



Timing is everything: Survival of Atlantic salmon *Salmo salar* postsmolts during events of high salmon lice densities

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Abstract

1. Atlantic salmon in aquaculture act as reservoir hosts and vectors of parasites like salmon lice and this parasite is shown to harm wild salmonid populations.
2. In this study, $n = 29,817$ tagged Atlantic salmon were studied in four release trials. Half of the released fish were given prophylactic treatment against lice, the other half represented sham control fish. We used a nested design comparing years with low and high lice density and seasonal dynamics in infestation pressure. The released Atlantic salmon thus experienced highly variable lice infestation pressures, which we linked to survival and growth in returning fish. The fish were released in a protected 'National Salmon Fjord' and $n = 559$ Atlantic salmon were recaptured after spending 1–4 years at sea.
3. In most experimental groups 1%–2.5% of the fish were recaptured at return. However, survival of unprotected fish was extremely low for the trial released at the highest density of lice: only 0.03% of these Atlantic salmon returned to the river, compared to 1.86% in the protected group.
4. *Synthesis and applications.* We document that high lice density can cause more than 50 times higher mortality risk in Atlantic salmon on their sea migration, even in a fjord with protected status. Fine-tuned and hard-to-predict year-to-year differences in timing, both for the wild smolt migration and the population build-up of lice released from aquaculture, means life or death to wild salmon. Management actions such as spatial segregation of farmed fish and lice (e.g. closed farm pens), and/or moving farms away from vulnerable habitats for wild salmonids (fjords and coastal areas), may be needed to ensure sustainable coexistence of wild and farmed Atlantic salmon.

KEYWORDS

aquaculture, Atlantic salmon, management, parasite-induced mortality, randomized controlled trials, salmon lice, wild and farmed fish interactions

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1 | INTRODUCTION

To complete its complex life cycle, wild Atlantic salmon *Salmo salar* postsmolts migrate from the rivers to their feeding grounds in the sea during spring and return as mature adults 1–4 years thereafter to their native river. The survival of the Atlantic salmon during its entire marine migration is typically (much) less than 10%, and most of the mortality occurs shortly after the fish has left the rivers (Thorstad et al., 2012).

Salmon farming has become a major industry in Norway during the recent decades. Atlantic salmon is farmed in net pens in the fjords and along the coast and serves as a host to the parasitic salmon louse *Lepeophtheirus salmonis* (Krøyer, 1837). This ectoparasite has pathogenic impacts on Atlantic salmon by feeding on their blood and tissue, causing skin lesions, osmoregulatory challenges and physiological stress responses in the host. The pathogenic effect is a well-studied topic (Costello, 2009; Thorstad et al., 2015; Torrissen et al., 2013).

With an estimated stock of 386 million farmed salmon (January 2017; Statistics Norway, 2017), compared to about 0.5 million returning wild Atlantic salmon (Anon, 2018), the number of hosts for the salmon louse has increased by several orders of magnitude since the early eighties (Heuch & Mo, 2001). Moreover, the stated political aim is to increase the production of Atlantic salmon and trout with 500% by 2050 (Vollset et al., 2017), which will scale up already documented negative effects of salmon lice.

These problems have led to a new regulatory framework, the so-called 'traffic light system' where green, yellow and red lights represent potential increase, stagnation or decrease in the volume of produced fish, respectively, in 13 predefined production zones along the Norwegian coast. The colour-coded impact categories come from a single indicator, i.e. from the effect of lice on wild salmon within each of the independent production zones: 'Green light' is used when 0%–10% of the wild population of salmon is likely to die because of lice, 'yellow light' is used at mortality rates from 10% to 30% and 'red light' is used at mortality rates >30%. Fish farms are in addition obliged to keep lice levels below 0.2 adult female lice per salmon during the smolt migration period (the rest of the year has a threshold of 0.5 adult female lice).

A mature female salmon louse carries two eggstrings with a total fecundity of about 500–1,000 eggs per brood, for farmed and wild Atlantic salmon respectively (Heuch & Mo, 2001). Hatched eggs develop into infective copepodids that may be transported over long distances with the water currents (Asplin et al., 2014). Infective lice copepodids have a life span depending on the ambient temperature (Samsing et al., 2016), and at 10 degrees they can drift for 17 days before they need to find a salmonid host, otherwise dying of starvation. Thus, it is likely that they are spread in most of the migration route of wild salmon smolts, and consequently, aquaculture may negatively impact wild Atlantic salmon. Previous studies have identified salmon lice as one of the two largest threats to wild salmon in Norway (Forseth et al., 2017; Taranger et al., 2015).

To study the effects of lice, a series of field experiments with parallel releases of treated versus untreated Atlantic salmon smolts,

have been performed in Norway and Ireland (Gargan, Forde, Hazon, Russell, & Todd, 2012; Jackson et al., 2013; Krkošek et al., 2013; Skilbrei et al., 2013). The results are conflicting, but a meta-analysis of all studies from Norwegian systems confirms that lice have a negative effect, but primarily in years when the natural mortality is high. When baseline mortality was high, the positive effect of antiparasitic treatment was high: risk ratio (RR) 1.77—meaning that 1.77 times more fish survive and return in the treated group compared to the control. When baseline mortality was low, no significant difference could be detected (RR ~1.00; Vollset et al., 2016). Thus, conflicting evidence and the lack of a clear link between infestation pressure from lice originating from fish farms and direct effects on e.g. mortality in wild Atlantic salmon makes the scientific controversy still largely unresolved (Vollset, 2019; Vollset, Qviller, Skår, Barlaup, & Dohoo, 2018).

Our study site, the Hardangerfjord system, is a 160-km long fjord on the south-western (SW) coast of Norway. This area is a hotspot for salmonid aquaculture industry. In Hardangerfjord, it has been documented that the proportion of returning fish is lower for fish that originate from rivers further away from the coast, i.e. deeper into the fjords, which may be related to longer time periods of exposure to lice or predators in the environment (Vollset, Skoglund, et al., 2014). Moreover, the *timing* of the migration of the salmon smolt seems to be crucial. Early migrating fish meet a much lower infestation pressure from lice than late migrating fish (Kristoffersen et al., 2018). This is related to the seasonal dynamics of the louse, which have a temperature-dependent population boom in late spring/early summer (Samsing et al., 2016).

Hardangerfjord was from 2010 to 2017 subjected to synchronized fallowing in order to control lice infestations on both farmed and wild salmonids. Accordingly, all farms in the outer part of the Hardangerfjord were emptied of farmed Atlantic salmon in March 2013 but had full production in 2014 (Guarracino, Qviller, & Lillehaug, 2018; Halttunen et al., 2017). We took advantage of the expected low-to-high lice density shift in the years 2013 versus 2014 and performed a large-scale experiment in the river Etne in Hardangerfjord. We released $n = 29,817$ Atlantic salmon smolts, using first generation hatchery-reared smolts originating from river Etne brood stock. Our experimental design combined four randomized controlled trials (RCTs) over 2 years (May and June releases nested within 2013 and 2014) with 50% of the smolts in each trial treated with prophylaxis and 50% given sham control treatment. With this setup, we were able to evaluate the effects of manipulated low and high lice infestation pressure on the survival and growth of recaptured Atlantic salmon upon their return to the river as adults. Moreover, a National research platform with dedicated staff and a fish trap (Resistance Board Weir) with a capture efficacy for wild salmon at about 90% (Skaala et al., 2015) was operational in the Etne River from 2013, (Skaala et al., 2015), minimizing potential capture bias.

We hypothesized that higher lice density causes increased mortality in sea run Atlantic salmon (H_1), and higher lice density causes a reduced growth rate in returned Atlantic salmon (H_2).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in River Etne, draining in the outer parts of Hardangerfjord, in Hordaland county, western Norway (Figure 1). The Hardangerfjord is among the most intensively used areas on the Norwegian coast for salmon production, with a standing stock of farmed Atlantic salmon of about 80,000 and 95,000 metric tonnes in 2013 and 2014 respectively (Fiskeridirektoratet, 2019). For further details on the study area see Halttunen et al. (2018).

2.2 | Experimental design

The experiment started in 2013 and was replicated in 2014; two groups of Atlantic salmon were released in May and June, each year (Table 1). All fish were released close to the mouth of River Etne. Returning adult individuals were caught in the trap in River Etne after 1–4 years at sea.

Fish used in this study were first generation, 1-year old hatchery-reared Atlantic salmon postsmolts produced from eggs and sperm stripped from broodstock caught in River Etne. Fish were reared at

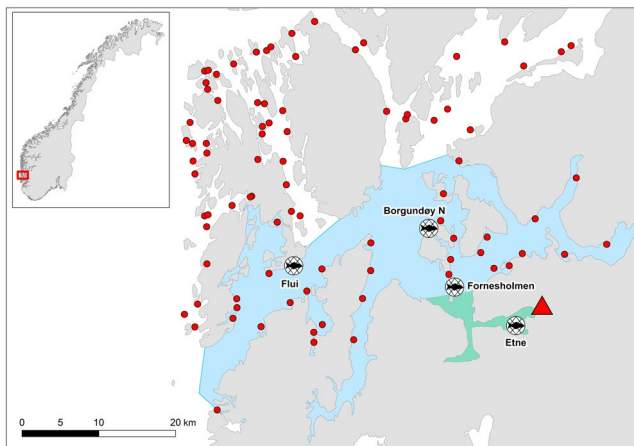


FIGURE 1 Map of the study area. Blue colour shows that the outer management area were farms that were followed in March 2013. Red triangle denotes the outlet of River Etne, green area shows the area protected from salmon farming (National Salmon Fjord), red dots denote salmon farming sites and black fish symbols show sentinel cages used in the study

TABLE 1 Summary of released salmon smolts and sample sizes for treatment (prophylaxis) and control groups in the four trials. Fish weights in gram \pm SD

Year	Release date	Prophylaxis	Control	Weight (g)
2013	18 May	3,791	3,972	72 \pm 21
2013	9 June	3,801	3,868	74 \pm 16
2014	18 May	3,819	3,818	47 \pm 11
2014	9 June	3,770	2,978	42 \pm 10

Matre Research Station (IMR) and made ready for release in salt water. Prior to release, all salmon smolts were tagged using coded wire tags inserted in their snout, which enable fish identification to (a) treatment/control and (b) timing of release. In addition, all fish had their adipose fin removed to enable us to distinguish experimental fish from wild fish in the trap on return to the river.

For the prophylactic antiparasitic treatment, we used a 30-min bath of Substance EX (Pharmaq), hereafter termed SubEX, at a concentration of 2 p.p.m in oxygenated water. This treatment was applied to 50% of the fish, randomly selected, securing a balanced design. SubEX protects the fish by preventing attached copepodids to develop into the next life stage for up to 16 weeks after treatment (Skillbrei, Espedal, Nilsen, Garcia, & Glover, 2015). Identical (sham) treatment was performed on the control fish. This process was performed 3 days before each of the four releases to allow recovery of the treated fish.

After tagging and treatment, fish were transported in closed oxygenated tanks to Etne by car to a 5 m³ cage in the sea, close to the outlet of River Etne. The fish were kept in the cage for approximately 48 hr before they were released by lowering the net in the cage. The release was done by night to reduce predation from birds. Prior to release a sample of 30 fish (randomly picked from the net) were killed to measure length and weight.

From 2014 to 2017, i.e. 1–4 years after release, all experimental fish returning to River Etne were caught in the fish trap and killed (wild Atlantic salmon not belonging to the experiment were released above the trap). Data on body length, weight and sex were registered at the return date.

2.3 | Estimation of lice infestation pressure

Salmon lice densities were estimated based on sentinel cages (Bjørn et al., 2011) stocked with 30 farmed Atlantic salmon postsmolts and positioned in the area the fish would migrate through (Figure 1). We extracted lice counts from periods that approximately matched the times of release for the fish, i.e. in a 14-day period after 18 May and 9 June in 2013 and 2014. We included all life stages of lice (from copepodites to adult stages) and calculated the total added number of lice per fish for a standardized period of 14 days (using modelled means of each cage mean, cf. Figure 2). These numbers were used to represent the environmental infestation pressure of lice in this study, hereafter termed *Lice Infestation Pressure*, for each of the four experimental releases. The positioning of the cages was the same between years.

To visualize the spatial distribution of lice infestation pressure in the whole area of interest (Figure 3) we used the Relative Operating Characteristic method to identify where the lice densities from the hydrodynamic lice dispersion model (see www.lakselus.no) were low (<1 lice per fish), medium (1–10 lice per fish) or high (>10 lice per fish; Sandvik et al., 2016). The hydrodynamic lice model has been described in detail in earlier studies (Johnsen, Fiksen, Sandvik, & Asplin, 2014; Myksvoll et al., 2018).

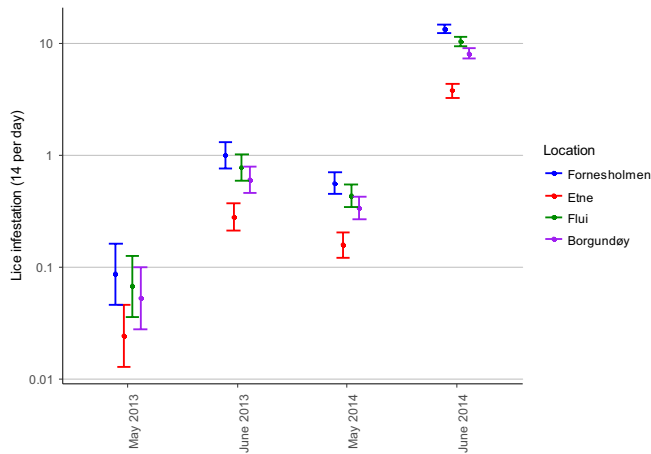


FIGURE 2 Salmon lice infestation pressure in outer Hardangerfjord in the four release trials in May and June 2013 and 2014. Lice infestations denote numbers of lice with 95% CIs per fish after 14 days of exposure, estimated as modelled means from each smolt cage locality (GLM model). Note the log scale

2.4 | Risk ratio

The RR or relative risk quantifies how much more likely the treated group is to return to the home river, compared to the control group. We analysed differences in return rates between treated and non-treated fish, for each of the four experimental releases, with the following formulae:

$$RR = \frac{ET / (ET + NT)}{EC / (EC + NC)} = \frac{ET (EC + NC)}{EC (ET + NT)}, \quad (1)$$

where *ET* is the number of return events (*E*) in the treatment (*T*) group; *NT* is the number of non-return events (*N*) in the treatment (*T*) group; *EC* is the number of return events (*E*) in the control (*C*) group and *NC* is the number of non-return events (*N*) in the control (*C*) group.

RR values higher than 1 show higher adult salmon returns of treated fish as compared to control fish, RR values lower than 1

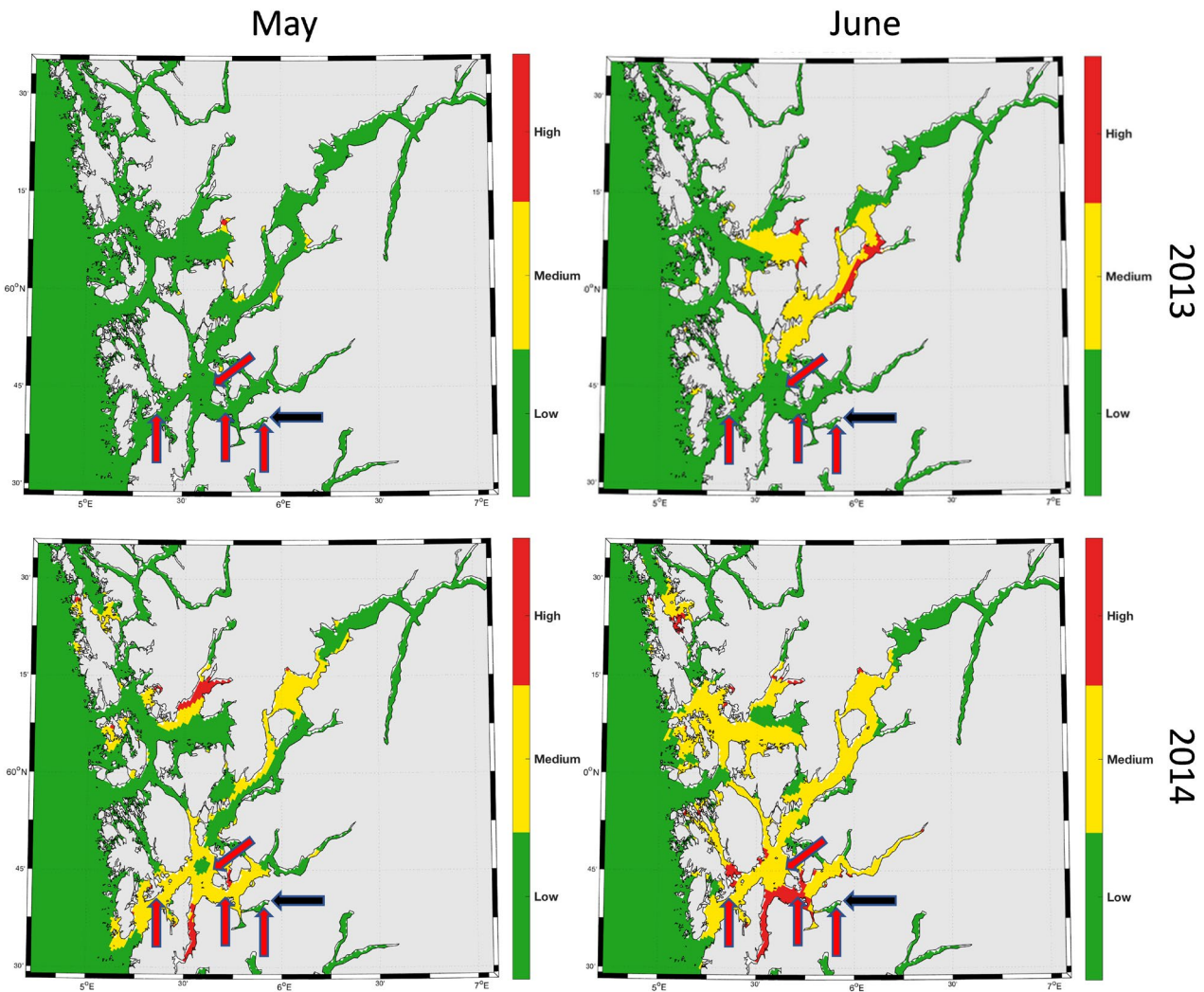


FIGURE 3 Maps showing areas of modelled low (green), moderate (yellow) and high (red) lice infestation pressure using the Relative Operating Characteristic method as described in Sandvik et al. (2016). The lice infestation pressures represent summarized values from the consecutive 14 days after release of salmon smolts, i.e. 18 May to 1 June (left panels) and 9–23 June (right panels) in 2013 and 2014. Black arrows show the release site at River Etne and red arrows show the locations of the sentinel cages

show higher returns of the controls. We calculated confidence intervals for the RR with the formulae:

$$\text{Ln}(\widehat{\text{RR}}) \pm Z \sqrt{\frac{(n_1 - x_1)/x_1}{n_1} + \frac{(n_2 - x_2)/x_2}{n_2}}, \quad (2)$$

where n_1 and n_2 = sample size of treated and non-treated fish released, respectively; x_1 and x_2 are the sample size of returned fish in the treated and control groups respectively. For 95% CIs we used $z = 1.96$.

2.5 | Survival probability

The survival probability (probability of return) was modelled by logistic regression:

$$\text{glm}(\text{Returned fish} \sim \text{Lice Infestation Pressure} \\ \times \text{Treatment}, \text{family} = \text{'binomial'}), \quad (3)$$

where *Returned fish* represents the probability for surviving 1–4 years in the sea and returning to the river (1 for returning fish, 0 for non-returning fish), *Lice Infestation Pressure* is the estimated environmental infestation pressure (standardized with mean = 0 and SD = 2) of lice and *Treatment* is prophylaxis against lice versus control. We also tested whether *Releaseweight* (average fish weight for the group at release) was a significant covariate in the model. As *Releaseweight* was a non-significant covariate (Estimate = -0.0054, $Z = -1.471$, $p = 0.14$), and did not improve the model (using Akaike Information Criterion), we used a simpler model without this factor. For model validation, we inspected residuals and re-run the model excluding one outlier fish. However, as the results were practically the same, we decided to include all data points.

2.6 | Growth at sea

The growth of the fish during its sea migration was evaluated with a linear regression model:

$$\text{lm}(\text{Weight} \sim \text{Lice Infestation Pressure} \\ + \text{Treatment} + \text{Seawinter} + \text{Sex}), \quad (4)$$

where *Weight* is individual fish body mass at return, *Lice Infestation Pressure* is the environmental lice infestation pressure (standardized with mean = 0 and SD = 2), *Treatment* is prophylaxis or control, *Seawinter* is the number of years at sea before returning to the river (standardized for 2 SW fish by subtracting 2 from the number of seawinters) and *Sex* differentiates males from females. Fish that spent four winters at sea were excluded from the analysis since these were only observed in one of the trials. We standardized *Lice Infestation Pressure* and *Seawinter* in order to have comparable effect sizes between factors and covariates in the model (Schielzeth, 2010). For model validation, residuals were inspected visually (vs. fitted values and leverage, quantile-quantile plot,

scale-location). We also re-run the model without two potential outliers, but decided to include all fish in the dataset.

Statistical analyses were carried out in R statistical package version 3.5.1 (R Developmental Core Team, 2019).

3 | RESULTS

3.1 | Salmon lice infestation pressure

Data from the sentinel cages showed that the lice infestation pressure increased about 10-fold from May to June (0.06–0.66 lice per fish after 14 days; average values from all locations) in 2013, and about 25-fold from May to June (0.37–8.87 lice per fish after 14 days) in 2014 respectively (Figure 2). The lowest lice density was found consistently in the protected inner locality of Etne (Figure 2). In 2013, when farmed salmon was removed by fallowing, the lice infestation pressure on fish was reduced by 84%–92% in May and June, respectively, compared to the full production year 2014 (Figure 2).

The modelled density and distribution of infective lice copepodids showed lower lice densities in the migration route of salmon smolts from the River Etne in May and June 2013 (Figure 3, upper panels). From May to June 2013, a marked increase in lice was observed in the middle part of the fjord, where there was full production of salmon in aquaculture. In 2014, when the outer part of the fjord (including the migration route of salmon smolts from River Etne) had full production of salmon, much higher densities of lice were present in this area (Figure 3, lower panels). Again, the lice density increased from May to June (Figure 3).

3.2 | Survival, duration of ocean migration and risk ratio

Both treated and control fish released in May and June 2013 predominantly returned after 2 years at sea (Figure 4). This pattern was not affected by treatment. For the May 2014 release, a similar proportion of the fish stayed at sea for 1, 2 and 3 years, and again, this was not affected by treatment. Fish released in June 2014 showed that treated fish returned mainly after 2 or 3 years at sea. From this release, $n = 70$ Atlantic salmon (1.86%) returned to the river. In contrast, only a single fish (0.03%) returned from the control group (Figure 4). This latter group was a clear exception since the return rate of Atlantic salmon for most groups was 1%–2.5%.

From the May 2013 release, about twice as many salmon from the control group returned as compared to the treated salmon (RR = 0.52, 95% CI: 0.35–0.76; Figure 5). From the June 2013 and May 2014 releases, slightly more treated fish returned compared to the control group, but there were no significant differences in the return rate between treated and control fish, RR = 1.05 and 1.13 (95% CI: 0.81–1.42 and 0.85–1.50) respectively (Figure 5). For the June 2014 release, the RR was exceptionally high and significant (RR = 55.3, 95% CI: 7.7–398) (Figure 5), reflecting that 70 fish (out of 3,770) returned in the treated group and that only a single fish (out of 2,978) returned in the control group.

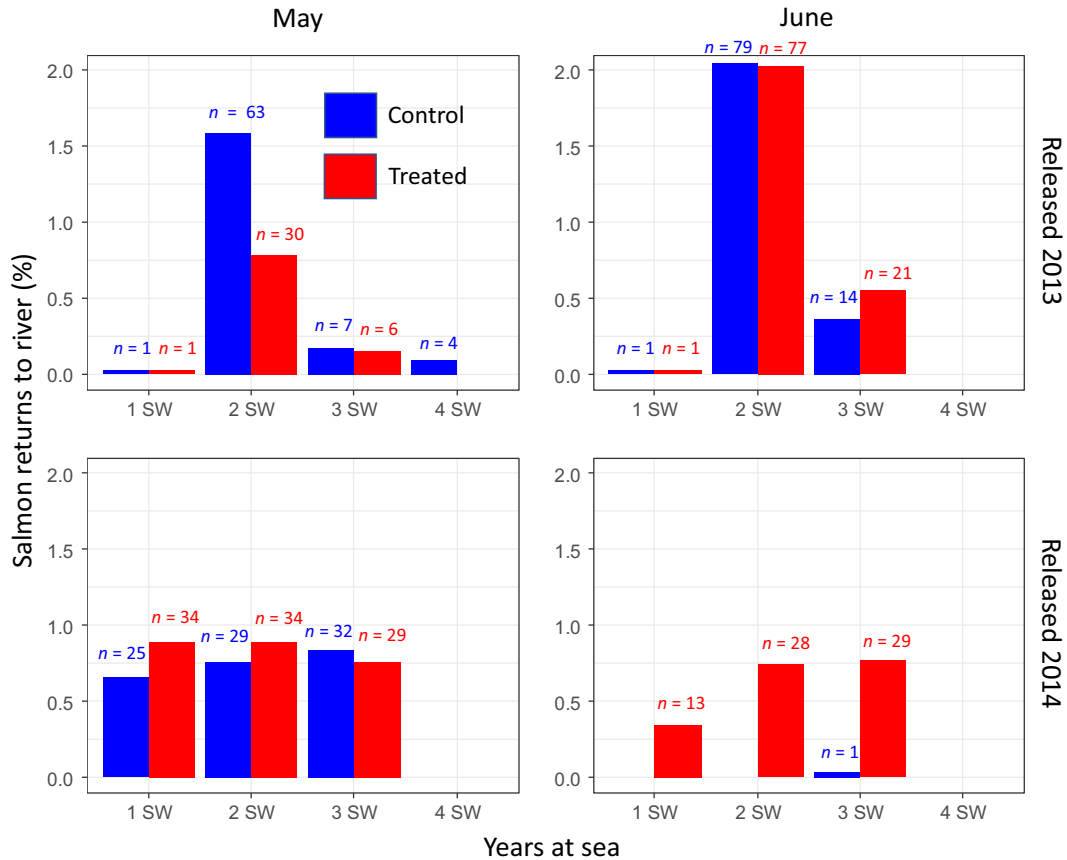


FIGURE 4 Adult salmon return in percent and number of years at sea for salmon treated with prophylaxis and control fish, released in May and June 2013 and 2014

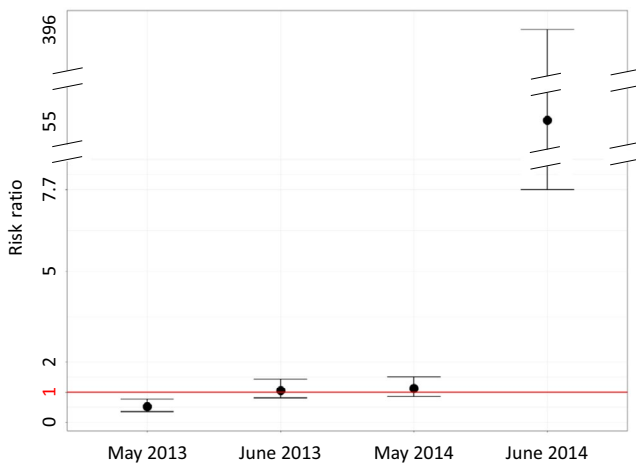


FIGURE 5 Risk ratio (RR) with 95% CIs of treated versus control fish, from the four experimental releases. RRs higher than 1 indicate higher likelihood of treated fish to return. Differences in RRs are statistically significant when the confidence intervals do not contain the value of 1

Lice Infestation Pressure, *Treatment* and the interaction between these were all significantly contributing to the probability of return of adult salmon ($p < 0.0001$ for all, Table 2). Increasing lice infestation pressure had a negative effect on the probability of return. *Treatment* had a positive effect in the centre and at high lice densities, but the

TABLE 2 Results from the GLM model testing survival (i.e. return and recapture in river) as a function of *Lice Infestation Pressure*, *Treatment* and the interaction between these

	Estimate	SE	z-value	p-value
Intercept	-4.5559	0.1488	-30.618	<0.0001
<i>Salmon lice</i>	-2.7587	0.5149	-5.358	<0.0001
<i>Treatment</i>	0.6629	0.1597	4.150	<0.0001
<i>Salmon lice</i> × <i>Treatment</i>	2.7125	0.5274	5.143	<0.0001

interaction effect with *Lice* indicated that *Treatment* was beneficial for the fish at high lice densities but negative at low lice infestation pressures.

3.3 | Growth at sea

The weight of returning salmon increased approximately linearly with increasing number of winters at sea and the fish added about 2–3 kg of body weight per year (Figure 6). We could not trace any effect of treatment on the size of returning fish ($p = 0.58$, linear regression, Table 3).

Fish released in June showed a general reduction in weight at return compared to fish released in May the same year (the only

FIGURE 6 Weight of Atlantic salmon returning from the sea 1, 2, 3 and 4 years after the four release trials in May and June 2013 and 2014. Horizontal bars show median size, boxes show interquartile range, whiskers extend to the farthest observations <1.5 the interquartile range and points show single observations outside this range. Numbers above the boxes denote sample size

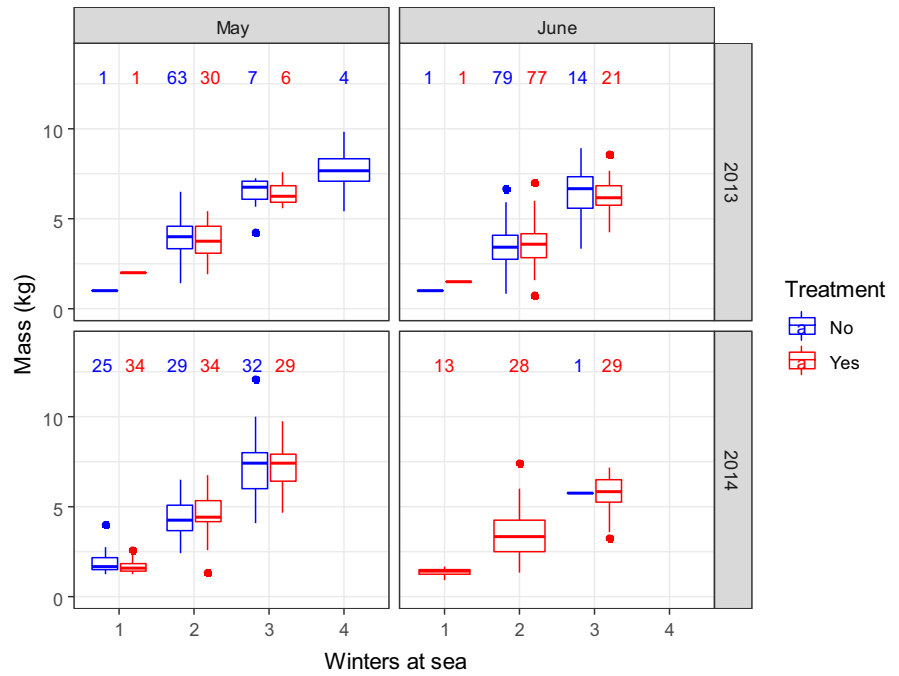


TABLE 3 Results from the linear regression model testing for relationships between individual fish *Weight* at return and lice infestation pressure (*salmon lice*), *Treatment*, *Seawinter* and *Sex*

	Estimate	SE	df	t-value	p-value
Intercept	-1,060.46	238.52	510	-4.446	<0.001
<i>Salmon lice</i>	-606.25	137.84	510	-4.398	<0.001
<i>Treatment</i>	60.34	108.0	510	0.56	0.577
<i>Seawinter</i>	2,498.38	92.7	510	26.96	<0.001
<i>Sex</i>	-297.62	112.0	510	-2.66	0.008

exception was for females released in 2013). This effect was much stronger for fish released in 2014 and consistent among females and males. Fish released in June 2014 were about 500 g lighter at return for each winter spent at sea, compared to fish released in May (Figure 7).

4 | DISCUSSION

4.1 | Lice-induced mortality

We present a unique documentation of mortality effects on Atlantic salmon, caused by salmon lice. Salmon smolts (unprotected control fish) that were released by their native river and exposed to high lice density (June 2014) suffered a 99.97% mortality rate. This was much higher than smolts in the paired release group protected with prophylaxis, where the mortality was 98.1%. The difference between the treatment and control groups in this trial thus resulted in the exceptionally high RR of 55.3:1, i.e. more than 50 times higher likelihood of survival and return for treated fish. This outcome nearly doubles the highest RR described in the 118 Norwegian release trials analysed in a recent meta-analysis (Vollset et al., 2016) and is a very strong support for our hypothesis (H_1) that lice, at high densities do have a large effect on the mortality of Atlantic salmon. If we let the surviving individuals from the treated group (1.9% of the released fish) represent the expected baseline survival for returning adult spawners, the control group suffered a 98.4% *added mortality*. This can be attributed directly to the effect of lice since RCTs are particularly directed at studying the effect of a single stressor, i.e. the factor that the treated group is protected against (here lice) and which the control group is vulnerable to. Our data confirm and strengthen the theoretical/model-based understanding that lice is a key driver of mortality

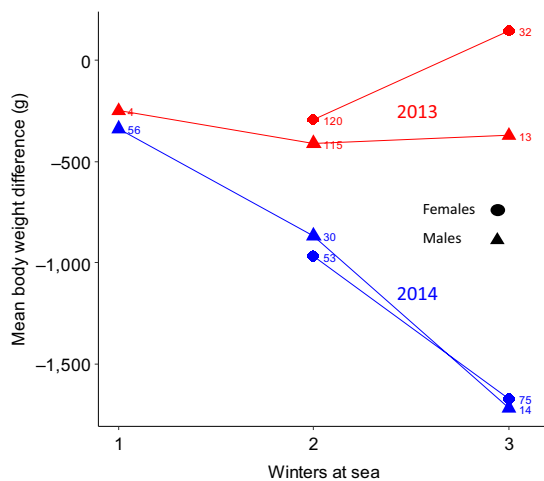


FIGURE 7 Body weight mass difference at return between smolt released in June (treated and control fish pooled since these groups did not differ in the growth model) as compared to fish released in May, in 2013 (red) and 2014 (blue), separately for females (circles) and males (triangles). Points show observed mean differences after 1, 2 and 3 seawinters. Numbers indicate sample sizes of weighed fish at return

risk in migrating Atlantic salmon smolts (Kristoffersen et al., 2018; Vollset, 2019), and also illustrate that the ultimate consequence of a high lice density may mean that the mortality can be close to 100% if the fish migrates under high lice infestation pressures. Modeled mortality estimates near 100% for migrating smolts have been published (worst case scenarios), and illustrate what may happen when the migration period is delayed, prolonged, or when the fish show low progression rates in their migration (Kristoffersen et al., 2018).

4.2 | Effects on growth

There was no overall effect of treatment on the weight of returning fish. We thus rejected our hypothesis that salmon lice density caused a reduced growth rate in Atlantic salmon (H_2). However, we made an interesting observation related to the body size of returning fish; treated smolts released in June 2014, at the highest lice density, were about 500 g lighter for each year spent at sea, compared to fish released the same year in May. This pattern was consistent in both females and males. Although some of this weight difference (loss) may be explained by a longer growing season the first year (3 weeks longer), we argue that this result also may have been caused by lice. The prophylactic agent we used (SubEX) does not prevent attachment of copepodids on the fish, it only prevents development of lice into later life stages (Skilbrei et al., 2015). Hence, the fish may still respond with stress reactions to attaching or attached lice, potentially leading to reduced growth rates at high lice densities, i.e. as observed in our data. Further studies are recommended to clarify this issue.

The interpretation of results from studies of both mortality and growth in the same groups of fish is not straightforward. Negative effects on growth caused by lice infestation in salmonids may be masked by size-selective mortality (Thorstad et al., 2015). Given our high mortality rates, any size-selective mortality may cause a bias in the growth data. Moreover, it is likely that a stress factor which can cause mortality to an individual also may reduce the growth rate in the same fish. Therefore, negative effects of lice on the growth of the fish are easily masked. Reduced growth rates in Atlantic salmon, due to lice infections, are shown previously, both from field and laboratory studies (Skilbrei & Wennevik, 2006; Skilbrei et al., 2013; Susdorf et al., 2018; Tveiten, Bjørn, Johnsen, Finstad, & McKinley, 2010), but depend on marine survival (Vollset, Barlaup, & Friedland, 2019).

4.3 | Challenges in the study design of lice-induced effects on salmonid fish

There are remaining methodological and statistical challenges related to the study of how lice affect wild salmonid populations: (a) the large variability in lice abundance on individual fish in the host population, typically including a relatively high proportion of fish with zero lice, many fish with a few lice and some fish with hundreds of lice; (b) the

large variability in lice density within a single season as well as between years and (c) the high complexity and significant inter-annual fluctuations in a range of environmental factors. These environmental factors influence the timing, development and survival of both the salmon lice and its Atlantic salmon host. Therefore, ideally, several RCT trials should be conducted consecutively within the same study. With such a study design, the outcome of the Atlantic salmon sea migration can be compared at different densities of lice.

Our four large-scale and long-term field experiments enabled comparisons of lice effects on Atlantic salmon at different lice densities, played out under natural conditions. Whereas the year 2013 had low lice densities (due to following—removal of salmon in aquaculture in spring), the year 2014 had normal (full) production of Atlantic salmon and had much higher lice densities. In addition, we released experimental groups of fish in May and June to include the seasonal (within-year) increase in lice.

We used two independent methods to determine the lice infestation pressure; firstly, lice counts on Atlantic salmon in sentinel cages, and secondly, modelled density and distribution of infective lice copepodids (Sandvik et al., 2016). Both these methods indicated that: (a) the following regime was highly effective in reducing the lice density in 2013 and (b) the lice density increased strongly from May to June in both years.

The lice counts on experimental Atlantic salmon in cages indicated that lice density increased about 10–25 fold from May to June. Also, the estimated density of lice decreased by approximately 90% when fish was removed by spring following (2013 vs. 2014). The high efficiency of following for reducing lice from the environment indicates that salmon farming is a key determining factor for the infestation pressure of lice.

4.4 | Toxicity of treatment against lice may have caused biased mortality estimates in previous studies

An interesting observation in our study was that twice as many fish returned from the control group ($RR = 0.52$, compared to the treated fish) in the May 2013 release, when the density of lice was at its lowest. The higher survival in the control group when the lice density was low, indicates a negative cost of the treatment with SubEX in our experiments. If SubEX, or other prophylactic treatments, have a negative effect on the salmon smolts (e.g. toxicity), this may in fact mask the true effects of lice in similar experiments. The scientific literature is sparse on potential negative effects of treatment against lice. One laboratory study showed no effect on fish growth after treatment with SubEX (Skilbrei et al., 2015), and Gjelland and co-workers speculated that intracoelomic (body cavity) treatment with emamectin benzoate (another prophylactic agent against lice) induced behavioural responses in sea trout (Gjelland et al., 2014).

Negative or toxic effects of prophylactic treatment against lice would only be observable in field experiments when the density of lice is low or negligible. At medium or higher densities of lice, i.e. when negative effects start to hamper the fish, a toxic effect of

SubEX would be compensated or masked by the positive effect of the protection against lice. In the June 2013 and May 2014 releases of salmon, when the lice densities were intermediate, we argue that the results, i.e. RRs not significantly different from 1, indicate a balancing effect of the toxicity of SubEX and the improved conditions for the fish by being protected from lice.

Importantly, if a prophylactic treatment (SubEX or others) is toxic to the experimental fish, research may underestimate the real effects of lice. For example, the meta-analysis performed by Vollset and co-workers, using data from 118 release groups and more than 650,000 individual fish, found no effect of treatment (RR ~1.00) when the baseline survival of the fish was high (Vollset et al., 2016). We argue that this result may be systematically biased by a potential toxic effect of the treatment. In other words, a real and significant mortality to the Atlantic salmon smolts, caused by a moderate lice density, may not be observed in experiments since the effect is masked by a similar mortality caused by the chemical treatment. This issue merits further investigation.

Vollset and co-workers have shown that lice may cause a delayed return in Atlantic salmon, which also alter the age-distribution in spawning populations (Vollset, Barlaup, Skoglund, Normann, & Skilbrei, 2014). Such effects could be caused by selective mortality in early maturing Atlantic salmon individuals, or, perhaps more likely, that lice infestations lead to reduced growth, which delay both maturation and the return to the river.

Our results (within-year and within-treatment-group comparisons, both years) show that a higher proportion of the fish spent more years at sea when they were released at high lice infestations (June), i.e. giving some support to the hypothesis that high lice infestations can delay the return of sea run Atlantic salmon.

4.5 | Size and efficiency of protected areas

Interestingly, the Etne fjord, where we released our experimental smolts, is a protected 'National Salmon Fjord' without any aquaculture production. This is clearly reflected in the low lice infestation pressure observed inside the Etne fjord, compared to other parts of the outer Hardangerfjord (cf. Figures 2 and 3). However, as the Etne fjord only covers a minor part of the migration route of the salmon smolts on their way to the open ocean, the protection status can be of limited value or even totally misleading. Our data document that experimental smolts, which migrated out during a high lice infestation pressure, had an extremely low probability of survival despite being released in a protected fjord. This illustrates an important argument on a management level: protected areas need to cover a significant part of the area where the organism under protection experiences relevant stress factors (Bjørn et al., 2011; Serra-Llinares et al., 2014). In the case of the Etne fjord, the defined area under protection as a 'National Salmon Fjord' is too small to secure wild populations of Atlantic salmon if lice infestation pressure reaches levels near what we observed in June 2014. A deadly level of lice in early to mid-June

would also imply that late migrating natural smolts would be highly vulnerable to harm.

4.6 | Stronger lice-induced effects with longer migration routes?

In River Guddal, situated in the central part of the Hardangerfjord, about 30 km North of River Etne, the smolt migration of Atlantic salmon has its peak in mid-to-late May (Skaala et al., 2019). If the smolt-migration in the River Etne follows the pattern in River Guddal, most of the natural smolts probably migrate through the fjord system marginally before, or partially overlapping with the period where we observed the deadly high levels of lice in 2014. According to our oceanographic model, the sharp increase in lice density started already around 20 May 2014 and may thus have contributed to the mortality in the natural smolt that year.

Our results are also relevant for smolts migrating from the inner rivers in the Hardangerfjord. Wild Atlantic salmon from these rivers will likely use longer time for their migration and thus arrive at the outer region of the fjord later than smolts from rivers closer to the fjord outlet. Consequently, Atlantic salmon populations migrating long distances in the fjord are expected to be more seriously affected by lice. For example, in the Vosso River, lice-induced mortality has been estimated to surpass 30%, which illustrates a more general trend: wild Atlantic salmon populations from the inner part of the fjord have lower population densities (Vollset, Skoglund, et al., 2014). This supports the hypothesis of increased lice-induced mortality in populations with long fjord migrations.

4.7 | Timing is everything

To improve management, it is now crucial to understand the population dynamics and not least the *timing* of lice blooms, which needs to be compared to the *timing* of the salmon smolt migration, in all individual rivers where lice can be a threat. Moreover, the timing of both lice development and smolt migration will be affected by climate change, but not necessarily in a synchronized manner. The inter-annual variation in *timing* for the smolt migration varies about 3–4 weeks from year to year in Norwegian rivers (Kristoffersen et al., 2018) and includes triggers (e.g. precipitation, snow melting, river discharge, etc.) that are not expected to affect the timing of lice blooms. Thus, climate change may cause asynchronous shifts in *timing* of fish migrations and lice blooms, with unknown consequences.

4.8 | Conclusions and policy recommendations

By combining four RCTs (prophylaxis vs. control) under vastly different (manipulated) lice densities and increased recapture efforts on returning individuals, we were able to provide compelling evidence that lice

at high densities can have a devastating impact, i.e. causing an *added* mortality of 98.4% (i.e. on top of the baseline mortality). Moreover, we highlight that *timing* is crucial: in years with little overlap between lice blooms and Atlantic salmon smolt migration, only minor effects can be expected. Conversely, in years with a strong overlap in timing, serious mortality effects can be expected. This is a major challenge for the management system since this timing cannot be controlled, it undergoes unpredictable variation from year to year and is expected to be altered by coming changes in climate. To cope with the problems created by lice, various chemical, mechanical/thermal and biological treatments have been, and are still used to delouse fish in aquaculture (particularly in the period where wild fish smolts migrate from the rivers). However, all delousing methods have their limitations; chemical treatments have become less efficient due to resistance (Aaen, Helgesen, Bakke, Kaur, & Horsberg, 2015) and may also pollute the environment, mechanical/thermal and biological treatment has unresolved animal welfare issues as well as increased risk of escapes (both of salmonids and cleaner fish; Brooker et al., 2018; Bui, Oppedal, Sievers, & Dempster, 2019; Overton et al., 2019; Staven et al., 2019). Thus, lice persist as a core challenge for the interaction between aquaculture and wild salmonids. Problems experienced this far have been related to an increasing biomass of fish in aquaculture and the future management may need to adapt to new conditions, such as climate change and altered biomass of fish. To understand the full context, one also needs to factor in the stated political goal to expand the production of salmon and trout by 500% within 2050 (Vollset et al., 2017).

Nevertheless, the lice challenges can be solved. For policy recommendations, we argue that there is a great potential for limiting the negative effects of lice by spatial separation. Fish in aquaculture can be isolated (totally or partially) from both the lice and from wild salmon fish: (a) salmon aquaculture may use closed farming pens (on land or in the sea), which will give near total control over the lice; (b) salmon aquaculture may use improved constructions of farming pens that limit the exposure of farmed fish to lice, for example by using pens with 'snorkel system' that segregates lice and fish vertically, or by semi-closed pens with protective skirts; (c) farming may also be moved away from vulnerable habitats for wild salmonids (fjords and near coastal areas); e.g. by increasing the size of protected areas, or move pens out at sea where the volume of water will dilute and thus reduce, but not solve, the problems with lice.

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AUTHORS' CONTRIBUTIONS

T.B., K.Ø.G., R.M.S.-L., B.F., R.N., Ø.K., A.D.S., O.T.S., Ø.S. and P.A.B. conceived the ideas and designed methodology; R.M.S.-L., R.N.,

A.D.S., Ø.S. and K.M.S.E. collected the data; T.B., K.Ø.G., R.M.S.-L., R.P. and A.D.S., analysed the data; T.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication (except O.T.S. who died before its completion).

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.zw3r2285d> (Bøhn et al., 2020).

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