

RESEARCH ARTICLE

Salmon louse infestation levels on sea trout can be predicted from a hydrodynamic lice dispersal model

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Abstract

1. The abundance of the parasitic salmon louse has increased with the growth in aquaculture of salmonids in open net pens. This represents a threat to wild salmonid populations as well as a key limiting factor for salmon farming. The Norwegian 'traffic light' management system for salmon farming aims to increase aquaculture production while securing sustainable wild salmonid populations. However, this system is at present solely focusing on mortality in wild Atlantic salmon, while the responses of sea trout with different ecological characteristics are not included.
2. We analyse lice counts on sea trout from surveillance data and use Bayesian statistical models to relate observed lice infestations to the environmental lice infestation pressure, salinity and current speed. These models can be used in risk assessment to predict when and where lice numbers surpass threshold levels for expected serious health effects in wild sea trout.
3. We find that in production areas with the highest density of salmon farms (West coast), more than 50% of the sea trout experienced lice infestations above the levels of expected serious health effects.
4. We also observed high lice infestations on sea trout in areas with salinities below louse tolerance levels, indicating that fish had been infested elsewhere but were returning to low-saline waters to delouse. This behavioural response may over time disrupt anadromy in sea trout.
5. The observed infestations on sea trout can be explained by the hydrodynamic lice dispersal model, which provides continuous estimates of lice exposure along the whole Norwegian coast. These estimates, which are used in Atlantic salmon research and management, can also be used for sea trout.
6. *Synthesis and applications.* Wild sea trout, spending its entire feeding migration in fjords and coastal areas, is at higher risk than wild Atlantic salmon to lice infestations from industrial salmon farming. The high levels of lice infestation we observed on sea trout question the environmental sustainability of the current

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aquaculture industry in areas with intensive farming. We discuss the complex responses of sea trout to salmon lice and how the Norwegian 'traffic light' management system may include data on sea trout.

KEYWORDS

aquaculture and wild fish interactions, management, parasite-induced health effects, salmon lice, sea trout, surveillance data

1 | INTRODUCTION

The ecto-parasitic salmon louse *Lepeophtheirus salmonis* (Krøyer, 1837) has benefited from the growing aquaculture industry along the Norwegian coastline and elsewhere, leading to altered parasite–host interactions (Aldrin et al., 2019). A key driver for the altered interactions is the increase in number of hosts for lice by several orders of magnitude over the last decades (Garlock et al., 2020; Heuch & Mo, 2001). Extensive research on salmonids has identified health risks associated with the increasing amounts of salmon lice, which feed on skin, mucus and blood, causing osmoregulatory and physiological stress responses in the fish (Finstad et al., 2000; Fjellidal et al., 2020; Grimnes & Jakobsen, 1996).

Sea trout *Salmo trutta* (L.) is an anadromous phenotype of brown trout. Brown trout must reproduce in freshwater, but may have facultative sea migrations that may last from weeks to months each year (Klemetsen et al., 2003). It may smoltify at a size of 12–25 cm (about 10–200 g weight) and make marine foraging migrations during late spring and summer to enhance the growth and reproductive potential (Elliott, 1994), that is at the time when both temperature and salmon lice production increases (Serra-Llinares et al., 2016; Vollset et al., 2018). In the marine environment, sea trout typically move actively around in the fjord system or in near-coastal areas, mostly remaining within 10–20 km from the river outlet (Flaten et al., 2016; Gjelland et al., 2014), where they feed in the upper water column, and therefore potentially overlap with the highest salmon lice concentrations (Eldøy et al., 2017; Johnsen et al., 2014). Moreover, sea trout are exposed to lice infestations over a much longer period compared to the Atlantic salmon (Bjørn et al., 2007; Thorstad et al., 2016).

The management system in Norway has acknowledged that salmon farming may lead to lice infestation levels threatening wild Atlantic salmon populations. In response, a new regulatory framework was recently implemented that uses a 'traffic light' system to evaluate how 13 separate production areas can achieve sustainable growth, using regional lice-induced mortality on out-migrating salmon post-smolts as the indicator. Decision-making is thereby based on scientific data to decide whether the farm production of fish should be reduced, kept on the same level or allowed to grow further (when expected lice-induced mortality on salmon post-smolts is >30%, 10%–30% and below 10% respectively). Such adaptive management may dampen the environmental impact from salmonid farming and improve the sustainability of Norwegian aquaculture. However, potential negative

effects on wild populations of other important fish species susceptible to salmon lice infestation, that is sea trout and Arctic char *Salvelinus alpinus*, are not assessed in the 'traffic light' system. This is not due to a lack of data on lice infestations on sea trout. The Institute of Marine Research and other institutions have been monitoring lice infestations on sea trout and Arctic char along the entire Norwegian coast since the program began in 1992 (Heuch et al., 2005).

While the surveillance program has accumulated long time series of data covering the Norwegian coast, major analytical challenges have hampered the understanding of negative effects of lice on sea trout. Firstly, lice infestations on fish typically present zero-inflated, right-skewed distributions, with a significant proportion of the fish (20%–40%) having zero lice. Secondly, lice infestations on fish show strong seasonal dynamics as well as spatial and between-year variability (Hurford et al., 2019; Jansen et al., 2012; Sandvik et al., 2016) and sea trout may respond to high lice infestations by prematurely returning to freshwater to regain osmotic balance and survive (Birkeland & Jakobsen, 1997; Halttunen et al., 2018; Pert et al., 2009). Finally, site- and time-specific data on key environmental variables (temperature, salinity, current and lice infestation pressure) where the fish has been sampled have not been available (Helland et al., 2015).

The use of coupled hydrodynamic-biological (hereafter termed hydrodynamic) models has recently increased the understanding of how infective lice larvae are dispersed in space and time (Asplin et al., 2020; Murray & Gillibrand, 2006). Hydrodynamic models cover the full Norwegian coastline, and daily data on lice infestation pressure, temperature, salinity, current speed and direction can be generated for any locality (Asplin et al., 2020). This enables an improved understanding of lice infestation patterns on sampled wild salmonids.

In this article, we use Bayesian statistical models to analyse salmon lice count data on sea trout sampled in 2019 from 40 study sites, that is covering the full south–north gradient of the Norwegian coastline. We attempt to predict lice infestation on fish caught in the wild using averaged (20 km, week) subsets of lice infestation pressure, current strength and salinity from our hydrodynamic model.

We hypothesize that: (1) the observed infestations on sea trout collected in the marine environment can be predicted from site (mean over 20 km)- and time (mean over week)-specific modelled data on (a) lice infestation pressure, (b) current strength and (c) salinity; and (2) a modelled threshold level for the infestation pressure of lice in the environment can be translated into expected negative health effects on wild sea trout.

2 | MATERIALS AND METHODS

2.1 | Study area, fish sampling and management/production areas

More than 1,100 locations are approved for aquaculture production along the Norwegian coast, but 600–700 are simultaneously active in production. These locations are distributed in 13 management/production areas (hereafter production areas; Figure 1). The production areas were defined to minimize cross-dispersion (Ådlandsvik, 2015).

We analysed a dataset of $n = 2937$ sea trout <200 g, sampled at 40 different sites in 2019 (the most recent data at the onset of this work; Figure 1). The fish was caught in traps and gillnets (17–21 mm mesh size) in week numbers 20–31 (mid-May to end of July) with a gradual delay from south to north (Table 1). The sampling thus targeted post-smolts recently migrated out from the rivers, a migration that is delayed from south to north by about 6–8 weeks (Johnsen et al., 2020; Kristoffersen et al., 2018). An approval for the work was granted from the animal ethics committee under The Food Safety Authority (FOTS Id 14809).

2.2 | Lice counts and expected health effects on fish

Lice counts on sea trout were performed in the field immediately after collection. Fish from traps were anaesthetized before sampling (Benzocaine 200 mg/ml diluted by 15–20 ml/100 L water) and released to the sea after recovery. Trout from gillnets were killed. Lice counts were performed with the fish submerged in a white plastic tub (5–10 L) using a strong headlamp (>500 lumen). Counts were performed by certified personnel and the following categories were quantified: copepodid, chalimus 1, chalimus 2, pre-adult, adult male

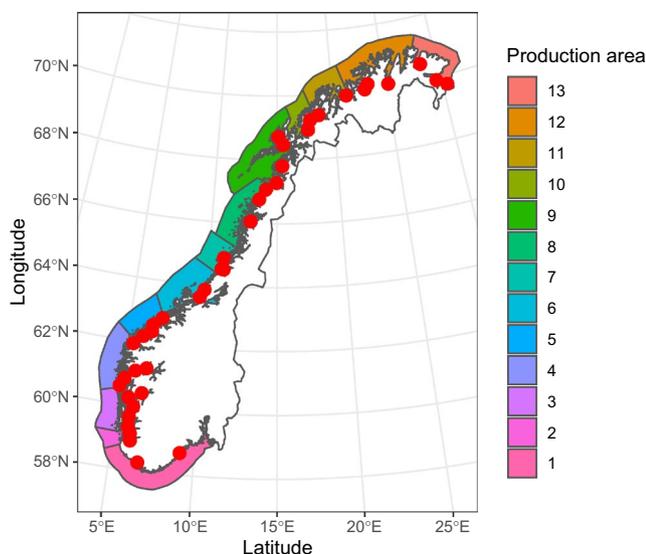


FIGURE 1 Map of the study area. Red dots show sampling sites and polygons represent the 13 production areas along the Norwegian coast

and adult female. Fish length in millimetre and mass in gram were recorded. Based on previous studies, we defined infestations of 0–0.1 salmon lice per gram as a low dose of salmon lice on sea trout. Doses of 0.1–0.3 and >0.3 were defined as moderate and critical doses, respectively, expected to result in health effects on the fish. Doses above 0.3 lice per gram trigger physiological stress responses with return to freshwater for sea trout <150 g (Taranger et al., 2015).

2.3 | Hydrodynamic model for environmental variables

The *lice infestation pressure* in the environment was estimated by combining: lice counts from all active aquaculture sites along the Norwegian coast (weekly counts of adult female lice), temperature at 3 m depth, monthly number of fish per farm and a hydrodynamic dispersion model system (Albretsen et al., 2011; Myksvoll et al., 2018; Sandvik et al., 2020).

From the hydrodynamic model, we extracted median values of *lice infestation pressure*, *salinity* and *current* in the upper 2 m of the water column from a 20-km radius around the catch site of each sea trout. We averaged the data over weeks to compare with time periods the fish samples were grouped into (cf. Table 1), and used *lice infestation pressure*, *salinity* and *current* as explanatory variables in the zero-altered gamma models.

2.4 | Zero-altered gamma (ZAG) models to predict salmon lice on the fish

We modelled *lice infestation* (lice/g) on the fish as a response to variation in the environmental variables *lice infestation pressure*, *current* and *salinity*. The variable *lice infestation pressure* was first square-root transformed, subsequently all variables were standardized to zero mean and unit standard deviation before inclusion into our main model:

$Lice\ infestation \sim Lice\ infestation\ pressure + Current + Salinity$, using $Site = random$. (1)

We ran separate analyses for (i) the total number of lice and (ii) the number of sessile young stages (copepodids, chalimus 1 and 2 only).

The model was implemented in the INLA package (Lindgren & Rue, 2015) for R (R-Developmental-Core-Team, 2019). Due to the zero-inflated and right-skewed nature of the response variable, the number of salmon lice per gram fish, we used a ZAG random effects modelling framework:

$$Y_i \sim ZAG(\mu_i, \pi_i) \text{ or } Lice\ on\ fish_i \sim ZAG(\Gamma_i, Bernoulli_i), \quad (2)$$

$$Mean(Y_i) = \pi_i \times \mu_i \text{ and } var(Y_i) = \frac{\pi_i \times r + \pi_i - \pi_i^2 \times r}{r} \times \mu_i^2, \quad (3)$$

$$\log(\mu_i) = \beta_1 \times Lice\ Inf\ Pressure + \beta_2 \times Current + \beta_3 \times Salinity + u_i, \quad (4)$$

$$\text{logit}(\pi_i) = \gamma_1 \times Lice\ Inf\ Pressure + \gamma_2 \times Current + \gamma_3 \times Salinity + v_i, \quad (5)$$

TABLE 1 Week, production area and the number of sea trout we counted lice on

Week	Production area												
	1	2	3	4	5	6	7	8	9	10	11	12	13
20	32	0	0	0	0	0	0	0	0	0	0	0	0
21	31	165	162	73	38	0	0	0	0	0	0	0	0
22	39	92	45	197	100	0	0	0	0	0	0	0	0
23	0	65	92	185	259	25	43	0	0	0	0	0	0
24	0	0	0	43	165	28	121	36	8	0	0	0	0
25	0	0	0	0	11	26	79	58	39	0	0	0	0
26	0	0	0	0	0	0	0	42	51	0	0	0	0
27	0	0	0	0	0	0	0	0	17	57	19	0	0
28	0	0	0	0	0	0	0	0	0	194	0	32	0
29	0	0	0	0	0	0	0	0	0	30	15	41	68
30	0	0	0	0	0	0	0	0	0	0	0	16	40
31	0	0	0	0	0	0	0	0	0	0	0	0	58

where Y_i is the observed number of lice on sea trout and follows a ZAG distribution. There are two components in the model: a binary Bernoulli part for lice presence or absence, with the mean π_i and a logistic link, and a gamma part for positive values of lice, with the mean μ_i and a log link (Zuur & Ieno, 2018).

In addition to other model validations, we also performed simulation tests to explore the ability of the ZAG model to cope with the proportion of zeros in the dataset (23% and 30% zeros for the total and sessile young lice respectively) and compared the observed versus expected values from the final ZAG model. The model was able to cope with the zeros (21% and 28% zeros were the modes in the simulation output, for the total and sessile young lice, respectively, Appendix Figure I), but showed a compressed set of expected values (up to about 1.5 lice/g) compared to the observed values, where a small number of fish had extremely high level of infestations (up to 9.1 lice/g; Appendix Figure II). We ran a series of cross-validation tests (with a simpler mixed model—*lmer* in R) to explore (i) whether single or few Sites were able to drive the main trends, and (ii) whether repeated random sampling of 80% ('training set') of the data could predict the last 20% of the data ('test-set'), using the R package `GROUPDATA2`. The cross-validation confirmed our main results from the ZAG model (Appendix Figures IX–XI).

3 | RESULTS

3.1 | Salmon lice in the environment and on the fish

The highest loads of actual *lice infestation* on sea trout, as well as the highest *lice infestation pressure* in the environment, were seen in production areas 4 and 5 (Figure 2), that is on the western coast of Norway (cf. Figure 1). Infestations were clearly lower in the far south and in the north, with intermediate values in between.

The proportion of sea trout with *lice infestation* above 0.3 lice per gram (critical dose) was below 20% in production areas 1, 2, 3, 8, 9,

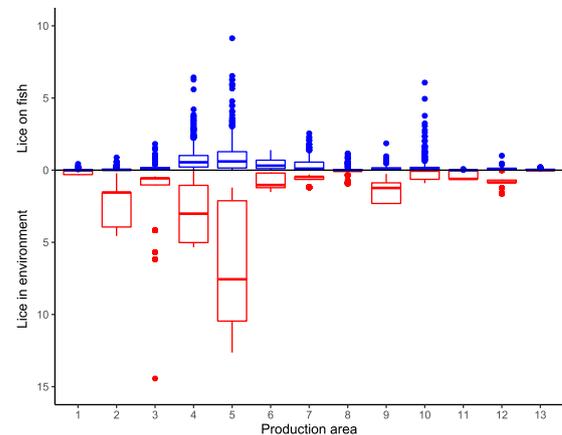


FIGURE 2 *Lice infestation* observed on the fish (all stages included, blue) versus modelled *lice infestation pressure* in the environment (red) in the 13 production areas along the Norwegian coast

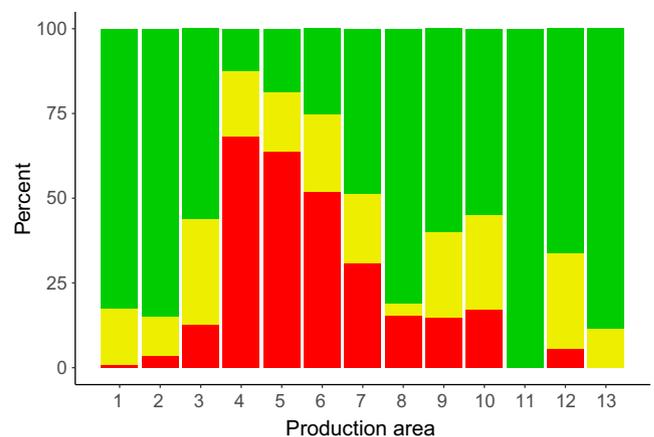


FIGURE 3 Proportion of fish with <0.1 lice (green), 0.1–0.3 lice (yellow) or >0.3 lice (red) per gram fish, respectively, in the 13 production areas

10, 11, 12 and 13 (Figure 3). In production area 7, this proportion was around 30%, and in production areas 4, 5 and 6, between 52% and 68% of the sea trout had such high doses of lice (Figure 3). In most of the production areas, about 10%–30% of the fish had between 0.1 and 0.3 lice per gram fish (moderate dose). Production area 11 showed only fish with <0.1 lice per gram.

3.2 | Observed lice on sea trout as a function of modelled environmental variables

3.2.1 | *Lice infestation pressure*

The number of lice observed per gram sea trout was strongly and positively related to the environmental infestation pressure (ZAG model, Figure 4; Table 2). This relationship was seen both for the total number of lice and for sessile young stages of lice per gram fish. Infestations were, as expected, generally higher when all lice stages were included. Moreover, the variability in lice infestations on individual sea trout was large along the full range of environmental lice infestation pressures.

The prediction line from the model indicated that fish exposed to an environmental lice infestation pressure above about 2.5 copepodids per 100 m² (confidence bands covering 1.5–4.5) can be expected to have more than 0.3 lice per gram of salmon lice (critical dose).

The random effects of *location* were also significant, both in the Bernoulli and the gamma models, demonstrating high variability along the coastline (Table 2).

3.2.2 | *Current strength*

Both the probability of lice infestation (Bernoulli component of model) and the level of infestation (gamma component) were

significantly and positively correlated with *current* (Figure 5; Table 2). The effect size was 0.41 as compared to 2.06 for *lice infestation pressure* in the binomial part of the model (having an infection or not), but as high as 0.35 as compared to 0.51 for the *lice infestation pressure* in the gamma part of the model (infestation intensity; Table 2).

3.2.3 | *Salinity*

Salinity had the weakest predictive power in the model with a non-significant trend (Figure 6; Table 2). Interestingly, even in areas where salmon lice are not expected to live, that is below a salinity of 15–20, relatively many individual fish were observed with high infestation levels.

4 | DISCUSSION

In this study, we found that the hydrodynamic model used to calculate salmon lice dispersal along the Norwegian coast can be used to predict lice infestation on sea trout caught at sea. The hydrodynamic lice dispersal model incorporates temperature-dependent lice development, lice attraction to light and high salinity, and lice mortality to calculate spatio-temporal salmon lice concentrations (infestation pressure), see Sandvik et al. (2016) for details. Our statistical modelling couples this infestation pressure to observed infestations and expected health effects on wild sea trout. Firstly, we document how a spatially heterogeneous host–parasite interaction, characterized by a zero-inflated data structure can be resolved with a Bayesian statistical model. Secondly, we contribute with important empirical support for the hydrodynamic model, which monitor the spread and distribution of infective salmon lice larvae along the entire Norwegian coast (for updated weekly estimates, see www.lakselus.no).

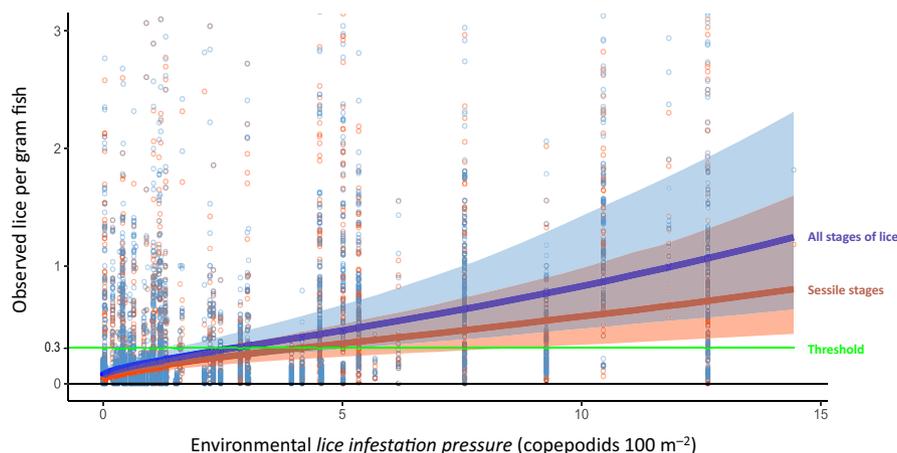


FIGURE 4 Observed (dots) and predicted (line with 95% confidence band from ZAG model) number of salmon lice per gram of sea trout at different lice infestation pressures in the environment. Blue coloured dots, lines and confidence bands represent the total number of lice, orange colour represents only sessile young stages. Green line indicates threshold of 0.3 lice per gram. Note, the y-axis is truncated, $n = 48$ fish had more than three (max = 9.1) lice per gram fish

TABLE 2 Parameter values for the underlying Bernoulli (presence/absence of lice) and gamma (positive values of lice) mixed models (that were glued together in the ZAG model). For graphical output from Bernoulli and gamma models, see Appendix Figures III–VIII

Bernoulli model	Mean	SD	0.025 quantile	0.975 quantile
Fixed effects				
Intercept	1.75	0.32	1.13	2.39
Lice infestation pressure	2.06	0.24	1.61	2.53
Current	0.41	0.17	0.09	0.74
Salinity	-0.18	0.19	-0.57	0.19
Random effects				
Location (40 groups)	1.87	0.26	1.43	2.44
Gamma model	Mean	SD	0.025 quantile	0.975 quantile
Fixed effects				
Intercept	-1.60	0.16	-1.93	-1.28
Lice infestation pressure	0.51	0.11	0.30	0.72
Current	0.35	0.09	0.18	0.52
Salinity	-0.13	0.07	-0.25	0.002
Random effects				
Location (40 groups)	0.97	0.12	0.76	1.24

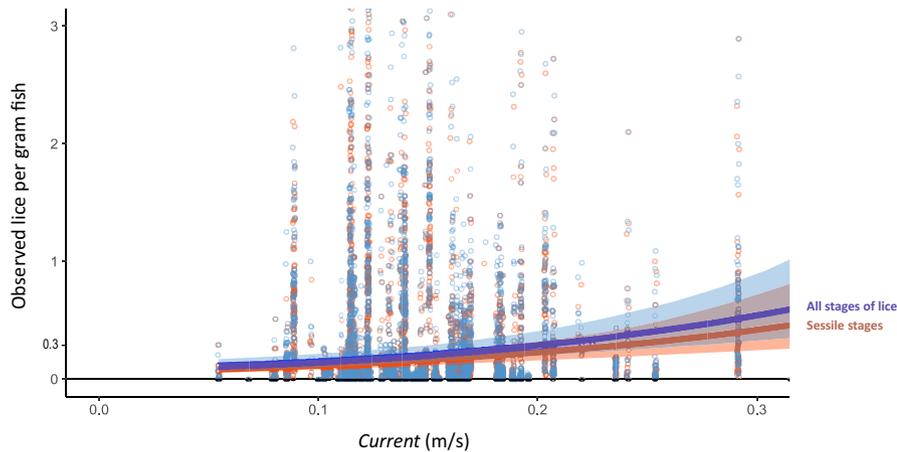


FIGURE 5 Observed (dots) and predicted (line with 95% confidence band) number of salmon lice per gram of sea trout at different current strengths in the environment. Blue coloured dots, lines and confidence bands represent the total number of lice, orange colour represents only sessile young stages

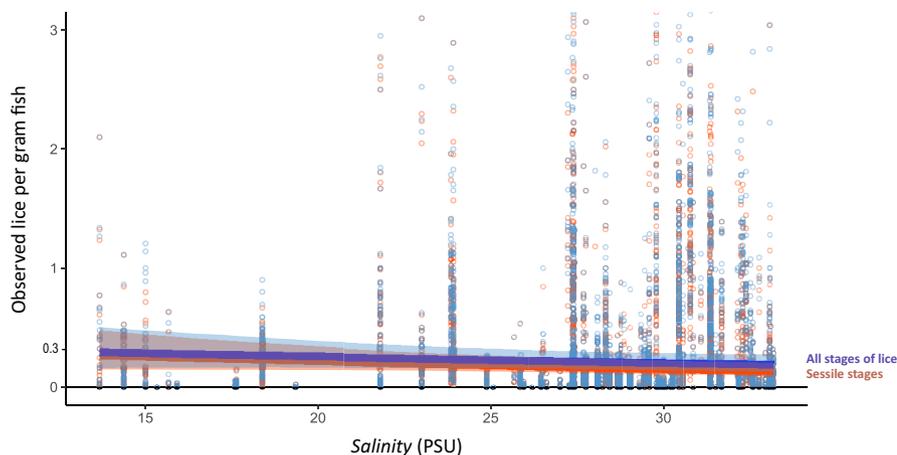


FIGURE 6 Observed (dots) and predicted (line with 95% confidence band) number of salmon lice per gram of sea trout at different salinity levels in the environment. Blue coloured dots, lines and confidence bands represent the total number of lice, orange colour represents only sessile young stages

no). By bringing the hydrodynamic model and the wild fish surveillance program together, we integrate two of the management tools available to understand the impact of salmon lice on wild salmonids.

4.1 | The role of environmental variables for lice infestation—*lice infestation pressure*

We document a strong positive correlation between *lice infestation* on sea trout and *lice infestation pressure* at the catch location of sampled fish. However, there was a large variation around the estimates along the full range of environmental lice infestation pressures. This can in part be explained by a lack of information on the migration history of individual fish and the patchiness in the infestation pressure. Sea trout display a diversity of marine migration patterns and life-history strategies (Davidsen et al., 2014). Thus, samples of sea trout collected will likely consist of several subpopulations with different lice infestation rates and distributions, depending on marine residence time and habitat use (Diserud et al., 2020). Sea trout with high lice infestations have a higher probability of dying or prematurely returning to freshwater (Serra-Llinares et al., 2020), and this group may therefore be under-represented in catch samples. Despite the challenging complexity in the analysis of salmon lice distributions on sea trout from surveillance data (loss of fish that dies, zero-inflated data, unavailable information on how long the fish was exposed to the parasites, etc.), our Bayesian model was still able to predict numerical estimates of lice burdens on sea trout, with confidence intervals, based on the modelled environmental variables. And these estimates indicate when and where sea trout are expected to get pathological effects, based on laboratory studies (Taranger et al., 2015).

The positive correlation between lice loads on wild sea trout and lice dissemination from surrounding fish farms is theoretically well-founded, and has previously been extensively documented in Norway, Scotland and Ireland for sea trout and Atlantic salmon (Gargan et al., 2012; Helland et al., 2015; Johnsen et al., 2020; Serra-Llinares et al., 2020; Vollset et al., 2017). The novelty with the present approach is the integration of space and time-specific model predictions of (a) dispersal of infective copepodids from fish farms, (b) water currents and (c) salinity in all 40 localities where we caught sea trout and counted salmon lice. This allows for a separation of the effects governing copepodid survival until host encounter (as computed with the hydrodynamic model), and the link between copepodid density and host infestation. The hydrodynamic model is an important management tool for the 'traffic light' system in the evaluation of lice effects on wild Atlantic salmon populations. Previous studies have shown that this hydrodynamic model can explain infestation levels on hatchery-reared Atlantic salmon post-smolts in sentinel cages (Sandvik et al., 2016, 2020), and, in combination with a virtual post-smolt migration model, estimate wild Atlantic salmon post-smolt mortalities for 401 rivers in Norway (Johnsen et al., 2020). However, the present work is, to our knowledge, the first published paper that translates the density of lice in the

environment into expected negative health effects on individual sea trout. We argue that this fills a scientific knowledge gap, with great relevance for the management system.

Farms in areas with intensive aquaculture activities in 2019, such as production areas 4, 5 and 6 (with 50–60, 20–30 and 60–70 million fish respectively) on the Norwegian west coast (cf. Figure 1), produced and spread large amounts of salmon lice that may infect wild sea trout. Accordingly, in these areas, we found that more than 50% of the sampled sea trout had more than 0.3 lice per gram fish, that is a critical infestation level (Taranger et al., 2015). In contrast, the lice infestation on wild fish in areas with little farm activities, in southern and northern Norway, and within fjords protected from salmonid farming, was much lower. This also conforms to earlier studies (Serra-Llinares et al., 2014, 2016). The suggested threshold for critical health effects in salmonids at 0.3 lice per gram fish, both for sea trout (preliminary return to freshwater) and Atlantic salmon (mortality), depends on the stage of the parasite (Taranger et al., 2015). The impact on the fish increases with the stage of the lice with full impact from pre-adult and adult lice. As we used counts of lice that included young stages, the mortality rate of developing lice on the fish should be considered. Previous experimental studies have shown significant mortality of lice on Atlantic salmon, mainly in the pre-adult and adult stages (Bui et al., 2016; Hamre & Nilsen, 2011). Other studies have shown that nearly 100% of the lice survives to pre-adult and adult stages (Bui et al., 2018), except at extreme temperatures not relevant for Norwegian field conditions (Dalvin et al., 2020). Therefore, lice mortality rates on the fish seem small, with some uncertainty whether experimental testing in the laboratory is representative for what happens in nature (Hamre et al., 2009). Overall, we argue that the threshold lice level of 0.3 lice per gram fish, causing critical health effects in sea trout, can be used also when young and sessile lice have been counted on the fish.

4.2 | The role of environmental variables for lice infestation—*current*

We found that *current* had the second-most important predicting power (among the tested variables) for the number of lice on sea trout in our analyses, next to the *lice infestation pressure*. Faster water currents contributed positively to increased lice infestations in sea trout. This result implies increased encounter rates between sea trout and copepodids at stronger currents, independent of the actual infestation level.

Laboratory experiments with farmed Atlantic salmon have shown that lice attachment increases with the water current, due to increased encounter rate (Samsing et al., 2015). It has also been shown in the field that stronger currents may slow down the fish (progression rates) and prolong the time exposed to high lice infestation pressure for Atlantic salmon smolts (Halttunen et al., 2018). The fact that we find a positive effect of water current on the probability for being infested, as well as on the infestation intensity,

underlines the importance of individual behaviour. Active fish will tend to gain higher lice infestation than less active fish. Active fish will presumably also find more food and grow better than less active fish, but an increased parasite toll by high activity may offset this advantage.

4.3 | The role of environmental variables for lice infestation—salinity

Salmon lice larvae may adjust their vertical positioning depending on external stimuli (Crosbie et al., 2019). In the salmon lice dispersion model, low-salinity avoidance increases with the amount of freshwater influence (Sandvik et al., 2020). A study that analysed salmon lice infestations on sea trout, using data from 2004 to 2010, found that increasing freshwater influence strongly reduced the number of lice on the fish (Helland et al., 2015). A weakness in that paper was that data on salinity were not available for the stations where the fish was sampled, and therefore had to be roughly estimated from the influx of freshwater in local rivers. In the present data, we were able to base our analyses on modelled weekly salinities from each of the 40 sites where the fish was sampled.

We expected lower lice infestation at lower salinity, but the data showed a weak opposite result, although the parameter estimate was not significantly different from zero. That many sea trout with high salmon lice infestations were found in areas where the salinity was low (<20) suggests that the fish had been infested elsewhere and were seeking brackish or fresh water, where they could re-establish their salt balance and reduce or get rid of their lice burdens (Bjørn et al., 2001; Eldøy et al., 2020; Gjelland et al., 2014). Such behavioural response to lice has been shown to significantly reduce the time sea trout spend for feeding and growing in the marine environment. For example, in an experimental field study that compared sea trout with added lice burdens to control fish (without added lice), sea trout with a high lice infestation reduced the time spent in the sea from 100 to 18 days on average (Serra-Llinares et al., 2020).

4.4 | Evolution and anadromy

During the last decades, the abundance of sea trout has declined markedly in many regions (ICES, 2013). Only 20% of the 430 sea trout populations evaluated in Norway were in good condition (Thorstad et al., 2019). Recent findings from several other countries indicate similar decreases, and for some areas it is hypothesized that this is a consequence of reduced marine survival caused at least in part by changes in food supply or increased parasite infestations related to fish farming (Shephard et al., 2016, 2019). In sea trout populations, mortality in the freshwater phase is often density dependent and can have a population regulating effect. In contrast, mortality in the marine phase is density independent and not regulatory, but has a population reducing effect (Jonsson & Jonsson, 2011). Hence, it is not believed that there are compensatory mechanisms

for additional mortality in the marine phase, and elevated marine mortality rates may therefore result in a reduction in the number of spawning adults. Because sea trout predominantly are females (Jensen et al., 2012), additional marine mortality has an accentuated potential to negatively affect population recruitment by reducing the egg supply. The marine phase is therefore a particularly important life stage of sea trout.

An increase in mortality of brown trout that migrates to sea can lead directly to reductions in the number of subsequent spawners. Mortality may also be induced indirectly through reduced growth rates from lice-induced physiological stress, resulting in an increased predation risk due to a prolonged period in the size-spectrum susceptible to gape-limited predators (Krkosek et al., 2011). Reduced growth associated with lice infestation, as well as premature return, will also reduce the reproductive output of surviving migrants. Increased mortality and reduced reproductive output from marine survivors can also result in indirect changes in migration propensity across generations, resulting from selection on underlying genetic mechanisms (ultimate effect). Hence, salmon lice infections over time may severely impact the rewards of marine migrations, thereby altering population dynamics and demography in populations with migratory brown trout. An individual brown trout has no way of assessing what the conditions are on its potential marine migration route or destination habitat. Thus, its migration decisions are informed not by present conditions, but rather by the Darwinian fitness of its ancestors, which drove either positive or negative natural selection for genes favouring anadromy. This natural selection for anadromy has been going on at least since the last ice-age, that is some 10,000 years ago. Only very recently, say for the last 5–10 generations and in high-production aquaculture regions, this natural selection includes the added environmental stressor of salmon lice at high densities. Therefore, brown trout in areas with high densities of salmon lice may still become anadromous despite low rewards for their migration to the sea. If aquaculture is not able to resolve the problems with salmon lice, natural selection may work against anadromy and over time reduce life-history variation in sea trout.

4.5 | Recommendations for future studies

Two specific ways to improve further studies are to detail the information on individual fish sampled: (a) genetic analysis that reveals from where each sampled sea trout have originated would reduce the variability and improve our ability to predict lice infestations on the fish (Diserud et al., 2020); (b) analyses of scales may reveal the migratory history of the individual fish. Most important is the *timing* of the shift from freshwater to sea water. With a high-resolution method that told us when the fish arrived at sea, our ability to calculate and understand the rates of infestation on the fish would improve significantly.

Our analyses in this article from a single year should be used as a stepping-stone for multi-year datasets and time-series analyses, which may help understand trajectories and drivers on larger scales, such as long-term climate change and aquaculture trends.

4.6 | Sea trout is not included in the 'traffic light' system

On top of other regulations, the Norwegian 'traffic light' system regulates the aquaculture salmon industry when negative effects of lice threaten wild populations of Atlantic salmon, that is at certain threshold mortalities for the migrating Atlantic salmon smolts. These threshold mortalities are estimated separately in the 13 production areas defined along the coast. However, since only a single indicator, that is wild Atlantic salmon mortality caused by lice, is used, the system may fail to represent a complex reality (Kongsvik et al., 2010) and to protect biodiversity in a wider sense. With a single indicator, other specific issues and broader scale impacts will be given less attention (Amundsen et al., 2019), for example escaped fish from aquaculture, pollution by chemicals or nutrients around salmon farm facilities, etc. Potential negative effects of salmon lice on sea trout (and Arctic char) are this far not considered in the Norwegian 'traffic light' system. However, recent methodological advances have shown promising attempts for implementing sea trout in the Norwegian 'traffic light' system, despite the complex biological response of the sea trout to salmon lice (i.e. compared to Atlantic salmon). Instead of looking solely at mortality, a method for describing changes in marine living area (reduced marine living area—RML) and marine feeding time (reduced marine feeding time—RMT) has been proposed as sustainability indicators for first-time migrant sea trout (Finstad et al., 2021). This has been done on the basis that high salmon lice densities exclude sea trout from otherwise usable habitat and can necessitate an early return to freshwater. Further, a biophysical model method has been developed to serve as a proxy for this indicator (Sandvik et al., 2021). The new methods include the spatial extent of sea trout and account for fish size and migration timing. Reduced marine living area and feeding time are well-suited for estimating the impact of salmon lice on sea trout populations (Finstad et al., 2021). However, it still remains to be seen if this model can be implemented within the present 'traffic light' system for Atlantic salmon (Vollset, Dohoo, et al., 2018).

5 | CONCLUSIONS

We provide new models and analyses that fill knowledge gaps on how sea trout is affected by salmon lice. We document worryingly high lice infestation in certain areas of the Norwegian coast and argue that sea trout in general has a more vulnerable life history than Atlantic salmon, due to extended exposure times to salmon lice. We also present improved analyses that identify threshold levels at which lice infestation pressure translates into expected serious health effects on individual sea trout. This indicates that the hydrodynamic lice dispersal model has unused potential for improving the risk assessment of salmonid fishes. We combine several management tools, and thereby provide empirical validation (a reality check) to the hydrodynamic model that calculate the spread and density of salmon lice, continuously along the Norwegian coastline. By using complementary data

sources, we provide new knowledge that may be used in improved risk and sustainability assessments on sea trout. As a final knowledge-based advice, we argue that new methodological advances should be used to include sea trout in the 'traffic light' system.

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CONFLICT OF INTEREST

None of the authors have conflicts of interest.

AUTHORS' CONTRIBUTIONS

T.B., R.N., A.D.S., Ø.K. and R.M.S.-L. conceived the ideas and designed the methodology; T.B., R.N., A.D.S., Ø.K. and R.M.S.-L. collected the data; T.B., K.Ø.G., M.B., A.D.S. and R.P. analysed the data; T.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.9ghx3ffjj> (Bøhn et al., 2021).

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