

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

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1 Executive Summary

- We investigated the relationship between parasitic sea lice on farmed and wild salmon in the Broughton Archipelago between 2001 and 2021, as well as the effects of these parasites on wild salmon returns
- We observed a positive relationship between the number of sea lice on salmon farms in the Knight Inlet-Tribune Corridor-Fife Sound (KTF) and the number of sea lice on wild juvenile salmon in these waterways
- We found a clear, negative association between sea louse infestation and survival of wild pink salmon at the population level
- Despite the recent decommissioning of two KTF salmon farms (Glacier and Burdwood), the predicted mortality due to sea lice on wild juvenile salmon was 15.2% for pink salmon returning in 2020, and 6.1% in 2021
- These continued elevated levels of mortality from sea lice may be due to the outsized infection pressures from Humphrey, Sargeaunt, and Doctor farms, and the fact that juvenile salmon are exposed to these farms early in their migration, when fish are smallest and most vulnerable to the effects of infestation
- Pursuant to the recommendations of the Steering Committee established by the Letter of Understanding between 'Namgis First Nation ('Namgis), Mamalilikulla First Nation (Mamalilikulla) and Kwikwastu'inuxw Haxwa'mis First Nation (KHFN) and the Province of British Columbia (Recommendations), and the tenure conditions of those farms, 'Namgis, Mamalilikulla and KHFN will decide if those farms will continue to operate beyond 2023 and 2024. Those decisions have not yet been made.
- While the link between sea louse infestation and population returns of wild pink salmon is clear, continued monitoring after the potential decommissioning of those farms would provide clarity on the lasting impact of farm removal in the Broughton
- Population-level analyses such as this one will be more difficult to perform moving forward due to the decline in monitoring of in-river salmon escapement by DFO

2 Supplemental Methods

2.1 Data Collection and Collation

2.1.1 Sea Lice on Farmed Salmon

Farm-level data on the abundance of sea lice and the number of domesticated 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 MOWI Canada West and Cermaq via the Broughton Archipelago Transition Initiative (BATI). The number of adult female lice in the Broughton Archipelago was then estimated by calculating the total sum of adult female lice on each farm (i.e. the number of adult female 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.?? Harrington et al. (2022)).

2.2 Sea Lice on Wild Juvenile Salmon

We used data describing sea-louse infestations on wild juvenile salmon in the Broughton Archipelago from the publicly available dataset from Salmon Coast Field Station's long-term monitoring program ([<https://github.com/salmoncoast/Sea-lice-database>]), 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 is described in detail in Peacock et al. (2016), but briefly, at three sampling sites in the Broughton Archipelago, 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 seasonal progression is a key predictor of sea-louse abundance and therefore an important variable in our models, we excluded three under-represented weeks (9, 28, and 33), which, across all years, accounted for less than 0.1% of our samples.

Through the years of this survey, due to slight differences in sampling protocols, there were variable numbers of copepodites and motiles that were identified to species (CITE TABLE). Chalimus-stage lice were also never identified to species due to the limitations of the live-lic ing method (Krkošek et al., 2005). We estimated the number of lice on wild juveniles by accounting for the number

of motile, chalimus, and copepodite lice separately (see scenario 1 below), using year-level predictions. To assess the sensitivity of our results to the assumptions implicit in Scenario 1, we contrasted it to 4 alternate scenarios, one using the same model but an individual-based prediction (Scenario 2), and the other three using different models (Scenarios 3-5). For each of these alternate scenarios, we re-ran the analysis and compared the values of the modelled effect of sea lice from salmon farms on juvenile pink salmon, c , described below, and compared the estimates of c between all scenarios here, plus the scenarios described further in this section.

Using these sea-louse data, we estimated the mean abundance of *L. salmonis* per wild juvenile salmon in each year as in Peacock et al. (2013). Briefly, we fit a generalized linear mixed-effects model (GLMM) to the sea-louse data described above, with year as a fixed effect and sample site (Fig. ??) and week-of-year as random effects. The model employed a negative-binomial error distribution, and was fit using the glmmTMB package ((Magnusson et al., 2017; Brooks et al., 2017))

2.2.1 Scenario 1 - *L. salmonis* Only, Year-level Predictions

The first scenario was the one used in the analysis presented in the main report. 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.

For 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. S1) and motile (Fig. S2) data.

We calculated the mean proportion of *L. salmonis* in a given year/stage and applied that to all individual observations via random a random draw from a Bernoulli distribution, with a weighted 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 more than one unidentified adult louse, this draw was repeated for each individual louse. This is more biologically realistic than ascribing 0.639 lice to a fish.

We then estimated the number of *L. salmonis* chalimus-stage 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.

2.2.1.1 Scenario 2 - *L. salmonis* Only, Individual-level Predictions

Scenario 1 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 the total number of lice. 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 therefore decided to test this assumption using Scenario 2.

Scenario 2 was done in the same manner as Scenario 1, except that for each fish that did not have speciated motiles or copepodites, we model-predicted a single proportion value of *L. salmonis* from our fit models, using the number of total 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 more than one unidentified adult louse, this draw was repeated for each individual louse.

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. S3).

2.2.3 Scenario 3 - 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. S3).

The reason we did not use this method for our main analysis, and instead used Scenario 1, is while this is still a valid method for predicting the proportion of *L. salmonis* at high values, the model structure forces an intercept of the regression line through the origin, which is not necessarily as robust of an assumption to make, as opposed to choosing a model structure that can use a Maximum Likelihood Estimation to find the intercept.

2.2.4 Scenario 4 - Beta-regression

One problem with the approach employed in Scenario 3, is that the model is forced to pass through the zero intercept (see Figure S3). To compare the Scenario 3 approach to a version of that model that does not force an intercept at the origin, we fit a beta-regression to the yearly average number of lice on wild juvenile fish, 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 Figure , and corroborates the Scenario 3 in that it predicts a value of 1.0 for the *L. salmonis* proportion in 2001. This is a useful confirmation with a slightly more realistic model, and it 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.

2.2.5 Scenario 5 - All lice estimate

Since both lice species are associated with negative effects on 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. 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 (NuSEDS - 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

We followed the same general procedure for estimating recruitment as Peacock et al. (2013). These recruitment estimates (i.e., the offspring from a given cohort of spawners that would have survived to spawn in the absence of commercial fisheries) drew on additional exploitation data for Area 12 (Van Will, unpublished data) and Areas 7-10 (English et al., 2018).

We estimate escapement 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.

The one deviation to the methods used by Peacock et al. (2013) for estimating recruitment was that we included populations in the main analysis which had three or more spawner-recruit (S-R) pairs (i.e., years of data), rather than those with at least 20 pairs. This approach is consistent with recent work not related to sea lice (e.g., Connors et al. (2010); Wilson et al. (2022)). We compared our approach to that of Peacock et al. (2013) by re-running the analysis with a cut-off of 20 pairs to see whether this assumption influences the estimated effect of sea lice. The final data set used in the primary analysis presented in the main report (i.e., $\zeta = 3$ S-R pairs), included 78 rivers and 2,744 S-R pairs across 149 populations (even- and odd-years considered as separate populations). The final dataset for the alternate approach (i.e., $\zeta = 20$ S-R pairs) included 41 rivers and 1,855 S-R 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 (Price et al., 2017) (Figs. S5, S6)

2.4 Relationship Between Farm Lice & Wild Juvenile Lice

We compared the annual estimates of sea-louse abundance on wild juveniles to the annual number of lice on salmon farms in the region. To do this, we compared three different groupings of salmon 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 the farms in the Knight-Tribune Fife Sound corridor (KTC) (Fig. ??), and c) the number of lice on three focal farms - Humphrey, Sargeant, and Doctors. We assess three different farm groupings because 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 wile juvenile salmon from farms may differ, making it challenging to know which farms are major sources of sea lice for wild juvenile salmon. This analysis was done using the glmmTMB package (Magnusson et al., 2017; Brooks et al., 2017).

A preliminary regression analysis revealed that the number of lice on both a) all farms, and b) KTC farms explained the number of lice on wild lice well (Fig. S7) across all scenarios. Given that the KTC grouping has an almost equivalent R^2 value to the "all farms" grouping across all scenarios and it represents a more biologically relevant selection of farms (as the juvenile salmon sampling sites are within the KTC corridor), we chose to use the KTC grouping farms moving forward, as in Peacock et al. (2013).

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. Here, $W_{a,t-1}$ is the number of sea lice in each area a in time $t-1$. As in Peacock et al. (2013), we assume the number of lice in areas 7-10 to be zero since sea-louse abundances on juvenile salmon on the Central Coast are extremely low in the absence of salmon farms (Gottesfeld et al., 2009). The mean abundance of lice per juvenile salmon per year in area 12 was estimated from the GLMM described previously. The term $cW_{a,t-1}$ is the modelled effect of sea lice from salmon farms on the juvenile pink salmon. The estimated percent mortality of pink salmon due to sea lice on wild juvenile salmon is therefore $1 - \exp(-cW_{a,t-1})$ (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 are equivalent to zero prior to 1991.

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 θ_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 et al. (2013), we fit the Ricker model in a linear form

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

in the lme4 package. 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 calculate the predicted % mortality in years beyond the S-R dataset (i.e., return years 2017-2021), 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

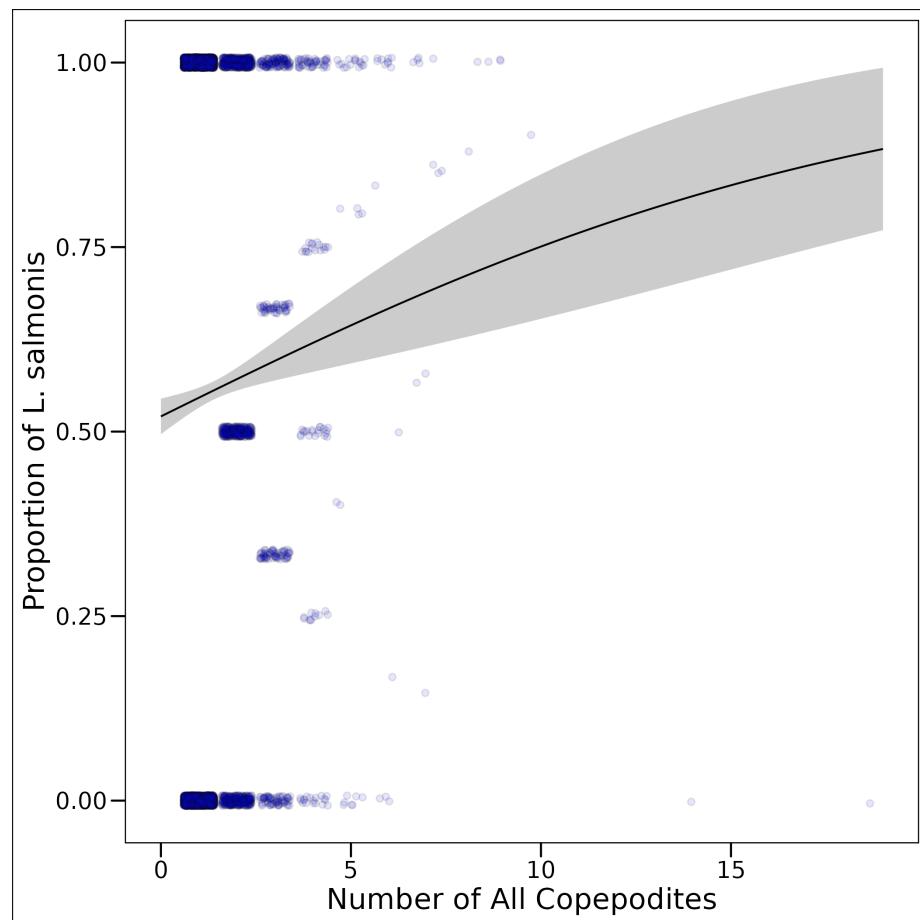


Fig. S1: Proportion of *L. salmonis* copepodite lice over increasing total number (*L. salmonis* and *C. clemensi*) of copepodite lice of per fish.

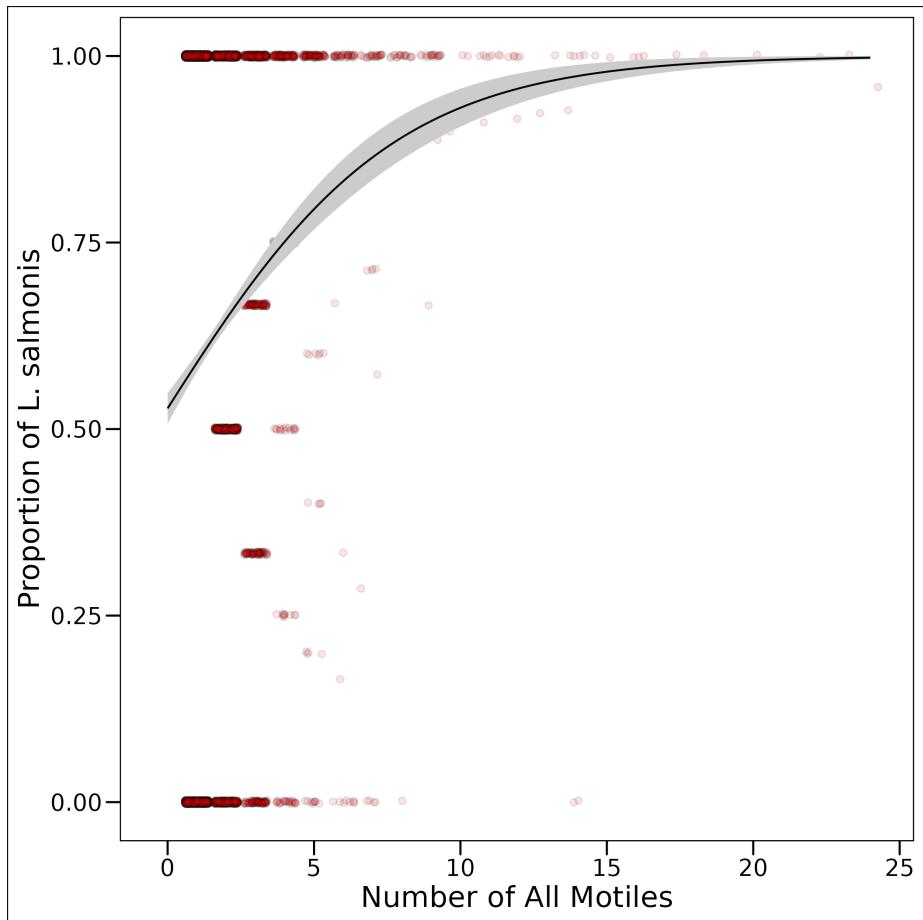


Fig. S2: Proportion of *L. salmonis* motile lice over increasing total number (*L. salmonis* and *C. clemensi*) of motile lice of per fish.

Year	Stage & Species ID							
	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 S1: 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.

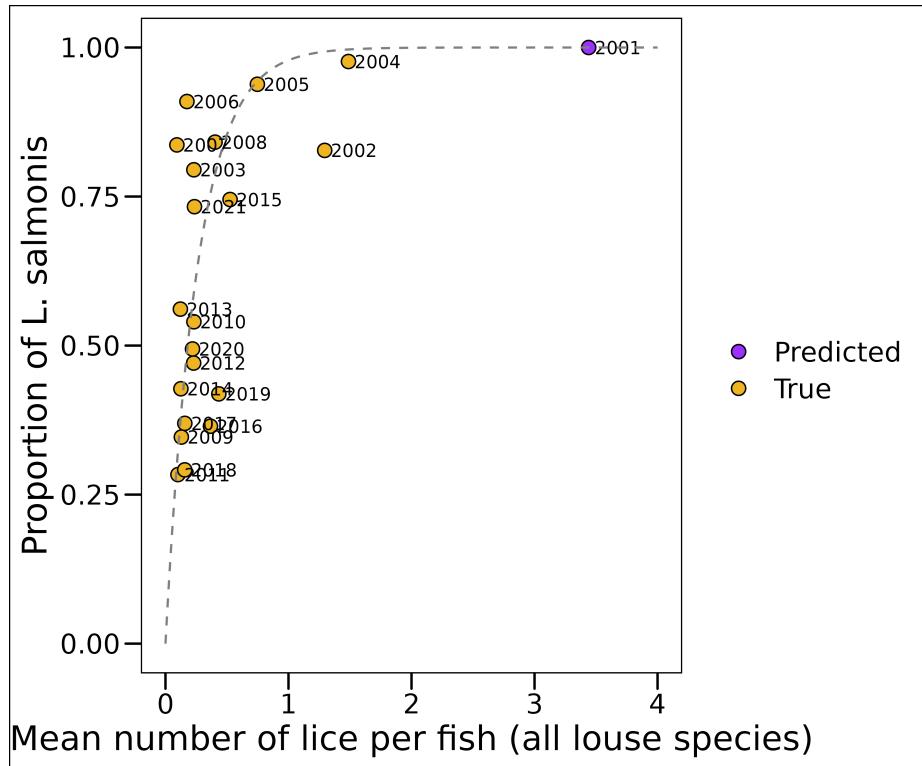


Fig. S3: Proportion of *L. salmonis* lice over increasing total number (*L. salmonis* and *C. clemensi*) of lice of per fish. Yellow points represent data, the purple point represents a predicted value.

Proportion Estimates		
Year	<i>L. copepodite</i>	<i>L. motile</i>
2001	Predicted	Predicted
2002-2004	Predicted	Empirical
2005-present	Empirical	Empirical

Table S2: Different year/stage combinations were given by either an empirical proportion or a model-predicted proportion.

Model	AIC	Neg. Log-Likelihood	ΔAIC
Alternative Model	11575.6	-5633.8	0
Null Model	11588.8	-5641.4	13.2

Table S3: Model comparison for null model and alternative model assessing if including a term for lice infestation improved fit of model of survival.

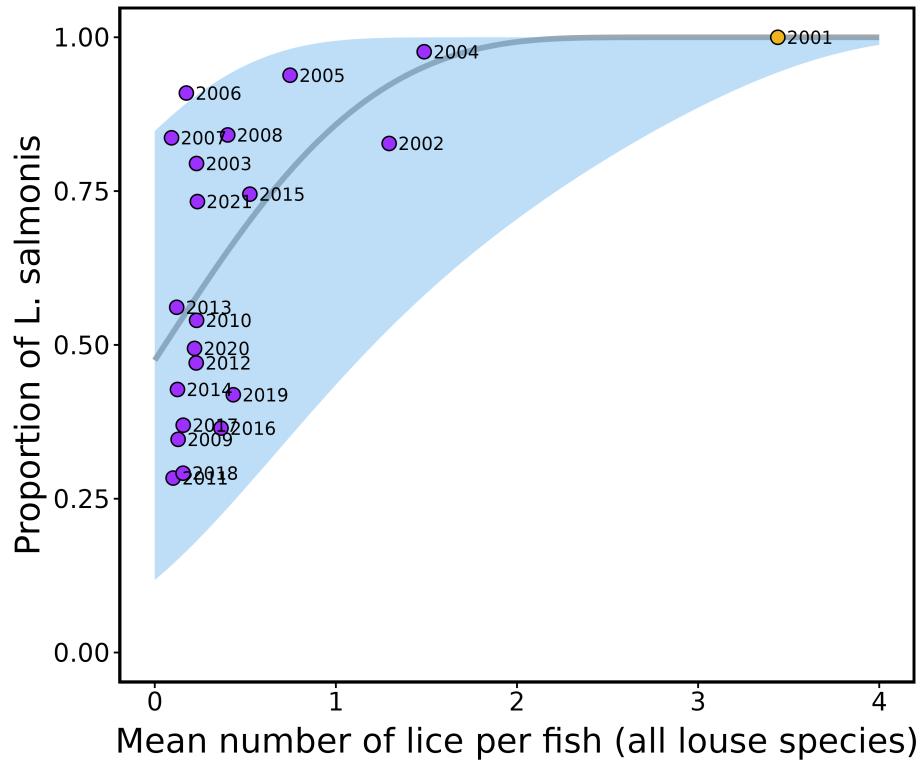


Fig. S4: Proportion of *L. salmonis* lice over increasing total number (*L. salmonis* and *C. clemensi*) of lice of per fish. The grey line indicates the model predicted values, and the blue envelope denotes the 95% confidence interval. Purple points denote data points, and the yellow point represents a predicted value.

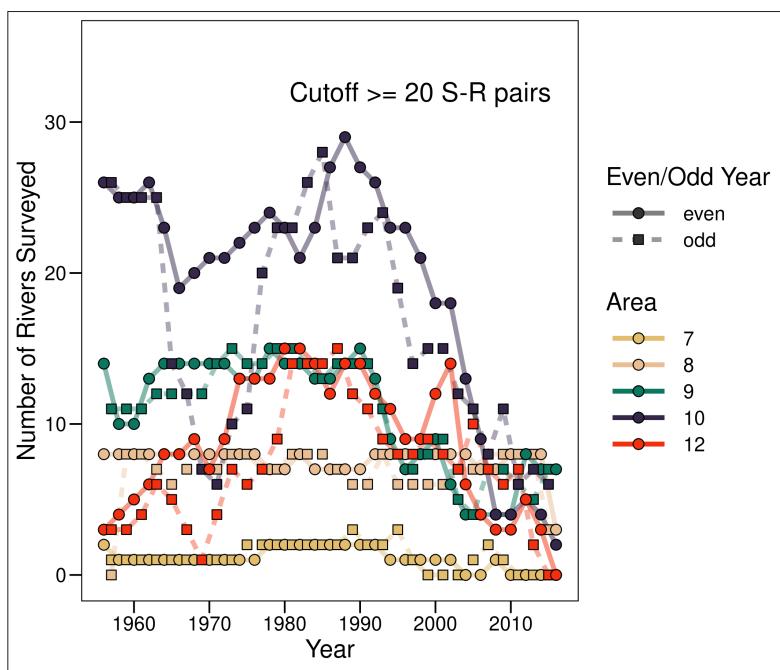


Fig. S5: Number of rivers in each year and each area that were surveyed by DFO to enumerate the number of spawners. Here the cutoff to define the number of spawner-recruit pairs to include a population is 3 pairs.

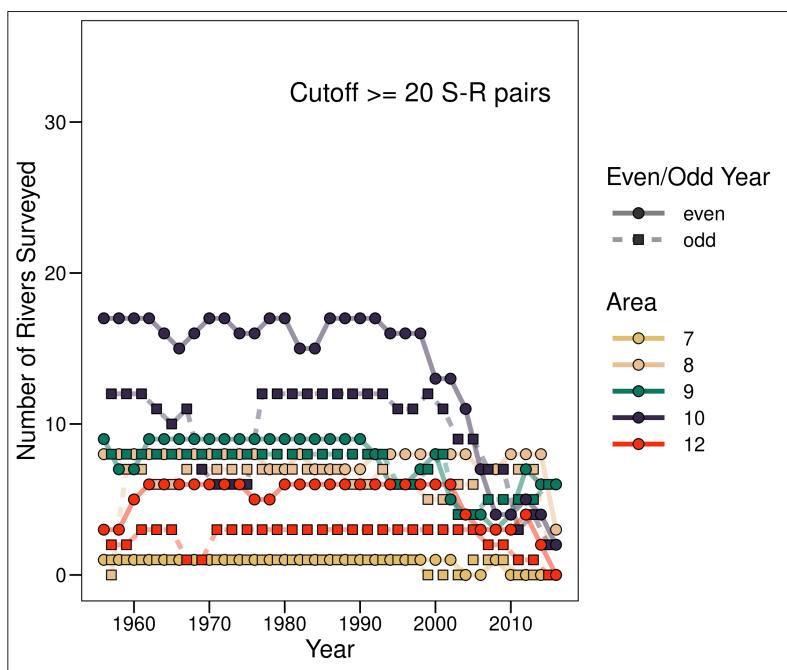


Fig. S6: Number of rivers in each year and each area that were surveyed by DFO to enumerate the number of spawners. Here the cutoff to define the number of spawner-recruit pairs to include a population is 20 pairs.

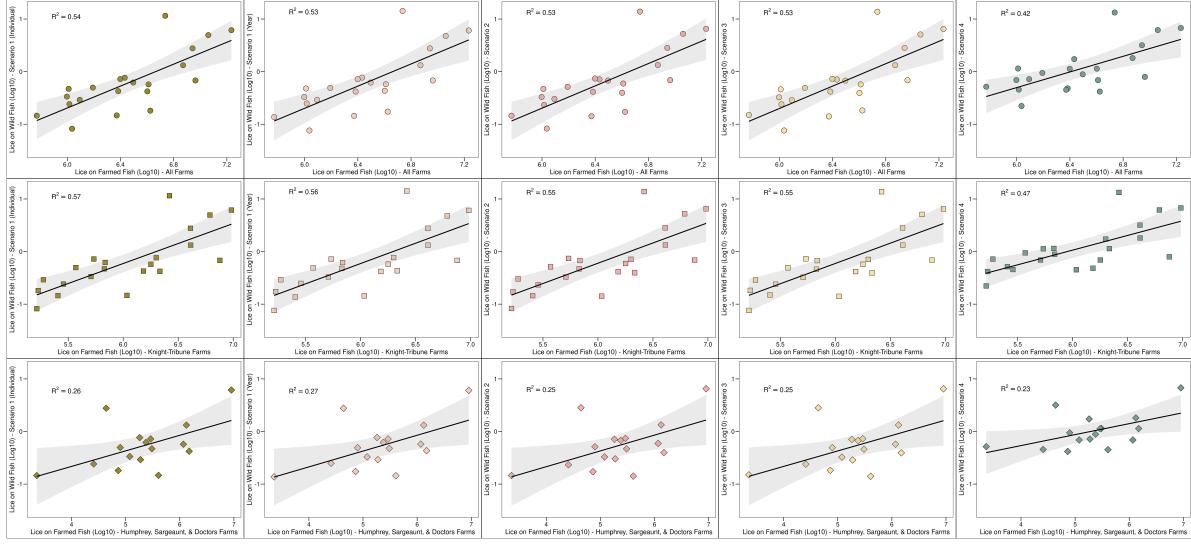


Fig. S7: A comparison of the relationship between the number of lice on wild salmon (on a \log_{10} scale), and the number of lice on the three sets of farm comparisons (also a \log_{10} scale). Here the comparison is across all 5 scenarios, and both the options for minimum population counts.

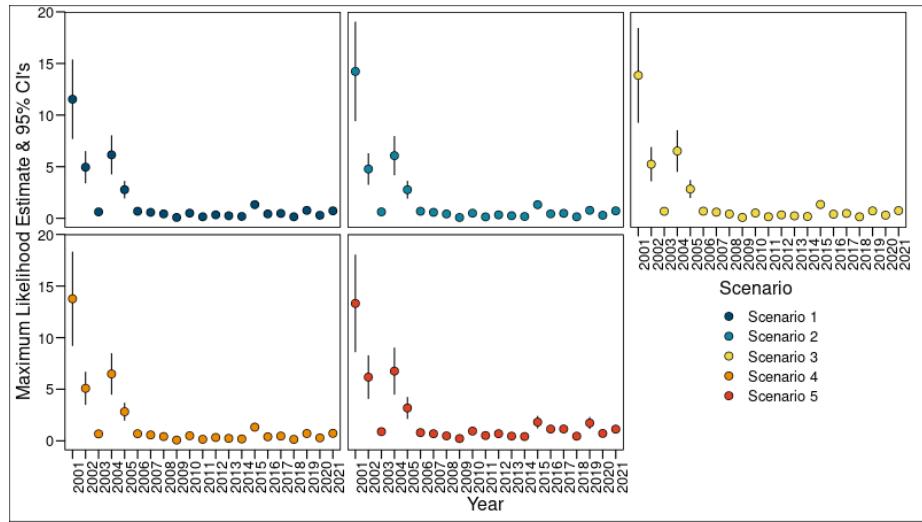


Fig. S8: Estimated number of lice per wild juvenile pink salmon in all available years. The points represent the estimated value, with the error bars giving a 95% confidence interval.

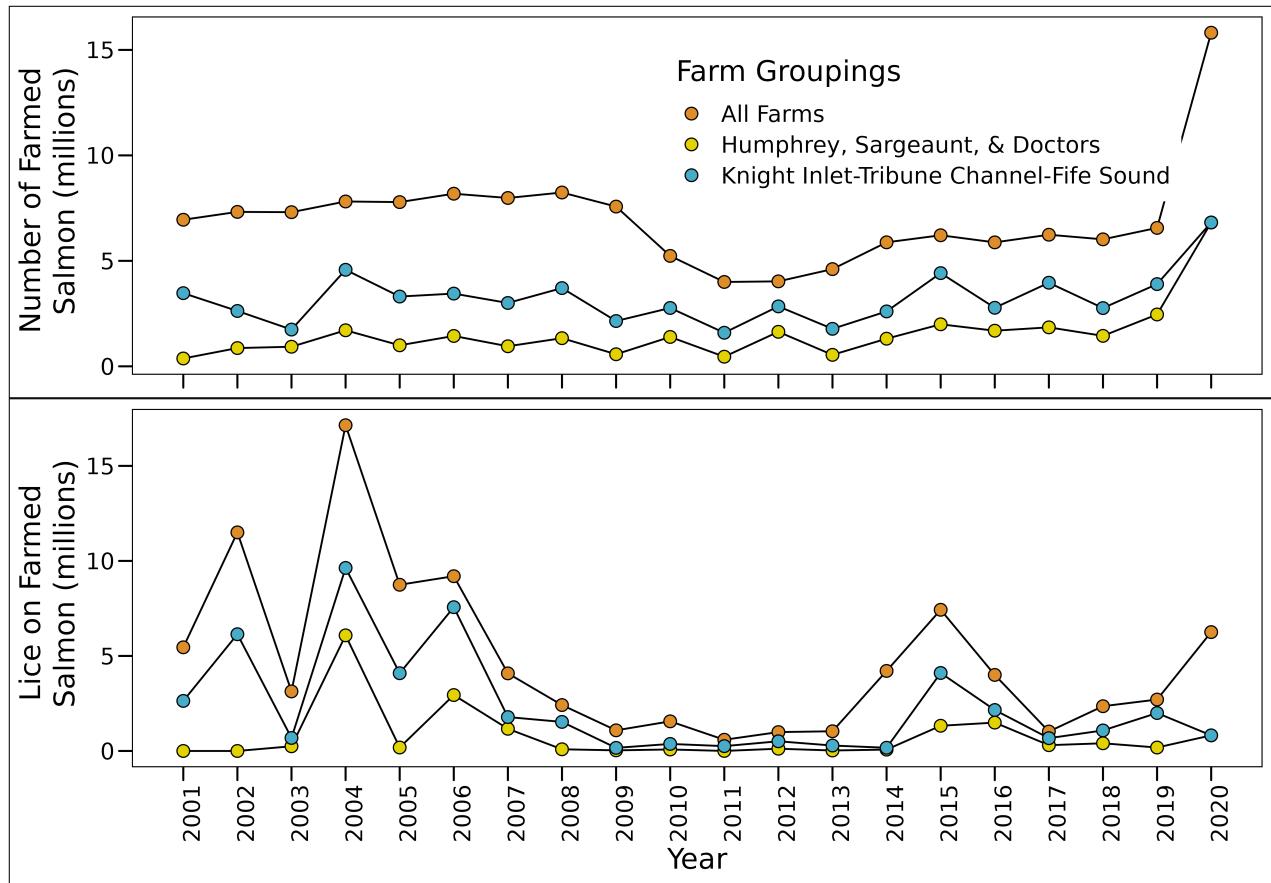


Fig. S9: Total number of salmon and lice on those salmon across farms. Values are given as sums across all farms in each category, and averaged between March & April, the only two months that were relevant to the present analysis. Farms are divided into Knight-Tribune Corridor (KTF) farms, non-KTF farms, and the sum of those two values - "All".

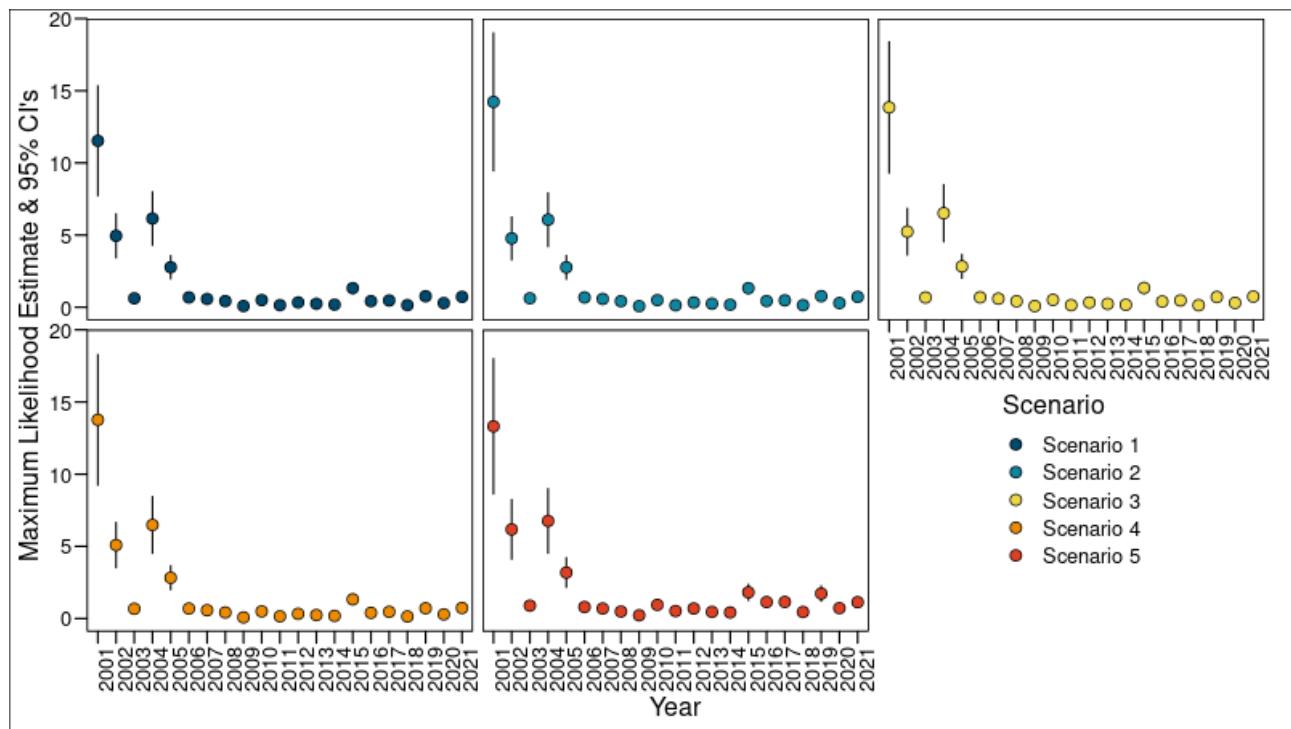


Fig. S10: Comparison between scenarios of log-log regressions between the number of lice on wild fish and farmed fish.

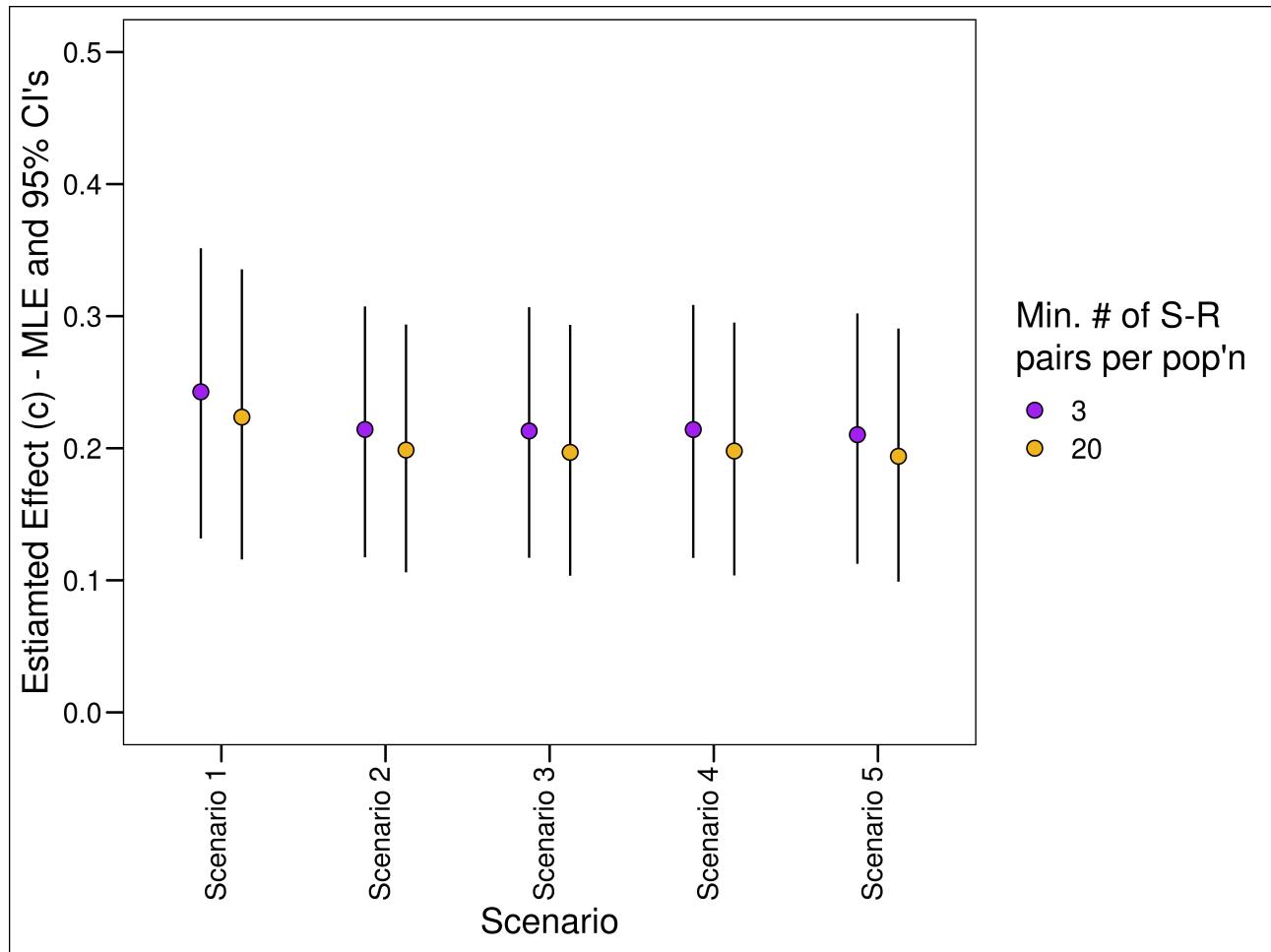


Fig. S11: Comparison of the estimates of c across all five scenarios and the two assumptions of pairs. Note that while the values for scenarios 2-5 look to be identical, they are not identical (see Table S2)

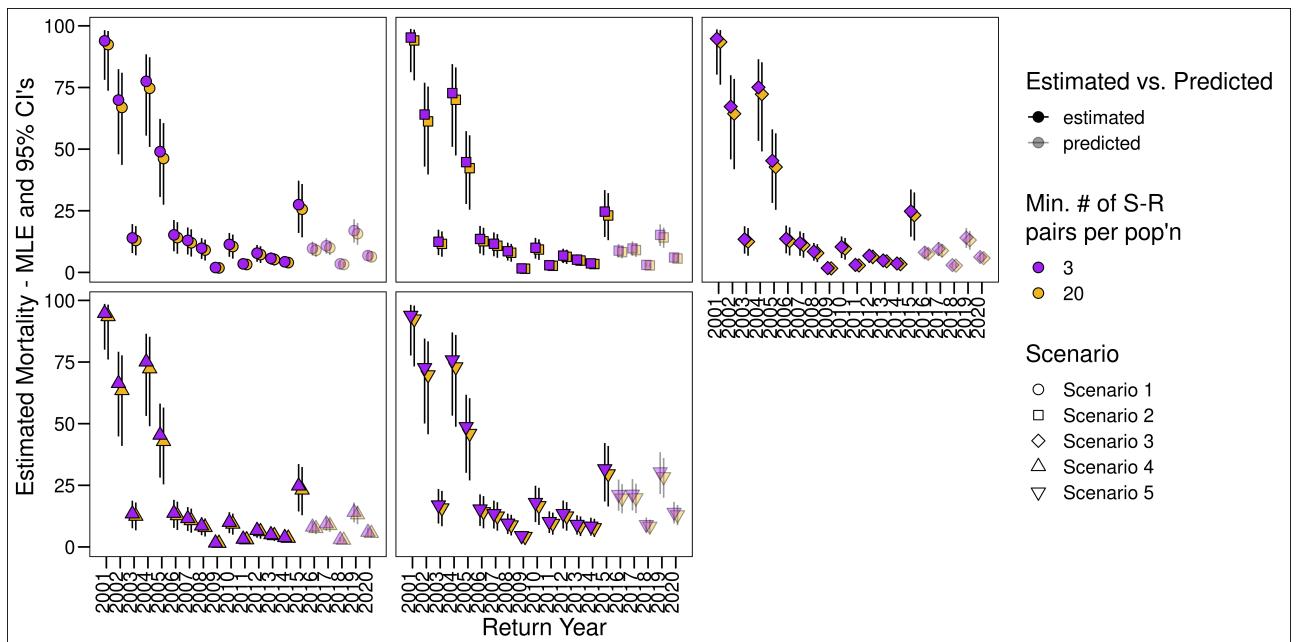


Fig. S12: Estimated and predicted percentage of the mortality in a given outmigration year, due to sea lice infestations of juvenile salmon $1 - \exp(-cW_{a,t-1})$. The points for the estimated values represent maximum likelihood estimates, and the error bars are 95% confidence intervals. The error bars on the predicted values are not *true* 95% CI's, but are a best-estimate of those bounds.

References

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