

Recent failure to control sea louse outbreaks on salmon in the Broughton Archipelago, British Columbia

Andrew W. Bateman, Stephanie J. Peacock, Brendan Connors, Zephyr Polk, Dana Berg, Martin Krkošek, and Alexandra Morton

Abstract: The advent and growth of salmon farming has changed the epidemiology of some salmon diseases. In 2015, in the salmon-farming region of the Broughton Archipelago, British Columbia, an outbreak of native ectoparasitic copepods (sea lice; *Lepeophtheirus salmonis*) recurred in wild juvenile salmon after a decade of effective control. We draw on a 15-year data set of sea lice on wild and farmed salmon in the area to assess the evidence for four factors that may explain the recent outbreak: (i) poorly timed parasiticide treatments of farmed salmon relative to wild salmon migration, (ii) evolution of resistance to parasiticide treatments in sea lice, (iii) anomalous environmental conditions promoting louse population growth, and (iv) a high influx of lice with an abundant pink salmon (*Oncorhynchus gorbuscha*) return in 2014. We propose that a combination of poorly timed treatments and warm environmental conditions likely explains the outbreak. Where wild salmon conservation is a concern, a more effective approach to managing sea lice on wild and farmed salmon could incorporate the out-migration timing of wild juvenile salmon and information on environmental conditions.

Résumé : L'apparition et la croissance de la salmoniculture ont changé l'épidémiologie de certaines maladies du saumon. En 2015, dans la région salmonicole de l'archipel Broughton, en Colombie-Britannique, une éclosion de copépodes ectoparasites indigènes (le pou du saumon; *Lepeophtheirus salmonis*) est réapparue chez des saumons juvéniles sauvages après une décennie de lutte antiparasitaire efficace. Nous avons utilisé un ensemble de données de 15 ans sur les poux du saumon chez les saumons sauvages et d'élevage dans cette région pour évaluer les preuves à l'appui de quatre facteurs qui pourraient expliquer l'éclosion récente, à savoir : (i) le mauvais choix du moment de traitements parasitocides des saumons d'élevage par rapport à la migration de saumons sauvages, (ii) l'évolution de la résistance aux traitements parasitocides des poux du saumon, (iii) des conditions ambiantes anormales qui favoriseraient la croissance de la population de poux et (iv) un important afflux de poux associé à l'abondant retour des saumons roses (*Oncorhynchus gorbuscha*) en 2014. Nous proposons qu'une combinaison de mauvais choix du moment des traitements et de conditions ambiantes chaudes explique vraisemblablement l'éclosion. Dans les régions où la conservation des saumons sauvages est préoccupante, une approche plus efficace de gestion des poux du saumon chez les saumons sauvages et d'élevage devrait incorporer le moment de la dévalaison des saumons juvéniles sauvages et des données sur les conditions ambiantes. [Traduit par la Rédaction]

Introduction

The salmon aquaculture industry has undergone rapid global expansion (Goldburg and Naylor 2005; Asche et al. 2013), altering the dynamics of some infectious diseases in coastal ecosystems and affecting wild salmon populations (Ford and Myers 2008; Costello 2009b; Foreman et al. 2015; Madhun et al. 2015). One such case is that of sea lice (*Lepeophtheirus salmonis* and *Caligus* spp.), ectoparasites that can transmit between farmed salmon, held in flow-through net pens, and nearby wild salmon (Krkošek et al. 2005a; Costello 2009b). Sea lice are naturally occurring parasitic copepods that feed on the epidermal tissues of their host fish.

Farmed salmon act as reservoir hosts that can amplify natural sea louse abundances and disrupt the migratory allopatry that typically protects out-migrating juvenile salmon from pathogens of their adult counterparts (Krkošek et al. 2009). Sublethal infections cause physiological and behavioural changes in hosts (Krkošek et al. 2011b; Brauner et al. 2012), and high infection levels can result in direct host mortality (Krkošek et al. 2006, 2009). Both sublethal and lethal effects may contribute to louse-associated reductions in survival seen in wild salmon populations (Gargan et al. 2012; Krkošek et al. 2013). Accordingly, sea lice are a costly problem for aquaculture operations and wild salmonid management alike (Costello 2009a, 2009b).

Received 14 March 2016. Accepted 10 May 2016.

A.W. Bateman.* Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada; Salmon Coast Field Station, Simoom Sound, BC V0P 1S0, Canada.

S.J. Peacock.*† Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

B. Connors. ESSA Technologies, Vancouver, BC V6H 3H4, Canada; School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

Z. Polk. Salmon Coast Field Station, Simoom Sound, BC V0P 1S0, Canada.

D. Berg. Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada.

M. Krkošek. Salmon Coast Field Station, Simoom Sound, BC V0P 1S0, Canada; Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada.

A. Morton. Salmon Coast Field Station, Simoom Sound, BC V0P 1S0, Canada; Raincoast Research Society, Sointula, BC V0N 3E0, Canada.

Corresponding author: Stephanie J. Peacock (email: stephanie.j.peacock@gmail.com).

*These authors contributed equally.

†Present address: Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from RightsLink.

The Broughton Archipelago, in British Columbia (BC), Canada, has been at the centre of research and debate surrounding the impacts of salmon aquaculture on wild Pacific salmon. Recent analyses of data collected through a joint industry–government–academic monitoring program have identified local patterns of louse infestation and associations between louse levels on salmon farms and those on wild juvenile salmon (Patanasatienkul et al. 2015; Rees et al. 2015). Sea lice associated with farms in the area have been correlated with declines in wild pink (*Oncorhynchus gorbuscha*) and coho (*Oncorhynchus kisutch*) salmon in the early 2000s (Krkošek et al. 2011a), although the connection has been debated (e.g., Marty et al. 2010 versus Krkošek et al. 2011b). Over the last decade, management of sea lice on salmon farms has greatly reduced outbreaks of both farmed and wild salmon, and declines in the productivity of some wild salmon populations have been reversed (Peacock et al. 2013).

Regulatory policy of aquaculture practices in BC requires farms to either harvest or treat their fish with emamectin benzoate (EMB; industry name SLICE) when on-farm louse counts exceed a “treatment threshold” of three motile-stage lice per fish (Fisheries and Oceans Canada 2015a). This policy is in place to protect wild salmonids from sea louse outbreaks, and it has been associated with effective control of sea louse abundances on wild juvenile salmon in the Broughton Archipelago over the last several years (Peacock et al. 2013). Many variables may influence louse population growth, however, and it may not yet be clear if current policy is sufficient to accommodate the environmental, biological, and management variation that can lead to outbreaks. For example, environmental conditions such as temperature and salinity that affect sea louse development, as well as the connectivity of regional sea louse populations, are relevant in designing coordinated area management plans for sea lice on salmon farms (Brooks 2009). Even where treatment has been successful in the past, sea lice can evolve resistance to treatment (Lees et al. 2008; Aaen et al. 2015). While resistance to EMB has not been reported in BC (Saksida et al. 2013), it presents a potential complication to louse management.

Here, we report on a 2015 outbreak of sea lice on juvenile wild salmon, identified through monitoring of migrating pink and chum (*Oncorhynchus keta*) salmon in the Broughton Archipelago. We also report on experiments to assess the potential evolution of resistance to EMB in *L. salmonis* in BC, and we explore other factors that may have contributed to elevated numbers of sea lice in spring 2015, drawing on data from industry, government, and nongovernmental organisations.

Methods and data acquisition

Monitoring sea lice on wild salmon

Juvenile wild salmon have been monitored for sea lice at three locations in the Broughton Archipelago (4, 5, and 6 in Fig. 2) since 2001. The resulting 15-year data set with detailed metadata is publicly available (Peacock et al. 2016). Details of the sampling methodology and louse-identification methods are in the online supplement¹, and published elsewhere (Morton and Williams 2003; Morton et al. 2004; Krkošek et al. 2005b; Peacock et al. 2013). Briefly, juvenile pink and chum salmon were collected by beach seine and nonlethally examined for sea lice using a 16× magnification hand lens. Attached sea lice were identified to stage (copepodid, chalimus, and motile), and motile lice were identified to species (*L. salmonis* and *Caligus clemensi*; Fig. S1¹).

We estimated the expected number of motile-stage *L. salmonis* from 2001 to 2015 using a generalized linear mixed-effects model with fixed effects for year and louse stage and random effects for week-of-year (Patanasatienkul et al. 2013, 2015) and location-year

combination (to account for differences in infection levels among locations due to farm activity or environmental factors). We fit the model to data on copepodid, chalimus, and motile stages to increase our ability to estimate the random effects, but report the motile estimates only to avoid confusion with *Caligus* copepodite- and chalimus-stage lice (see supplement for additional results¹). We pooled data from both pink and chum salmon hosts, as past work has not detected a related species effect on sea louse abundance (Patanasatienkul et al. 2013). We assumed a log link function and a negative binomial distribution to account for overdispersion of parasites among hosts (Fig. S3¹). To readily accommodate non-normal errors, hierarchical structure, and the large sample sizes involved (31 103 salmon sampled over 15 years), we fit the model in a Bayesian framework using uninformative priors (Table S1¹). In the online supplement¹, we provide details of the model-fitting and further analyses of sea louse prevalence, abundance of nonmotile stage lice (which have not been consistently identified to species), and temporal and spatial patterns of the 2015 outbreak.

As sea lice have been correlated with reduced productivity of pink and coho salmon populations (Krkošek et al. 2011a; Peacock et al. 2013), we calculated the population-level mortality of pink salmon predicted to result from the 2015 outbreak. To do this, we multiplied the mean sea louse abundance on juvenile salmon in 2015 (all stages) by previously published parameter estimates for the effect of sea lice on survival (Peacock et al. 2013). This estimate of population-level mortality includes both compensatory and noncompensatory ecological effects of parasites (Krkošek et al. 2011b; Godwin et al. 2015) and is therefore more relevant at the population scale than laboratory estimates of louse-induced mortality (e.g., Jones and Hargreaves 2009). We accounted for uncertainty in both parameter estimates and louse abundance using a Monte Carlo approach; see the online supplement for details¹.

Sea lice and treatment on farms

We compiled data on the abundance of motile *L. salmonis* on farmed salmon and the timing of EMB treatments in the Broughton Archipelago from publicly available sources (Marty et al. 2010; Cohen Commission 2011; Fisheries and Oceans Canada 2015b). The data include monthly estimates of the number of motile *L. salmonis* per farmed salmon for each farm in the study area and whether the farm was treated with EMB. The compiled data set is available in the online supplement¹.

To investigate trends in precautionary versus reactionary treatment timing, we compared the number of treatments that occurred during the winter months before the wild juvenile salmon out-migration (November through February; precautionary) with those that occurred during the out-migration (March through June; reactionary) in each year. If poor timing of treatments on farmed salmon were responsible for the high abundance of lice on adjacent wild salmon in 2015, we would expect to see proportionately fewer precautionary treatments in the winter months and proportionately more spring treatments in reaction to crossing the three-lice-per-fish threshold (Fisheries and Oceans Canada 2015a) than in previous years when louse abundance on wild juvenile salmon has remained low.

We also examined the farm data for instances in which farms did not treat when required by their license conditions; once the number of sea lice on a farm exceeds the three-lice-per-fish threshold, the farm has 15 days to treat if the threshold is crossed between 1 March and 30 June or 30 days to treat if the threshold is crossed between 1 July and 28 February (Fisheries and Oceans Canada 2015a). Using the available data, reported at monthly intervals, we recorded cases of noncompliance with license conditions when there was no treatment or harvest reported within

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0122>.

1 month (1 March through 30 June) or 2 months (1 July through 28 February) of counts exceeding the treatment threshold. Harvest dates were not always available, so we assumed that a farm had been harvested if it did not report louse counts for 2 months after the treatment threshold was crossed. This last assumption seems reasonable, as the license conditions require an increased frequency of monitoring once the treatment threshold is crossed (Fisheries and Oceans Canada 2015a). We report the rate of non-compliance as the annual proportion of instances in which an on-farm treatment threshold was exceeded but treatment was not initiated within the mandated time period. If changes in the rate of compliance with license conditions were responsible for the 2015 outbreak, we would expect to see an elevated rate of non-compliance compared with previous years when outbreaks on adjacent juvenile salmon did not occur.

To illustrate how treatment timing affects on-farm louse abundance, we considered one case of noncompliance and used models fit by Rogers et al. (2013) to predict the louse abundances that would have resulted if the license conditions had been followed. The model predictions assume exponential growth of louse populations prior to treatment and exponential decline after treatment. We calculated 95% confidence regions for the predictions by allowing uncertainty in the model-averaged prediction (normally distributed on the log scale) to propagate from each time step to the next.

Sea louse chemical resistance

We performed bioassays to determine the effect of EMB on survival of *L. salmonis* collected from wild juvenile salmon captured by beach seine in the Broughton Archipelago in the springs of 2012 and 2015. If the emergence of resistance to EMB were responsible for the anomalously high louse numbers observed in 2015, we would expect to see a decline in EMB effectiveness between 2012 (the time period of no outbreaks) and 2015 (when an outbreak occurred). Bioassays followed the protocols described by Westcott et al. (2008), and we describe our methods in more detail in the online supplement¹.

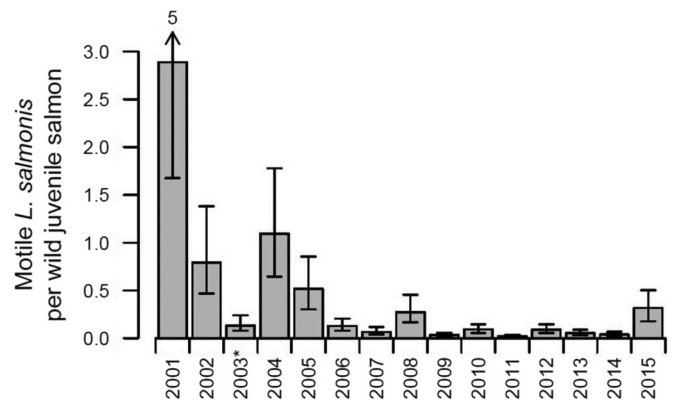
We analysed the proportion of sea lice that survived exposure to EMB using binomial generalized linear mixed-effects models with fixed effects for EMB concentration, louse sex, year, and all possible interactions and a random effect for sampling date (Table S2¹). If resistance to EMB was responsible for the 2015 outbreak, we would expect to see strong support for louse survival models, including an interaction between year and concentration. From the survival models, we calculated the effective concentration of EMB that resulted in 50% survival of sea lice (EC₅₀).

Sea surface temperature

The developmental rate of sea lice is strongly influenced by temperature, with development from infectious to adult stages ranging from about 50 days at 7 °C to about 20 days at 15 °C (Stien et al. 2005). Reports of anomalously high eastern Pacific ocean temperatures in 2015 (i.e., “the Blob”; Kintisch 2015) prompted us to investigate how sea surface temperature has varied in the study region over the past 15 years. If high ocean temperatures were responsible for the anomalously high louse numbers in 2015, we would expect ocean temperatures in 2015 to have been high in comparison with previous years when outbreaks on adjacent juvenile salmon did not occur.

We used temperature measurements from 2000 through 2015 at Pine Island lighthouse, near the Broughton Archipelago (Fisheries and Oceans Canada 2015c), to calculate standardized deviations in sea surface temperature by subtracting the mean monthly temperature across our period of study and dividing by the standard deviation in temperature. We used multiple linear regression to interpolate missing data at Pine Island lighthouse using measurements at Chrome Island, Egg Island, and Kains Island lighthouses (Fisheries and Oceans Canada 2015c; see online supplementary

Fig. 1. The estimated abundance (mean \pm 95% credible interval) of motile *L. salmonis* per wild juvenile pink and chum salmon from 2001 to 2015. The upper estimate in 2001 was 8.2 motile *L. salmonis* per juvenile salmon (not shown). *In 2003, the farms adjacent to juvenile salmon sampling sites and most farms along the migration route we sampled — 11 in total — were followed (Morton et al. 2005).



material for details¹). We also report temperatures measured during juvenile salmon monitoring between 2001 and 2015, given as the standardized deviations of mean monthly sea surface temperature from the overall mean.

While salinity also influences sea louse biology (Brooks 2005), we did not include salinity in our analysis because the spring freshets that cause biologically relevant reductions in salinity in the Broughton Archipelago generally occur after the juvenile salmon out-migration (Brooks 2005, 2009). Further, salinity varies considerably with proximity to freshwater inputs, making it difficult to meaningfully characterize annual fluctuations on a regional scale. For completeness, we present salinity values with our monitoring data in the supplementary material¹.

Wild salmon returns

Sea lice are transmitted from adult wild salmon to farmed salmon in the autumn, when wild salmon return to their natal rivers to spawn. The number of returning pink salmon therefore influences the abundance of sea lice on farmed salmon the following winter (Marty et al. 2010). If returning adult pink salmon (and the sea lice they hosted) in the summer and fall of 2014 contributed to the anomalously high louse numbers in the spring of 2015, we would expect the abundance of adult pink salmon spawners to have been higher in 2014 than in earlier years associated with low louse abundance on farmed and wild juvenile salmon (2005–2013). We report the estimated number of pink salmon spawners in Broughton Archipelago watersheds comprising a mean of 94.4% (range: 85.7%–99.4%) of reported spawners in the area (Fisheries and Oceans Canada 2015d; see online supplementary data¹).

Results

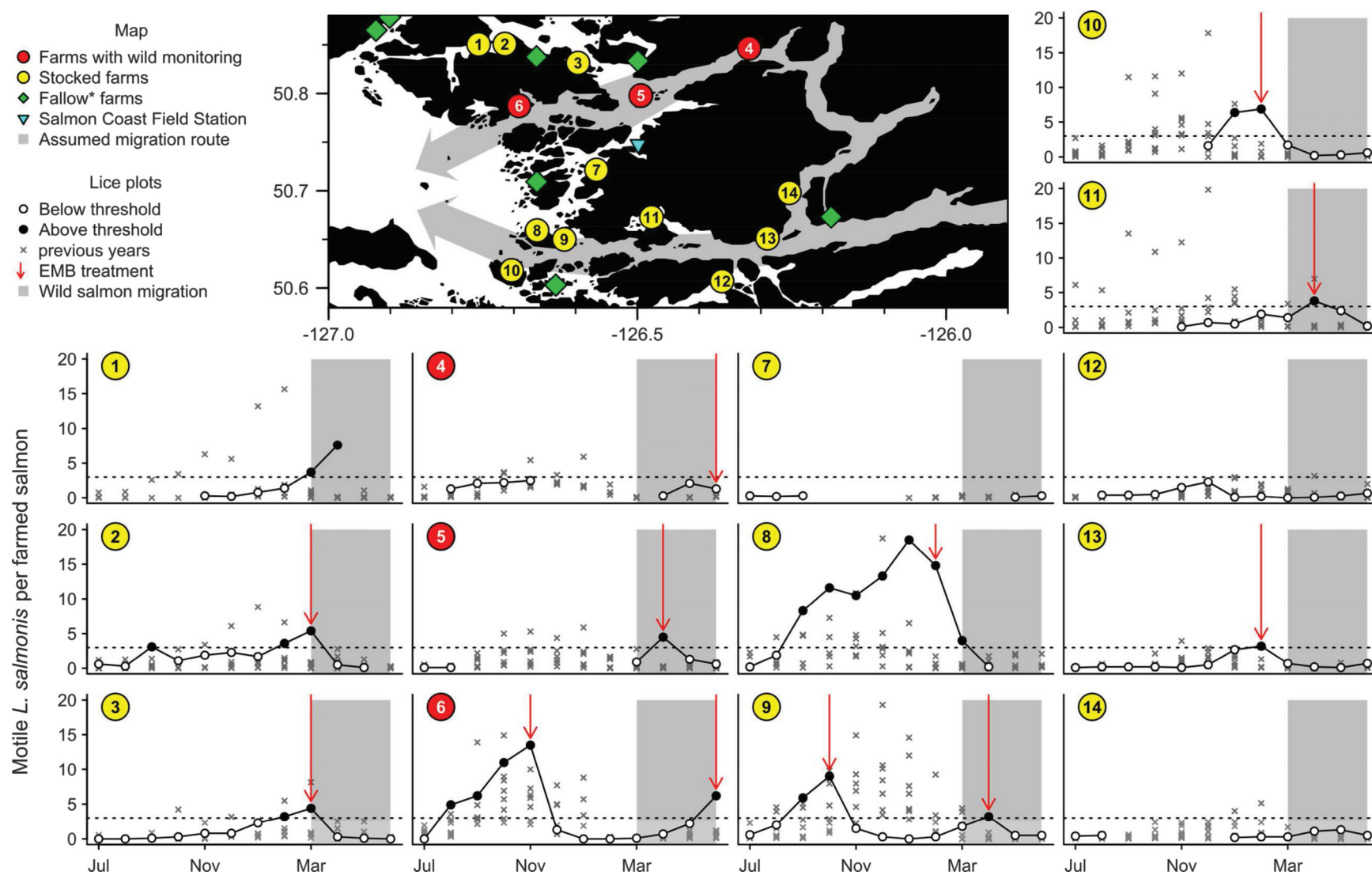
Monitoring sea lice on wild salmon

The mean abundance of motile *L. salmonis* on juvenile pink and chum salmon in 2015 was the highest observed in a decade, but not as high as in the early 2000s (Fig. 1). Using previous model estimates for the effect of sea lice on pink salmon survival (Peacock et al. 2013), the sea louse abundance on juvenile salmon in 2015 corresponds to predicted louse-induced mortality of 9%–39% (mean 23%; Fig. S10¹).

Sea lice and treatment on farms

The abundance of motile lice on farmed salmon, prior to the juvenile salmon out-migration, was high relative to recent years, triggering spring treatments on several farms (Fig. 2). When treatments were applied in February (e.g., farms 8, 10, and 13 in Fig. 2),

Fig. 2. The mean number of motile *L. salmonis* per farmed salmon on farms in the Broughton Archipelago, BC, that were active* in March – June 2015 (light and dark numbered circles on the map; see numbers). Data for previous years are from July 2005 through June 2014. Treatments with emamectin benzoate (EMB) are indicated by arrows for July 2014 through June 2015 only. *Fallow farms (diamonds) are those that did not contain salmon in any month from March through June 2015. One additional farm was excluded even though it contained fish in March to May 2015, because it is only used temporarily and has reported only 4 months of sea lice data since 2010. The map was produced using the R package PBSmapping (Schnute et al. 2015) with shoreline data from the GSHHG (Global Self-consistent, Hierarchical, High-resolution Geography). Database available from <http://www.soest.hawaii.edu/pwessel/gshhg/> [accessed 25 May 2016]. [Colour online.]



they were effective at reducing louse abundances during the out-migration. Some farms, however, including those operated by the same company (e.g., farms 8 and 9 in Fig. 2), had treatment schedules that were offset, suggesting that treatments among farms could have been better coordinated.

In several cases, farms did not treat or harvest all of their fish within 30 days of when sea louse counts exceeded the three-lice-per-fish treatment threshold (e.g., farms 6 and 8 in Fig. 2). Meta-data from farm reports (Fisheries and Oceans Canada 2015b) indicated that some farms postponed treatments until February, just before the juvenile salmon out-migration.

A change in the timing of treatments relative to the pink and chum out-migration period was apparent in 2015, compared with previous years, by the proportion of treatments in the winter versus during the out-migration. A high proportion of winter treatments has been associated with fewer lice on both farmed and wild salmon (Peacock et al. 2013), but 2015 saw a higher number of treatments during the wild salmon migration than precautionary treatments prior to the migration (Fig. 3a). Although this pattern also occurred prior to 2005, since 2005 there has been a higher number of winter treatments and corresponding low sea louse abundance on farmed salmon during the spring wild salmon out-migration (Fig. 3a).

The proportion of farms delaying management action (treatment or harvest), apparently in contravention of license conditions, was not out of the ordinary for the year ending 30 June 2015 (Fig. 3b). We note that rates of noncompliance were low from 2009 through 2013 (except for 2012), coinciding with multiple years of low overall treatment rates (Fig. 3b). While noncompliance was not widespread in 2014–2015, delayed treatment does appear to have resulted in high sea louse abundance on some farms prior to the wild salmon out-migration (Fig. 2).

From the model predictions, sea louse dynamics on farm 8 in 2014–2015 behaved as expected (Fig. 4a). If treatment on farm 8 had been postponed to the latest date in compliance with license conditions (30 days after the treatment threshold was crossed), the louse abundance would have likely been low throughout the winter, but would have recovered to levels exceeding the treatment threshold during the late spring (Fig. 4b). If the frequency of louse monitoring had been increased as soon as lice on farm 8 neared the treatment threshold, treatment could have been administered as soon as the threshold was crossed, and the model indicates that treatment would have been more effective at reducing louse abundance and slowing recovery (Fig. 4c). In this latter “precautionary” case, the model indicates that there likely would have been a similar mean abundance of sea lice during the wild salmon out-migration as was actually observed. Louse abundances on farm 8 over the intervening winter months, however, would likely have been greatly suppressed (Fig. 4c).

Sea louse chemical resistance

Sea lice collected from wild juvenile salmon were sensitive to EMB, with no evidence of reduced sensitivity in 2015 relative to 2012 (Fig. 3c).

Sea surface temperature

The sea surface temperature at Pine Island lighthouse was anomalously high in the early months of 2015, as were the mean monthly temperatures during the juvenile salmon monitoring in April–June 2015 (Fig. 3d). The interpolated temperature in January 2015 was higher than the mean temperature across all months in all years of study (2000–2015). These elevated temperatures may have contributed to more rapid development and reduced generation times for sea lice on farmed salmon over the winter of 2015 (Stien et al. 2005; Groner et al. 2014).

Wild salmon returns

Finally, while the returns of pink salmon to rivers of the Broughton Archipelago in fall 2014 were the highest on record since 2001 (corresponding to the 2002 wild salmon out-migration: Fig. 3e), they were similar to returns in 2004 and 2009. Nonetheless, the size of the pink salmon return likely contributed to high sea louse abundance on farms in early 2015, as the abundance of returning pink salmon has been found to correlate well with sea lice numbers on farmed salmon the following April (Marty et al. 2010).

Discussion

The spring of 2015 saw the recurrence of a sea louse outbreak on juvenile pink and chum salmon in the Broughton Archipelago, BC, with the abundance and prevalence of *L. salmonis* similar to levels seen in 2005 — the highest in the previous decade (Fig. 1; Figs. S4, S5¹). This corresponded to anomalous environmental conditions in early 2015 (Kintisch 2015). While the sea louse outbreak was not on the same scale as those seen between 2000 and 2004, the elevated louse counts in 2015 also correspond to high numbers of sea lice on salmon farms and mark a departure from almost a decade of successful louse management on salmon farms in the area (Peacock et al. 2013). The louse counts we observed in 2015 agree with industry observations, matched for sampling time and location (Mainstream Biological Consulting 2015; Fig. S14¹). Based on a previously published model of salmon productivity in relation to sea louse abundance (Peacock et al. 2013), the overall infestation levels observed on wild juveniles in 2015 are predicted to result in 9%–39% additive mortality in wild pink salmon (see online supplement; Fig. S10¹), although this prediction may be biased if environmental conditions in 2015 altered salmon migration timing relative to our standardized sampling window (see below).

Combined with the recent failure of chemical parasiticide treatments in other salmon-farming areas of the world (Lees et al. 2008; Aaen et al. 2015), the 2015 sea louse outbreak raised concern about the prospect of chemical resistance. Elsewhere, elevated louse counts have followed years of effective management once resistance evolves (Penston and Davies 2009). Our bioassays, however, showed that *L. salmonis* collected from wild salmon in the Broughton Archipelago remain sensitive to EMB. The effective EMB concentration killing 50% of pre-adult stage II lice (EC₅₀) was unchanged from 2012 to 2015, consistent with recent reports by other researchers that EMB remains effective in BC (Saksida et al. 2013; Aaen et al. 2015). Theoretical study suggests that a large, wild sea louse population, such as that found in the Pacific Ocean, might delay or preclude the evolution of resistance (McEwan et al. 2015). The sea lice we collected from wild salmon appear to have been more sensitive to EMB than previously assayed farm-origin lice (Saksida et al. 2013), perhaps indicating differential sensitivity to EMB in lice undergoing resistance selection on farms or variation in experimental conditions or procedures.

Overall, our results suggest that the 2015 sea louse outbreak in the Broughton Archipelago may have been influenced by a combination of factors that each contributed to louse population growth, including elevated sea surface temperatures, timing of EMB treatments on salmon farms that was not well-matched to the salmon outmigration period, and a large influx of sea lice to the region with a healthy pink salmon return in the autumn of 2014 (Fig. 3). Although the proportion of treatments that occurred during the 2015 wild salmon out-migration was higher than in non-outbreak years, treatment timing did not contravene license conditions more than in non-outbreak years (Figs. 3a, 3b). This points to factors other than changes in compliance with license conditions driving the 2015 outbreak.

Ocean temperatures in 2015 were anomalously high, with the January estimate exceeding the mean temperature — across all months — over the previous decade (Fig. 3c). This likely accelerated

Fig. 3. Potential factors influencing the number of sea lice on juvenile wild salmon in the Broughton Archipelago, BC, plotted against the relevant wild salmon out-migration year. (a) Mean (95% CI) motile *L. salmonis* lice per farmed salmon (left axis and points) during juvenile wild salmon migration (March–June) and total number of treatments in winter (November–February; open bars) and during the migration (March–June; shaded bars) on salmon farms in the region. (b) Proportion of instances where treatment threshold was exceeded but management action was not taken within 1 month (March–June) or 2 months (July–February); numbers above bars count instances when the threshold was exceeded between July of the previous year and June of the given year. (c) Effective concentrations of EMB at which survival of sea lice was 50% (EC_{50}), as estimated from bioassays using pre-adult male (circles) and female (triangles) *L. salmonis*. (d) Deviations in sea surface temperature (ΔSST) at Pine Island lighthouse in BC. Dotted line segments show temperatures interpolated using data from three nearby lighthouses. Points show the mean monthly deviation in SST measured during juvenile salmon monitoring. Horizontal dashed line indicates the interpolated Pine Island temperature in January 2015. (e) The number of pink salmon (millions) returning to the four main salmon-bearing rivers in the Broughton Archipelago, BC. Compared with panels (a–d), the time axis in panel (e) is shifted because pink salmon returns in the autumn influence infestation of juveniles the following spring.

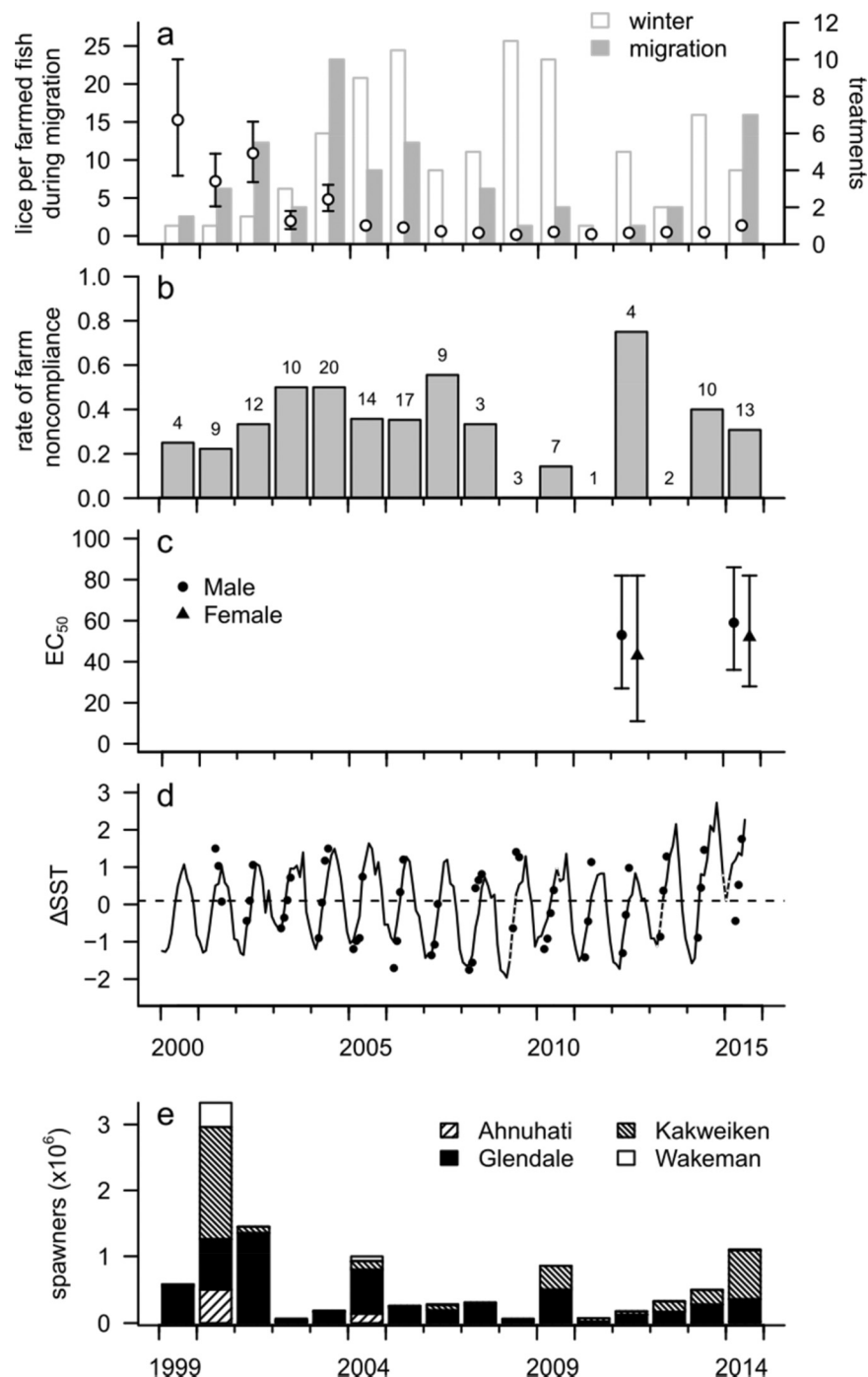
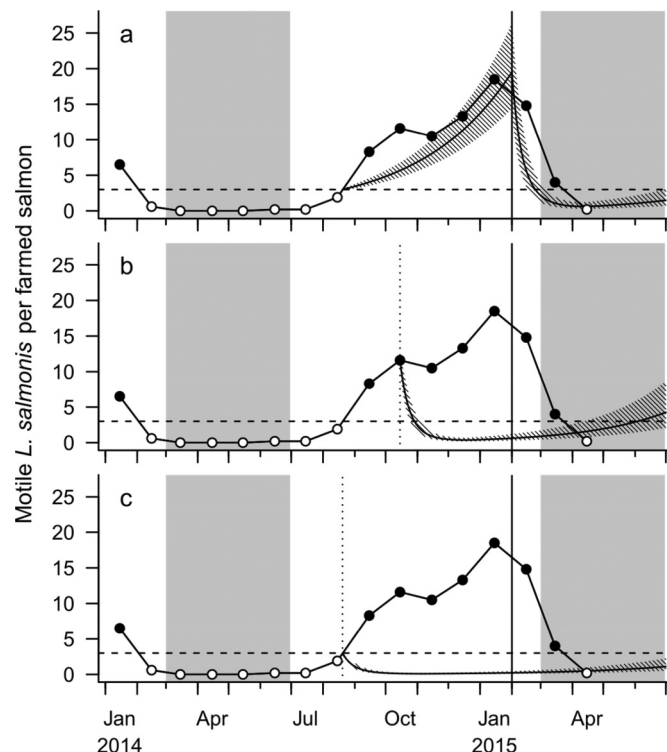


Fig. 4. Motile *L. salmonis* per farmed salmon for farm 8 in Fig. 3, with predicted louse abundances between and during juvenile wild salmon out-migration (shaded regions) under different treatment scenarios: (a) the actual treatment date in February 2015 (solid vertical line), (b) treatment in October 2014 (vertical dashed line), 30 days after the three-lice-per-fish threshold was reported to be exceeded in September, as per license conditions (Fisheries and Oceans Canada 2015a), and (c) treatment in August 2014 (vertical dashed line), immediately when the treatment threshold is crossed (i.e., precautionary treatment). Predictions used model-averaged parameters from Rogers et al. (2013); hatching delimits 95% confidence regions produced when uncertainty in the mean growth rate compounds in successive time steps.



the developmental rates of *L. salmonis* (Stien et al. 2005; Groner et al. 2014). Such elevated ocean temperatures are consistent with coast-wide reports of unseasonably warm seas (colloquially “the Blob”; Kintisch 2015). Although this year’s high temperatures were anomalous, ocean temperatures are likely to rise because of anthropogenic global warming over the coming decades (Overland and Wang 2007; Mauger et al. 2015), and accelerated louse development may become common.

The metadata associated with publicly reported louse counts on farms (Fisheries and Oceans Canada 2015b) indicated that anti-louse treatments were sometimes delayed until just before the beginning of the wild salmon out-migration. On at least one farm in the Broughton Archipelago, our model predictions suggest that delayed treatment resulted in high louse abundance throughout the winter preceding the 2015 pink and chum out-migration (Figs. 2, 4), which may have increased louse transmission to other farms in the area. In other salmon-farming regions, farm clusters have been shown to act as connected metapopulations, with local farmed salmonid density influencing louse abundance on farms (Adams et al. 2012; Jansen et al. 2012; Kristoffersen et al. 2013). Because the Broughton Archipelago’s salmon farms contribute to regional sea louse infestation pressure (Stucchi et al. 2011), farms may infect and reinfect each other, indicating that a more coordinated area-based management approach is needed.

Although the strategy of delaying treatment may be intentioned as precautionary management to reduce lice just before the wild salmon out-migration, the result in 2015 was several months in which louse numbers were allowed to remain high (Fig. 4a), increasing production of free-living larval sea lice. Sea louse abundance was higher than usual on salmon farms just prior to the usual wild salmon out-migration period (Fig. 2). Through louse population growth on the wild juvenile pink and chum salmon (Krkošek et al. 2005a, 2006), those wild juveniles may act as sources of farm re-infection, effectively becoming vectors that better connect the farm metapopulation. Warm winter weather is known to advance juvenile salmon incubation (Alderdice and Velsen 1978; Murray and McPhail 1988) and may have resulted in advanced development of wild pink and chum salmon in 2015 (juveniles were larger than on the same calendar day in previous years; Fig. S11¹). If out-migration was indeed earlier than normal for salmon in 2015, then treatments delayed until the typical out-migration window could have resulted in increased infestation of early migrating wild pink and chum. This, in turn, could have exacerbated the 2015 sea louse outbreak. Alternatively, warmer ocean conditions could have led to early spring algal blooms and more rapid early marine growth for wild juvenile salmon.

Towards cooperative coordinated area management

Given that there were no changes in compliance with sea louse management policy associated with the 2015 outbreak, our analyses indicate that current policy is not sufficient to accommodate the variation in biological, environmental, and management factors that can combine to generate an outbreak. One solution may be to change policy from a focus on treatment thresholds on individual farms to a focus on area-based integrated pest management (Brooks 2009). In addition to a management threshold on individual farms, a successful coordinated area management plan might incorporate environmental information, knowledge of salmon biology, and the network structure of interfarm parasite transmission (Adams et al. 2012; Jansen et al. 2012; Kristoffersen et al. 2013).

Furthermore, broader sharing of real-time information among research groups from government, industry, academia, and non-governmental organisations could help improve management. For example, multiple industry, government, and nongovernmental organizations noticed high louse levels early in 2015 (Hume 2015; Mainstream Biological Consulting 2015). Meanwhile, relevant understanding of the system (Brooks 2009; Stucchi et al. 2011) and information — such as climate forecasts — existed that might have helped identify 2015 as a year that was vulnerable to an outbreak. Increased sharing and discussion of information could have improved the prospects of management actions before sea lice on salmon farms exceeded treatment thresholds and before the wild juvenile salmon out-migration. Maintaining open communication, collaborative monitoring, and coordinated area management may help facilitate early detection and outbreak control. This proactive approach to parasite management is succinctly expressed in the following Haiku:

Communication,
cooperation towards
coordination

While it is not possible to pinpoint the factors that led to the 2015 Broughton Archipelago sea louse outbreak, the data we examined suggest that unusual environmental conditions, combined with delayed farm management actions, likely played a role by increasing louse abundance on salmon farms and transmission to juvenile wild salmon. We did not pursue a quantitative evaluation of our hypotheses for the 2015 outbreak because the data were too sparse. In the future, evaluating factors, considered here

qualitatively in a quantitative framework would provide a rigorous basis for predictive modelling that could inform management.

The outbreak in 2015 occurred despite ordinary compliance with the existing three-lice-per-fish treatment threshold requirements for farms (Fisheries and Oceans Canada 2015a), compelling us to suggest that on-farm management may benefit from a more holistic approach. Under the paradigm of coordinated area management, such an approach may involve proactive treatment in response to environmental conditions and wild fish migration timing, applied in conjunction with existing on-farm parasite treatment thresholds (Brooks 2009). Past work has shown that treatment of farmed salmon with parasiticides in the winter months can minimize the mean louse abundance on migrating juvenile wild salmon in the spring (Peacock et al. 2013; Rogers et al. 2013). Rather than relying on treatment in reaction to louse abundance exceeding a threshold on a farm-by-farm basis, managers might consider treatments in advance of the wild salmon out-migration period that are coordinated among nearby farms and informed by forecasts for environmental conditions known to affect sea louse development. Striving to improve management promises benefits to salmon farmers and those who depend on wild salmon alike (Costello 2009a).

Acknowledgements

This work would not have been possible without the dedicated contributions of dozens of volunteers — too many to name — who participated in weekly sea louse monitoring during wind-lashed and rain-drenched springs in the Broughton Archipelago. Thanks also to all those who provided advice, transportation, food, warmth, and welcoming safe havens for a decade and a half of fieldwork at Salmon Coast Field Station. This work was supported by NSERC and Killam postdoctoral fellowships to AWB, an NSERC Discovery Grant to M.A. Lewis (University of Alberta) that supported SJP, an NSERC Discovery Grant and Sloan Fellowship to MK, a Global Greengrant from the Marisla Foundation, and an infrastructure grant from the Pacific Salmon Foundation. The manuscript was improved by comments from two anonymous referees.

References

Aaen, S.M., Helgesen, K.O., Bakke, M.J., Kaur, K., and Horsberg, T.E. 2015. Drug resistance in sea lice: a threat to salmonid aquaculture. *Trends Parasitol.* 31(2): 72–81. doi:10.1016/j.pt.2014.12.006. PMID:25639521.

Adams, T., Black, K., MacIntyre, C., MacIntyre, I., and Dean, R. 2012. Connectivity modelling and network analysis of sea lice infection in Loch Fyne, west coast of Scotland. *Aquac. Environ. Interact.* 3(1): 51–63. doi:10.1007/s10005.012.00052.

Alderice, D.F., and Velsen, F.P.J. 1978. Relation between temperature and incubation time for eggs of chinook salmon (*Oncorhynchus tshawytscha*). *J. Fish. Board Can.* 35(1): 69–75. doi:10.1139/f78-010.

Asche, F., Roll, K.H., Sandvold, H.N., Sørvig, A., and Zhang, D. 2013. Salmon aquaculture: larger companies and increased production. *Aquac. Econ. Manag.* 17(3): 322–339. doi:10.1080/13657305.2013.812156.

Brauner, C.J., Sackville, M., Gallagher, Z., Tang, S., Nendick, L., and Farrell, A.P. 2012. Physiological consequences of the salmon louse (*Lepeophtheirus salmonis*) on juvenile pink salmon (*Oncorhynchus gorbuscha*): implications for wild salmon ecology and management, and for salmon aquaculture. *Philos. Trans. R. Soc. B Biol. Sci.* 367(1596): 1770–1779. doi:10.1098/rstb.2011.0423. PMID:22566682.

Brooks, K.M.K. 2005. The effects of water temperature, salinity, and currents on the survival and distribution of the infective copepodid stage of sea lice (*Lepeophtheirus salmonis*) originating on Atlantic salmon farms in the Broughton Archipelago of British Columbia, Canada. *Rev. Fish. Sci.* 13(3): 177–204. doi:10.1080/10641260500207109.

Brooks, K.M. 2009. Considerations in developing an integrated pest management programme for control of sea lice on farmed salmon in Pacific Canada. *J. Fish Dis.* 32(1): 59–73. doi:10.1111/j.1365-2761.2008.01013.x. PMID:19245631.

Cohen Commission. 2011. Exhibit 1696: BC Salmon Farmers Association Sea Lice Module Files 2010 [online]. Available from <http://www.watershed-watch.org/resources/cohen-commission-exhibit-1696-spreadsheet-bc-salmon-farmers-association-sea-lice-module-files-2010-jan-1-2010> [accessed 31 August 2015].

Costello, M.J. 2009a. The global economic cost of sea lice to the salmonid farming industry. *J. Fish Dis.* 32(1): 115–118. doi:10.1111/j.1365-2761.2008.01011.x. PMID:19245636.

Costello, M.J. 2009b. How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proc. R. Soc. B Biol. Sci.* 276(1672): 3385–3394. doi:10.1098/rspb.2009.0771.

Fisheries and Oceans Canada. 2015a. Finfish aquaculture licence under the Pacific Aquaculture Regulations. Part B: License conditions [online]. Available from <http://www.pac.dfo-mpo.gc.ca/aquaculture/licence-permis/docs/licence-cond-permis-mar-eng.pdf> [accessed 30 June 2015].

Fisheries and Oceans Canada. 2015b. Public reporting on aquaculture — sea lice [online]. Available from <http://www.pac.dfo-mpo.gc.ca/aquaculture/reporting-rapports/lic-pou-eng.html> [accessed 30 June 2015].

Fisheries and Oceans Canada. 2015c. Data from BC lighthouses [online]. Available from <http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html> [accessed 5 August 2015].

Fisheries and Oceans Canada. 2015d. NuSEDS V2.0 Regional adult salmon escapee database pink: 1999–2014 [online]. Available from <http://open.canada.ca/data/en/dataset/c48669a3-045b-400d-b730-48aaf8c5ee6> [accessed 12 August 2015].

Ford, J.S., and Myers, R.A. 2008. A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biol.* 6(2): e33. doi:10.1371/journal.pbio.0060033. PMID:18271629.

Foreman, M.G.G., Guo, M., Garver, K.A., Stucchi, D., Chandler, P., Wan, D., Morrison, J., and Tuele, D. 2015. Modelling infectious hematopoietic necrosis virus dispersion from marine salmon farms in the Discovery Islands, British Columbia, Canada. *PLoS ONE*, 10(6): e0130951. doi:10.1371/journal.pone.0130951. PMID:26114643.

Gargan, P.G., Forde, G., Hazon, N., Russell, D.J.F., and Todd, C.D. 2012. Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. *Can. J. Fish. Aquat. Sci.* 69(2): 343–353. doi:10.1139/f2011-155.

Godwin, S.C., Dill, L.M., Reynolds, J.D., and Krkošek, M. 2015. Sea lice, sockeye salmon, and foraging competition: lousy fish are lousy competitors. *Can. J. Fish. Aquat. Sci.* 72(7): 1113–1120. doi:10.1139/cjfas-2014-0284.

Goldburg, R., and Naylor, R. 2005. Future seascapes, fishing, and fish farming. *Front. Ecol. Environ.* 3(1): 21–28. doi:10.1890/1540-9295(2005)003[0021:FSFAFF]2.0.CO;2.

Groner, M.L., Gettinby, G., Stormoen, M., Revie, C.W., and Cox, R. 2014. Modelling the impact of temperature-induced life history plasticity and mate limitation on the epidemic potential of a marine ectoparasite. *PLoS ONE*, 9(2): e88465. doi:10.1371/journal.pone.0088465. PMID:24505493.

Hume, M. 2015. May. Sea lice infestation could kill up to “millions” of wild salmon [online]. The Globe and Mail, Vancouver, B.C. Available from <http://www.theglobeandmail.com/news/british-columbia/sea-lice-infestation-could-kill-up-to-millions-of-wild-salmon/article24300307/> [accessed 22 February 2015].

Jansen, P.A., Kristoffersen, A.B., Viljugrein, H., Jimenez, D., Aldrin, M., and Stien, A. 2012. Sea lice as a density-dependent constraint to salmonid farming. *Proc. R. Soc. B Biol. Sci.* 279(1737): 2330–2338. doi:10.1098/rspb.2012.0084.

Jones, S.R.M., and Hargreaves, N.B. 2009. Infection threshold to estimate *Lepeophtheirus salmonis*-associated mortality among juvenile pink salmon. *Dis. Aquat. Organ.* 84(2): 131–137. doi:10.3354/dao02043. PMID:19476283.

Kintisch, E. 2015. “The Blob” invades Pacific, flummoxing climate experts. *Science*, 348(6230): 17–18. doi:10.1126/science.348.6230.17. PMID:25838359.

Kristoffersen, A.B., Rees, E.E., Stryhn, H., Ibarra, R., Campisto, J.-L., Revie, C.W., and St-Hilaire, S. 2013. Understanding sources of sea lice for salmon farms in Chile. *Prev. Vet. Med.* 111(1–2): 165–175. doi:10.1016/j.prevetmed.2013.03.015. PMID:23628338.

Krkošek, M., Lewis, M.A., and Volpe, J.P. 2005a. Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proc. R. Soc. B Biol. Sci.* 272(1564): 689–696. doi:10.1098/rspb.2004.3027.

Krkošek, M., Morton, A., and Volpe, J.P. 2005b. Nonlethal assessment of juvenile pink and chum salmon for parasitic sea lice infections and fish health. *Trans. Am. Fish. Soc.* 134(3): 711–716. doi:10.1577/T04-133.1.

Krkošek, M., Lewis, M.A., Morton, A., Frazer, L.N., and Volpe, J.P. 2006. Epizootics of wild fish induced by farm fish. *Proc. Natl. Acad. Sci.* 103(42): 15506–15510. doi:10.1073/pnas.0603525103. PMID:17021017.

Krkošek, M., Morton, A., Volpe, J.P., and Lewis, M.A. 2009. Sea lice and salmon population dynamics: effects of exposure time for migratory fish. *Proc. R. Soc. B Biol. Sci.* 276(1668): 2819–2828. doi:10.1098/rspb.2009.0317.

Krkošek, M., Connors, B.M., Morton, A., Lewis, M.A., Dill, L.M., and Hilborn, R. 2011a. Effects of parasites from salmon farms on productivity of wild salmon. *Proc. Natl. Acad. Sci.* 108(35): 14700–14704. doi:10.1073/pnas.1101845108. PMID:21873246.

Krkošek, M., Connors, B.M., Ford, H., Peacock, S., Mages, P., Ford, J.S., Morton, A., Volpe, J.P., Hilborn, R., Dill, L.M., and Lewis, M.A. 2011b. Fish farms, parasites, and predators: implications for salmon population dynamics. *Ecol. Appl.* 21(3): 897–914. doi:10.1890/09-1861.1. PMID:21639053.

Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B., and Todd, C.D. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. *Proc. R. Soc. B Biol. Sci.* 280(1750): 1–8. doi:10.1098/rspb.2012.2359.

Lees, F., Baillie, M., Gettinby, G., and Revie, C.W. 2008. Factors associated with changing efficacy of emamectin benzoate against infestations of *Lepeophtheirus salmonis* on Scottish salmon farms. *J. Fish Dis.* 31(12): 947–951. doi:10.1111/j.1365-2761.2008.00969.x. PMID:19017071.

- Madhun, A.S., Karlsbakk, E., Isachsen, C.H., Omdal, L.M., Eide Sørvik, A.G., Skaala, Ø., Barlaup, B.T., and Glover, K.A. 2015. Potential disease interaction reinforced: double-virus-infected escaped farmed Atlantic salmon, *Salmo salar* L., recaptured in a nearby river. *J. Fish Dis.* **38**(2): 209–219. doi:10.1111/jfd.12228. PMID:24467305.
- Mainstream Biological Consulting. 2015. Prevalence of sea lice on juvenile salmonids captured in the Broughton Archipelago [online]. A report prepared for Marine Harvest Canada. Campbell River, B.C. Available from <http://marineharvest.ca/globalassets/canada/pdf/asc-dashboard-2016/broughton-archipelago-sea-lice-2015.pdf> [accessed 22 February 2016].
- Marty, G.D., Saksida, S.M., and Quinn, T.J. 2010. Relationship of farm salmon, sea lice, and wild salmon populations. *Proc. Natl. Acad. Sci. U.S.A.* **107**(52): 22599–22604. doi:10.1073/pnas.1009573108. PMID:21149706.
- Mauger, G.S., Casola, J.H., Morgan, H.A., Strauch, R.L., Jones, B., Curry, B., Busch Isaksen, T.M., Whitely Binder, L., Krosby, M.B., and Snover, A.K. 2015. State of knowledge: climate change in Puget Sound [online]. Report prepared for the Puget Sound Partnership and the National Oceanic and Atmospheric Administration. Climate Impacts Group, University of Washington, Seattle, Wash. doi:10.7915/CIG93777D. Available from <https://cig.uw.edu/publications/state-of-knowledge-climate-change-in-puget-sound/> [accessed 8 March 2016].
- McEwan, G.F., Groner, M.L., Fast, M.D., Gettinby, G., and Revie, C.W. 2015. Using agent-based modelling to predict the role of wild refugia in the evolution of resistance of sea lice to chemotherapeutants. *PLoS ONE*, **10**(10): e0139128. doi:10.1371/journal.pone.0139128.
- Morton, A.B., and Williams, R. 2003. First report of a sea louse, *Lepeophtheirus salmonis*, infestation on juvenile pink salmon, *Oncorhynchus gorbuscha*, in near-shore habitat. *Can. Field-Nat.* **117**(4): 634–641.
- Morton, A., Routledge, R., Peet, C., and Ladwig, A. 2004. Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada. *Can. J. Fish. Aquat. Sci.* **61**(2): 147–157. doi:10.1139/f04-016.
- Morton, A., Routledge, R.D., and Williams, R. 2005. Temporal patterns of sea louse infestation on wild Pacific salmon in relation to the fallowing of Atlantic salmon farms. *N. Am. J. Fish. Manage.* **25**(3): 811–821. doi:10.1577/M04-149.1.
- Murray, C.B., and McPhail, J.D. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. *Can. J. Zool.* **66**(1): 266–273. doi:10.1139/z88-038.
- Overland, J., and Wang, M. 2007. Future climate of the North Pacific Ocean. *Eos*, **88**(16): 178–182. doi:10.1029/2007EO160003.
- Patanasatienkul, T., Sanchez, J., Rees, E.E., Krkošek, M., Jones, S.R.M., and Revie, C.W. 2013. Sea lice infestations on juvenile chum and pink salmon in the Broughton Archipelago, Canada, from 2003 to 2012. *Dis. Aquat. Organ.* **105**(2): 149–161. doi:10.3354/dao02616. PMID:23872858.
- Patanasatienkul, T., Sanchez, J., Rees, E.E., Pfeiffer, D., and Revie, C.W. 2015. Space-time cluster analysis of sea lice infestation (*Caligus clemensi* and *Lepeophtheirus salmonis*) on wild juvenile Pacific salmon in the Broughton Archipelago of Canada. *Prev. Vet. Med.* **120**(2): 219–231. doi:10.1016/j.prevetmed.2015.03.006. PMID:25869117.
- Peacock, S.J., Krkosek, M., Probošycz, S., Orr, C., and Lewis, M.A. 2013. Cessation of a salmon decline with control of parasites. *Ecol. Appl.* **23**: 606–620. doi:10.1890/12-0519.1. PMID:23734489.
- Peacock, S.J., Bateman, A.W., Krkošek, M., Connors, B., Rogers, S., Portner, L., Polk, Z., Webb, C., and Morton, A. 2016. Sea louse parasites on juvenile wild salmon in the Broughton Archipelago, British Columbia, Canada. *Ecology*, **97**(7): 1887. doi:10.1002/ecy.1438.
- Penston, M.J., and Davies, I.M. 2009. An assessment of salmon farms and wild salmonids as sources of *Lepeophtheirus salmonis* (Krøyer) copepodids in the water column in Loch Torridon, Scotland. *J. Fish Dis.* **32**(1): 75–88. doi:10.1111/j.1365-2761.2008.00986.x. PMID:19245632.
- Rees, E.E., St-Hilaire, S., Jones, S.R.M., Krkosek, M., DeDominicis, S., Foreman, M.G.G., Patanasatienkul, T., and Revie, C.W. 2015. Spatial patterns of sea lice infection among wild and captive salmon in western Canada. *Landsc. Ecol.* **30**: 989–1004. doi:10.1007/s10980-015-0188-2.
- Rogers, L.A., Peacock, S.J., McKenzie, P., DeDominicis, S., Jones, S.R.M., Chandler, P., Foreman, M.G.G., Revie, C.W., and Krkošek, M. 2013. Modeling parasite dynamics on farmed salmon for precautionary conservation management of wild salmon. *PLoS ONE*, **8**(4): e60096. doi:10.1371/journal.pone.0060096. PMID:23577082.
- Saksida, S.M., Morrison, D., McKenzie, P., Milligan, B., Downey, E., Boyce, B., and Eaves, A. 2013. Use of Atlantic salmon, *Salmo salar* L., farm treatment data and bioassays to assess for resistance of sea lice, *Lepeophtheirus salmonis*, to emamectin benzoate (SLICE®) in British Columbia, Canada. *J. Fish Dis.* **36**(5): 515–520. doi:10.1111/jfd.12018. PMID:23106395.
- Schnute, J.T., Boers, N., and Haigh, R. 2015. PBSmapping: mapping fisheries data and spatial analysis tools [online]. R package version 2.69.76. Available from <https://CRAN.R-project.org/package=PBSmapping> [accessed 25 May 2016].
- Stien, A., Bjørn, P.A., Heuch, P.A., and Elston, D.A. 2005. Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. *Mar. Ecol. Prog. Ser.* **290**: 263–275. doi:10.3354/meps290263.
- Stucchi, D.J., Guo, M., Foreman, M.G.G., Czajko, P., Galbraith, M., Mackas, D.L., and Gillibrand, P.A. 2011. Modeling Sea Lice Production and Concentrations in the Broughton Archipelago, British Columbia. In *Salmon lice: an integrated approach to understanding parasite abundance and distribution*. Edited by S. Jones and R. Beamish. John Wiley & Sons, Chichester, UK. pp. 117–150.
- Westcott, J.D., Stryhn, H., Burka, J.F., and Hammell, K.L. 2008. Optimization and field use of a bioassay to monitor sea lice *Lepeophtheirus salmonis* sensitivity to emamectin benzoate. *Dis. Aquat. Organ.* **79**(2): 119–131. doi:10.3354/dao01887. PMID:18500028.