



## Original Article

# Salmon lice infestations on sea trout predicts infestations on migrating salmon post-smolts

Knut Wiik Vollset,<sup>1,\*</sup> Elina Halttunen,<sup>2</sup> Bengt Finstad,<sup>3</sup> Ørjan Karlsen,<sup>2</sup> Pål Arne Bjørn<sup>2</sup> and Ian Dohoo<sup>4</sup>

<sup>1</sup>Uni Research, LFI - Freshwater Biology, Nygårdsporten 112, 5006 Bergen, Norway

<sup>2</sup>Institute of Marine Research, PO Box 6404, NO-9294 Tromsø, Norway

<sup>3</sup>Norwegian Institute for Nature Research, PO Box 5685 Sluppen, N-7485 Trondheim, Norway

<sup>4</sup>University of Prince Edward Island, Charlottetown, Canada

\*Corresponding author: tel: +4755584723; e-mail: [knut.vollset@uni.no](mailto:knut.vollset@uni.no).

Vollset, K. W., Halttunen, E., Finstad, B., Karlsen, Ø., Bjørn, P. A., and Dohoo, I. Salmon lice infestations on sea trout predicts infestations on migrating salmon post-smolts. – ICES Journal of Marine Science, 74: 2354–2363.

Received 9 February 2017; revised 18 April 2017; accepted 30 April 2017; advance access publication 1 June 2017.

Impacts of sea lice (*Lepeophtheirus salmonis* or *Caligus spp.*) on wild salmonids is currently one of the most important issues facing management of fish farms in salmon producing countries in the northern hemisphere. Surveillance of sea lice on wild Atlantic salmon (*Salmo salar*) is often hampered by the ability to catch enough migrating post-smolts. Therefore, sea lice abundance on anadromous trout (*Salmo trutta*) is often used to infer sea lice abundance on migrating salmon post-smolt. However, the assumption that there is a relationship between the abundance of lice on salmon and trout has never been tested. Here we use a dataset of sea lice on salmon post-smolt and sea trout that have been caught simultaneously in trawl hauls, to evaluate the correlation in abundance of sea lice between the two species using various statistical models. We demonstrate that trout generally has higher abundances of sea lice than salmon. Average lice per gram fish on sea trout (log transformed) predicted the abundance of lice on salmon best. Negative binomial models of lice counts were preferable to using trout lice counts as direct estimates of salmon lice abundance, and they had better predictive ability than logit models of high (vs. low) lice counts. Including the size of the salmon increased the predictive ability of the model, but these data are not generally available. The effect of salmon weight may have been a direct effect of body size, or an indirect effect of time spent in marine waters. Finally, we predict lower salmon lice counts on migrating salmon with our selected binomial model than with the current method of using trout lice counts as a direct estimator on salmon lice counts, and demonstrate that management advice would change considerably depending on the chosen method.

**Keywords:** aquaculture, conservation, fish farming, *Lepeophtheirus salmonis*, management, parasite, salmonids, salmon lice, *Salmo salar*.

## Introduction

The impact of sea lice (here referring to *Lepeophtheirus salmonis* and *Caligus spp.*) on wild salmon stocks are currently one of the most controversial topics in the debate surrounding the marine survival and conservation of salmon species. Sea louse (or salmon louse when only referring to the most prevalent lice on salmonids, *L. salmonis*) is an ecto-parasite that attaches to the surface of the skin of salmonids and creates lesions which causes osmoregulatory stress for the host (Grimnes and Jakobsen, 1996; Finstad *et al.*, 2000; Wagner *et al.*, 2008). This can lead to secondary

infections (Wells *et al.*, 2007), higher risk of predation mortality (Godwin *et al.*, 2015; Peacock *et al.*, 2015), or in conditions of high infection levels, death (Birkeland, 1996; Grimnes *et al.*, 1996; Bjoern and Finstad, 1997, 1998; Finstad and Grimnes, 1997; Finstad *et al.*, 2000). The reason for the controversy related to the interaction between lice and salmon is that salmon farms have been identified as an important source of infestations on wild fish (Bjorn *et al.*, 2011; Serra-Llinares *et al.*, 2014, 2016). This can lead to unnaturally high levels of lice, and affect the seasonal timing of infestations (Krkosek *et al.*, 2006; Vollset and Barlaup, 2014) and

disrupt the natural migratory allopatry of adult and young fish which helps protect young fish from infestations (Krkosek *et al.*, 2006). Moreover, several studies have demonstrated that lice can lead to reduction of returning adult spawners (Krkosek *et al.*, 2013; Skilbrei *et al.*, 2013; Vollset *et al.*, 2015), although the magnitude of this impact on population levels has been debated (Jackson *et al.*, 2014; Krkošek *et al.*, 2014). In addition, sub-lethal effects of salmon lice such as reduced growth and increased age at return have also been demonstrated (Skilbrei *et al.*, 2013; Vollset *et al.*, 2014). For this reason Norwegian salmon farms are obliged to adhere to strict national regulations, not exceeding a certain number of female or mobile lice and in some regions conduct co-ordinated delousing to keep infestation pressure on migrating wild post-smolts to a minimum (Torrissen *et al.*, 2013).

To monitor infestation levels of lice, wild fish are caught using trawling with specialized equipment (FISH-LIFT, Holst and McDonald, 2000), trap nets (Barlaup *et al.*, 2013), seine nets or gill-nets (Bjorn *et al.*, 2011). These levels can then be compared with threshold levels of lice which are believed to be physiological harmful or lethal based on laboratory studies, modelling studies or expert opinions (or a combination of the three) (Taranger *et al.*, 2015). In the case of Atlantic salmon (*Salmo salar*), which in the Atlantic is the species with the highest cultural, recreational and commercial interest, direct sampling of migratory young salmon is difficult, costly and time consuming. Most efficient is the use of pelagic trawls using specialized equipment (FISH-LIFT, Holst and McDonald, 2000). However, even though salmon post-smolts are caught most years, most of the trawls are often done over only a few days, usually whenever the boat happens to encounter an aggregation of migrating post-smolts (Finstad *et al.*, 2000). Consequently, these samples are usually lumped together in time and space and thus are not representative of the entire smolt-run. In addition, due to cost and time, trawling data are only available from a select few fjords, and in some years catches are very small or absent. Sea trout, on the other hand, are easily catchable most likely because they have different marine behavior compared with Atlantic salmon. In contrast to salmon, who swim relatively fast off-shore, sea trout stay close to the coast throughout their marine sojourn where they are easily catchable using low cost methods such as gill nets or trap nets (Thorstad *et al.*, 2016). The availability of sea trout and the lack of good data from migratory salmon post-smolts, has forced management to utilize salmon lice levels on sea trout as a proxy indicator for infestation levels of salmon. For example, Taranger *et al.* (2015) suggested a method of estimating percent likelihood of survival for salmon based on lice levels on sea trout during the time of migration of salmon post-smolt. However, to date no data has been presented that can test if this relationship is valid. To test the assumption that lice levels of sea trout reflect the lice levels on salmon we collected trawl data where salmon and sea trout has been caught simultaneously and attempted to correlate different parasite measurement across the two species. Thus, this is the first attempt to validate the assumption that sea trout can be used as a proxy indicator for parasite load on Atlantic salmon post-smolts.

## Material and methods

### Sampling

The Institute of Marine Research (IMR) and the Norwegian Institute for Nature Research are, to the best of our knowledge, the only two institutions that have conducted trawling for post-smolts in Norway. All available data were obtained from these

two institutions and it was evident that both trawling methods and data recording had changed over time. However, trawling was performed every year when wild salmon post-smolts migrate from the rivers to the sea during weeks 18–28 in years 1998–2015. A specially designed FISH-LIFT trawl (Holst and McDonald, 2000) was used for sampling in order to avoid loss of both scales and lice on the caught fish. FISH-LIFT sorts the fish into a closed aquarium, connected to the trawl cod-end, such that it allows large numbers of fish to continue to swim unharmed in the aquarium once caught. The ca. 15 m long trawl was deployed once or twice per day with speeds of ca. 3 knots ~4 h at a time, for distances of 6–20 nautical miles. The trawled stretch varied according to the weather, currents and the amount of by-catch. In order to sample fish which represented the accumulated infestation over the whole fjord migration route, the trawling was concentrated in the outer parts of the sampled fjords, as close as possible to the shore line.

The fish were transferred from the floating aquarium to a basin on board the research vessel, retrieved rapidly with a small hand held net, put into individual plastic bags, and euthanized with a blow to the head. The lice on the fish were counted either immediately, or frozen and counted later in the lab. The fish were handled with utmost care to avoid loss of scales and lice. However, apparent scale loss or other injuries were noted along with other individual characteristics (species, length and weight) during lice counting. Stages of salmon lice were distinguished to the stages copepodites, chalimus, preadult, adult male and adult female. The results are reported yearly by IMR (Svåsand *et al.*, 2015; Nilsen *et al.*, 2016).

### Data selection criteria for analysis

The original data file contained records from the years 1998 to 2015 in nine regions (Hardangerfjorden, Trondheimsfjorden, Namsenfjorden, Osterfjorden, Sognefjorden, Frohavet, Nordfjorden, Altafjorden, Malangen). In some of these regions trawling was not done consistently in the same geographic location and the definition of a region is therefore somewhat ambiguous. In the data from the later periods, the exact geographic track of the trawls was available, in others, only the start and stop location and time was available. In addition, in some cases the exact location of the trawling was not possible to identify in the old data. For simplicity and due to relatively few data points we have decided to broadly categorize the trawl hauls into “fjords” where the trawling had taken place. Furthermore, while the catches of trawls consisted of several trawl hauls, we decided to pool data within a week in a year in order to get sufficient fish number at each data points. As a result, the data were pooled into “groups” which consisted of all fish caught in 1 week within a given fjord and our research objective was to compare lice counts from trout and salmon within the same group.

Reviewing the original data it was also clear that trout catch data were in many cases missing. Personnel involved in trawling indicated that there had been some inconsistency in whether or not trout had been kept for lice counting. This was especially evident in the older data, where no data on trout existed. After excluding groups without trout or salmon counts, the remaining dataset contained data from weeks 18–28 in years 2004–2015 in six fjords (Hardangerfjorden, Trondheimsfjorden, Namsenfjorden, Nordfjorden, Osterfjorden, Sognefjorden). In all these data trawling had been conducted in the outer part of the fjord.

Salmon louse, which is an external parasite, can for various reasons be scraped off during trawling or handling. To avoid using individuals with high loss of salmon lice we excluded individuals that had a documented scale loss of >50% ( $n = 122$ ). Furthermore, in some instances only total lice were recorded (not divided into attached and mobile), or weight and length of the fish was not recorded. These cases were all excluded ( $n = 254$ ). Another 15 trout that were very large >750 g were also excluded. The final dataset contained 99 groups from 6 fjords over a period of 12 years (2004–2015) with a total of 2762 individuals (2474 salmon and 288 trout).

For statistical reasons, our final exclusion criterion was that each group should contain at least three specimens from each species. This final criterion reduced the dataset to 316 salmon and 228 trout, and the number of fjords was reduced to 4 (Hardangerfjorden, Trondheimsfjorden, Sognefjorden and Namsenfjorden) over a period of 10 years.

### Data analysis

Descriptive statistics were computed and quantile plots used to compare the distributions of trout and salmon lice counts. A scatterplot of group mean counts (salmon vs. trout) was used to explore the unconditional relationship in the final dataset.

In general, our goal was to attempt to predict the number of lice on individual salmon post-smolt based on the average number of lice on trout in that group. To correct for the fact that different groups had very different number of trout records (meaning the predictor was measured with highly variable precision), each data point was weighted according to the number of trout records in the group.

Three types of statistical models were fitted to the data; (i) negative-binomial, (ii) logistic, and (iii) linear. In all models, a random effect for group (i.e. each week/fjord/year combination) was included to account for the lack of independence among lice counts on salmon.

In the negative-binomial models the *number of lice per salmon* was the response variable. Predictors evaluated are described below. To evaluate the predictive ability of the negative binomial model, correlations between observed and predicted salmon lice counts were computed and scatterplots created. Diagnostics plots were used to evaluate the normality and homoscedasticity of the random effects and residuals were examined for extreme values.

The logistic model was used to estimate the *odds that a salmon had a lice count above 0.1 lice/g*. This threshold was chosen because it is believed to be the threshold where salmon post-smolts first experience physiological impacts from salmon lice, once the lice develops into mobile stages (Wagner *et al.*, 2008). In practical terms, this would mean 2 lice on 20 g salmon post-smolt, or 5 lice on a 50 g salmon post-smolt. To present the predictive ability of the logistic model, sensitivity (Se) and specificity (Sp) were calculated for the raw data and for the best fitting model along a range of cut-points. Model diagnostics were similar to those for the negative binomial model.

In the linear model we attempted to predict *the lice per gram for salmon post-smolt*. However, these models were discarded for a couple of reasons. It was not possible to appropriately weight the trout data in the multilevel linear model, and the assumption of normality of residuals at all levels was not well met, so no further results from these models are presented.

In total seven competing models with different predictors were used to predict the lice levels of salmon. These included:

~average total lice per trout  
 ~log (average total lice per trout)  
 ~log (average (total lice per trout/trout weight))  
 ~log (average (total lice per trout/trout weight)) + salmon weight  
 ~log (average attached lice per trout)  
 ~log (average (attached lice per trout/trout weight))  
 ~log (average (attached lice per trout/trout weight)) + salmon weight

Given that the predictors were all continuous, the linearity of the relationships between each predictor and the relevant outcome was evaluated using lowess smoothed curves and by adding quadratic terms to the models. For the negative binomial models, results from models in which the trout lice counts were included as linear and quadratic functions are presented.

Finally, we also modelled *attached lice* on salmon post-smolt, replicating all models that were built for the total lice counts on salmon post-smolt. However, these results were almost identical to the results using total lice. The reason for this was that total and attached lice counts were very highly correlated ( $\rho = 0.976$ ). Consequently, the results from the modelling exercise using attached lice are not presented here.

Estimates of model fit (Akaike information criterion; AIC and  $r^2$ ) may not reliably reflect the predictive ability of the model because the estimates were based on the same data used to build the model. In order to validate the model a cross-validation procedure of the best fitting model was carried out as follows. The selected model (M3) was fit using data from 20 of the 21 groups and this model was then used to predict values in the one group omitted. The procedure was repeated until predicted lice counts were obtained for all groups in the dataset. The correlation between these values and the observed mean salmon lice counts was computed.

### Implications for management advice

In Norway, sea trout captured in trap-nets are used to predict population level effects in both salmon and trout populations through a simple multinomial relationship between lice per gram fish and likelihood of mortality (in percent) due to the lice infestation (Sväsand *et al.*, 2015; Taranger *et al.*, 2015). In epidemiology, this percent mortality is referred to as the attributable fraction (i.e. the reduction in the probability of survival given that the individual does not die from another cause). Samples of trout that are assumed to represent salmon post-smolt (mostly taken in trap-nets or gill nets) are taken during the period of time when salmon are thought to be migrating.

For salmon, only lice counts from trout under 150 g are used. These counts are divided into four categories based on number of lice/gram fish weight (0–0.1, 0.1–0.2, 0.2–0.3, >0.3) that are assumed to be related to probabilities of mortality of 0, 20, 50, and 100%, respectively. A weighted average mortality for the entire sample is then calculated. These overall estimates (deemed “population level effects”) are further categorized according to assumed sustainability (0–10% green, 10–30% yellow, >30% red) (Taranger *et al.*, 2012).

In contrast, our approach attempts to use *the average number of lice on trout* as a predictor of number of lice on salmon post-smolt, instead of using the trout counts directly as a predictor of

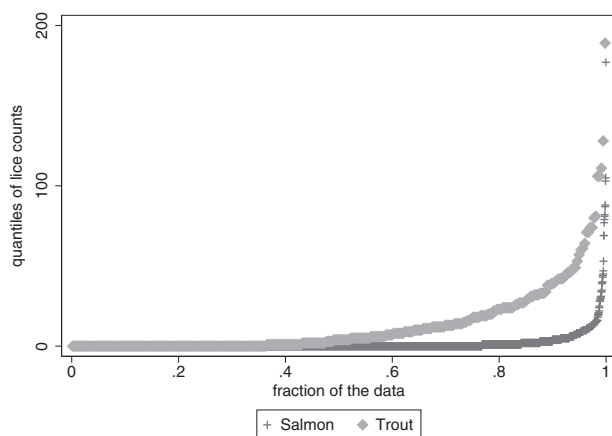
lice on salmon. To illustrate what effect our approach would have on management advice, we used an independent dataset of trout collected with a trap net in 2009–2015 in the Herdlefjorden outside Bergen (<https://doi.pangaea.de/10.1594/PANGAEA.873663>) to calculate the “population level effects” as calculated in the management system (see above). The sampling area was the outer fjords of the Osterfjord, where several salmon populations migrate past, and it is believed that this is the region where migrating salmon mainly encounters salmon lice (Vollset *et al.*, 2016). The estimated “population level effects” derived directly from trout lice counts was compared with those based on predicted salmon lice counts derived from our best-fitting negative binomial model.

## Results

In the original dataset (numbers of salmon and trout, from nine regions over a 17-year period) most fish had zero lice and the two species had comparable maximum lice counts (salmon max = 177, trout max = 189). However, the trout had clearly fewer zeroes and overall higher lice counts (Figure 1). This finding corresponds to earlier observations that sea trout generally have higher levels of lice than salmon (Nilsen *et al.* 2016). The max lice counts in the subset of data used in the analysis (316 salmon and 228 trout from four fjords over a 10-year period) were somewhat lower (salmon max = 104, trout max = 106). Figure 2 presents the quantile plot comparison of all the remaining study groups. Figure 3 presents a scatter plot of the group average lice counts of salmon vs. trout.

### Negative binomial models

The predictors, AIC and  $r^2$  for the seven models are presented in Table 1. The table also includes the results from models with quadratic terms for the various measures of lice count, as these rendered a slightly lower AIC and (in most cases a slightly higher  $r^2$ ). The main results can be summarized as follows; (i) log transforming the counts on trout clearly increased the model fit, (ii) using lice per gram trout was a better predictor than using only counts of lice as a predictor, (iii) correcting for the size of the salmon increased the predictive ability of the model, and (iv) using attached lice per trout instead of total lice (M5–M7) gave a better prediction before correcting for size of the trout but a poorer



**Figure 1.** Quantile plot of all salmon and trout lice counts in original dataset. Data from 2474 salmon and 288 trout in 98 groups.

prediction when correcting for size of the trout. The correlation coefficient ( $r^2$ ) between observed and fitted values for the best model (M4) was 0.72 for the linear model and 0.74 for the model including the quadratic term.

In the preceding models, fjord was included as a random effect. To explore the role of fjord on the predictive outcome, we added fjord as fixed effects. This had little impact on the parameters. Likewise, we explored the effect of between-year variation by adding year as a fixed effect. This strongly reduced the between group variance as there were 10 years and only 21 groups (fjord/week/year combinations). Fortunately, it had very little effect on the parameter estimates, and we are therefore relatively confident that our estimates are robust.

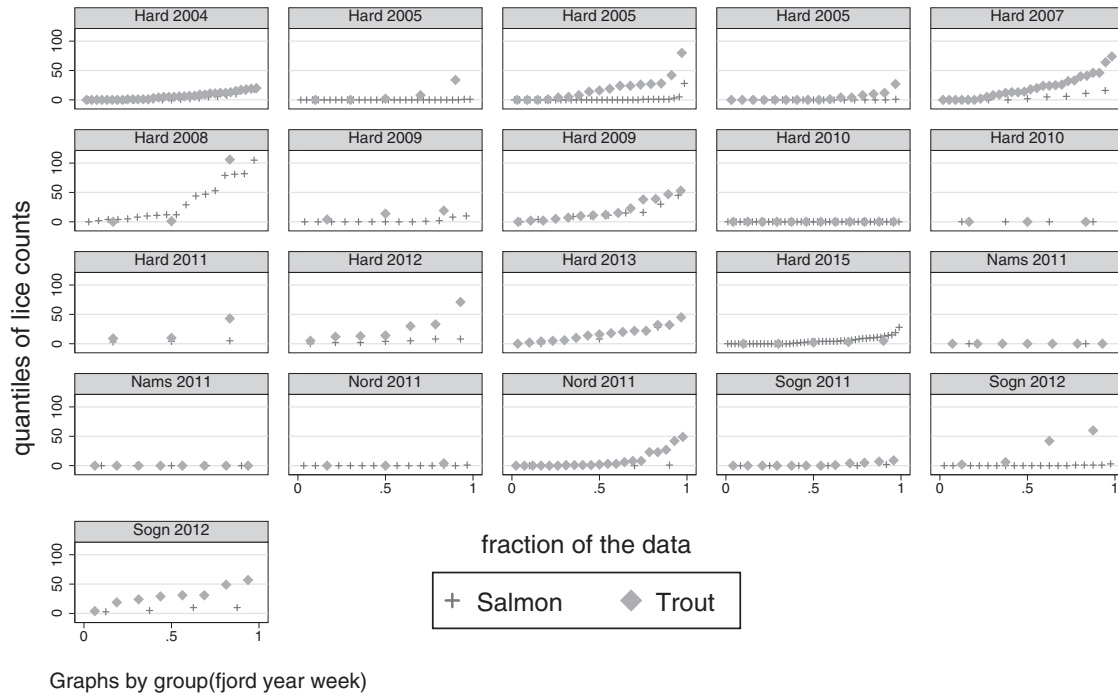
Including salmon weight (M4) improved the model fit; it resulted in a slight decrease in the coefficient for the trout lice count variable from 1.59 to 1.46, and the linear and quadratic coefficients for salmon weight were +0.096 and  $-0.0007$ , respectively. However, in the following text we have chosen to focus on the model not including salmon weight. The rationale behind this is that our aim is to use trout in a sampling area where we lack samples of salmon to predict number of lice on salmon. Consequently, in these areas we will not have information on the size of the salmon, thus it will not be possible to base predictions on a model, which requires knowledge of salmon weights.

The correlation coefficients of the observed and fitted values for the model, not including size of salmon (M3), was 0.67 for the linear model and 0.71 for the quadratic model. As seen in Figure 4 adding the quadratic term had very little impact on the actual predictions the model made with the exception that the quadratic model produced some much smaller predicted values for three groups. For simplicity we have, in the following text, focused on the linear model (M3). The parameter estimates for model M3 are shown in Table 2. The cross validation exercise (model M3—linear) showed relatively little reduction in the correlation between predicted and observed salmon lice counts ( $r$  dropped from 0.67 to 0.59), suggesting that the estimate of the predictive ability was only biased in a positive manner to limited extent. This positive bias would have been present for all models so would not have affected the ranking of models in terms of predictive ability.

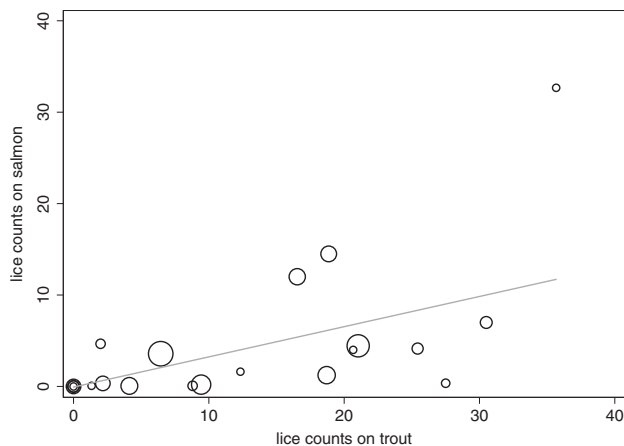
### Logistic models

The AIC and Se and Sp for the logistic models are shown in Table 3. The results mirror those of the negative-binomial models; (i) log transforming the number of lice on trout increased predictive ability (M11 vs. M12), (ii) adjusting for weight of the trout increased the predictive ability (M12 vs. M13), (iii) adding weight of the salmon increased the predictive ability, and (iv) using attached lice as a predictor rather than total lice did not give a better prediction after correcting the size of the trout.

Similar to the negative binomial model, we focus on the model that does not correct for the weight of the salmon. The model parameters for model M13 are shown in Table 4. The predicted probability of a salmon having high total lice count ( $>0.1$  lice/g) across range of mean trout lice counts shown in Figure 5. At  $\sim 0.1$  lice/g trout, the expected prevalence of high lice counts in salmon was about 14%, while at  $\sim 0.3$  lice/g trout the expected prevalence of high lice counts in salmon was 56%.



**Figure 2.** Quantile plots of all salmon and trout lice counts from dataset used in analysis. Data from 316 salmon and 228 trout in 21 groups which contained a minimum of 3 salmon and 3 trout.



**Figure 3.** Scatterplot of salmon total lice counts vs. trout counts from dataset used in analysis. Point size represents weight assigned to point. Data from 316 salmon and 228 trout in 21 groups which contained a minimum of 3 salmon and 3 trout.

The  $Se$  and  $Sp$  of the best fitting model (M14) were 75 and 63, respectively, while the  $Se$  and  $Sp$  of model M13 were 99 and 55, respectively (both based on predicted probability cutpoints of 0.01). In comparison, when trout counts in each group were used directly by choosing cut offs of 0.1 or 0.2 lice/g trout, the  $Sp$  and  $Se$  were 20.9/97.8 and 49.4/59.3, respectively.

To explore how the  $Se$  and  $Sp$  (i.e. using the model as a diagnostic test), varied with the predicted probability cutpoint

chosen, we plotted how  $Se$  and  $Sp$  changed with different cutoff points (and their corresponding trout lice count cut offs). Essentially, this asks the following question: how sensitive and specific would a “diagnostic” test be at predicting salmon with high or low lice counts, given a predictive cutoff point of lice per gram trout? In Figure 6, it is easy to see that a balance between  $Se$  and  $Sp$  is achieved at a cutpoint of approximately 0.2 (equivalent to a trout lice count of 12.1). However, at this cutpoint, both the  $Se$  and  $Sp$  are quite low (~65%) meaning that salmon with high and low counts are both misclassified ~35% of the time.

**Implications for management advice**

In the second dataset (from Herdlefjorden) the estimated likelihood of mortality of migrating salmon post-smolt (in %) based on the weighted average mortality calculated directly from lice counts on sampled trout below 150 grams (method by Taranger et al. 2015 described earlier), for 1 May–31 July in years 2009–2015 divided into five 2-week periods, is presented in Table 5a. In Table 5b, we present the same estimated likelihood of mortality based on predicted lice counts [predictions based on model 3 using all sampled trout data, adjusted for the average weight of the salmon post-smolts in the trawl data (23 g)]. The pairwise comparison of the two sets of mortality estimates are also plotted in Figure 7. These demonstrate how the mortality estimates based on the model predictions using all trout are clearly lower than the weighted average mortality using direct lice counts on trout under 150 g. Out of the 35 samples, 4 groups went from category “yellow” to category “green”, while 6 went from category “red” to category “yellow”. In addition, one sample went from category “green” to category “yellow”.

**Table 1.** Comparison of negative binomial models for total lice counts on salmon with various forms and combinations of predictors included in the model.

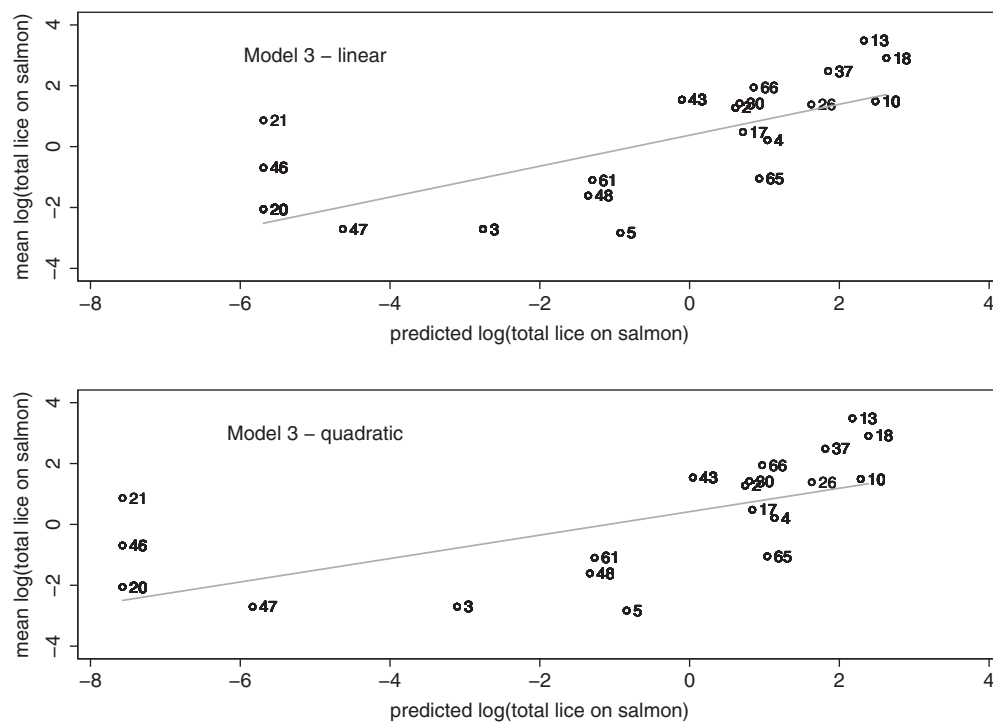
Model	Outcome	Predictor(s)	Quadratic		Linear	
			AIC	Corr. <sup>a</sup>	AIC	Corr. <sup>a</sup>
M1	total lice	total lice per fish (tlpf) <sup>b</sup>	10466	0,49	10481	0,51
M2	"	log(total lice per fish (tlpf)) <sup>c</sup>	10438	0,55	10442	0,57
M3*	"	log(tlpf) adjusted for weight	10200	0,71	10205	0,67
<b>M4</b>	"	<b>M3 + salmon weight</b>	<b>10088</b>	<b>0,74</b>	<b>10092</b>	<b>0,72</b>
M5	"	log(trout attached lice per fish (tapf)) <sup>d</sup>	10385	0,59	10389	0,60
M6	"	log(tapf) adjusted for weight	10269	0,62	10275	0,68
M7	"	M6 + salmon weight	10145	0,68	10152	0,71

<sup>a</sup>correlation between observed and predicted log(counts).

<sup>b</sup>correlations based on average predicted value for the group.

<sup>c</sup>mean total lice count on trout in the group.

<sup>d</sup>mean attached lice count on trout in the group.



**Figure 4.** Plots of observed mean lice counts on salmon vs. predicted values. (Based on M3 linear and M3 quadratic models). Lines of linear fit and observation identifiers have been included.

**Table 2.** Model parameters from logistic model M3 from Table 1.

Fixed effect					
	Coef.	Std. Err.	z	P >  z	[95% CI]
Constant	1.59	0.08	20.44	<0.01	[1.43, 1.74]
LN (TLPGM)	3.69	0.16	23.16	<0.01	
Over-dispersion parameter	1.20	0.04	27.41	<0.01	[1.18, 1.30]
Random effect					
Group	Coef.	Std. Err.	[95% CI]		
	0.54	0.09	[0.39, 0.75]		

The model was based on 316 individuals in 21 groups. LN (TLPGM) is the log normal lice counts on trout divided by the weight of the trout.

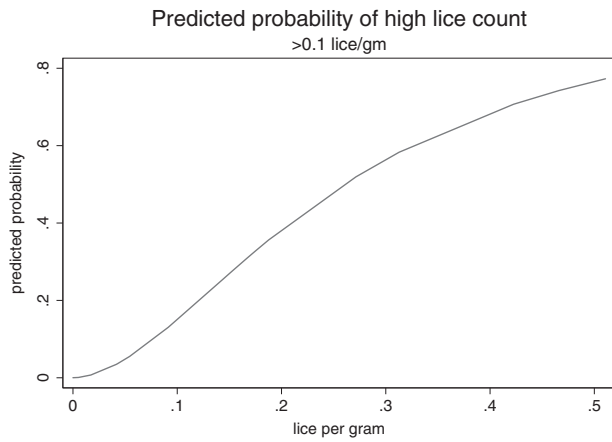
### Discussion

This study is the first study that demonstrates that there is a correlation between lice levels on sea trout and migrating salmon post-smolts. This result should be highly relevant for management, which for a number of years has estimated the impact of salmon lice on Atlantic salmon using lice counts from sea trout (Svåsand *et al.*, 2015; Taranger *et al.*, 2015). However, it must be stressed that there is large variance around the relationship between the lice levels of the two species, and that the predictive ability of using lice levels on trout to predict lice levels on salmon post-smolts is relatively low so predictions will be rather imprecise.

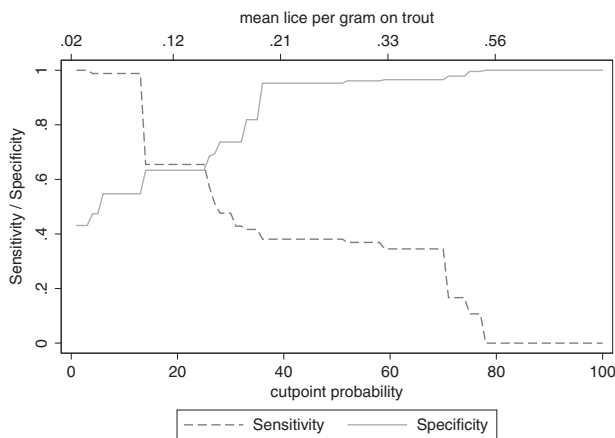
**Table 3.** Comparison of logistic models for total lice counts on salmon with various forms and combinations of predictors included in the model.

Model	Outcome	Predictor(s)	AIC	Se <sup>a</sup>	Sp <sup>b</sup>
M11	high lice <sup>c</sup>	total lice per fish (tlpf <sup>d</sup> )	2832	57	52
M12	"	log(total lice per fish (tlpf))	2831	66	47
M13*	"	log(tlpf) adjusted for weight	2673	99	55
<b>M14</b>	"	<b>M13 + salmon weight</b>	<b>2485</b>	<b>75</b>	<b>63</b>
M15	"	log(trout attached lice per fish (tapf <sup>e</sup> ))	2795	66	61
M16	"	log(tapf) adjusted for weight	2693	99	55
M17	"	M16 + salmon weight	2493	82	64

<sup>a</sup>Probability of correctly classifying a positive salmon.  
<sup>b</sup>Probability of correctly classifying a negative salmon.  
<sup>c</sup>High lice burden was >0.1 lice/g of salmon.  
<sup>d</sup>Mean total lice count on trout in the group.  
<sup>e</sup>Mean attached lice count on trout in the group.



**Figure 5.** Predicted probability of a salmon having a high lice count (>0.1 lice/g) across the range of mean trout lice values (based on model 13 with log transformed, weight adjusted lice counts as sole predictor).

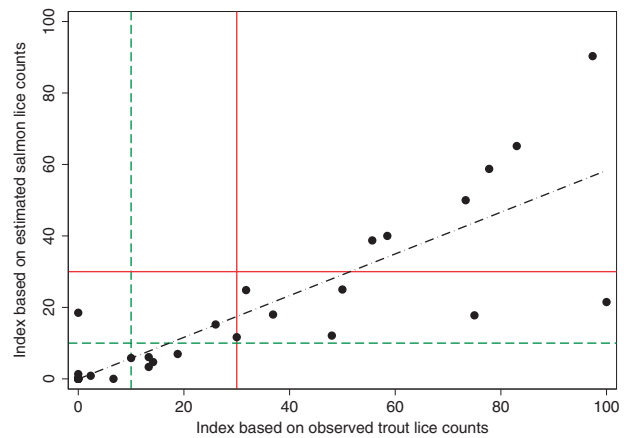


**Figure 6.** Plot of Se and Sp estimates derived at cutpoint probabilities (%) ranging from 0 to 100 (lower x-axis)—based on model M13 with log transformed, weight adjusted lice counts as the sole predictor. Upper axis shows equivalent total lice counts (per g) at cutpoints (1, 20, 40, 60, and 80%).

**Table 4.** Model parameters from logistic model M13 from Table 3.

Fixed effect					
	Coef.	Std. Err.	z	P> z	[95% CI]
Constant	2.44	0.25	9.59	<0.01	[1.94, 2.94]
LN (TLPGM)	1.81	0.14	13.23	<0.01	[1.55, 2.08]
Random effect					
	Coef.	Std. Err.	[95% CI]		
Group	1.21885	0.212472	[0.86, 1.72]		

The model was based on 316 individuals in 21 groups. LN (TLPGM) is the log normal lice counts on trout divided by the weight of the trout.



**Figure 7.** Scatter plot showing index values based on observed counts in trout under 150 g and predicted counts in salmon. Dashed lines demarcate edge of “green zone” (10% mortality), solid lines demarcate edge of “red zone” (30% mortality) and dash-dot line shows linear fit of the points.

One of our main findings was that the sea trout generally had higher levels of lice than salmon. A plausible explanation for this can be that the two species have very different marine life-history strategies and near-shore habitat use. While Most trout (and especially smaller trout) spend all of their time near shore (Thorstad *et al.*, 2016), salmon post-smolt migrate relatively fast from their river of origin and outwards towards the open sea. The average progression rate of salmon during their early marine migration is somewhere around 0.4–3.0 body lengths per second (Thorstad *et al.*, 2012; Vollset *et al.*, 2016). This means that salmon post-smolt can spend everything from a few days up to several weeks (sometimes over a month) migrating in near shore environment (depending on topography) where they are most likely to encounter salmon lice. Thus, most salmon post-smolt caught by a trawl will have had lice that have not yet developed to mobile stages (Finstad *et al.* 2000). Trout on the other hand, may have been residing in the marine near shore environment for several months depending on the life-history strategy of the individual, and therefore amassed a wider range of lice life-stages. However, we suspect that even though we do catch a lot of trout with high levels of lice in the trawls, we might not catch the most affected trout due to mortality and premature return migration to the fresh water (Birkeland, 1996; Birkeland and Jakobsen,

**Table 5.** Estimated “population level effect” of salmon lice based on the method described in Taranger *et al.* (2015).

(a)					
Year	1–15 May	16–31 May	1–15 June	16–30 June	1–31 July
2009	0.0 (3)	2.4 (17)	18.8 (17)	13.3 (9)	50.0 (2)
2010	0.0 (4)	26.0 (55)	55.7 (23)	83.0 (30)	(0)
2011	6.7 (3)	(0)	10.0 (12)	0.0 (2)	(0)
2012	14.2 (12)	31.8 (17)	58.5 (20)	77.8 (9)	5.0 (2)
2013	0.0 (1)	0.0 (5)	0.0 (8)	36.9 (16)	(0)
2014	0.0 (6)	13.3 (9)	73.3 (3)	97.4 (57)	(0)
2015	0.0 (4)	100.0 (3)	48.0 (5)	0.0 (1)	30.0 (4)
(b)					
Year	1–15 May	16–31 May	1–15 June	16–30 June	1–31 July
2009	0.0 (7)	0.9 (23)	7.0 (23)	3.3 (12)	25.0 (4)
2010	0.0 (7)	15.2 (69)	38.8 (32)	65.2 (33)	(0)
2011	0.0 (17)	6.3 (8)	5.8 (24)	0.0 (4)	(0)
2012	4.7 (34)	24.8 (31)	40.0 (27)	58.8 (16)	17.8 (9)
2013	0.0 (20)	0.0 (23)	0.0 (21)	18.0 (25)	(0)
2014	1.3 (15)	6.1 (23)	50.0 (8)	90.3 (63)	(0)
2015	18.5 (20)	21.5 (20)	12.1 (19)	0.0 (8)	11.7 (12)

The upper table (a) is based on estimates using trout <150 g, while the lower (b) is based on trout predictions from model 3. Number inside brackets indicates number of fish used to calculate the “population level effect”. Note that N is lower for (a) compared with (b) because they only utilize trout smaller than 150 g.

1997). Therefore, even the highest levels of lice on trout might be underestimations.

Different species and populations of salmonids are known to have different susceptibility and immune response to lice. Dawson *et al.* (1997) found that significantly more lice settled on hatchery-reared sea trout compared with hatchery-reared salmon (~400–500 g). Although, salmon lice numbers declined more rapidly on sea trout than on salmon, the number at the end of the experiment was higher on trout than on salmon. If salmon lice prefer trout as a host compared with salmon, this may explain the lower abundance of lice on salmon compared with trout in our study. From a life-history perspective trout may be a high risk—high gain host from the perspective of the parasite, as they remain closer to the coast where the likelihood of encountering another host is high, but the likelihood of survival in areas affected by freshwater runoff is lower (Thorstad *et al.*, 2015). In contrast Glover *et al.* (2003) found higher lice abundance on a farmed salmon group compared with a different population of trout, contrasting the finding by Dawson *et al.* (1997). However, farmed fish may differ from wild salmon, and in a follow up study Glover *et al.* (2004) found that wild fish from the river Dale had lower susceptibility than farmed salmon and wild salmon from the nearby river Vosso. Another mechanism that may amplify the lice burden on individual fish is that fish infested with salmon lice are also more susceptible to new infestations (Ugelvik *et al.*, 2016).

Interestingly, lice levels on salmon post-smolt were strongly affected by the size of the fish. Increased size may be linked to swimming speed and consequently the encounter rate with lice. For example, Samsing *et al.* (2015) demonstrated that lice encounter is dome-shaped with the highest encounter rate at intermediate swimming speeds. A larger individual will also create a larger pulse of water around the head, which may trigger the salmon lice copepodite to swim towards the fish. Heuch *et al.* (2007) demonstrated that salmon lice reacts to the pulse of water from a model salmon head pushed forward into a tank, jumping towards the head. Higher lice numbers on larger fish have also been observed in experimental infestation studies (Glover *et al.*, 2003, 2004, 2005). Another plausible explanation is that size reflects growth during the marine phase. Consequently, size will be

correlated with time spent in marine waters and therefore larger post-smolt will have a longer exposure history than smaller fish. If this is the case, the trawl samples a distribution of fish with various exposure histories. Thus, the abundance on lice on the sampled fish must be viewed as an underestimation for populations with long exposure histories and an overestimation for populations with a low exposure history. Ideally, trawling should be conducted after the post-smolt have left the exposure area for lice from fish farms. However, the few attempts to capture fish in open waters after they have left fjords have generally been unsuccessful with very small catches (Bengt Finstad, pers. comm.).

Even though our binary approach that modelled the likelihood that a salmon had either high (>0.1 lice/g fish weight) or low (<0.1 lice/g fish weight) did support the hypothesis that lice on trout was a significant predictor of high or low lice counts on salmon, the results from this method were not promising. The advantage of using such a binary model is that it can be used as diagnostic tool to define a fish in a category of either “sick” or “not-sick”, and with this one can calculate the Sp and Se of the model. This provides information on how good the diagnostic tests are. However, clearly the optimal balance between Se and Sp indicated that the model was a poor diagnostic tool. For example, increasing the Sp to more than 60% would strongly compromise the Se and vice versa. Furthermore, a binary system does not allow for a calculation of estimated mortality on salmon post-smolt as suggested in Taranger *et al.* (2015). Therefore, our recommendation is to utilize the numerical values of counts (from the negative binomial model described earlier) to predict lice numbers on salmon instead of predicting it categorically.

Currently a new management system is being implemented in Norway where the allowable production of salmon in different regions in Norway will be based on (among other things) advice on the impact of salmon lice on wild fish (Karlsen *et al.*, 2016). More specifically, the current threshold values that are to be implemented state that the production biomass is not allowed to increase if the estimated mortality of local salmonid populations based on lice counts from wild caught fish exceeds 10%, and the allowable biomass will be reduced if the estimated mortality



exceeds 30%. Using an independent dataset on trap-net caught trout, we demonstrated how our model would lead to a clear reduction in the estimated mortality for salmon post-smolts compared with the currently used method, and that in many cases the advice given based on the above mentioned threshold would change.

In this study, we have used the relationship between salmon lice on sea trout and Atlantic salmon as a global relationship and applied it to another system and sampling method when calculating the infestation pressure on salmon. We are aware that this has limitations. The relationship between salmon lice on sea trout and Atlantic salmon are most likely strongly dependent on temporal and spatial scales. *Fjord* came out as an important random effect in our analysis indicating that lice counts varied substantially among fjords and it is quite plausible that the trout lice count—salmon lice count relationship is different at different overall lice levels. In theory, the relationship between any specific trawling station and trap-net location may be inherently different because of a range of reasons, e.g. the geography/bathymetry and position of the sample locations, the rivers in the vicinity, and salmonid population attributes in these rivers. However, to date there are not enough available data to do an analysis that can unravel this complexity.

Although there seems to be a consensus that in fish farm intensive areas there are higher infestation levels of lice on wild fish (Bjorn *et al.*, 2011; Serra-Llinares *et al.*, 2014, 2016), documenting negative population level effects on salmonids in general, and on Atlantic salmon particularly, remains controversial. There are several reasons for this controversy, but the difficulty of getting accurate estimates of sea lice loads on migrating wild post-smolt salmon is perhaps the largest, as this leads to uncertainties in estimating the lice induced mortality of salmon. Our advice is to increase the trawling effort on salmon post-smolts in the Norwegian fjords. More data can thereafter be used to validate to what degree the relationship found in this study is globally valid and to validate potential spatially explicit salmon lice models such as hydrodynamic particle tracking models. Also, based on this analysis, we suggest that using sea trout lice counts directly to predict expected mortality on salmon is not appropriate. However, trout lice counts may be used to predict salmon lice counts, with these estimates then being combined with information from other sources for decision making in the management system.

## Acknowledgements

Karin Kroon Boxaspen, Rune Nilsen, Nils Arne Hvidsten, Julius Dahle, Arild Refsnes, and Arve Kristiansen are acknowledged for providing the trawling data used in this study. Arve Kristiansen is also acknowledged for providing information on trawling practices. The trawl data was obtained by the National Salmon Lice Monitoring Program on wild Salmonids in Norway funded by the Institute of Marine Research, Norway, the Norwegian Food Safety Authority, the Norwegian Environment Agency and the Norwegian Institute for Nature Research.

## Funding

Knut Wiik Vollset and Ian Dohoo were supported by the Norwegian Research Council (Project. Nr. 243912/E50) during the writing and analysis of this study. All authors from IMR and NINA funded by internal grants from the Institute of Marine Research and the Norwegian Institute for Nature Research, respectively.

## References

- Barlaup, B. T., Gabrielsen, S. E., Loyland, J., Schlappy, M. L., Wiers, T., Vollset, K. W., and Pulg, U. 2013. Trap design for catching fish unharmed and the implications for estimates of sea lice (*Lepeophtheirus salmonis*) on anadromous brown trout (*Salmo trutta*). *Fisheries Research*, 139: 43–46.
- Birkeland, K. 1996. Consequences of premature return by sea trout (*Salmo trutta*) infested with the salmon louse (*Lepeophtheirus salmonis* Kroyer): Migration, growth, and mortality. *Canadian Journal of Fisheries and Aquatic Sciences/Journal Canadien des Sciences Halieutiques et Aquatiques*. Ottawa 53: 2808–2813.
- Birkeland, K., and Jakobsen, P. J. 1997. Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. *Environmental Biology of Fishes*, 49: 129–137.
- Bjoern, P. A., and Finstad, B. 1997. The physiological effects of salmon lice infection on sea trout post smolts. *Nordic Journal of Freshwater Research*, 73: 60–72.
- Bjoern, P. A., and Finstad, B. 1998. The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected post smolts of sea trout (*Salmo trutta*). *Canadian Journal of Zoology/Revue Canadien de Zoologie*, 76: 970–977.
- Bjorn, P. A., Sivertsgard, R., Finstad, B., Nilsen, R., Serra-Llinares, R. M., and Kristoffersen, R. 2011. Area protection may reduce salmon louse infection risk to wild salmonids. *Aquaculture Environment Interactions*, 1: 233–244.
- Dawson, L. H. J., Pike, A. W., Houlihan, D. F., and McVicar, A. H. 1997. Comparison of the susceptibility of sea trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) to sea lice (*Lepeophtheirus salmonis* (Kroyer, 1837)) infections. *Ices Journal of Marine Science* 54: 1129–1139.
- Finstad, B., Bjoern, P., Grimnes, A., and Hvidsten, N. 2000. Laboratory and field investigations of salmon lice [*Lepeophtheirus salmonis* (Kroyer)] infestation on Atlantic salmon (*Salmo salar* L.) post-smolts. *Aquaculture Research*, 31: 795–803.
- Finstad, B., and Grimnes, A. 1997. Registreringer av lakselus på laks, sjøørret og sjøøye i 1996 (Registrations of salmon lice on Atlantic salmon, sea trout and Arctic charr in 1996). NINA Oppdragsmelding, 485: 1–27.
- Glover, K. A., Aasmundstad, T., Nilsen, F., Storset, A., and Skaala, O. 2005. Variation of Atlantic salmon families (*Salmo salar* L.) in susceptibility to the sea lice *Lepeophtheirus salmonis* and *Caligus elongatus*. *Aquaculture*, 245: 19–30.
- Glover, K. A., Hamre, L. A., Skaala, Ø., and Nilsen, F. 2004. A comparison of sea louse (*Lepeophtheirus salmonis*) infection levels in farmed and wild Atlantic salmon (*Salmo salar* L.) stocks. *Aquaculture*, 232: 41–52.
- Glover, K. A., Skaala, Ø., Nilsen, F., Olsen, R., Teale, A. J., and Taggart, J. B. 2003. Differing susceptibility of anadromous brown trout (*Salmo trutta* L.) populations to salmon louse (*Lepeophtheirus salmonis* (Kroyer, 1837)) infection. *Ices Journal of Marine Science*, 60: 1139–1148.
- Godwin, S. C., Dill, L. M., Reynolds, J. D., and Krkosek, M. 2015. Sea lice, sockeye salmon, and foraging competition: lousy fish are lousy competitors. *Canadian Journal of Fisheries and Aquatic Sciences*, 72: 8.
- Grimnes, A., Finstad, B., and Bjorn, P. A. 1996. Økologiske og fysiologiske konsekvenser av lus på laksefisk i fjordsystem (Ecological and physiological consequences of lice on salmonids in the fjord ecosystems). NINA Oppdragsmelding, 381: 1–37.
- Grimnes, A., and Jakobsen, P. J. 1996. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. *Journal of Fish Biology*, 48: 1179–1194.
- Heuch, P. A., Doall, M. H., and Yen, J. 2007. Water flow around a fish mimic attracts a parasitic and deters a planktonic copepod. *Journal of Plankton Research*, 29: I3–I16.

- Holst, J. C., and McDonald, A. 2000. FISH-LIFT: a device for sampling live fish with trawls. *Fisheries Research*, 48: 87–91.
- Jackson, D., Cotter, D., Newell, J., ODonohoe, P., Kane, F., McDermott, T., Kelly, S. et al. 2014. Response to M. Krkošek, C. W. Revie, B. Finstad, and C. D. Todd's comment on Jackson *et al.* Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar* L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. *Journal of Fish Diseases*, 37: 419–421.
- Karlsen, Ø., Finstad, B., Ugedal, O., and Svåsand, T. 2016. Kunnskapsstatus som grunnlag for kapasitetsjustering innen produksjons-områder basert på lakselus som indikator. Rapport fra Havforskningen nr. 14-2016. pp. 137.
- Krkošek, M., Lewis, M. A., Morton, A., Frazer, L., and Volpe, J. P. 2006. Epizootics of wild fish induced by farm fish. *Proceedings of the National Academy of Sciences of the United States of America*, 103: 15506–15510.
- Krkošek, M., Revie, C. W., Finstad, B., Todd, C. D., Comment on Jackson *et al.* 2014. Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar* L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality'. *Journal of Fish Diseases*, 37: 415–417.
- 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. *Proceedings of the Royal Society B-Biological Sciences*, 280: 20122359.
- Nilsen, R., Bjørn, P. A., Serra-Llinares, R. M., Asplin, L., Sandvik, A. D., Johnsen, I. A., Karlsen, Ø. et al. 2016. Lakselusinfeksjonen på vill laksefisk langs norskekysten i 2015. Enn fullskalatest av modellbasert varslings og tilstandsbekreftelse. Rapport fra Havforskningen nr. 2-2016. pp. 60.
- Peacock, S. J., Krkošek, M., Bateman, A. W., and Lewis, M. A. 2015. Parasitism and food web dynamics of juvenile Pacific salmon. *Ecosphere*, 6: 1–16.
- Samsing, F., Solstorm, D., Oppedal, F., Solstorm, F., and Dempster, T. 2015. Gone with the flow: current velocities mediate parasitic infestation of an aquatic host. *International Journal for Parasitology*, 45: 559–565.
- Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M., and Asplin, L. 2014. Salmon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. *Aquaculture Environment Interactions*, 5: 1–16.
- Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., and Asplin, L. 2016. Nearby farms are a source of lice for wild salmonids: a reply to Jansen *et al.* (2016). *Aquaculture Environment Interactions*, 8: 351–356.
- Skilbrei, O. T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F., and Strand, R. 2013. Impact of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 1997–2009. *Journal of Fish Diseases*, 36: 249–260.
- Svåsand, T., Boxaspen, K. K., Karlsen, Ø., Kvamme, B. O., Stien, L. H., and Taranger, G. L. 2015. Risikovurdering norsk fiskeoppdrett-2013. Fisken og havet, særnummer: 2-2015.
- Taranger, G. L., Karlsen, Ø., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., Kvamme, B. O. et al. 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *ICES Journal of Marine Science: Journal du Conseil*, 72: 997–1021.
- Taranger, G. L., Svåsand, T., Bjørn, P. A., Jansen, P. A., Heuch, P. A., Grøntvedt, R. N., Asplin, L. et al. 2012. Forslag til førstegenerasjons målemetode for miljøeffekt (effektindikatorer) med hensyn til genetisk påvirkning fra oppdrettslaks til villaks, og påvirkning av lakselus fra oppdrett på villevende laksefiskbestander.
- Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E. et al. 2015. Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta*-a literature review. *Aquaculture Environment Interactions*, 7: 91–113.
- Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E. et al. 2016. Marine life of the sea trout. *Marine Biology*, 163: 1–19.
- Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., and Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81: 500–542.
- Torrisen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O. T., Nilsen, F., Horsberg, T. E. et al. 2013. Salmon lice - impact on wild salmonids and salmon aquaculture. *Journal of Fish Diseases*, 36: 171–194.
- Ugelvik, M. S., Mo, T., Mennerat, A., and Skorping, A. 2016. Atlantic salmon infected with salmon lice are more susceptible to new lice infections. *Journal of Fish Diseases*, 40: 311–317.
- Vollset, K. W., and Barlaup, B. T. 2014. First report of winter epizootic of salmon lice on sea trout in Norway. *Aquaculture Environment Interactions*, 5: 5.
- Vollset, K. W., Barlaup, B. T., Mahlum, S., Bjørn, P. A., and Skilbrei, O. T. 2016. Estimating the temporal overlap between post-smolt migration of Atlantic salmon and salmon lice infestation pressure from fish farms. *Aquaculture Environment Interactions*, 8: 511–525.
- Vollset, K. W., Barlaup, B. T., Skoglund, H., Normann, E. S., and Skilbrei, O. T. 2014. Salmon lice increase the age of returning Atlantic salmon. *Biological Letters*, 10: 20130896.
- Vollset, K. W., Krontveit, R. I., Jansen, P. A., Finstad, B., Barlaup, B. T., Skilbrei, O. T., Krkošek, M. et al. 2015. Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. *Fish and Fisheries*, 17: 714–730.
- Wagner, G. N., Fast, M. D., and Johnson, S. C. 2008. Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. *Trends in Parasitology*, 24: 176–183.
- Wells, A., Grierson, C. E., Marshall, L., MacKenzie, M., Russon, I. J., Reinardy, H., Sivertsgard, R. et al. 2007. Physiological consequences of "premature freshwater return" for wild sea-run brown trout (*Salmo trutta*) postsmolts infested with sea lice (*Lepeophtheirus salmonis*). *Canadian Journal of Fisheries and Aquatic Sciences/Journal Canadien des Sciences Halieutiques et Aquatiques*, 64: 1360–1369.

Handling editor: Mark Gibbs