. The survival of the pink salmon cohort was not statistically different from a reference region without salmon farms. Although repeated use of a single parasiticide can lead to resistance, reducing louse transmission from farmed salmon may help conserve some wild Pacific salmon populations.

Keywords: aquaculture, conservation, salmon, sea lice.

Introduction

An increase in sea lice (*Lepeophtheirus salmonis*) infestations of wild juvenile pink (*Oncorhynchus gorboscha*) and chum (*Oncorhynchus keta*) salmon above those typically observed in nature have been linked with salmon farms in Pacific Canada (Morton and Williams, 2003; Morton *et al.*, 2004, 2008; Krkošek *et al.*, 2005a, 2006). The infestations are associated with high mortality of wild juvenile salmon (Morton and Routledge, 2005; Krkošek *et al.*, 2006) and depressed populations of wild salmon (Krkošek *et al.*, 2007a; Ford and Myers, 2008). The sea louse is a native marine ectoparasitic copepod that commonly infects adult wild and farmed salmonids, feeding on host surface tissues and causing morbidity and mortality (Pike and Wadsworth, 2000; Costello, 2006). Although adult Pacific salmon are commonly infested (Nagasawa, 2001; Beamish *et al.*, 2005), juvenile Pacific salmon tend to be protected from lice because they enter the ocean uninfested and are spatially separated from large adult salmon populations for the first 2–3 months of marine life (Krkošek *et al.*, 2007b). Because lice are found on juvenile Pacific salmon at prevalences typically <5% in areas without salmon farms, it is likely that the elevation—or bioamplification—of the numbers of sea lice by salmon farms leads to infestations (Krkošek, 2010). Lice have a direct life cycle, with non-infectious nauplii and infectious copepodites that disperse

in the plankton, followed by a developmental progression of parasitic stages from copepodites, to chalimi, and then motiles. Motiles include adult lice that sexually reproduce on host fish, with females extruding eggstrings from which planktonic nauplii hatch. Transmission of lice among host fish and between wild and farmed salmon is predominantly via the planktonic stages as well as through motile lice, which can move among fish (Ritchie, 1997; Connors *et al.*, 2008).

The threat of sea-louse transmission to wild Pacific salmon is likely mediated by siting and management of farms as well as biotic and abiotic factors (Krkošek, 2010). Two possible management options to reduce louse exposure of wild juvenile salmon are removing salmon farms from wild salmon migration routes and treating farmed salmon with chemical therapeutants (Morton *et al.*, 2005; Orr, 2007). In Canada, fallowing salmon farms during the juvenile outmigration is not practical yearly because farmed salmon require more than a year in the marine pens to reach harvest size. In one year, a British Columbia management plan that emptied salmon farms on one route was associated with reduced abundance of sea lice on juvenile pink and chum salmon in the Broughton Archipelago (Morton *et al.*, 2005), and the cohort of juvenile pink salmon subjected to the fallow experienced exceptionally high marine survival (Beamish *et al.*, 2006). As it is not practical to fallow farms every year during the salmon outmigration, there has been a movement towards the coordinated

application of a chemical therapeutant, emamectin benzoate (EM), which is administered in salmon feed. EM is a crustacean neurotoxin and is associated with reduced abundance of sea lice on farmed salmon for several weeks following application (Gustafson *et al.*, 2006; Orr, 2007). Reliance on EM has caused concern about resistance (Denholm *et al.*, 2002). The relative efficacy of fallowing and chemical treatment for reducing louse exposure of wild juvenile salmon has not been evaluated.

We studied the distribution of sea lice in the Broughton Archipelago in 2007 in relation to salmon farming activity as well as the corresponding survival of wild juvenile pink and chum salmon. The study is divided into three parts. First, we studied the distribution of planktonic larval sea lice—nauplii and copepodites—in the months preceding the outmigration of juvenile salmon. This yielded information on the likely sources of lice present in the marine environment when juvenile salmon begin their seaward migration. Plankton data were analysed to seek evidence for an association with salmon farm activity (grower, harvest, fallow, chemical treatment) and abiotic factors (exposure, currents, temperature, salinity). Second, we collected data on the abundance of sea lice on juvenile pink and chum salmon as they travelled down one migration corridor containing two fallowed farms and another migration corridor containing several active farms. These data were analysed using statistical models to evaluate the effects of farms and abiotic covariates on the abundance of sea lice. Further, a mechanistic model was applied to estimate sea-lice transmission and juvenile salmon survival, similar to Krkošek *et al.* (2006). Finally, in the third part, pink salmon escapement data were used to compare the survival of the studied cohorts in the Broughton Archipelago with an unexposed reference region north of the Archipelago, which we refer to as the central coast, where there are no fish farms. The results shed light on the efficacy of fallowing and chemical treatment as management interventions to reduce the threat of transmitting sea lice to wild juvenile salmon.

Methods

Plankton sampling

Plankton tows were made between 2 February and 2 April 2007 at 19 sites on at least two different dates throughout the Broughton Archipelago, British Columbia (Figure 1). The sites sampled each week included five estuaries, one broodstock fish farm, two farms in the process of harvesting mature salmon, one farm holding 2-year-old fish, four farms holding year-1 smolts, three farms with pens but no fish, and five control sites. Control sites were those that had no fish farms but similar oceanographic characteristics (temperature, salinity, embayment) to the sites containing fish farms. One farm was treated with EM part way through the study, providing an opportunity to investigate whether there was a response in the planktonic louse populations nearby. To investigate site-specific factors at locations with non-zero louse abundance (active farm sites), tows were conducted at several locations: between the pens and the shore, between the farm and open water, and down- and up-current from the farms. At fallow and smolt farms, sampling was between the farm and the shore.

We used a plankton net of 250- μ m mesh and dimensions 0.5 m diameter \times 2.48 m length on a towline 24.4 m long towed for 20 min at an average speed of 48.3 cm s⁻¹ (12.5 s.d.) at each site. Speed and volume were calculated using a G.O. Environmental flowmeter # 21333. During the first week of sampling, the net was towed without weights several centimetres below the surface. On subsequent sampling trips, a 0.45-kg weight was attached to the net, lowering the opening of the net to some 2 m below the surface (calculated by the angle of the tow line). At one site where lice were abundant (Sir Edmund), we also sampled with additional weights, lowering the net to 6 m and to 8 m for two additional tows between the farm and shore. After 20 min of towing, the net was pulled to the boat and its outside washed down with seawater to flush any plankton adhered to the inside of the net into the codend. The contents of

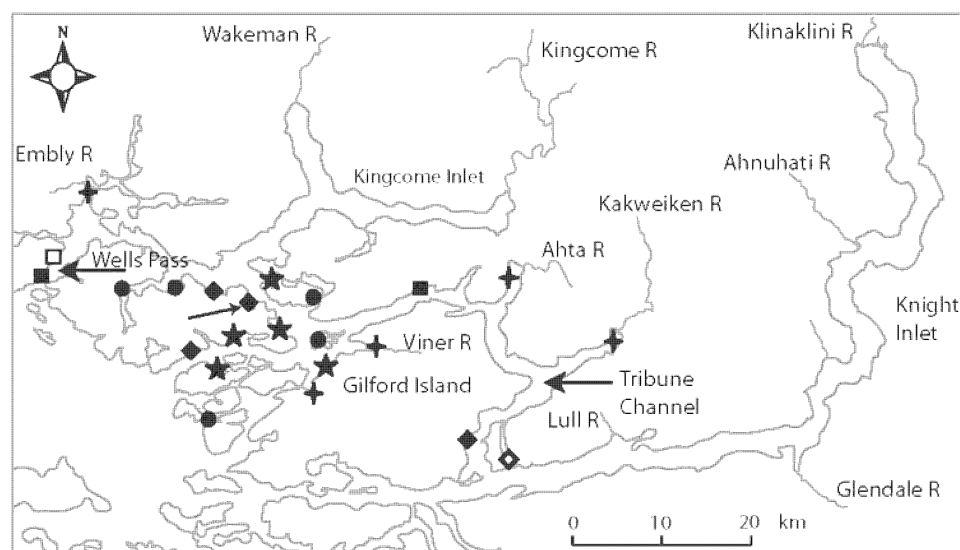


Figure 1. Map of the Broughton Archipelago showing plankton sample sites. Squares are fallow farms; circles are smolt farms; diamonds are farms with adult salmon; stars are control sites; and crosses are estuary sites. The open square and open diamond are farm locations that were not sampled. The arrow shows the farm treated with EM near the end of the study. The Broughton Archipelago is located east of northern Vancouver Island, British Columbia.

the codend were then poured into jars and the contents examined under $\times 10$ magnification within 6 h. *Lepeophtheirus salmonis* nauplii and copepodites were identified according to Galbraith (2005).

Analysis of plankton data

To test the null hypothesis that sea-louse nauplii were distributed independently of proximity to farmed fish, we conducted a χ^2 test for the presence or absence of lice in individual tows vs. site category (unexposed sites: control, estuary, and empty; farm sites: brood, smolt, grower, and in-harvest). At active farm sites, where nauplii were sufficiently abundant to support analysis of site-specific correlates, we conducted a Poisson regression analysis of (i) farm status as grower or in-harvest; (ii) farm location in a sheltered bay; (iii) recent treatment with "Slice"TM (EM); (iv) sampling between the farm and the nearest shore; (iv) sampling down-current of the farm; and (v) sampling behind the farm when facing out to more open water. In addition, surface salinity and temperature, date of the tow, and the weight attached to the net (to make it sink deeper) were included as continuous covariates. The analysis was conducted with the function "glm" in the statistical analysis package R (with the logarithm of the volume of water sampled included as an offset variable to control for variation in the volume of water sampled between tows; Selvin, 1998). The model was fitted iteratively by a backward elimination procedure, with the term with the largest of any p -values > 0.05 dropped sequentially.

Sampling juvenile salmon

In spring 2007, sea lice presence on juvenile pink and chum salmon was studied along two migration routes in the Broughton Archipelago. The fish likely originated from three rivers (Embley, Wakeman, and Kingcome) that are enumerated by Fisheries and Oceans, Canada, and known to produce pink and chum salmon (Figure 2). One migration route contained two salmon farms that were followed. The other migration route contained five salmon farms each holding Atlantic salmon. Along each route, we collected juvenile pink and chum salmon at intervals of 1–3 km to enumerate sea lice. The fallow transect contained 13 sample sites spanning 14 km from the Embley River to Queen Charlotte Strait (Figure 1). Both fallowed farms were empty of fish except for ~ 10 d when several pens at the more western farm were stocked with young smolts at the onset of the season (19 March 2007). From 1 April on, however, that farm remained empty for the duration of this study. The transect along the active route contained 23 sample sites spanning 40 km from near the Wakeman River to Queen Charlotte Strait (Figure 2). The farms along that route contained salmon that ranged in age from young smolts to broodstock (Figure 2). Each of the two transects was sampled three times, generating three paired active/fallow datasets, collected during the periods on 7–17 April, 19–28 April, and 9–16 May.

Fish were collected with a beach-seine 30 m long, 1.5 m deep, and 1.6-cm mesh. Twice near the Wakeman River, fish were

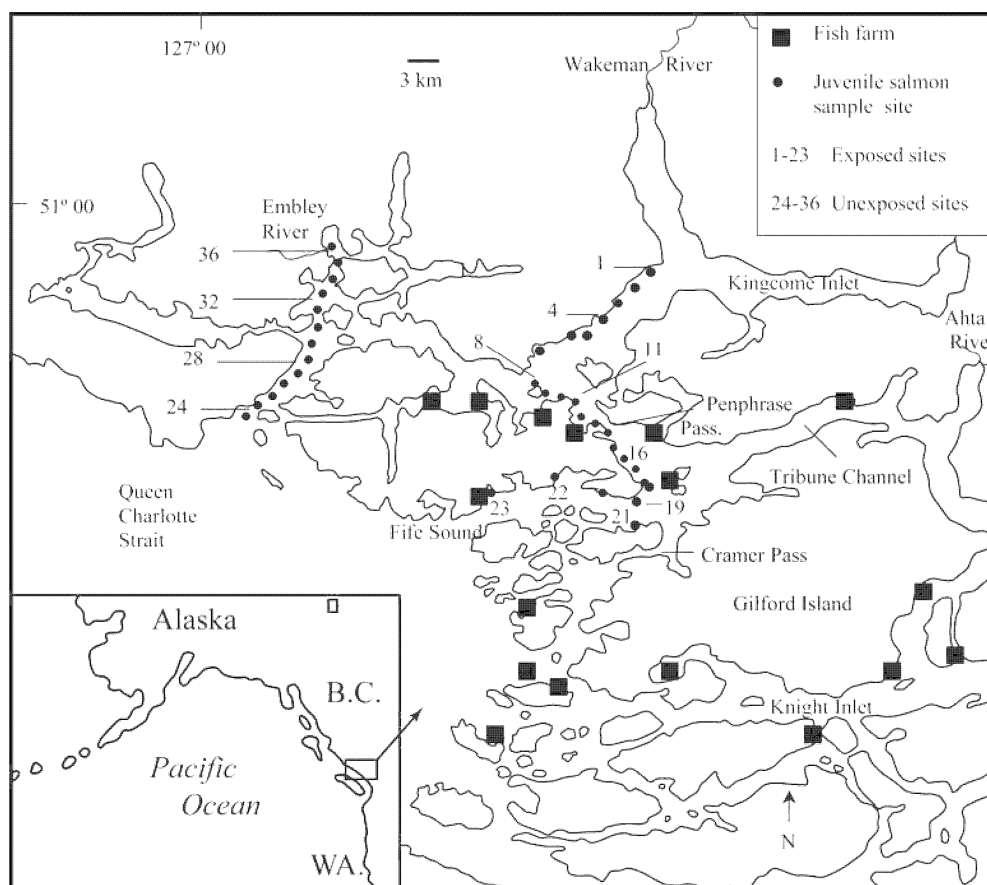


Figure 2. Map of the study area showing salmon farms and the transects of juvenile salmon sampling sites along the active migration route (sites 1–23) and the fallow migration route (sites 24–36). Wells Pass is along the fallow migration route identified by the transect with sample sites 24–36.

situated only under sheer cliff slopes, preventing beach-seining, so on those occasions we used a dipnet 45 cm in diameter with 5-mm knotless mesh to capture fish. Always, the fish were transferred into buckets by 10-cm² dipnets, and 100 were examined. We determined the species of each fish (usually pink and chum salmon) and examined each fish for sea lice using the non-lethal sampling method of Krkošek *et al.* (2005b), and identified lice to five developmental stages: copepodite, chalimus I or II, chalimus III or IV, pre-adult, and adult, following Galbraith (2005). Lice were separated into two species (*L. salmonis* or *Caligus clemensi*) at the copepodite and adult stages. Several categories of surface tissue damage related to louse feeding and/or attachment were recorded: abdominal pinching, haemorrhaging, lesions, puncture wounds, grazed gill plates, and dark blemishes associated with chalimus lice. The fish were held in buckets by periodically exchanging the contents for fresh seawater, then released at the site of capture, after examination was complete.

Analysis of salmon data

Empirical statistical analyses and mechanistic modelling were applied to evaluate the relationship between sea lice on juvenile salmon and the migration routes studied. Using generalized linear models (GLMs) with the Poisson error, we tested whether total abundance of sea lice was equal on fallow and active migration routes, whether there was a difference in louse abundance at locations before and after the fish passed a farm, and whether the difference in louse abundance between locations before and after passing the farm differed between active and fallow migration routes. In each of these analyses, sampling replicate was included as a nominal variable, and temperature and salinity as continuous covariates. Model selection was conducted by a backward process whereby the full model was specified, the least significant of the insignificant terms was removed, then the model was refitted. The procedure was repeated until only significant terms remained. The analysis was applied to copepodites, chalimi, motiles, and total lice. The GLM approach was conducted in the statistical package R. We also applied a cluster analysis using Procedure Cluster in SAS, with both Ward's and the centroid clustering methods. The cluster analysis was applied to average abundance estimates for each of three life stages of sea lice at each site across the three replicate sets of samples. The life stages were (i) copepodite, (ii) chalimus I and II combined, and (iii) chalimus III and IV.

The mechanistic model was an extension of the transmission model for sea lice described by Krkošek *et al.* (2005a, 2006) and presented in the Supplementary material. The model treats each migration route as a one-dimensional habitat—lice and fish only move seawards or landwards along narrow migration corridors, but not in other horizontal or vertical directions. Nauplii are assumed to originate from one of two sources: farms or natural. Farms are modelled as discrete points, natural sources as continuously and uniformly distributed over the entire region. The spread of planktonic nauplii and copepodites is modelled as an advection–diffusion–decay process, with two components to their movement: a systematic (advective) component corresponding to the mean surface current through the region, and a random (diffusion) component corresponding to turbulence caused by wind, tides, and random movement of the individual organisms. Nauplii and copepodites experience some mortality (a decay component) as well as development from the nauplius to the copepodite stage.

The model assumes that fish move along their one-dimensional migration route at a constant velocity from their natal rivers to sea. Attachment of copepodites to a passing fish is assumed to be proportional to the local density of unattached copepodites. Fish mortality is allowed to depend on the numbers of chalimus-stage and motile lice on the fish at a given time, with the strength of parasite-induced host mortality coming from estimates derived from experimental studies (Krkošek *et al.*, 2009). The equations are given in Krkošek *et al.* (2005a, 2006) and the Supplementary material. Similar to Krkošek *et al.* (2006), parameter values in the model associated with planktonic nauplii and copepodite mortality and development were obtained from the literature, whereas parameters associated with attachment, development, and mortality of parasitic lice were estimated by fitting the model to the data using maximum likelihood (see Supplementary material). An important extension to the previous applications of the model is that both the fallow and active routes were modelled simultaneously, with a common value for the parameter associated with the abundance of nauplii from natural sources.

There are a number of approximations in the mechanistic model, notably the one-dimensional representation of a complex three-dimensional habitat, a steady-state approximation for louse production on farms, and non-varying abiotic factors such as temperature and salinity. Another approximation is that because the first two farms on the active migration route were in proximity, the production of larvae by these two farms was modelled as a single point source situated halfway between the two farms. The same approximation was applied to louse production by the third and fourth farms on the active route because they too are in proximity to each other. This was done to reduce the number of free parameters in the model-fitting procedure and because past analyses indicated a limited ability to distinguish between point sources situated in proximity (e.g. 2–3 km) because the spatial spread of lice from farms is an order of magnitude larger (~30 km; Krkošek *et al.*, 2006). Note that, in addition to the mechanistic model, the GLM approach was pursued to accommodate potentially confounding abiotic factors better as well as to relax the assumptions and approximations of the mechanistic model. The mechanistic model was applied independently to each of the three replicate datasets using a genetic algorithm and subsequent simplex optimization in R. With the best fit of the model, the estimated spatial distributions of lice originating from farmed and wild sources were evaluated along with the survival of wild juvenile salmon.

Survival estimates from stock assessments

The final part of the analysis involved estimating and comparing the survival of populations of pink salmon in the Broughton Archipelago relative to populations from a reference region where there are no salmon farms. The unexposed region comprises a portion of the central coast of British Columbia, specifically Fisheries and Oceans Canada's Management Areas 7, 8, 9, and 10, and is detailed in Krkošek *et al.* (2007a). For both regions, only populations that had escapement estimates for both 2006 and 2008 were used. Fishing mortality for that cohort of pink salmon from both the Broughton Archipelago and the central coast was assumed to be negligible, because commercial fisheries on the stocks have declined substantially, with harvest rates near or below 5%. The survival estimates were generated by first dividing the escapement estimate in 2006 (the parental generation) by the escapement estimate in 2008 (the year our study cohort

Table 1. Summary of plankton data, organized by exposure category to farmed salmon, subcategories of site status within the farm exposure categories, number of tows conducted for each status category, and the number of sample sites within each status category.

Exposed?	Status	Tows	Sites	Nauplii	Average temperature (°C)	Average salinity (psu)
No	Control	14	5	0	7.0 (0.55)	28.6 (4.3)
	Empty	9	3	0	7.3 (0.39)	29.8 (2.6)
	Estuary	10	5	0	6.9 (0.65)	23.8 (8.2)
Yes	Smolt	9	4	0.11	6.8 (0.80)	29.1 (4.0)
	Grower	16	2	0.5	7.3 (0.41)	28.9 (4.8)
	Harvest	27	2	0.74	5.8 (0.99)	24.9 (4.2)
	Brood	2	1	0.5	6.25 (–)	18.5 (–)

Data associated with the status categories are the proportion of tows with *L. salmonis* present, and the average temperature and salinity (s.d.).

returned to the rivers), then taking the natural log. We used Student's *t*-tests to test whether survival differed between the Broughton Archipelago and the central coast and also compared the difference in survival between regions with the estimated mortality attributable to sea lice in the Broughton Archipelago.

Results

Lice in the plankton

In all, 87 plankton tows were carried out, and 256 *L. salmonis* nauplii, 37 *L. salmonis* copepodites, and 2 adult male *C. clemensi* were captured. All the lice were found in tows close to stocked fish farms (Table 1); there were no lice in samples from control sites or sites with net pens but no fish. We found 95% of the nauplii, 97% of the copepodites, and both of the adult *Caligus* within 2 m of the surface. Differences in louse frequencies between site categories at the level of status subcategory (grower, smolt, estuary, empty, etc.) and at the level of exposure to farmed salmon were both highly significant (χ^2 tests, $p < 0.0002$ for both). Lice prevalence increased as the age of the farmed fish increased: smolt, grower, to in-harvest, except for the oldest (broodstock), which had fewer pens than the other active farms and therefore likely fewer fish than the other active farms (Table 1). There was no obvious relationship between the frequency of nauplii presence in tows with either salinity or temperature (Table 1). At the farms where tows were made in different locations around the farms, the best yields were between the farm and the nearest shore (average abundance 10.3, with 10.0 s.d.) and downstream of the farms (average abundance 4.5, with 6.1 s.d.), as opposed to upstream of the farms (average abundance and s.d. zero) and between the farm and open water (average abundance 0.5, with 1.2 s.d.). Tow location relative to individual farms was included in the Poisson regression analysis below.

For the Poisson regression analysis, surface salinity and sampling date were dropped from the model because they were insignificant. The weight attached to the net was then only significant ($p = 0.050$). All other terms were highly significant ($p = 0.002$ for sampling date, $p < 0.0001$ for all others). (The residual deviance was also used to test for extra-Poisson variation which was significant; $p = 0.013$.) However, further analysis of the deviance residuals showed that this significance was largely attributable to two plankton tows that contained no nauplii in conditions where they would otherwise be expected. Hence, the

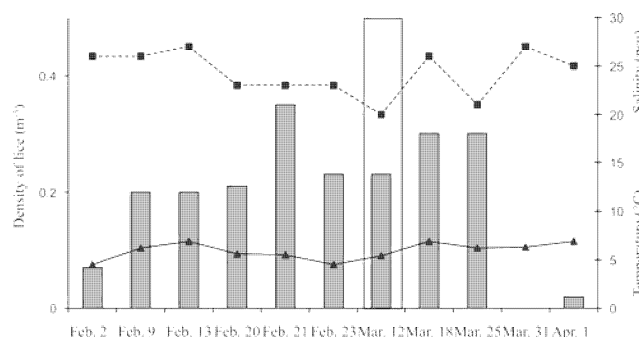


Figure 3. Density of nauplii (grey bars) caught in weekly plankton tows at the salmon farm before and after the farm fish were treated with EM during the first week in March (shown by the clear vertical rectangle). Also shown are trends in salinity (squares; in psu) and temperature (triangles; in °C).

Table 2. Average fork length (L_F) of juvenile salmon, and temperature and salinity for the three replicate datasets of lice on juvenile salmon, with the s.d. value in parenthesis.

Species or parameter	Replicate		
	1	2	3
Pink salmon L_F (mm)	36.06 (2.65)	36.70 (3.12)	41.14 (6.84)
Chum salmon L_F (mm)	41.55 (3.77)	42.37 (4.51)	50.15 (9.05)
Temperature (°C)	7.77 (0.73)	9.08 (0.98)	10.60 (1.60)
Salinity (psu)	21.54 (7.84)	28.10 (4.47)	21.08 (8.06)

data seem reasonably consistent with the Poisson variance assumption. Significant terms retained in the model indicated that (i) nauplii abundance was higher both for samples taken near farms located in more sheltered sites and for farms containing more mature fish, (ii) abundance decreased significantly after the farm was treated with EM (Figure 3), (iii) abundance was greater when the sample was taken between the farm and the nearest shore, on the down-tide side, and on the opposite side of the farm from the passage to more open water, and (iv) more nauplii were caught when the surface water was warmer.

Lice on juvenile salmon

We examined a total of 9286 pink and chum salmon. The fish had average fork lengths (Table 2) of 37.4 mm (pink salmon) and 44.0 mm (chum salmon). Pink salmon averaged 1.09 mm more on the exposed route and chum salmon averaged 1.71 mm more on the unexposed route. Temperature rose steadily through the sampling rounds and average salinity remained relatively stable (Table 2). Two salinity and three temperature measurements were missed owing to malfunctioning equipment. Average louse abundance (all stages) on the exposed route was 0.31 (0.73 s.d.), compared with the average abundance of 0.03 (0.22 s.d.) of lice on the unexposed route. If the sites inland of farms (sites 1–7) on the exposed route are excluded, average louse abundance on the active route is 0.42 (0.82 s.d.). For the fallow route, which corresponds to ambient louse abundance, the low abundance is similar to prevalence (the percentage of fish infested), which is 2.8%.

The GLM indicated that louse abundance on juvenile salmon was greater on the migration route with active farms than on the

fallow migration route ($p < 0.00001$ for each of copepodites, chalimi, motiles, and total lice) and that temperature and salinity were also significant covariates ($p < 0.05$ in each case), except for motile lice, where temperature was not significant ($p > 0.05$). Sea lice abundance differed significantly among replicate datasets for chalimi, motiles, and total lice ($p < 0.02$ in each case), but not for copepodites. Chalimi and total lice were more abundant on chum salmon than pink salmon ($p < 0.02$), but this was not evident for either copepodites or motiles ($p > 0.05$). The abundance of all stages of sea louse as well as their total abundance was greater at locations seaward of farms relative to locations inland of farms ($p < 0.02$). The difference in louse abundance between sites seaward of farms relative to sites inland of farms was less on the fallow relative to the active migration route, for copepodites, chalimi, and total lice ($p < 0.02$, for each case), but not for motiles ($p > 0.05$).

The cluster analysis indicated an association between sea lice on juvenile salmon and the salmon farms (Figure 4). All sites on the active route that were inland and hence unexposed to the farms, up Kingcome Inlet, and along the Wells Pass fallowed route, separated into a single cluster characterized by low abundance of all three life stages of lice. The result for the remaining sites, those seaward of active farms, depended slightly on the clustering method. Nonetheless, both the centroid and Ward's methods identified two further clusters, related to differences in relative abundances of the copepodite vs. older life stages. Fish caught at sites that were close to active farms contained relatively more copepodites. Sites that were farther away contained relatively more of the older chalimus-stage lice.

The centroid method, which tends to isolate single units in separate clusters, did so with two sites: (i) site 23, which was close to the Wicklow farm and the last site along the migration route with active farms, contained the highest numbers of lice overall, and (ii) site 16, which was intermediate between the Sir Edmund and Burdwood farms and contained a relatively large number of older chalimus-stage lice (a feature not visible in the plot). Ward's clustering method, which tends to identify more clusters of equal size, incorporated both these sites into the upper cluster. The centroid method unequivocally placed site 23 in a separate cluster, and showed virtually equal preference for isolating

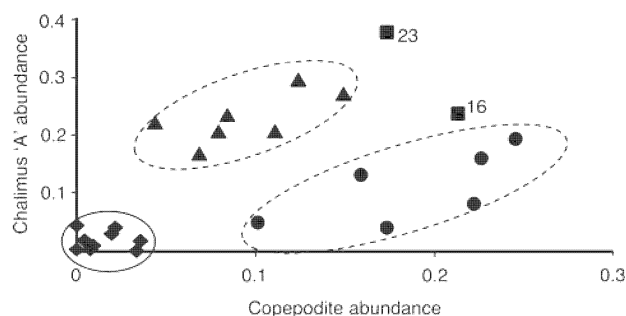


Figure 4. Cluster analysis of lice on juvenile wild salmon using the centroid method. Sites within the solid ellipse were all unexposed to farms. The analysis showed a clear, unambiguous separation between these sites and the others. Sites within the lower right, dashed ellipse (designated by circles) were close to active farms; sites within the other dashed ellipse (designated by triangles) were farther from active farms. The separation among these two sets and the two single-site clusters was subject to minor ambiguities, as explained in the text.

site 16 in a separate cluster rather than including it in the upper cluster. When the clustering was re-run using only the copepodite and chalimus I/II abundances, site 16 was placed in the lower cluster. No other sites showed comparable instability in the clustering.

The transmission model fitted the spatial distributions of sea lice on both active and fallow migration routes (Figures 5–7). For each dataset, there was a distinct spatial pattern in the abundance of sea lice on the exposed migration route that was related to the salmon farms; as the fish migrate past active farms, they become infested with copepodites which then mature through the chalimus and motile stages. The estimated distributions of planktonic copepodites indicated that transmission from salmon farms was large relative to the ambient infection pressure on both active and fallow migration routes. The relative strength of larval production at the farm locations varied among replicates, with the first farms being the larger source in the first replicate, and the last, most seaward, farm being the largest estimated source of lice in the second and third replicate. Across all replicates, the estimated louse production by farms was between 10 and 60 times ambient production (Table 3). The estimated abundance of copepodites from salmon farms exceeded ambient levels for about 30–40 km along the migration route per farm. There was a temporal trend evident in a progression towards increased abundance of older lice in later replicates. Parameter estimates indicated that pink salmon migrated more quickly through the area than chum salmon. The proportion of juvenile salmon showing evidence of louse damage to surface tissues increased therefore with louse abundance. The proportion of fish with louse-damaged surface tissues was ~50% at the seaward end of the migration route containing active farms, whereas it was markedly lower on the fallowed migration route (Figures 5–7). The estimated direct effect of infestation by sea lice on juvenile salmon survival was <10% on the active migration route and negligible on the fallow migration route.

Escapement and survival analysis

Survival among rivers, based on escapement data, was highly variable, and there was no detectable difference in mean survival for the Broughton Archipelago relative to the central coast (Table 4, t -test with $p = 0.48$). The high variability in the data is reflected by the large standard errors on the mean estimates of survival. From the rivers assessed in the Broughton Archipelago, only the Embly River clearly corresponds to the fallow migration route. That population experienced very poor survival, with a 90% decline, although it was subject to fallow intervention. Among the populations exposed to active farms, the Glendale population also experienced a 90% decline, whereas other populations fluctuated and some increased in abundance. Escapement data and survival for the central coast were also highly variable, with some populations increasing and others decreasing during the 2006–2008 pink salmon cohort.

Discussion

Previous studies have suggested that salmon farms cause an increase in the abundance of sea lice in the nearshore marine environment above that in areas without salmon farms during the early life history of juvenile pink and chum salmon (Morton and Williams, 2003; Morton *et al.*, 2004; Krkošek *et al.*, 2005a, 2006). The results of the study reinforce these findings, but also provide important new insights into the efficacy of management

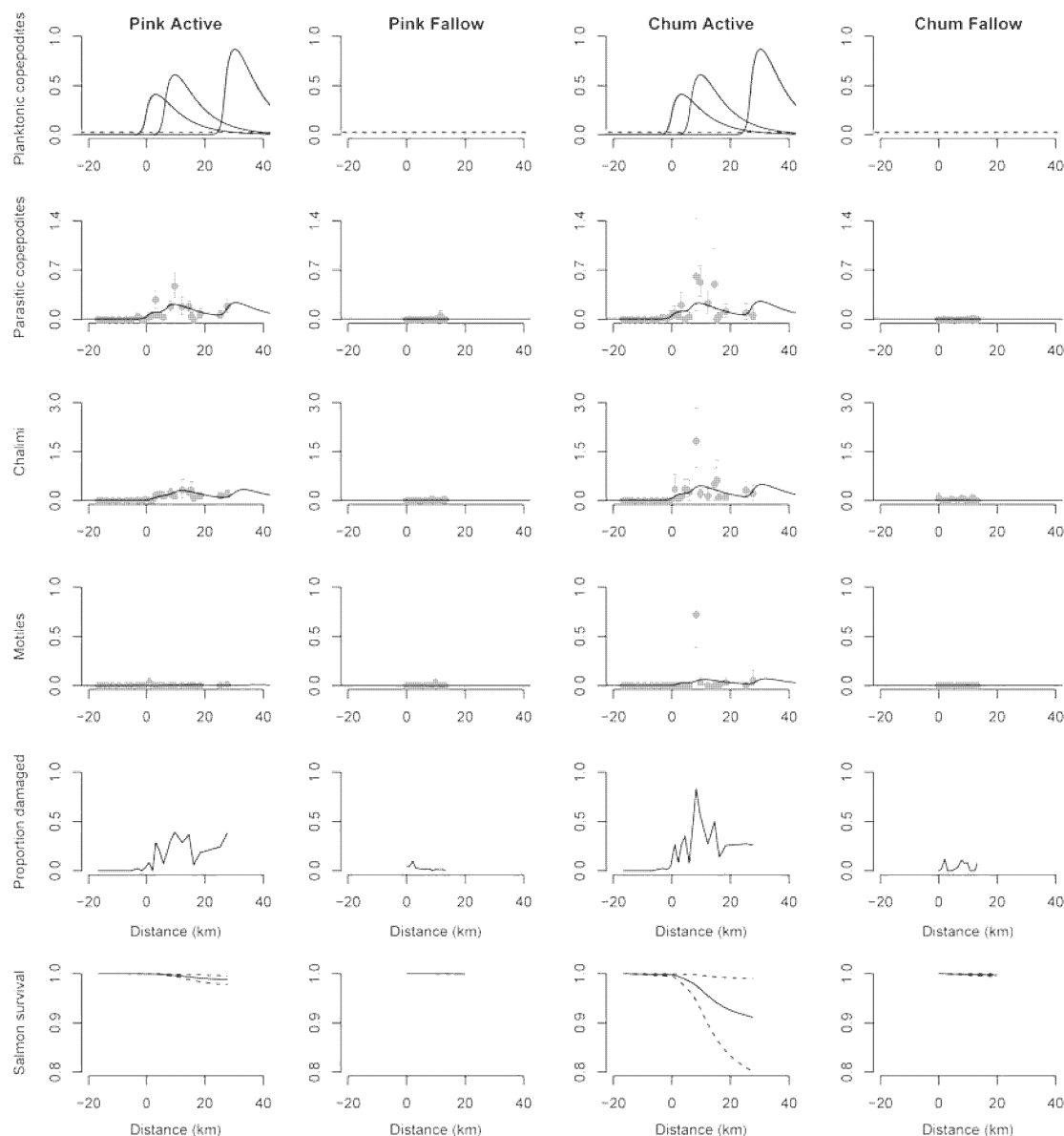


Figure 5. Fit of the transmission model to the abundance of sea lice on juvenile pink and chum salmon along one migration route containing active salmon farms and one migration route containing fallow salmon farms (Figure 1). There are five salmon farms on the active route: a pair clustered at $x = 0$, another pair clustered at $x = 6.5$, and a fifth farm situated at $x = 19.3$. For each cluster of two farms, the cluster was modelled as one source situated a distance halfway between the two farms. In the first row of panels, the thick grey line is the estimated spatial distribution of planktonic copepodites on a relative scale, with its component parts originating from the three salmon farm sources (thin solid lines) and the ambient distribution (thin dotted line). Shown also are the mean abundance ($\pm 95\%$ bootstrap confidence intervals) of parasitic louse developmental stages per fish (copepodites, chalimi, and motiles), along with the maximum likelihood fit of the transmission model. Below the louse-abundance panels are the proportion of juvenile salmon showing damaged surface tissues associated with louse feeding and the estimated proportion of juvenile salmon surviving louse parasitism along the migration route. Data are from the first replicate dataset (7–17 April).

actions implemented to reduce the risk of exposure to sea lice of juvenile wild salmon: fallowing and chemical treatment. The plankton component of our study indicates that nauplii were found primarily at locations containing active farms, but not at fallow farms or other control areas, and that chemical treatment on one farm was associated with a corresponding reduction, but not eradication, of planktonic nauplii nearby. The data indicate that farmed salmon were likely the primary sources of lice in the nearshore environment in the weeks preceding the juvenile

salmon outmigration. The analysis of data on sea lice on juvenile salmon reveals the characteristic spatial pattern of transmission of sea lice from farmed to wild salmon; as the juvenile salmon migrate past salmon farms, there is first an increase in copepodites infesting the fish, followed by a developmental progression through chalimus and motile stages as the fish transport the lice down the migration route. This spatial pattern was evident on the migration route containing active salmon farms, but not on the migration route containing fallow farms. Relative to previous

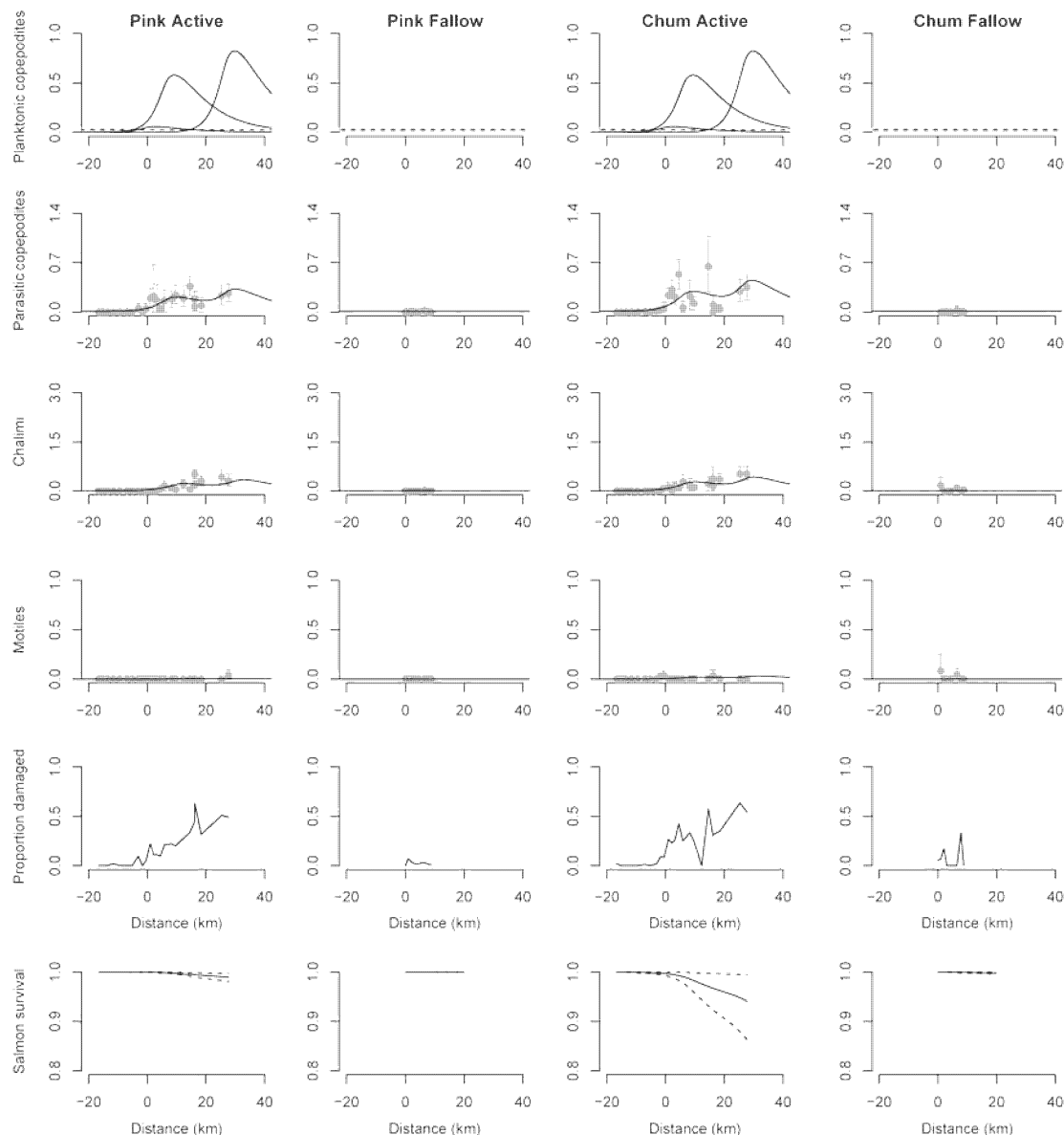


Figure 6. Fit of the transmission model to the abundance of sea lice on juvenile pink and chum salmon along one migration route containing active salmon farms and one migration route containing fallow salmon farms (Figure 1). There are five salmon farms on the active route: a pair clustered at $x = 0$, another pair clustered at $x = 6.5$, and a fifth farm situated at $x = 19.3$. For each cluster of two farms, the cluster was modelled as one source situated a distance halfway between the two farms. In the first row of panels, the thick grey line is the estimated spatial distribution of planktonic copepodites on a relative scale, with its component parts originating from the three salmon farm sources (thin solid lines) and the ambient distribution (thin dotted line). Shown also are the mean abundance ($\pm 95\%$ bootstrap confidence intervals) of parasitic louse developmental stages per fish (copepodites, chalimi, and motiles), along with the maximum likelihood fit of the transmission model. Below the louse-abundance panels are the proportion of juvenile salmon showing damaged surface tissues associated with louse feeding and the estimated proportion of juvenile salmon surviving louse parasitism along the migration route. Data are from the second replicate dataset (19–28 April).

infestations (Krkošek *et al.*, 2006), louse transmission on both routes was reduced and the estimated survival of juvenile salmon higher. This may be due to coordinated application of chemical therapeutants, but we did not have a comprehensive dataset on the timing and distribution of EM use throughout the Broughton Archipelago with which to test this hypothesis.

Potential natural host populations for lice in the nearshore marine environment preceding and during the juvenile salmon outmigration are natural overwintering salmonid populations of

subadult coho salmon (*Oncorhynchus kisutch*), Chinook salmon (*Oncorhynchus tshawytscha*), and possibly stickleback (*Gasterosteus aculeatus*; Jones *et al.*, 2006; Beamish *et al.*, 2007). Stickleback, however, are likely not a major producer of lice because no lice have been observed to reach the gravid female stage on them, possibly because stickleback are not a suitable host for lice to complete their life cycle (Jones *et al.*, 2006; Krkošek, 2010). From the plankton data, no nauplii were found in waters where there were no farmed salmon. However, this

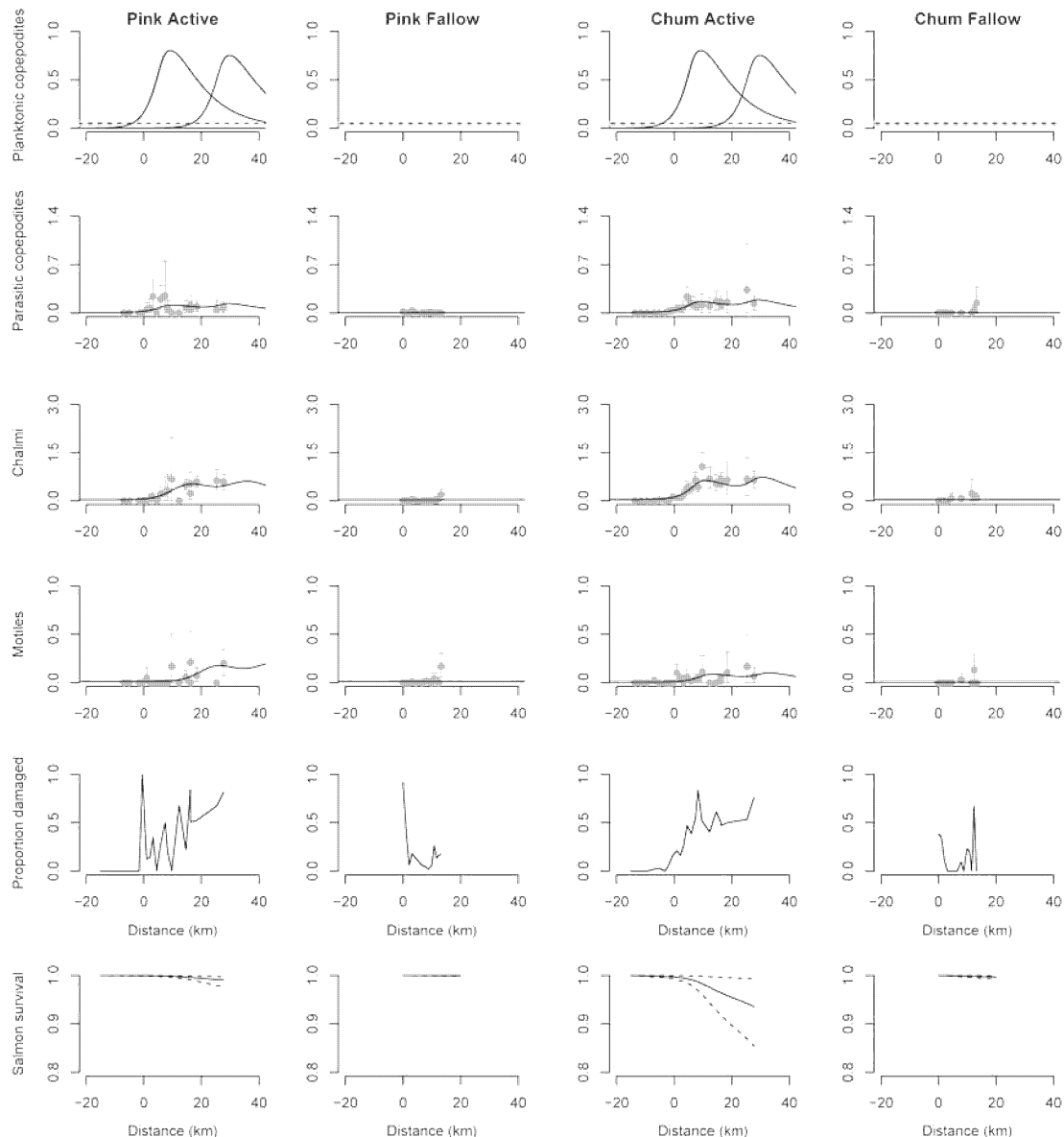


Figure 7. Fit of the transmission model to the abundance of sea lice on juvenile pink and chum salmon along one migration route containing active salmon farms and one migration route containing fallow salmon farms (Figure 1). There are five salmon farms on the active route: a pair clustered at $x = 0$, another pair clustered at $x = 6.5$, and a fifth farm situated at $x = 19.3$. For each cluster of two farms, the cluster was modelled as one source situated a distance halfway between the two farms. In the first row of panels, the thick grey line is the estimated spatial distribution of planktonic copepodites on a relative scale, with its component parts originating from the three salmon farm sources (thin solid lines) and the ambient distribution (thin dotted line). Shown also are the mean abundance ($\pm 95\%$ bootstrap confidence intervals) of parasitic louse developmental stages per fish (copepodites, chalimi, and motiles), along with the maximum likelihood fit of the transmission model. Below the louse-abundance panels are the proportion of juvenile salmon showing damaged surface tissues associated with louse feeding and the estimated proportion of juvenile salmon surviving louse parasitism along the migration route. Data are from the third replicate dataset (9–16 May).

does not imply that planktonic lice are absent from areas not containing salmon farms during the spring outmigration period for juvenile pink and chum salmon in the Broughton Archipelago. In fact, the presence (but low prevalence) of lice on fish on the fallow route as well as in regions with no farms (Krkošek *et al.*, 2007b) indicates that planktonic lice are likely present. Nonetheless, the plankton data analysed here suggest that alternative natural sources likely produce far fewer lice than salmon farms during the spring outmigration season for juvenile salmon. The

lice data derived from juvenile salmon and the results of the transmission model further indicate that the abundance of lice from natural sources was low. There was a low but general ambient infestation pressure from natural sources along all migration routes, evidenced by the presence of lice on juvenile salmon in the fallowed migration corridor as well as the close fit of the transmission model where the natural ambient infestation pressure was constrained to the same value on active and fallow migration routes. The data presented here plus those from regions without

salmon farms indicate that the production of lice by natural overwintering host populations generates a natural prevalence that is typically <5% infestation on juvenile pink and chum salmon (Krkošek *et al.*, 2007b; Krkošek, 2010).

Abiotic factors were tested in the analysis in addition to salmon farms. Temperature accelerates the rates of louse development (Stien *et al.*, 2005), which may increase the rate of production of louse larvae on farms. Correspondingly, we found a positive

effect of temperature on the abundance of nauplii caught in the plankton tows as well as on the abundance of lice on juvenile salmon. Although salinity is thought to affect louse survival in experimental conditions (Johnson and Albright, 1991), the results here did not show a significant effect of salinity on nauplii abundance. The effect of salinity on planktonic lice may be via a reduction in survival from nauplii to copepodites, which was not observed owing to the generally low abundance of planktonic copepodites at all sites. There was an association of salinity and louse abundance on juvenile salmon, possibly reflecting the reduced survival of planktonic lice and also the reduced success of copepodites at attaching to a host fish at low salinities (Bricknell *et al.*, 2006). However, as the fish were migrating from low salinity past the farms to higher salinity, the salmon examined in higher salinity had been exposed to more farms than those examined from lower salinity. Although there is a confounding correlation between salinity and exposure to salmon farms, the combination of large datasets, the appearance of the most juvenile lice stages at stocked salmon farms, and statistical modelling indicated that migration past salmon farms was an important predictor of lice on juvenile wild salmon.

Oceanographic processes are likely important to louse dispersion (Foreman *et al.*, 2006), evidenced by the increased abundance of nauplii in locations down-current from the farm as well as between farms and the nearest shore. The observed accumulation of lice between farms and shorelines may be important for wild juvenile salmon risk of infestation, because wild juvenile pink and chum salmon occupy nearshore (intertidal) habitats. Few planktonic copepodites were found during the study, perhaps because they are transported away from the immediate vicinity of the farms, that survival from nauplii to copepodite was poor, or that copepodites were not caught as efficiently as nauplii. Copepodites were caught in clusters and were

Table 3. Parameter estimates from the transmission model.

Parameter	7–17 April	19–28 April	9–16 May
Ratio of louse production by farms 1 and 2 relative to ambient	29	26	16
Ratio of louse production by farms 3 and 4 relative to ambient	47	28	33
Ratio of louse production by farm 5 relative to ambient	9	53	58
Diffusion coefficient of planktonic larvae ($\text{km}^2 \text{d}^{-1}$)	0.57	1.34	3.7
Survival of copepodites on pink salmon	0.34	0.33	0.59
Survival of copepodites on chum salmon	0.50	0.014	0.36
Survival of chalimi on pink salmon	0.02	0.34	0.62
Survival of chalimi on chum salmon	0.10	0.05	0.10
Distance pink salmon travel during the chalimus stage (km)	3.9	4.2	11.1
Distance chum salmon travel during the chalimus stage (km)	1.0	1.1	2.5
Pink salmon migration speed (km d^{-1})	0.39	0.42	1.11
Chum salmon migration speed (km d^{-1})	0.10	0.11	0.25

Table 4. Survival of pink salmon populations, based on escapement data from rivers in the Broughton Archipelago and the central coast of British Columbia.

Region	System	Escapement 2006	Escapement 2008	Survival	Average survival (s.e.)
Broughton	Ahta	4 156	1 218	1.23	–
	Kakweiken	33 761	74 818	–0.80	–
	Kingcome	2 057	3 423	–0.51	–
	Wakeman	3 646	14 661	–1.39	–
	Viner	61	7	2.16	–
	Lull	760	89	2.14	–
	Anhuhati	10 855	10 801	0.00	–
	Glendale	15 085	181 820	–2.49	–0.01 (0.21) ^a
	Embly ^b	5 040	49 459	–2.28	–0.21 (0.58) ^c
	Cheenis	32	55	–0.54	–
Central coast	Neekas	10 200	6 700	0.42	–
	Tankeeah	50	40	0.22	–
	Quartcha	750	450	0.51	–
	Clatse	2 300	3 250	–0.35	–
	Hook	150	65	0.84	–
	Elcho	800	400	0.69	–
	Dean	2 500	3 650	–0.38	–
	Milton	270	400	–0.39	–
	Kilbella	5 000	5 000	0.00	–
	Chuckwalla	10 000	31 000	–1.13	–
	Johnston	5 000	180	3.32	0.27 (0.32)

^aAverage survival is given along with the associated standard errors (s.e.) and is calculated for the Broughton Archipelago without the Embly River population included.

^bPopulation not exposed to salmon farms although in the Broughton Archipelago.

^cAverage survival is given along with the associated s.e. and is calculated for the Broughton Archipelago with the Embly River population included.

also observed attached to detritus. Both these characteristics suggest that the plankton sampling technique used was inadequate for that stage of sea louse.

The plankton data on abundance of larval sea lice are consistent with those of other work from Europe that found high abundances of nauplii near salmon farms (Costelloe *et al.*, 1996, 1998; Penston *et al.*, 2004, 2008). Those workers also found peak copepodite densities at varying distances from farm locations. The effect of oceanography on louse dispersion is reflected in the large spatial spread of copepodite lice estimated from the transmission model; approximately 30–40 km of elevated planktonic copepodite abundance on the migration route containing active farms. As copepodites are the infectious stage, understanding their distribution following release from farms is critical to understanding the infestation risk to wild juvenile salmon. As few copepodites were captured in the plankton tows, this study was clearly insufficient to quantify directly the abundance and distribution of planktonic copepodites. However, copepodites were observed on wild juvenile pink and chum salmon in the immediate vicinity of plankton tows that did not capture any copepodites. This suggests that planktonic copepodites must have been present in the marine environment and were in fact located around active salmon farms. Further insight into the spatial distribution and behaviour of planktonic copepodites is needed to evaluate the spread of planktonic copepodites from salmon farms.

The cluster analysis indicated an association between sea lice and salmon farms as well as some interesting patterns in how sites were clustered. In particular, the primary break between the low- and high-abundance sites was consistently strong, with high-abundance sites being seaward of farms on the active migration route. The instability in clustering results for site 16 also offers some interesting insight. Among the complex Broughton Archipelago waterways, there are locations where juvenile salmon runs converge, and site 16 falls into that category. In 2007, there were two adult/broodfish farms in eastern Tribune Channel (Figure 2). Young salmon from the Ahta and Kakweikan rivers travel west through Tribune Channel along the mainland shore and enter Fife Sound (Krkošek *et al.*, 2005a, 2006). The sea lice on these stocks had matured beyond the copepodite stage by the time they exited Tribune Channel on approach to site 16. At the confluence of migration routes, the abundance of sea lice may reflect mixing of populations with different infestation histories based on which route the fish traversed. This variation in local abundance of sea lice attributed to mixing of populations could also underlie some of the deviation in the data from the transmission model, particularly seaward of the salmon farms.

The seasonal progression identified in the statistical analysis as changes in abundance among replicates was readily apparent in the spatial distributions of lice in Figures 5–7. The abundance of louse developmental stages, particularly motiles, increased as the migration season progressed. This pattern indicates that the movement/migration pattern may be more complex than represented in the model as an average continuous and constant seaward movement of fish. In reality, fish migratory movements are probably sporadic, responding to abiotic factors such as salinity and biotic factors such as food availability (Olsson *et al.*, 2006). This could lead to local retention of fish, local developmental progression of lice, and accumulation of older lice as the season progresses. The seasonal progression is not captured in the transmission model, which treats each replicate dataset separately, so this becomes a challenge to future modelling initiatives aiming at capturing the full spatial and temporal pattern in the abundance of sea lice.

The parameter estimates suggest that pink salmon migrated more quickly than chum salmon. The migration speed was calculated by comparing the estimated value of the distance juvenile salmon migrate during the chalimus stage with a mean development time of ~10 d, taken from Stien *et al.* (2005). In the model, the higher migration speed means that the exposure period of faster-moving fish is shorter, affecting the model by reducing the overall abundance of lice on infested fish (the curves are lower for pink salmon than chum salmon), and also by smoothing out or broadening the spatial distributions of parasitic stages. We did not detect a systematic difference in louse survival between pink and chum salmon using the transmission model, although laboratory studies have indicated differences in the physiological response of pink and chum salmon to lice, with corresponding differences in louse survival (Jones *et al.*, 2007). The statistical modelling indicated that lice were significantly more abundant on chum than on pink salmon, as would be expected from the results of the laboratory work of Jones *et al.* (2007). According to the transmission model, the differences in louse abundance between pink and chum salmon reflect different migration speeds rather than differential levels of louse survival. The difference in estimated mortality between pink and chum juvenile salmon attributable to sea lice is also primarily a consequence of the difference in estimated migration speeds. As chum salmon were estimated to migrate more slowly, they were exposed to the lice longer, so were predicted to have experienced greater mortality.

The results presented here indicate that removing farm salmon hosts, i.e. fallowing, reduces louse abundance to levels and spatial distributions that would be expected in areas without salmon farms. The corresponding estimated louse-induced mortality of juvenile salmon travelling down the fallowed migration route was negligible. These findings are consistent with that of Morton *et al.* (2005), who found a reduction in the abundance of sea lice when farms were fallowed in the Broughton Archipelago in 2003, as well as with that of Beamish *et al.* (2006), who estimated high survival for that cohort of pink salmon. One limitation of our study was that the fallow migration route, although it contained two farms, was short relative to other studies of lice on migration routes containing salmon farms. In particular, the length of the fallow migration route (~14 km) was about half the distance that copepodites were estimated to spread from active farms. This means that it would be unlikely to carry the full developmental progression of lice on juvenile salmon migrating along the fallow route, as observed on the active route and in earlier work on longer migration routes in Tribune Channel (Krkošek *et al.*, 2005a, 2006), assuming that the migration speeds of salmon among these migration routes are roughly similar. This, therefore, makes the dataset from the fallow migration route more challenging to fit to the transmission model and to estimate parameters. However, the fallow migration route was long enough to observe louse development through the early developmental stages (copepodites and chalimi), making those data comparable among migration routes. Further, by fitting the transmission model simultaneously to both active and fallow datasets, the analysis uses information from both datasets, making comparisons between migration routes more informative than analysing each in isolation. More work is needed, particularly from longer migration routes with all farms in a fallowed state to understand the effects of fallowing better.

Although fallowing salmon farms likely reduces the risk of sea lice to wild salmon, a coordinated application of parasiticides such

as EM is an alternative management action used by industry in an attempt to protect wild juvenile salmon. Our results indicate that louse production on active farms exceeded the natural production of sea lice by 9–58 times, which is nevertheless a decline by approximately 100 times relative to earlier epizootics used in 2004 and 2005 (Krkošek *et al.*, 2006). The proportion of juvenile salmon showing signs of louse damage to surface tissues was ~50% after they passed farms, and the estimated direct mortality of wild juvenile salmon attributable to sea lice was <10% by the seaward end of the migration route. The mortality may be underestimated because the model does not track survival after the fish left the migration route, because parameters for the rates of parasite-induced host mortality may have been underestimated (Krkošek *et al.*, 2009), and because lice may reduce salmon survival indirectly in ways that have not yet been measured, such as increasing predation risk and competition with uninfested populations. The results do indicate that the use of parasiticides on farms can reduce the spread of lice to wild juvenile salmon, but further work is needed to evaluate the duration and general efficacy of this management option to protect wild salmon as well as the potential for lice to evolve resistance and toxicological effects on non-target organisms in the marine environment.

Based on escapement data, there were no significant differences in survival that corresponded to sea-lice abundance and juvenile salmon mortality on the migration route containing active farms relative to unexposed populations north of the Broughton Archipelago. Any effects of sea lice on wild salmon survival, be they direct mortality or indirect through increasing predation risk, at the abundances observed here are likely difficult to detect amid the high levels of environmental stochasticity inherent in pink salmon population dynamics. It is therefore difficult to quantify whether the abundances of lice observed in relation to fallowing and chemical treatment affect salmon survival. Therefore, to determine if management changes such as fallowing and chemical treatment have the desired effect of reducing sea-lice abundance and improving salmon survival, more data are needed. Specifically, there is a need for multiple years of replication to evaluate the consistency of reductions in abundance of sea lice as well as to accumulate sufficient sample size in the corresponding escapement estimates to provide powerful statistical tests for changes in productivity of pink salmon. Moreover, inference from differences in productivity between the Broughton Archipelago and the reference populations on the central coast relies on the assumption that there is no factor (other than sea lice) that systematically biases populations to have different survival between the two regions. Although it is not impossible that such a confounding factor exists, no such factor has been identified despite the efforts of several large research programmes (Fraser *et al.*, 2009). The comparison is further supported by the tendency for the populations in these regions to vary synchronously, indicating shared environmental drivers of mortality (Pyper *et al.*, 2001).

The results presented here indicate that when salmon farms are fallowed, the abundance and distribution of sea lice approaches that expected in areas without salmon farms. In addition, the use of EM as a parasiticide on farmed salmon may reduce the spread of lice to wild salmon, but not to the same extent as fallowing. To further substantiate these findings, the following are needed: (i) research with experimental designs following the principles of randomization and control on fallowing as a management strategy on longer migration routes; (ii) better understanding of the behaviour and distribution of copepodites; and (iii) detailed

analyses of louse population dynamics on farms following chemical treatment and the associated response in nearby migratory wild juvenile salmon populations. However, management and policy will have to consider alternative strategies other than chemical treatment, because lice may evolve resistance (Denholm *et al.*, 2002; Lees *et al.*, 2008) and because of unintended impacts on non-target organisms including crustaceans of ecological or economic importance. Such management strategies could include moving farms away from rivers and constricted wild salmon migration corridors, as well as closed containment technology that creates a physical impermeable barrier between the inside of a farm and the surrounding environment.

Supplementary material

Supplementary information is available at ICESJMS online, which details the transmission model used in the analysis. The transmission model is also described in Krkošek *et al.* (2006).

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