

# Sea lice are associated with reduced survival of pink salmon populations in the Broughton Archipelago: An updated analysis

Cole B. Brookson      Emma M. Atkinson

Andrew W. Bateman      Stephanie J. Peacock

Sean C. Godwin

October 2022

## 1 Executive Summary

- The impacts of open-net salmon farms on wild salmon survival have been of special interest in the Broughton Archipelago, particularly as they relate to the effect of ectoparasitic sea lice on juvenile salmon.
- We investigated the relationships between sea lice on farmed and wild salmon in the Broughton between 2001 and 2021, as well as the effects of these parasites on wild salmon returns
- We found a clear relationship between the number of sea lice on salmon farms and the number of sea lice on wild juvenile salmon
- We found a significant negative association between elevated sea lice and reduced survival of wild pink salmon in the Broughton Archipelago.
- The predicted mortality of wild pink salmon due to sea lice ranged from a low of 1.61%, for salmon returning to the Broughton in 2010, to a high of 95.3% , for those returning in 2002
- Despite BATI's farm-decommissioning process having left one KTF farm site (Glacier) empty of fish since 2019 and another (Burdwood) empty since 2020, overall sea-louse numbers in the KTF corridor have not declined significantly, resulting in 16.5% predicted mortality due to sea lice for pink salmon returning in 2020, and 6.6% in 2021

## 2 Supplemental Methods

### 2.1 Data Collection and Collation

#### 2.1.1 Sea Lice on Farmed Salmon

Data on the abundance of lice on farmed salmon were collated from two main sources. Data from 1999-2009 were collected from (Marty et al., 2010), and data from 2003 to 2021 were provided by the Broughton Archipelago Transition Initiative (BATI). Since records from Marty et al. (2010) are since not available through the original database, we default to data provided by BATI. These data consist separately of estimates of both the number of Atlantic salmon *S. salar* on the relevant farms of interest, and the average number of adult female sea lice *L. salmonis* per salmon per farm in the region (Main Fig. 1). The number of lice in the region was then estimated by calculating the total sum of lice on each farm (i.e. the number of lice multiplied by the inventory of the farm), and summing that value for all farms of interest (Orr, 2007; Marty et al., 2010; Peacock et al., 2013).

Given that some farms in the region contribute greater infestation pressures on wild juvenile salmon than others, we compared three different groupings of the farms. We looked at the relationship of lice on wild juveniles to a) the number of lice on all farms, b) the number of lice on farms in the Knight-Tribune corridor, and c) the number of lice on the three most influential farms - Humphrey, Sergeant, and Doctors (Fig. Fig. 1 Main Text).

#### 2.2 Sea Lice on Wild Juvenile Salmon

To account for sea lice on wild juvenile salmon, we used data collected from Salmon Coast Field Station that represent a long-term monitoring program, wherein juvenile pink salmon were sampled and examined for sea lice at weekly intervals from late March through June between 2001 and 2021. Collection of these data are described in a variety of publications including (Krkošek et al., 2005; Peacock et al., 2013), but briefly, at the sampling sites, shoals of juvenile salmon were identified visually and then collected in a seine net. The juvenile salmon were then transferred to buckets, then either placed individually into sample bags and frozen for subsequent analysis (2001-2004), or analyzed non-lethally on size using a hand lens and a visual assay method that compares favourably to dissecting scope-based assays on dead fish (Krkošek et al., 2005). Since not all weeks of the year were evenly represented in the data, and since week is an important variable in our models, we excluded three weeks (9, 28, and 33), which, across all years, accounted for less than 0.1% of our samples.

To accurately represent the effect of sea lice on wild juvenile salmon, we compared three scenarios. Since *L. salmonis* are salmon specialists whose infestation of wild salmon is more directly attributable to salmon farms than the generalist *C. clemenci*, we used our field sampling data to estimate the number of *L. salmonis* lice (copepodite, chalimus, and motile stage) on wild juvenile

salmon. We performed two permutations of this estimation process to test two competing assumptions. We compared this with the method previously used (by Peacock et al. 2013, described below), and a similar method that uses a different modeling approach. Last, we made an estimate of all lice on wild juveniles, regardless of louse species.

To compare these five scenarios, we made estimates of our spawner recruit parameter of interest,  $c$ , described below, and compared the estimates of  $c$  between all scenarios here, plus the scenarios described further in this section.

### 2.2.1 Scenario 1 - *L. salmonis* Only

Through the years of this survey, due to slight differences in sampling protocols, there were variable numbers of lice in all stages of interest (copepodids, chalimus, and motiles) that were identified to species.

For years in which copepodites were mostly speciated (i.e., 2005 - present), we estimated the number of unidentified copepodites that were actually *L. salmonis* using the empirical proportion of *L. salmonis* among the speciated copepodites. Similarly, for years in which motiles were mostly speciated (i.e., 2002 - present), we estimated the number of unidentified motiles that were actually *L. salmonis* using the empirical proportion of *L. salmonis* among the speciated motiles.

This method is a decision that makes an assumption about the process that drives *L. salmonis* proportions. We know from previous approaches (Peacock et al., 2013; Bateman et al., 2016) that the proportion of *L. salmonis* increases with an increase in the number of lice overall. However, previous approaches implicitly **only** assumed that increase was driven by inter-annual variation, such that for a given fish, the proportion of lice that were *L. salmonis* depended on the amount of lice more generally in the system in that year. The alternative assumption that could be made is that the proportion of *L. salmonis* is actually driven by an individual level process in that, regardless of the year, the proportion of *L. salmonis* on a given fish is determined by the total number of lice on that specific fish. While this may seem trivial, it is a relatively large assumption about the underlying drivers of this pattern we see with increasing *L. salmonis* proportions in accordance with increasing numbers of lice overall. So, we decided to test this assumption by permuting Scenario 1 with these two sub-scenarios.

For both sub-scenarios, regarding years in which copepodites (i.e., 2002 - 2004) and motiles (i.e., 2001) were counted but never speciated, we estimated the number of *L. salmonis* in these life stages using predicted *L. salmonis* proportions from simple logistic regressions fit to the speciated years' copepodite (Fig. 1) and motile (Fig. 2) data.

#### 2.2.1.1 Scenario 1.1 - Default to Individual-level Predictions

To default to individual level of predictions, for each fish that did not have speciated motiles or copepodites, we model-predicted a single proportion value

of *L. salmonis* from our fit logistic models, using the number of lice on that individual fish as our predictive value. Then, for each unidentified louse, we used that predicted proportion to weight a random sample of a Bernoulli trial. To expand on this, for a given fish, if it had some number of lice on it,  $n$ , that would result in a single-value model prediction,  $p$ , which for example let's assume is 0.75. For each unidentified adult louse, to decide if that louse was *L. salmonis*, we drew from a Bernoulli distribution, where the probability of drawing a 1 (and therefore counting that louse as an *L. salmonis* louse) was equal to 0.75. In circumstances where there were  $\geq 1$  unidentified adult lice, this draw was repeated for each individual louse.

### 2.2.1.2 Scenario 1.2 - Default to Year-level Predictions

To default to the year level of predictions, we calculated the mean proportion in a given year/stage and applied that to all individual observations via random sampling with a set probability according to our mean proportion. To illustrate this more clearly, for 2001 motiles, the average predicted portion of *L. salmonis* is 0.639. For each unidentified adult louse, to decide if that louse was *L. salmonis*, we drew from a Bernoulli distribution, where the probability of drawing a 1 (and therefore counting that louse as an *L. salmonis* louse) was equal to 0.639. In circumstances where there were  $\geq 1$  unidentified adult lice, this draw was repeated for each individual louse. This is more biologically realistic than ascribing 0.639 lice to a fish.

For both sub-scenarios, we then estimated the number of *L. salmonis* chalimus-staged lice by applying the average of the *L. salmonis* proportions for copepodites and for motiles. Since copepodites were counted as chalimus in 2001, we estimated the *L. salmonis* proportion for chalimus in that year using only the motile *L. salmonis* proportion.

### 2.2.2 Scenario 2 - Comparison to Previous Methods

To make useful comparisons to previous work (Peacock et al., 2013; Bateman et al., 2016), we followed the procedure outlined by the aforementioned works, wherein for all years all chalimus stage lice and all unidentified copepodites were counted as *L. salmonis* and for 2001 the proportion of unidentified motiles was estimated using a non-linear model as described by Bateman et al. (2016). Since the ratio of *L. salmonis* to all lice increases asymptotically as the number of total lice increases, we use a nonlinear regression, which takes the form

$$Y \sim a - (a - b)^{-cX}$$

where  $a$  is the maximum attainable  $Y$ ,  $b$  is the value of  $Y$  when  $X$  is 0 and  $c$  is the proportional relative rate of the increase in  $Y$  while  $X$  increases. In our case, since  $Y$  is continuous and bounded at 0 and 1,  $a$  was given the value of 1.0,  $b$  is 0.0 and  $c$  is fit.

This analysis indicates that the predicted proportion of *L. salmonis* in 2001 is  $> 0.95$  (Fig. 3).

### 2.2.3 Scenario 3 - Beta-regression

One noted problem with the approach employed in scenario 2, is that the model is forced to pass through the zero intercept by nature (see Figure 3). We decided it would be useful to compare the scenario 2 approach to a version of that model that does not force an intercept at the origin. To do this, we fit a beta-regression to the yearly average data, which predicted the proportion of *L. salmonis* in a given year as a function of the mean number of all lice species per fish.

The results of that model are shown in Fig. 4, and confirm what the previous approach (that calculated the values by year) suggested, which was a value of 1.0 for the prediction of *L. salmonis* proportions in 2001. This is a useful confirmation, as it takes a slightly more realistic model and also importantly allows for a quantification of uncertainty around our estimate in 2001. That is, given the presence of a lower bound on the estimate, we can run a version of the analysis using the lower end of the 95% confidence interval to see if changing our assumption on that value changes the overall conclusions of our analysis.

### 2.2.4 Scenario 4 - All lice estimate

Since both lice species are important in the understanding of mortality to wild salmon, we made our best estimate of all lice on wild salmon in the field sampling program, summing all stages and all species of lice to create an estimate for the average number of lice on salmon. Note that this did not require any models, as there was no need to infer the species or stage of unidentified lice.

## 2.3 Pink salmon spawner-recruit data

### 2.3.1 Spawner Abundance

To evaluate the population-level effect of sea lice on wild pink salmon using spawner-recruit models we assembled time series of spawner abundance and recruitment estimates for each population of interest. The spatial scope of the data includes focal populations in the Broughton Archipelago (DFO Pacific Fishery Management Area 12, hereafter DFO Area 12) as well as reference data from farm-free regions on the central coast (DFO Areas 7-10). For this analysis, we define a ‘population’ as a group of salmon of a given species that breed together at the same time and place – in this case, at the level of the river or stream. We treat odd- and even-year classes of pink salmon as separate populations, because their fixed two-year life cycle means that the two year classes are reproductively isolated from one another (Beacham et al., 2012).

We sourced annual river-level estimates of spawner abundance (the number of mature salmon that return to freshwater to spawn) from the publicly available Government of Canada New Salmon Escapement Database System (of Fisheries & Oceans, 2020). While methods for estimating spawner abundance vary depending on the system and time period, these data are generally collected through stream walking surveys, surveys conducted by helicopter, or in-stream fish counting technology such as resistivity/acoustic arrays.

### 2.3.2 Recruitment Estimates

To generate estimates of recruitment (the offspring from a given cohort of spawners that would have survived to spawn in the absence of commercial fisheries), we drew on additional exploitation data for Area 12 (Van Will, unpublished data) and Areas 7-10 (English et al., 2018).

When estimating escapement, we calculate that rate for each year and area as

$$\mu_{i,t} = \frac{C_{a,t}}{C_{a,t} + E_{a,t}}$$

where exploitation rate  $u_{i,t}$  is given for each river  $i$  and each year  $t$ , as the proportion of the catch  $C_{a,t}$  in each area  $a$  and year  $t$  relative to the sum of all estimated escapement  $E$  and catch  $C$ . Note that this assumes all rivers  $i$  within fishery management areas  $a$  to have the same exploitation rate in a given year  $t$ .

We estimate the recruits,  $R_{i,t}$  to each river  $i$  in each year  $t$  as

$$R_{i,t} = \frac{S_{i,t}}{1 - u_{i,t}},$$

where  $S_{i,t}$  is the spawner abundance of pink salmon from year  $i$  in year  $t$ , and  $u_{i,t}$  is the exploitation rate for river  $i$  in year  $t$ . Here we assume that populations within a given management area experience the same rate of exploitation, though that rate varies year to year. We included populations in the main analysis which had three or more spawner-recruit pairs (i.e., years of data), consistent with previous work (e.g., Connors et al. 2013, 2018, 2019).

We compared this to the approach of Peacock et al. (2013), who used a cutoff of 20 or more pairs. To carry this comparison through to see the effect of this assumption on the estimate of the effect of lice, we compare these two assumptions through all the following analysis. The final dataset, assuming min. three pairs, included 78 rivers and 2,744 spawner-recruit pairs across 149 populations (even- and odd-years considered as separate populations). The final dataset, assuming min. 20 pairs, included 41 rivers and 1,855 spawner-recruit pairs across 72 populations. Note that the number of rivers sampled in each year declined over the time series due to the coastwide reduction in escapement monitoring by DFO (Figs. 5, 6)

## 2.4 Relationship Between Farm Lice & Wild Juvenile Lice

In order to estimate the effect of lice on the returns of pink salmon, we needed to make estimates of the mean number of *L. salmonis* per wild juvenile salmon in each year, via data from weekly monitoring surveys in the years 2001-2021. We estimated the mean number of lice per year with a generalized linear mixed-effects model (GLMM) where year was a fixed effect and both sample site (Fig. 1 Main Text) and week were random effects. We then compared the annual estimate of the number of lice on wild juveniles to the number of lice on salmon farms in the region. To do this, we compared three different groupings of

salmon farms. Free-living, infectious-stage sea lice disperse according to complex ocean circulation patterns, primarily influenced by wind, tides, and river input. Depending on the farm location and currents, the relative infection pressure on wild juvenile salmon from farms may differ, making it challenging to know which farms are major sources of sea lice for wild juvenile salmon. We looked at the relationship of lice on wild juveniles to a) the number of lice on all farms, b) the number of lice on the farms in the Knight-Tribune corridor (KTF) (Fig. 1 Main Text), and c) the number of lice on three focal farms - Humphrey, Sargeant, and Doctors. This analysis was done using the glmmTMB package (Magnusson et al., 2017).

A preliminary regression analysis revealed that the number of lice on both a) all farms, and b) KTF farms explained the number of lice on wild lice well (Fig. 7) across all scenarios. While both the "All Farms" and KTF groupings provided high correlation with lice on wild juveniles, given that the KTF grouping has an almost equivalent  $R^2$  value in all scenarios and it represents a more biologically relevant selection of farms, we chose to use only KTF grouping farms moving forwards.

## 2.5 Model Analysis

To directly model the effect of sea lice on the survival of pink salmon populations, we used a hierarchical version of the classic Ricker model (Ricker, 1954), described in Peacock et al. (2013). This approach allowed us to treat populations in the Broughton region (area 12) as being exposed to salmon farms while populations in other regions (7-10) were not exposed to local salmon farms.

The hierarchical Ricker model can be described as

$$R_{i,t} = N_{i,t-2} \exp[r - b_i N_{i,t-2} - cW_{a,t-1} + \theta_t + \theta_{a,t} + \varepsilon_{i,t}]$$

where  $R_{i,t}$  is the number of recruits to population  $i$  in year  $t$ ,  $N_{i,t-2}$  is the number of spawners in population  $i$  at year  $t - 2$ . This  $t$  lag is to account for the two-year lifespan of pink salmon.  $r$  is the growth rate which is treated as singular across different populations, but  $b_i$  is the density-dependence parameter which is unique to each population, to represent the different habitat factors and competitive interactions each population  $i$  experiences independently. Further, the term  $cW_{a,t-1}$  is the modelled effect of sea lice from salmon farms on the juvenile pink salmon. Here,  $W_{a,t-1}$  is the number of sea lice in each area  $a$  in time  $t - 1$ . We assume the number of lice in areas 7-10 to be zero since there are no salmon farms in that region, and the mean number of lice per juvenile salmon per year in area 12, is estimated from the GLMM described previously. Thus, since  $W_{a,t-1}$  are data in this formulation, we fit  $c$  as the coefficient, giving the direct estimated percent mortality of pink salmon due to sea lice on wild juvenile salmon equal to  $1 - \exp(-cW_{a,t-1})$  (Krkošek et al., 2011; Peacock et al., 2013).

With respect to data on sea lice, no measurements of lice on wild juvenile salmon exist pre-2001, so in line with Peacock et al. (2013), we assume that  $W_{a,t-1}$  are "missing" data from 1991-2001, and pre-1991 are 0.

Stage & Species ID							
Year	L. cope	C. cope	Unid cope	Unid chal	L. mot	C. mot	Unid mot
2001				X			X
2002			X	X	X	X	
2003			X	X	X	X	
2004			X	X	X	X	
2005-present	X	X	X	X	X	X	

Table 1: Year and Louse Stage data availability in the Salmon Coast Field Station wild juvenile salmon sampling data. X’s denote year/stage combinations for which there are data available.

We account for three forms of stochasticity in this analysis. First, the environmental stochasticity which varies through time but is consistent in time  $t$  for all populations. This is modeled as  $\theta_t$ , a normally distributed random variable with a mean of zero and an estimated variance. Second, we account for environmental stochasticity which varies through time  $t$  and among areas, such that all populations within an area  $a$  are subject to the same effect. This is  $\theta_{a,t}$ , a normally distributed random variable with a mean of zero and an estimated variance. Last, we also account for residual environmental stochasticity that varies through years  $t$  and among populations  $i$ . This is  $\varepsilon_{i,t}$ , a normally distributed random variable with mean zero and estimated variance.

As in Peacock (2013), we fit the Ricker model in a linear form

$$\ln \frac{R_{i,t}}{N_{i,t-2}} = r - b_i N_{i,t-2} - c W_{a,t-1} + \theta_t + \theta_{a,t} + \varepsilon_{i,t}$$

in the *lme4* package (Bates, 2010). We compared the fit of this model to a null model version without any term accounting for effects from sea lice. To estimate variance around our maximum likelihood estimates, we calculated confidence intervals on our model parameters via parametric bootstrapping, described in detail in (Krkošek et al., 2007; Krkošek and Hilborn, 2011).

To predict the % mortality in future years, we used the predicted mean number of lice on juvenile salmon from our GLMM as our values for  $W_{a,t-1}$ , along with our fitted value for  $c$ . To get some measure of variance, we also took the 2.5th and 97.5th percentile values from the confidence interval of the GLMM predictions, and used those values for our values of  $W_{a,t-1}$  to predict an upper and lower bound.

All analysis presented here was performed in the R statistical computing language (Team, 2022).

### 3 Figures & Tables





Figure 1: Proportion of *L. salmonis* copepodite lice over increasing total number (*L. salmonis* and *C. clemensi*) of copepodite lice of per fish.

Proportion Estimates		
Year	L. copepodite	L. motile
2001	Predicted	Predicted
2002-2004	Predicted	Empirical
2005-present	Empirical	Empirical

Table 2: Different year/stage combinations were given by either an empirical proportion or a model-predicted proportion.

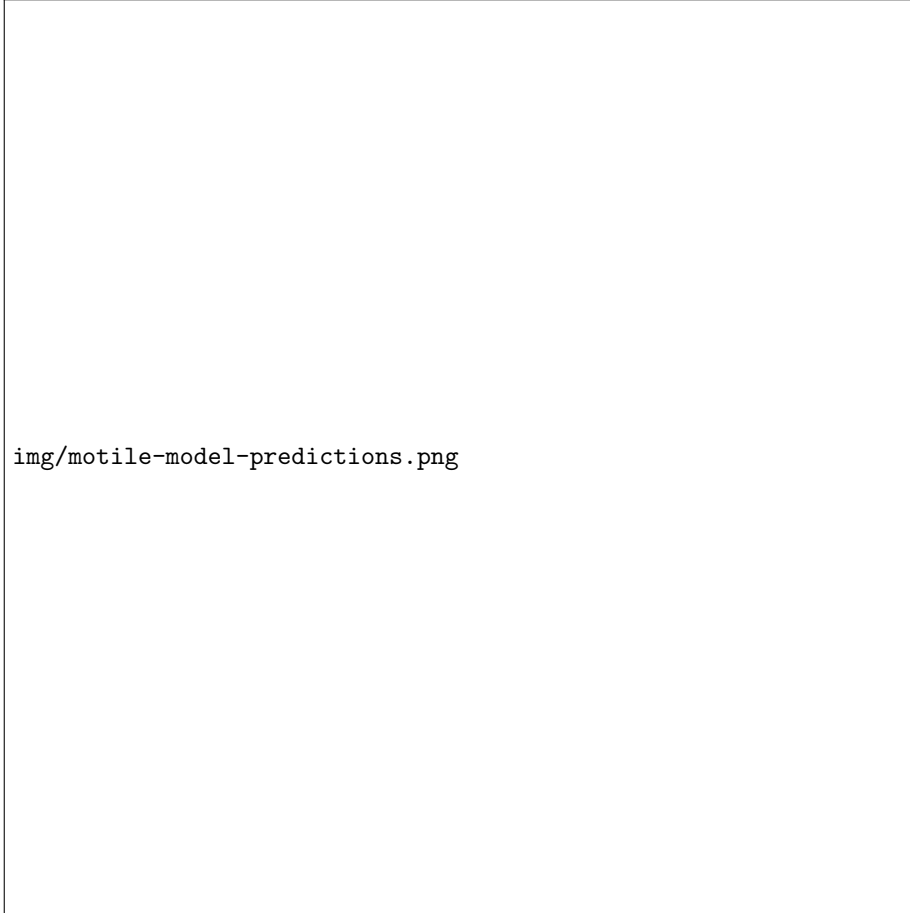


Figure 2: Proportion of *L. salmonis* motile lice over increasing total number (*L. salmonis* and *C. clemensi*) of motile lice of per fish.

Model	AIC	Neg. Log-Likelihood	$\Delta$ AIC
Alternative Model	11575.6	-5633.8	0
Null Model	11588.8	-5641.4	13.2

Table 3: Model comparison for null model and alternative model assessing if including a term for lice infestation improved fit of model of survival.

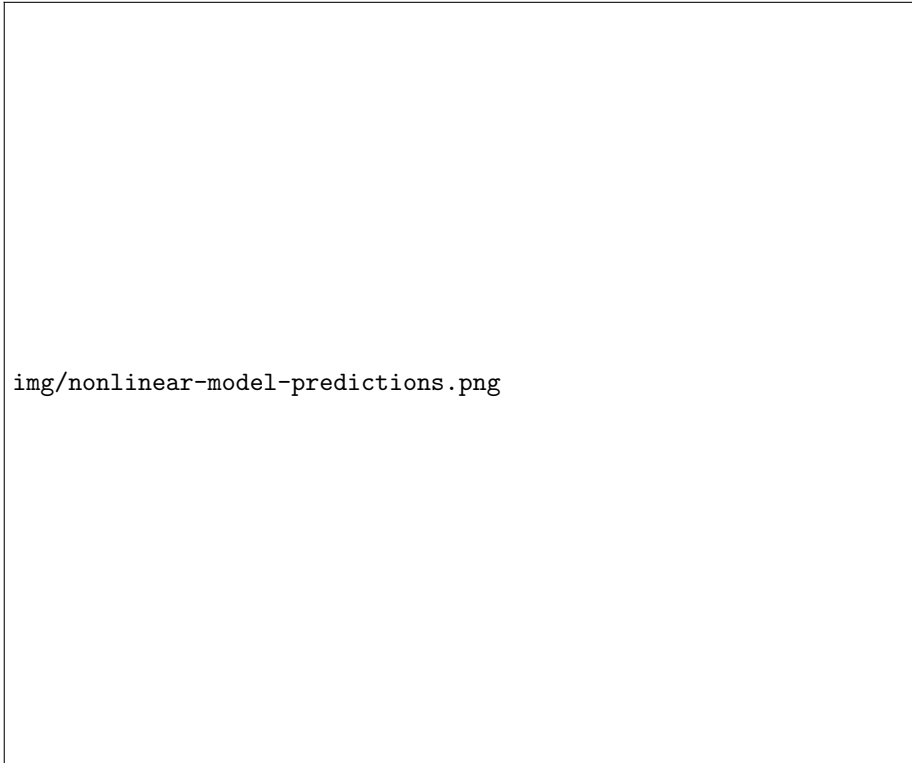


Figure 3: Proportion of *L. salmonis* lice over increasing total number (*L. salmonis* and *C. clemensi*) of lice of per fish. Yellow points represent data, the purple point represents a predicted value.

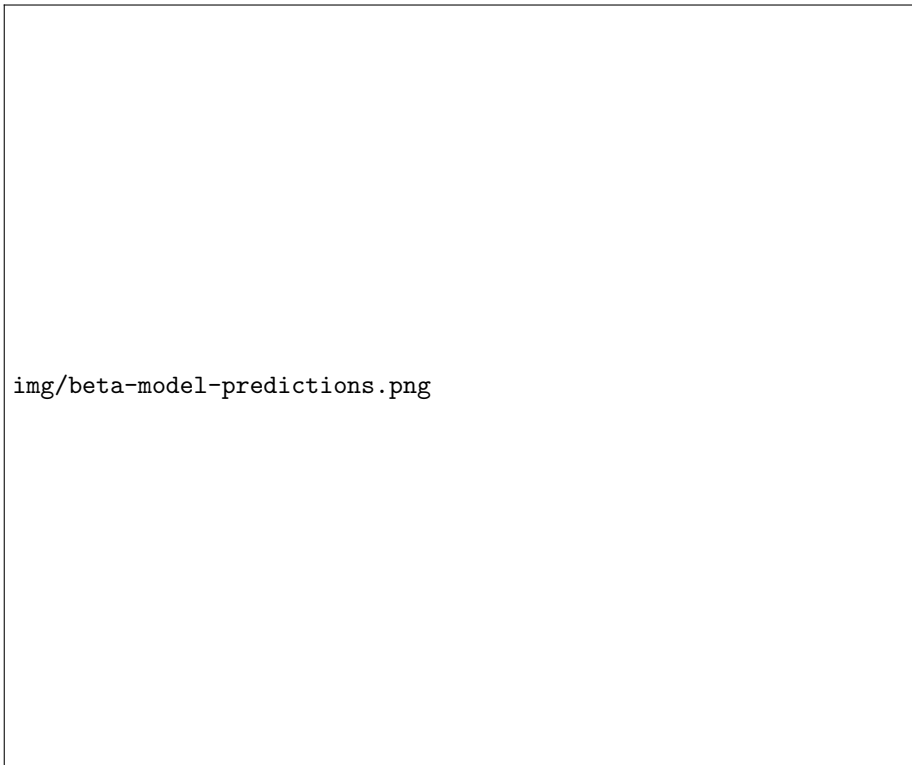


Figure 4: Proportion of *L. salmonis* lice over increasing total number (*L. salmonis* and *C. clemensi*) of lice of per fish. The grey line indicates the model predicted values, and the blue envelope denotes the 95% confidence interval. Purple points denote data points, and the yellow point represents a predicted value.

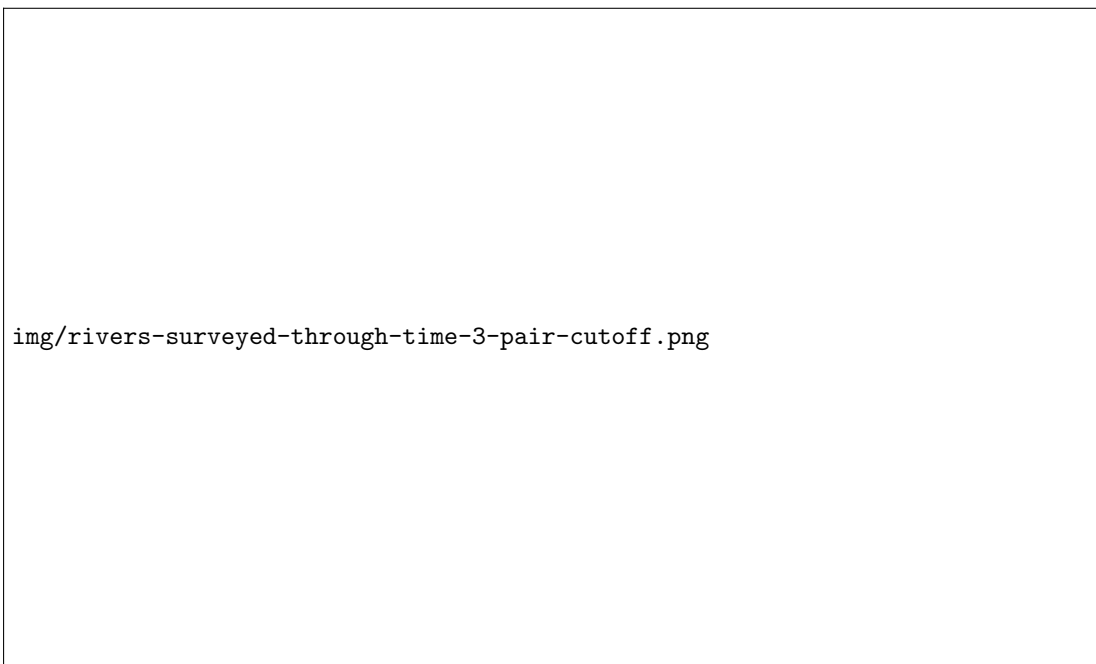


Figure 5: Number of rivers in each year and each area that were surveyed by DFO to enumerate the number of spawners. Here the cutoff to define the number of spawner-recruit pairs to include a population is 3 pairs.

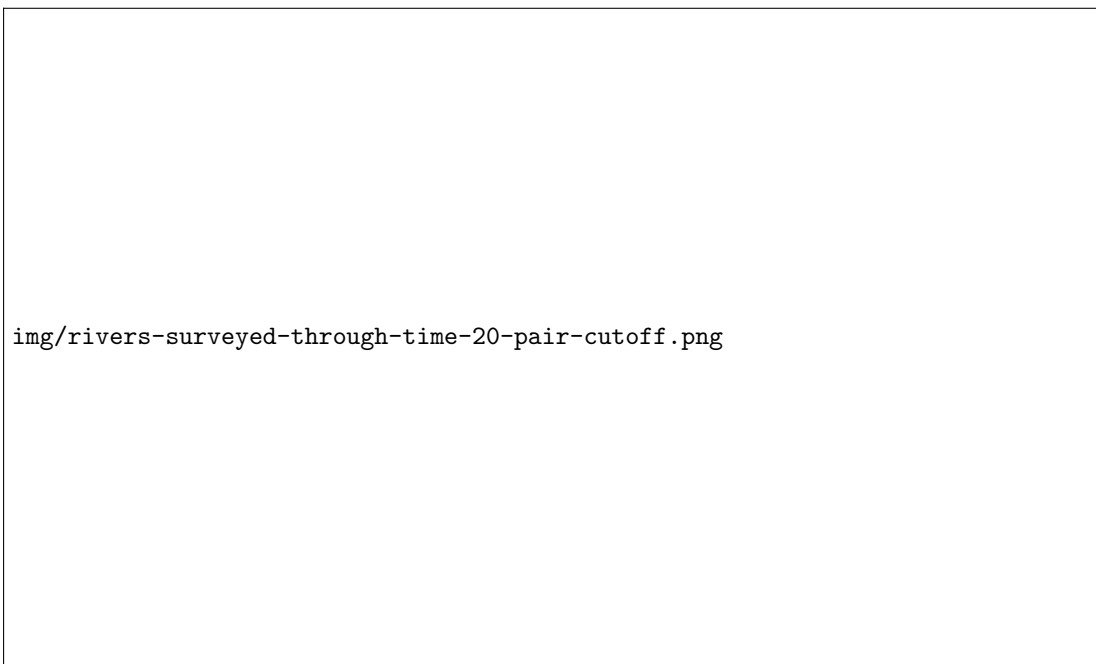
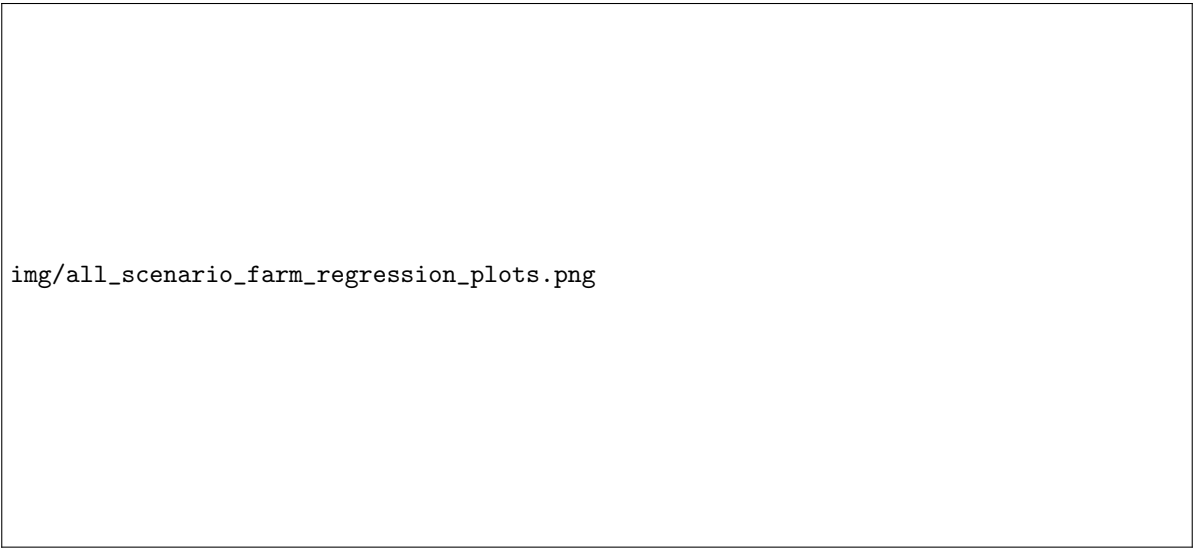
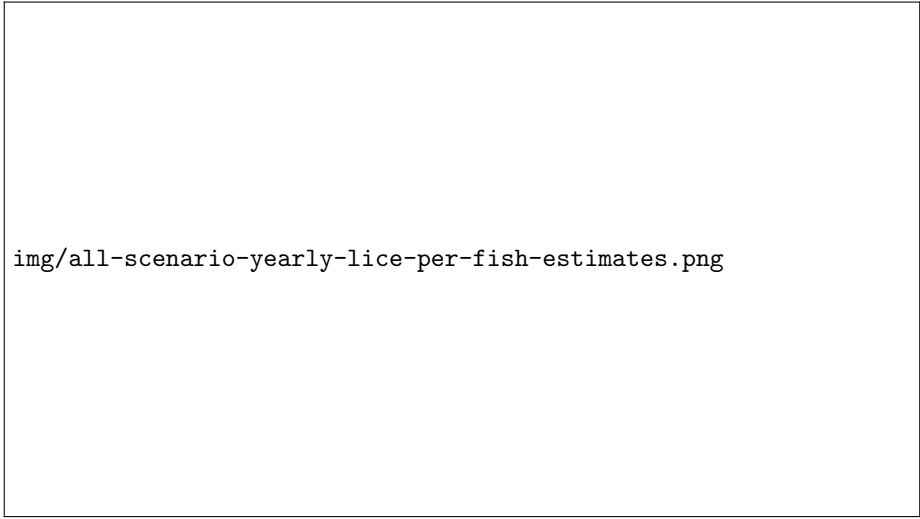


Figure 6: Number of rivers in each year and each area that were surveyed by DFO to enumerate the number of spawners. Here the cutoff to define the number of spawner-recruit pairs to include a population is 20 pairs.




img/all\_scenario\_farm\_regression\_plots.png

Figure 7: A comparison of the relationship between the number of lice on wild salmon (on a  $\log_{10}$  scale), and the number of lice on the three sets of farm comparisons (also a  $\log_{10}$  scale). Here the comparison is across all 5 scenarios, and both the options for minimum population counts.



img/all-scenario-yearly-lice-per-fish-estimates.png


Figure 8: Estimated number of lice per wild juvenile pink salmon in all available years. The points represent the estimated value, with the error bars giving a 95% confidence interval.



img/timeseries-lice-fish-abundance.png

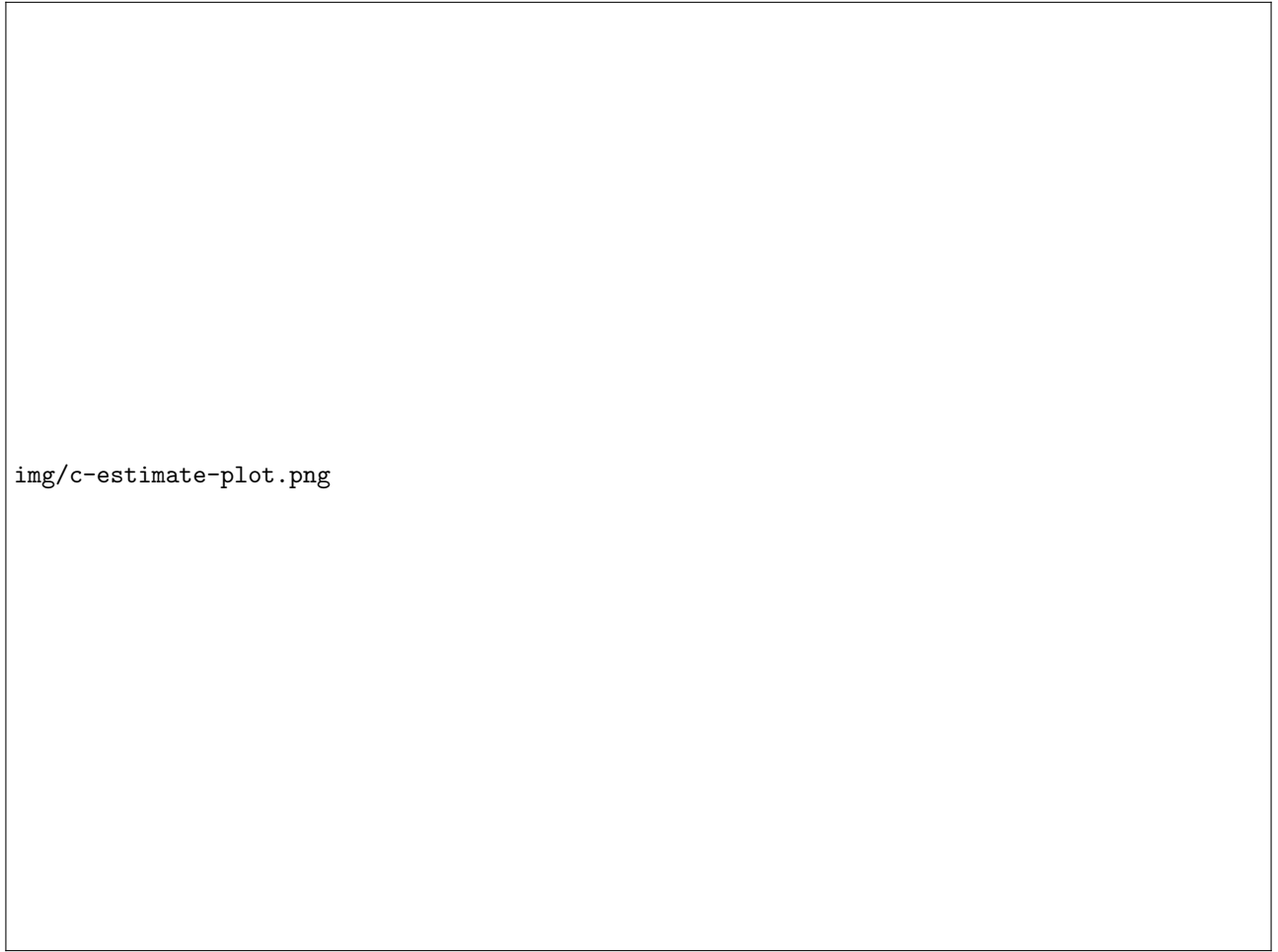
Figure 9: Total number of salmon and lice on those salmon across farms. Values are given as sums across all farms in each category, and averaged between March & April, the only two months that were relevant to the present analysis. Farms are divided into Knight-Tribune Corridor (KTF) farms, non-KTF farms, and the sum of those two values - "All".





img/all-scenario-yearly-lice-per-fish-estimates.png

Figure 10: Comparison between scenarios of log-log regressions between the number of lice on wild fish and farmed fish.



img/c-estimate-plot.png

Figure 11: Comparison of the estimates of  $c$  across all five scenarios and the two assumptions of pairs. Note that while the values for scenarios 1.2 - 4 look to be identical, they are not identical (see Table 2

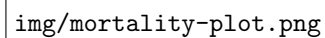
The image is a placeholder for a plot, indicated by the text 'img/mortality-plot.png' inside a rectangular frame. The plot itself is not visible.

Figure 12: Estimated and predicted percentage of the mortality in a given outmigration year, due to sea lice infestations of juvenile salmon  $1 - \exp(-cW_{a,t-1})$ . The points for the estimated values represent maximum likelihood estimates, and the error bars are 95% confidence intervals. The error bars on the predicted values are not *true* 95% CI's, but are a best-estimate of those bounds.

## References

- A. W. Bateman, S. J. Peacock, B. Connors, Z. Polk, D. Berg, M. Krkošek, and A. Morton. Recent failure to control sea louse outbreaks on salmon in the Broughton Archipelago, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(8):1164–1172, Aug. 2016. ISSN 0706-652X. doi: 10.1139/cjfas-2016-0122. URL <https://cdnsciencepub.com/doi/full/10.1139/cjfas-2016-0122>. Publisher: NRC Research Press.
- D. M. Bates. lme4: Mixed-effects modeling with R, 2010.
- T. D. Beacham, B. McIntosh, C. MacConnachie, B. Spilsted, and B. A. White. Population structure of pink salmon (*Oncorhynchus gorbuscha*) in British Columbia and Washington, determined with microsatellites. 2012.
- K. English, D. Peacock, W. Challenger, C. Noble, I. Beveridge, D. Robichaud, K. Beach, E. Hertz, and K. Connors. North and Central Coast Salmon Escapement, Catch, Run Size and Exploitation Rate Estimates for Each Salmon Conservation Unit for 1954–2017. *Pacific Salmon Foundation*, 2018.
- M. Krkošek and R. Hilborn. Sea lice (*Lepeophtheirus salmonis*) infestations and the productivity of pink salmon (*Oncorhynchus gorbuscha*) in the Broughton Archipelago, British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(1):17–29, 2011.
- M. Krkošek, A. Morton, and J. P. Volpe. Nonlethal Assessment of Juvenile Pink and Chum Salmon for Parasitic Sea Lice Infections and Fish Health. *Transactions of the American Fisheries Society*, 134(3):711–716, May 2005. ISSN 0002-8487, 1548-8659. doi: 10.1577/T04-133.1. URL <http://doi.wiley.com/10.1577/T04-133.1>.
- M. Krkošek, A. Gottesfeld, B. Proctor, D. Rolston, C. Carr-Harris, and M. A. Lewis. Effects of host migration, diversity and aquaculture on sea lice threats to Pacific salmon populations. *Proceedings of the Royal Society B: Biological Sciences*, 274(1629):3141–3149, Dec. 2007. doi: 10.1098/rspb.2007.1122. URL <https://royalsocietypublishing.org/doi/full/10.1098/rspb.2007.1122>. Publisher: Royal Society.
- M. Krkošek, B. M. Connors, A. Morton, M. A. Lewis, L. M. Dill, and R. Hilborn. Effects of parasites from salmon farms on productivity of wild salmon. *Proceedings of the National Academy of Sciences*, 108(35):14700–14704, Aug. 2011. doi: 10.1073/pnas.1101845108. URL <https://www.pnas.org/doi/abs/10.1073/pnas.1101845108>. Publisher: Proceedings of the National Academy of Sciences.
- A. Magnusson, H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, M. Brooks, and M. M. Brooks. Package ‘glmmTMB’. *R Package Version 0.2.0*, 2017.

- G. D. Marty, S. M. Saksida, and T. J. Quinn. Relationship of farm salmon, sea lice, and wild salmon populations. *Proceedings of the National Academy of Sciences*, 107(52):22599–22604, Dec. 2010. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1009573108. URL <https://www.pnas.org/content/107/52/22599>.
- D. of Fisheries & Oceans. NuSEDS-New Salmon Escapement Database System - Open Government Portal, 2020. URL <https://open.canada.ca/data/en/dataset/c48669a3-045b-400d-b730-48aafe8c5ee6>.
- C. Orr. Estimated Sea Louse Egg Production from Marine Harvest Canada Farmed Atlantic Salmon in the Broughton Archipelago, British Columbia, 2003–2004. *North American Journal of Fisheries Management*, 27(1): 187–197, 2007. ISSN 1548-8675. doi: 10.1577/M06-043.1. URL <http://onlinelibrary.wiley.com/doi/abs/10.1577/M06-043.1>. eprint: <https://afspubs.onlinelibrary.wiley.com/doi/pdf/10.1577/M06-043.1>.
- S. J. Peacock, M. Krkošek, S. Probošycz, C. Orr, and M. A. Lewis. Cessation of a salmon decline with control of parasites. *Ecological Applications*, 23(3): 606–620, 2013. Publisher: Wiley Online Library.
- W. E. Ricker. Stock and recruitment. *Journal of the Fisheries Board of Canada*, 11(5):559–623, 1954. Publisher: NRC Research Press Ottawa, Canada.
- R. C. Team. R: A language and environment for statistical computing 2022, 2022.