



Salmon lice-induced mortality of Atlantic salmon during post-smolt migration in Norway

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Johnsen, I. A., Harvey, A., Sævik, P. N., Sandvik, A. D., Ugedal, O., Ådlandsvik, B., Wennevik, V., Glover, K. A., and Karlsen, Ø. Salmon lice-induced mortality of Atlantic salmon during post-smolt migration in Norway. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsaa202.

Received 3 July 2020; revised 25 September 2020; accepted 28 September 2020.

The expansion of salmonid aquaculture has resulted in environmental challenges, including salmon lice that may infest both farmed and wild fish. For wild Atlantic salmon post-smolts that migrate from their rivers to the ocean, the first phase of their journey in the coastal zone, where aquaculture occurs, is critical when considering lice exposure. To evaluate the lice influence during the post-smolt migration we have developed a migration model. An archive with spatiotemporal concentrations of lice larvae in Norwegian coastal waters has been established using a combination of state-of-the-art hydrodynamic and lice biology models. To estimate lice-induced mortality of wild salmon from Norwegian rivers, the infestation level on the virtual post-smolts was calibrated to match that observed on wild post-smolts genetically assigned their rivers of origin. The lice infestation pressure was modelled on post-smolts from 401 rivers covering all of Norway. Based on this, aquaculture-produced salmon lice-induced mortality of wild salmon post-smolts was estimated to be <10% for 179 rivers, 10–30% for 140 rivers, and >30% for 82 rivers in 2019. Estimated mortalities were used together with other data sets to evaluate aquaculture sustainability in Norway. The aquaculture regulatory system represents a globally leading example of science-based management that considers the environmental impact.

Keywords: Atlantic salmon post-smolt, aquaculture, *Lepeophtheirus salmonis*, management, mortality, Norway, salmon lice, *Salmo salar*

Introduction

Aquaculture, and especially cage-based marine aquaculture, represents a rapidly growing form of global food production. The production of salmonids, which primarily consists of Atlantic salmon (*Salmo salar*) and to a lesser degree marine-farmed rainbow trout (*Oncorhynchus mykiss*), was first established in Norway in the early 1970s. Since its pioneering start, production has increased rapidly, reaching 1.44 million tons in Norway in 2019 (<https://www.ssb.no/en/jord-skog-jakt-og-fiskeri/statistikker/fiskeoppdrett>) and 2.25 million tons globally in 2016 (FAO, 2018). However, the growth of this industry has not been without

environmental challenges, and genetic interactions between wild conspecifics and farmed escapees, and salmon lice (*Lepeophtheirus salmonis*, Krøyer 1837) infestations on wild salmonids, are considered the most significant (Torrissen *et al.*, 2013; Taranger *et al.*, 2015; Glover *et al.*, 2017; Forseth *et al.*, 2017).

The salmon louse is an ectoparasitic copepod that consists of two allopatric sub-species in the Atlantic and Pacific oceans respectively (Skern-Mauritzen *et al.*, 2014). It is an obligate parasite of anadromous salmonids during the marine phase of the life cycle, feeding on the skin, blood and mucus of its host

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(Kabata, 1974; Wootten *et al.*, 1982). As a consequence of moderate-to-large infestations, lice may damage the skin of its host and make it more susceptible to secondary infections, causing physiological and osmoregulatory challenges, and ultimately death (Birkeland and Jakobsen, 1997; Bjørn and Finstad, 1998; Dawson *et al.*, 1999; Poole *et al.*, 2000; Bjørn *et al.*, 2001). Sublethal lice infestations may also affect growth, behaviour, and age of maturity of its host during its marine migration (Birkeland, 1996; Skilbrei *et al.*, 2013; Gargan *et al.*, 2015; Shephard *et al.*, 2016).

Due to an increasing number of salmon and trout farmed in open cages in coastal regions (405 million salmon and rainbow trout in Norway alone as of 1/1-2017; <https://www.ssb.no/en/jord-skog-jakt-og-fiskeri/statistikker/fiskeoppdrett>), the number and availability of hosts for salmon lice have increased (Heuch and Mo, 2001; Bergh, 2007). In an attempt to reduce the pressure of lice infestation on wild salmonids in aquaculture-dense regions of Norway, increasingly stringent regulations to limit the numbers of lice permitted on farmed fish have been imposed. However, regulations of the allowed lice level have not been able to compensate for the industry's almost continual expansion. Consequently, the infection pressure to which both farmed and wild salmonids have been exposed to in farming-dense regions of Norway has increased substantially with time (Taranger *et al.*, 2015). This situation has been exacerbated by the fact that lice increasingly display reduced sensitivity to chemotherapeutants (Espedal *et al.*, 2013; Ljungfeldt *et al.*, 2014; Kaur *et al.*, 2017), and are therefore increasingly difficult to control on farms.

The first three stages of the salmon louse life cycle are planktonic. Thus, depending on the prevailing conditions and temperatures, larvae may drift 100 km or more from their source of origin with ambient water currents before dying from starvation or senescence (Asplin *et al.*, 2014; Johnsen *et al.*, 2014; Johnsen *et al.*, 2016). Lice larvae produced on farmed fish may therefore infest both farmed and wild fish as demonstrated by the fact that lice displaying resistance to delousing chemotherapeutants are also found on wild salmonids in aquaculture-dense regions (Fjørtoft *et al.*, 2017, 2019).

Atlantic salmon post-smolts migrating from rivers are exposed to lice on their way to their oceanic feeding grounds. Due to their small size, the post-smolts are particularly vulnerable to the effects of lice infestation in aquaculture-intensive areas (Finstad *et al.*, 2000; Rikardsen *et al.*, 2004; Skaala *et al.*, 2014). The migration of salmon post-smolts usually commences from late April in southern Norway, and late June in northern Norway, and typically lasts 3–7 weeks (Orell *et al.*, 2007; Skaala *et al.*, 2012; Otero *et al.*, 2014; Haraldstad *et al.*, 2017). However, the majority of a river's smolt population migrates during a 1- to 2-week period (Hvidsten *et al.*, 1995; Davidsen *et al.*, 2005; Skilbrei and Wennevik, 2006; Urke *et al.*, 2013).

In 2017, the Norwegian Government implemented a new system for managing the growth of the aquaculture industry in the white paper “Predictable and environmentally sustainable growth in Norwegian salmon- and trout farming” (St. Meld. 16, 2014–2015). The system regulates future growth of the industry based upon the estimated salmon lice-induced mortality of wild salmon post-smolts within 13 management areas (MAs) that cover the entire Norwegian coastline. This is commonly referred to as the “Traffic Light System”, whereby each MA is determined as “green” if lice are estimated to cause <10% mortality of wild salmonid post-smolts, “yellow” if estimated mortality is 10–30%,

and “red” if estimated mortality is >30%. In turn, these colours reflect whether the industry in that zone will be allowed to expand (green), must reduce production levels (red), or shall maintain at current levels (yellow). Given that Atlantic salmon farming is an economically significant form of aquaculture, and that Norway is the largest salmon-producing country in the world, this regulatory system represents a globally leading example of science-based regulation of aquaculture based on its environmental impact.

Norway has a national program (NALO) for monitoring salmon lice infestation levels on wild Atlantic salmon post-smolts, sea trout (*Salmo trutta* L.), and Arctic char (*Salvelinus alpinus* L.) (Taranger *et al.*, 2015). Within the program, wild salmon post-smolts are captured by trawling in six fjord and coastal areas along the coastline. The salmon lice infestation levels on these post-smolts are used to estimate the proportion of fish in the MA that are likely to die from lice infestation according to threshold tolerance limits (Holst *et al.*, 2003; Taranger *et al.*, 2015). However, NALO does not cover the entire coast, nor does it take into consideration that within each of the 13 MAs, post-smolts captured during trawling originate from multiple rivers of varying characteristics, including differences in the distances and migration routes to the ocean. Genetic tools have been used to identify the compositional units of mixed-stock fisheries (Dahle *et al.*, 2018; Johansen *et al.*, 2018), including mixed salmonid fisheries (Beacham *et al.*, 2012; Ozerov *et al.*, 2017; Bradbury *et al.*, 2018). Harvey *et al.* (2019) recently identified the rivers of origin for many of the salmon post-smolts captured during the NALO trawling surveys in 2015–2019, using a similar approach to the previous studies, and to the genetic methods implemented in Norway to identify fish-farm escapees back to their farms of origin (Glover *et al.*, 2008; Glover, 2010). The genetic assignments provide the opportunity to look at river-specific infestation levels, and in turn, the ability to develop and validate more accurate models of post-smolt migration and lice infestation dynamics in Norwegian fjords.

The Norwegian coastline is estimated to be >25 000 km long (CIA, 2017) and has >400 rivers that may contain salmon. Clearly, it is not logistically feasible to monitor the lice infestation rates and corresponding mortality on post-smolts migrating from all of these rivers. Therefore, we developed a virtual post-smolt (VPS) model that estimates lice infestation during the salmon's migration to the ocean. Information about the lice larvae concentrations along the VPS migration routes was taken from the lice dispersion model (Sandvik *et al.*, 2020).

The VPS model was calibrated and validated by the lice level observed on the wild salmon post-smolts captured by trawling. The trawled post-smolts were identified to their rivers of origin through genetic assignment methods (Harvey *et al.*, 2019). Here, we present the VPS model with a sensitivity test and the estimated level of lice on the fish for all 401 rivers targeting a spawning biomass over 10-kg females (Anon, 2016). The mortality of Atlantic salmon during their migration from the river was estimated based upon the modelled level of lice.

Material and methods

Overview

To estimate the level of salmon lice-induced mortality of wild salmon post-smolts migrating towards the ocean, we built a VPS model using knowledge of migration speed and timing of start

migration from empirical observations. To estimate the lice infestation on the VPS, we combined lice larvae concentration from a previously published lice dispersion model (Johnsen *et al.*, 2016; Sandvik *et al.*, 2016, 2020; Mykssvoll *et al.*, 2018), and calibrated the infestation levels using measurements of lice infestation levels of wild salmon post-smolts that had been captured in the fjords in multiple years. Finally, by assuming tolerance of lice as given by Taranger *et al.* (2015), with a sensitivity test to altered limits, lice-induced mortality was estimated for all salmon rivers along the Norwegian coastline. A schematic overview of the model is presented in Figure 1, and the major elements upon which it is based are described in detail below.

Area description

The Traffic light regulation system of the entire Norwegian coastline, based on the estimated lice-induced mortality of wild salmon, requires mortality estimates for the salmon rivers along the coastline. Rivers are located from the outer coastline to the inner fjords, the longest fjord being over 200 km long. Data on the wild migrating Atlantic salmon post-smolts captured during the NALO trawling surveys have been made available for this study

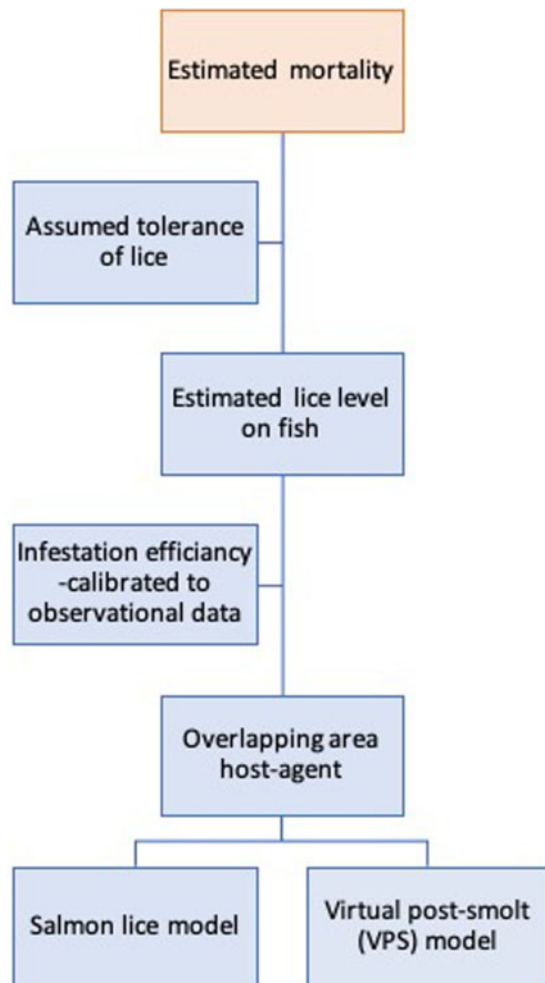


Figure 1. Schematic overview of the model system used to estimate the salmon lice (*Lepeophtheirus salmonis*) infestation level on out-migrating Atlantic salmon (*Salmo salar*) post-smolt from rivers along the Norwegian coast.

(www.nmdc.no). The post-smolts captured in 2015, 2016, 2017, 2018, and 2019 (Nilsen *et al.*, 2018a, b, c, d, e; Nilsen *et al.*, 2019a, b, c, d, Nilsen *et al.*, in prep) were used to calibrate the model predictions from the corresponding years. The rivers to which the captured fish were genetically assigned are given in Supplementary Table S3.

The temporal distribution of the start of the Atlantic salmon post-smolt migration varies between the rivers as well as inter-annually (Otero *et al.*, 2014). The temporal distribution of start migration used in our model is based on compilations of data on 25% annual catch of migrating smolts from 25 Norwegian rivers (Otero *et al.*, 2014; Karlsen *et al.*, 2016; Supplementary Table S1). In addition, we used information collected from several Norwegian technical reports giving sparser data on the temporal distribution of start migration for 18 rivers. In general, post-smolts begin their migration earlier in the south than in the north (Hvidsten *et al.*, 1998; Otero *et al.*, 2014). The temporal distribution of start migration does, however, also vary between rivers located at similar latitudes but at different positions within fjords (Hvidsten *et al.*, 1998; Vollset *et al.*, 2016a). This variation is probably caused by differences in catchment composition and height distribution that influence the development of water discharge and water temperature in spring. Based on the available data and expert judgement (see Nilsen *et al.* 2017 Appendix 2b), we assumed a probable distribution of start migration for each of the 401 rivers, and the time span of the migration was set to occur 10 d prior to the 25% migration time and the end of the migration was set to occur 30 d after the 25% timing date. The date of start, 25%, and end of the migration is given in Supplementary Table S1. Most rivers within a MA were given the same migration timing given by the observed median date for 25% migration from reference rivers with longer time series from that region. Rivers with more sparse migration data were compared to these reference rivers and the timing was adjusted if they deviated by more than a week in observed migration dates for the same years. For rivers without any data on smolt migration timing, rivers with low-altitude coastal catchments were given an earlier start date, whereas rivers with high-altitude inland catchments were given a later start date (usually a week) than the reference river(s) for that MA (Nilsen *et al.* 2017, Appendix 2b).

Observed fish used for model calibration and validation

Wild salmon post-smolts were captured by trawl in the outer parts of the fjords, using a specially designed fish-lift trawl (Holst and McDonald, 2000). This surface trawl is 35 m wide, 5 m deep, and is towed at 4–5 knots. The fish-lift trawl separates fish of relevant size and sorts them into an aquarium connected to the trawl cod-end. The system is designed to minimize scale loss and loss of lice. Trawling was performed in the outer part of fjords and genetic baselines established for all rivers in four MAs: MA2–5 made it possible to assign the captured post-smolts to their river of origin. Hence, we were enabled with an observational data set of captured wild post-smolts captured in weeks 18–24 in 2015–2019.

Genetic assignment methods were used to determine the river of origin for the post-smolts captured by trawling. Full details of the assignment methods are presented elsewhere (Harvey *et al.*, 2019), although a short summary is given here. A genetic baseline, consisting of data from 31 microsatellite DNA markers, was

established for 45 salmon populations in four MAs (Supplementary Table S2). Thereafter, this genetic baseline was used to identify post-smolts captured by trawling back to their rivers of origin using the individual assignment approach implemented in the program ONCOR (Kalinowski *et al.*, 2007). Individual post-smolts that were assigned with an assignment probability higher than 0.80 were accepted as correctly assigned (shown in Supplementary Table S3). Individuals not meeting these criteria or with sign of being hatchery reared post-smolts (tagged with PIT or adipose fin removed) were treated as unidentified. The hatchery-reared post-smolts were removed because they originate from scientific release trials and may be chemically protected against salmon lice, or artificially infested with salmon lice. Such fish may also have a different migration behaviour from wild post-smolts.

Salmon lice dispersion model

The biophysical salmon lice dispersion model calculated the daily concentration of lice by combining data from reported levels of lice at aquaculture sites along the Norwegian coast and hydrodynamic models (Albretsen, 2011; Asplin *et al.*, 2014; Johnsen *et al.*, 2014; Myksvoll *et al.*, 2018). The simulated daily concentration of lice was a calculated number of copodids residing in the upper 2 m of the water column that day and is hereby referred to as the *lice concentration*. The concentration field was limited to the upper metres, as the salmon post-smolts normally reside close to the surface (Davidsen *et al.*, 2009; Plantalech Manel-La *et al.*, 2009). The dispersion was influenced by their vertical positioning, as described in Johnsen *et al.* (2014); Crosbie *et al.* (2019). A more detailed description of the parameterization of the model lice behaviour used in this study can be found in Sandvik *et al.* (2020). The lice concentration has been demonstrated to be well correlated with observations of lice on fish (Samsing *et al.*, 2016; Sandvik *et al.*, 2016, 2020; Myksvoll *et al.*, 2018).

Similar use of hydrodynamic dispersion models to predict the distribution of salmon lice for management purposes has been widely made in the scientific community (Salama and Murray, 2011; Adams *et al.*, 2012; Salama *et al.*, 2013; Adams *et al.*, 2015; Adams *et al.*, 2016; Salama *et al.*, 2016; Samsing *et al.*, 2017; Salama *et al.*, 2018; Cantrell *et al.*, 2018).

VPS migration model

Parametrization of migration

The VPS migration model calculated the swimming routes of individual post-smolts on their way to the ocean. It was coupled with the predicted lice concentration from the salmon lice model. Behavioural responses of post-smolts to shifting environmental conditions are largely unknown. Therefore, the VPS were parameterized to swim towards the ocean by artificially implementing a *fjord-index* in the 800 m × 800 m horizontally resolved grid used by the salmon lice model. The fjord-index is shown for the Hardangerfjord (in MA3) in Figure 2. All grid-cells in open ocean, defined as >10 km from any land cell in the model, got a value of zero and the rest of the sea cells are initially undefined. Thereafter, the index was defined iteratively where undefined cells neighbouring a cell with value i got the value $i + 1$. This was repeated until all sea cells were defined. At every time step, each individual VPS checked the neighbour cells for a lower fjord-index (there was always at least one such neighbour) to find a local

direction out of the fjord. A stochastic element was added to the model to create individual variability in migration routes.

Using hourly time steps, the VPS could stay in the cell, move to a cell with lower fjord index, or move to a cell with higher index. Stochasticity in migration routes between the VPS was included as the probability for migration to a lower fjord index, and hence towards the ocean, was five times higher compared to staying at the current position or move to a grid with higher fjord index. If several neighbouring grids had a lower fjord index compared to the value at current position, there was an equal likelihood of migration between them. The modelled progression speed of VPS corresponds to a median value of 0.14 m s⁻¹ (25- and 75-percentiles of 0.12–0.16 m s⁻¹).

Empirical results from studies using tagging approaches show a great variability in progression speed, between 0.4 and 3.0 body lengths s⁻¹ (Thorstad *et al.*, 2004; Finstad *et al.*, 2005; Økland *et al.*, 2006; Davidsen *et al.*, 2009; Plantalech Manel-La *et al.*, 2009; Thorstad *et al.*, 2012; Urke *et al.*, 2013; Halttunen *et al.*, 2018). The divergent results may be explained by the different set-up of the experiments, as they are completed in different areas, shifting environments, and most of the results are obtained using hatchery reared post-smolts that tend to be larger than wild fish. The progression speed of the VPS was ~1 body length s⁻¹ for the size of wild salmon post-smolts (Rikardsen *et al.*, 2004). The modelled progression speed was in accordance with observed progression speed of wild tagged post-smolt (Urke *et al.*, 2013). The VPS was followed until they reach the open ocean, defined as a grid with fjord-index = 0 and further migration along the coast was not considered in the simulation.

Parametrization of lice infestation

The infestation efficiency (the likelihood of settlement on a host when residing in the same water masses) of salmon lice is influenced by salinity, temperature, water currents, and the age of the copepodite (Hevrøy *et al.*, 2003; Brooks, 2005; Bricknell *et al.*, 2006; Samsing *et al.*, 2015). The infestation efficiency as a function of these variables is, however, unknown. Therefore, we assumed a fixed infestation efficiency.

The number of salmon lice infestations on the VPS (NLice) was modelled using a negative binomial distribution with expectation μ and variance $\mu + \mu^2/\theta$,

$$\begin{aligned} NLice &\sim NB(\mu, \theta) \\ E(NLice) &= \mu \\ \text{Var}(NLice) &= \mu + \frac{\mu^2}{\theta}. \end{aligned}$$

The response variable was related to the infestation pressure (IP) by a log link, which ensured positive count values. The IP was defined as the migration time multiplied with the mean lice concentration along the migration route (h N lice m⁻³). Generally, this was proportional to the number of lice encountered by the salmon on its way to the sea.

GLMM regression was conducted to calibrate the model, using lice count data from trawled fish in the period 2015–2019. To estimate the IP experienced by trawled fish, a simulation was performed in which ten VPS from each river were generated per hour. Trawled fish were then assigned a lice pressure equal to the mean lice pressure experienced by matching VPS. A VPS was “matching” if it originated from the same river as the trawled fish and occurred in the trawling area on the same day as the fish that

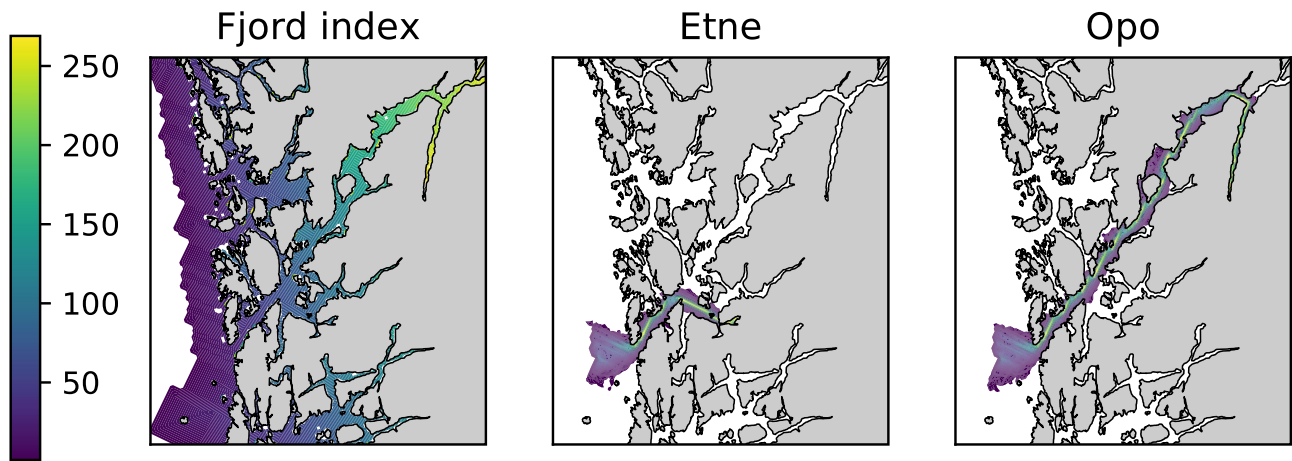


Figure 2. Fjord index used for model parameterization of migration (left panel). Modelled migration area for Atlantic salmon (*Salmo salar*) post-smolts from the rivers Etne (middle panel) and Opo (right panel) in the Hardangerfjord. Coloured area marks the area of migration, the number of fish increase from blue to yellow.

was captured. Trawled fish with no matching VPS (446 of 2125) were discarded from the analysis. These were either genetically misassigned or had a migration pattern that was different from the VPS.

A naïve regression model linking lice count and IP was

$$\log \mu_i = \text{Intercept} + \log IP_i, \quad (1)$$

where IP_i was the estimated IP for the i 'th trawled fish, measured in $h \ N \ \text{lice} \ m^{-3}$. This model was useful to check whether there was indeed a significant correlation between estimated IP and observed lice counts. It did, however, imply a nonlinear (power-law) relationship between lice count and IP, which was biologically questionable. In our main model, we therefore forced a linear relationship by defining IP as an offset variable. The resulting model made more biological sense but could not be used to confirm the correlation between IP and N_{Lice}. To account for possible systematic differences in modelled infestation efficiency between different years or rivers, we also included river and year as random intercepts. The main model then read

$$\begin{aligned} \log(\mu_{ijk}) &= \text{Intercept} + \text{offset}(\log(IP_{ijk})) + fYear_j + fRiver_k, \\ fYear_j &\sim N(0, \sigma_{Year}^2), \\ fRiver_k &\sim N(0, \sigma_{River}^2), \end{aligned} \quad (2)$$

with $fYear_j$ and $fRiver_k$ as the random effects of the j 'th year and k 'th river, respectively. We remark here that the intercept parameter (and its random effects) encompass a range of different factors relating to infestation efficiency, such as louse infestation success rate, fish swimming speed, oceanic turbulence and systematic errors in the modelled migration route or lice concentration. Regional or yearly differences in any of these factors will show up in the model as random effects.

All statistical analyses were conducted in RStudio 1.2.5019 (RStudio Team, 2020). GLMM regression was conducted using the package merTools (Knowles and Frederick, 2019).

Experimental studies have shown that between 30 and 50% of the newly attached salmon lice die before reaching the mobile stages that cause the heaviest damage to the host fish (Grimnes and Jakobsen, 1996; Stien *et al.*, 2005; Wagner *et al.*, 2008; Hamre

et al., 2009). Therefore, we assumed that 60% of the attached lice survive to the mobile stages, which was used when estimating the lice-induced mortality of salmon post-smolts.

Testing the model sensitivity

As the temporal distribution of the post-smolts start migration is to a large extent unknown for a majority of the rivers, the prevalence and mean intensity of the lice levels on the VPS were estimated for a range of temporal distributions for start migration. Six migration distributions were tested: Flat distribution, flat distribution moved 10 d forward and backward in time, left-skewed, right-skewed, and centred distribution, as illustrated in Supplementary Figure S1. All of the assumed start migration distributions extended over a 40-day period (Supplementary Table S1). With an exception of the flat distribution, the assumed migration distributions were calculated using a beta distribution. To obtain a *left skewed* distribution, the date for 25 and 50% migration was assumed to be 3 and 7 d earlier respectively. Correspondingly, the date for 25 and 50% migration was assumed to be 10 and 7 d later to obtain the *right skewed* distribution. The *centred* distribution was obtained by assuming the date of 25% migration to be 5 d later.

Estimating mortality

Using the smolt migration model, we calculated the number of lice on 1000 individual VPS from each of the 401 salmon rivers for the period 2012–2019, assuming migration period as presented in Supplementary Table S1 with a flat distribution. The simulated number of lice on the VPS were used to estimate the risk of mortality for individual fish, which then was summed for the river in question. The risk of mortality for a 20 g salmon post-smolt was assumed to be in accordance with previously proposed lice tolerance levels (Normal mortality in Table 1, Taranger *et al.*, 2015). To test the sensitivity of different tolerance levels, we calculated mortality with a lower and higher lice tolerance, (Table 1) as conducted previously (Kristoffersen *et al.*, 2018).

Table 1. Assumed tolerance limits for mortality of Atlantic salmon (*Salmo salar*) post-smolts with salmon lice (*Lepeophtheirus salmonis*).

Low mortality		Normal mortality		High mortality	
Lice per fish	Assumed mortality (%)	Lice per fish	Assumed mortality (%)	Lice per fish	Assumed mortality (%)
<2	0	<2	0	<2	0
2–3	10	2–3	20	2–3	40
4–6	25	4–6	50	>3	100
7–10	50	>6	100	–	–
>10	100	–	–	–	–

The limits correspond to the tolerance limit for a 20 g post-smolt in accordance to Taranger et al (2015) and Kristoffersen et al (2018).

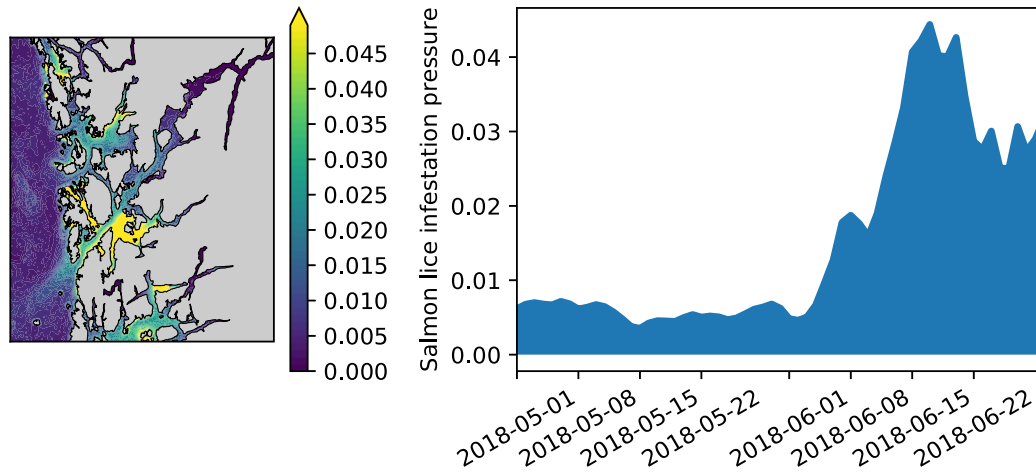


Figure 3. Mean simulated lice (*Lepeophtheirus salmonis*) distribution in the upper 2 m during May 2018 and June 2018 (left side) and daily averaged concentration of lice (ind $m^{-3} h^{-1}$) representing the infestation pressure in the assumed migration area for Atlantic salmon (*Salmo salar*) post-smolts from the river Opo during May 2018 and June 2018 (right side).

Results

Model migration

Figure 2 illustrates the modelled post-smolt migration routes from two rivers in the Hardangerfjord. From each of the rivers Etne and Opo, 1000 VPS were followed during their migration to the ocean. The fjord has several routes of exit to the ocean, but the parameterization of the model forced the VPS out the main fjord mouth, the opening with the shortest distance to open ocean. The shortest migration distances between the river and the ocean were 79 km for Etne and 224 km for Opo, giving average modelled migration times of 6.7 and 17.6 d, respectively.

The temporally averaged simulated salmon lice concentration in the upper 2 m during May and June 2018 is shown in Figure 3 (left panel). The daily average lice concentration in the assumed migration area for salmon from the Opo river (the coloured area in Figure 2) is assumed to represent the IP and is shown by shaded area in Figure 3 (right panel) for May and June 2018. The number of infective lice rapidly increased in the time period relevant for the migration of the VPS from this river, illustrating that migration timing can be an essential factor to consider.

Model infestation efficiency

When fitted to the trawl data, the simple model defined by (1) gave an expected louse count of

$$\log \mu = 1.9244 + 0.6351 \cdot \log(\text{IP}),$$

and a dispersion parameter of $\theta = 0.2740$. The standard error of

the IP coefficient is 0.0403, which implied a significant ($p < 0.01$) correlation between lice count and model IP. Fitting the main infestation efficiency model (2) to the trawl data, we obtained

$$\log \mu = 1.2844 + \log(\text{IP}),$$

with the intercept having a standard error of 0.3790. Dispersion was estimated to $\theta = 0.3695$. The random-effect variance was 1.4733 for fRiver and 0.4384 for fYear. For more details of inter-annual and river-specific data, see Supplementary Figure S2, Supplementary Tables S4 and S5. Reduced models with one or both random effects removed showed a larger AIC value and were rejected. The uncertainty was determined both by the standard error of the intercept and by the variance of the random effects.

Model sensitivity

The estimated lice level on the VPS varied between the simulations of different migration timing; altering the temporal distribution for migration in accordance to the curves in Supplementary Figure S1 altered the lice infestation level (Supplementary Figure S3). The left skewed distribution resulted in lower estimated prevalence and mean intensity lice on the VPS compared to the normal migration in MA 2–5 in all the simulated years. Correspondingly, the right skewed distribution estimated higher lice level compared to the normal migration. The centred, Flat – 10 d and Flat + 10 d distributions showed a similar prevalence and intensity of lice on the VPS as the flat (normal)

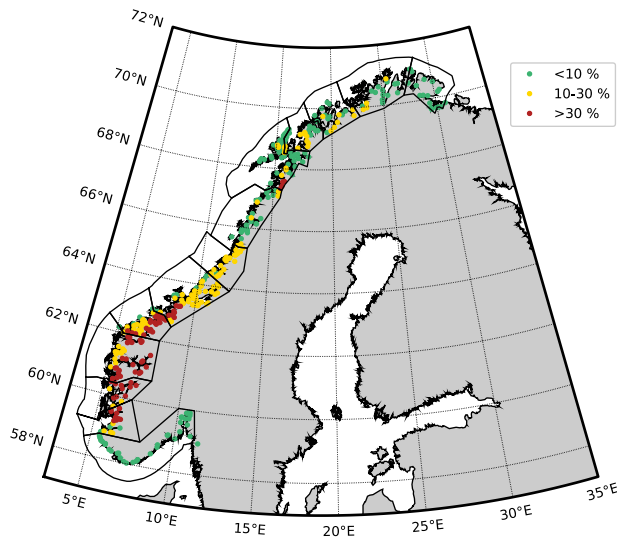


Figure 4. Estimated mortality of Atlantic salmon (*Salmo salar*) post-smolts from salmon lice (*Lepeophtheirus salmonis*) infestations during out migration in 2019. The estimated mortality is categorized into three classes: <10% mortality in green, 10–30% mortality in yellow and >30% mortality in red. The MAs are marked in black and are numbered from south to north.

migration in 2019. In 2018, the *Flat + 10 d* distributions predicted increased salmon lice infestation levels in MA2 and MA3 compared to the flat (*normal*) migration (not shown). The variability in influence between MAs and years reflects the seasonal and management dynamics in the salmon lice levels on the farms. Note that these results represent the average estimate between the rivers in the area, where all rivers were weighted equally.

Estimated mortality

In 2019, a total of 179 rivers were classified as having a low (<10%) mortality of migrating post-smolts, 140 as having a medium (10–30%) mortality of migrating post-smolts, and 82 rivers as having a high (>30%) mortality of migrating post-smolts using the established mortality tolerance limits (Table 1; Figure 4). When mortality among rivers was weighted equally, the average mortality was high in 2019 (>30%) in MA3 and 4, moderate (10–30%) in MA 2, 5, 6, 7, and 10, and low (<10%) in the remaining areas (MA1, 8, 9, 11, 12, and 13). Note that the average here was weighted equally between the rivers, not reflecting the different rivers salmon production. When estimating river-specific mortality, MA1 and 13 did not have estimated mortality exceeding 10% in any rivers during 2012–2019. The majority of the rivers displaying a high mortality of post-smolts were located in inner fjord locations. The simulations from 2012 to 2019 reveal that the proportion of rivers with low mortality (<10%) in MA 2–6 has decreased since 2012 and 2013 (Figure 5). MA3 is the only area with decreasing number of highly influenced rivers (mortality >30%) from 100% influenced rivers in 2016. Interannual fluctuation in the estimated influence can be seen in MA 4, 5 and 8, related to the production cycles in the MAs. The data set of the model estimates is published with river-specific data starting in 2012 (Johnsen et al., 2020).

Alterations in the assumed tolerance limit influenced mortality estimates (Figure 6). The median mortality between rivers in an MA altered classifications in 4 out of 13 MAs in 2019.

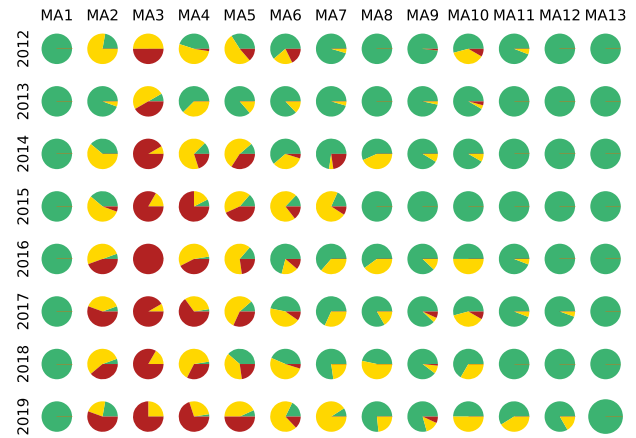


Figure 5. Distribution of river-specific estimated mortality of Atlantic salmon (*Salmo salar*) post-smolts due to salmon lice (*Lepeophtheirus salmonis*) infestations in 13 MAs during the years 2012–2019. The estimated mortality is categorized into three classes: <10% mortality in green, 10–30% mortality in yellow and >30% mortality in red.

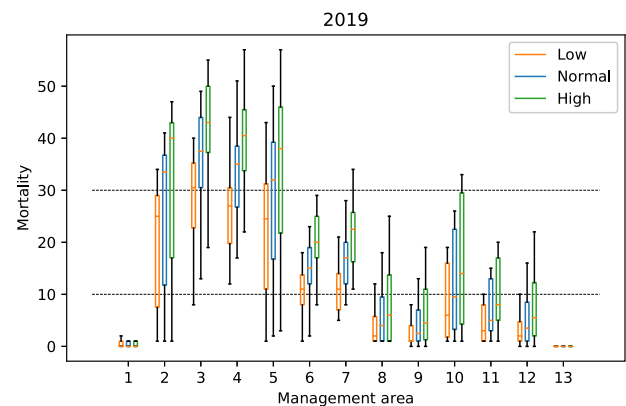


Figure 6. Estimated mortality of Atlantic salmon post-smolts due to salmon lice (*Lepeophtheirus salmonis*) infestations during migration to the ocean in 2019. The estimates are calculated based upon three different assumed tolerance limits.

Discussion

Here, we developed a VPS model to estimate the marine mortality of wild Atlantic salmon post-smolts resulting from infestation of salmon lice produced on commercial salmon farms. After parametrization and calibration against empirical data from the field, the model was implemented to estimate mortality for post-smolts from 401 rivers spanning Norway. Based on this, aquaculture-produced salmon lice-induced mortality of wild salmon post-smolts was estimated as <10% for 247 rivers, 10–30% for 122 rivers, and >30% for 32 rivers in 2019.

Management applications

The mortality estimates generated from this work are currently used as a major part of the Norwegian Government’s evaluation of the environmental impact of aquaculture. Here, the indicator used to describe this impact is the mortality of wild salmonids caused by salmon lice from fish farms in all 13 MAs. In implementing the Norwegian Government’s Traffic Light System for

regulating the aquaculture industry, all relevant available sources of data are considered and evaluated within each MA. This includes both the observed and modelled lice levels on wild fish (Nilsen *et al.*, 2018 a, b, c, d, e; Sandvik *et al.*, 2016; Kristoffersen *et al.*, 2018). As there are >400 rivers containing salmon in Norway, measuring the influence of salmon lice on post-smolts during migration to the ocean based upon field observations alone is logistically unfeasible. Thus, model results as presented here provide an important supplement to the empirical observations to evaluate potential environmental impacts from aquaculture.

The VPS model has been calibrated against observations of lice numbers on wild salmon post-smolts captured by trawling in the fjords over multiple years to ensure that the model predictions are in accordance with observed lice levels on out-migrating post-smolts from individual rivers. Ideally, the observational data set available for calibration should include fish from all MAs. Due to limitations in trawling effort and genetic baselines for all rivers, the available data set consists of targeted effort in the MAs with highest aquaculture intensity (MA2–5). A similar model was developed for estimating mortality of Atlantic salmon during post-smolt migration but calibrated using lice infestation levels on hatchery-reared salmon post-smolts kept in sentinel cages in the fjords for surveillance purposes (Kristoffersen *et al.*, 2018). Our model results predict higher lice infestation levels than the predictions from the previous study. As the lice concentration fields, migration model, temporal distribution of post-smolt start migrations, and observation data sets used for model calibration are different between these two studies, it is difficult to identify a single cause of the differences in the results between the two models. Whereas Kristoffersen *et al.* (2018) calibrated their model using observed number of lice kept in sentinel cages, the model presented here is calibrated using the number of lice observed on out migrating wild post-smolts captured by trawling. Given that both are calibrated to fit observations, it seems feasible that the different observational data sets represent a significant cause of different model outputs. Another source of difference is the dispersion models. Kristoffersen *et al.* (2018) disperse salmon lice larvae as a function of seaward distance, while our method is based upon a hydrodynamic model. The genetic assignment of the captured post-smolts provided a unique possibility to calibrate and evaluate the VPS model to the IP observed on wild Atlantic salmon post-smolts on a per-river basis (Harvey *et al.*, 2019). To our knowledge, the result from the VPS model is the only method that is shown to estimate lice levels in accordance with river-specific data.

For the VPS model, results from both modelled and observed approaches showed that, within each MA, rivers are differentially affected. That is, as illustrated here, salmon originating from inner-fjord rivers always displayed a higher lice-induced mortality compared to the outer-fjord or coastal rivers. The main reason is longer distance, and thereby extended time exposure to lice larvae in the fjord or coastal area. This is consistent with other studies that have demonstrated higher marine mortality for inner as opposed to outer fjord populations (Vollset *et al.*, 2016a). Therefore, future management regimes need to consider variation in aquaculture impact also within the 13 MAs covering Norway.

The VPS model predicted elevated lice-induced mortality of VPS in MA 2–12. In MA 2–5 the estimated mortality was low for <60% of the rivers during 2015–2018, and MA3 has not exceeded 33% green rivers during 2012–2019. With an exception of MA3

that has shown an improvement since 2016, the number of rivers with high estimated mortalities has increased the latter years. This indicates a negative development regarding the environmental impact on wild fish, considering salmon lice. The interannual fluctuations in the lice-induced mortality in MA 4 and 5 coincide with coordinated production between farms within these MAs, where there was high farmed biomass in the outer part of the MA during the years where high mortality was estimated for many of the rivers. Throughout the study period, the highest mortalities were found in MA 3 and 4 as a combined result of the lice concentration in the water masses and long migration routes.

Model sensitivity

The development of numerical models enables the possibility to monitor the environmental conditions and investigate the influence of aquaculture on wild oceanic migrating post-smolts. Further, models enable the possibility to explore the effect of different scenarios by varying different parameters, such as migration routes, tolerance limits, infestation efficiency, and so on. Here, we have assumed that the infestation efficiency of the lice is constant and not influenced by environmental conditions. It is shown that salmon lice increase their infestation efficiency with increasing temperatures (Skern-Mauritzen *et al.*, 2020). However, as salmon start their migration later in north compared to in the south, the sea temperature under seaward migration is not that different (Myksvoll *et al.*, 2018). The sensitivity analysis conducted here focused on the migration timing of the fish (the temporal distribution of start migration) and how tolerance limits of lice altered the estimated mortality.

For the estimated mortality of VPS, we assumed a migration where the VPS start their migration during a 40-day period for all rivers. This is probably seldom the case (e.g. Veselov *et al.*, 1998; Orell *et al.*, 2007). However, the temporal distribution of the start migration is strongly influenced by environmental cues that may also vary between rivers (Hvidsten *et al.*, 1995; Fjeldstad *et al.*, 2012; Jensen *et al.*, 2012; Jonsson and Jonsson, 2014). Water discharge, water temperature, and changes in these two factors, either alone or in combination, appear to be the most important environmental factors for interannual and inter-river variation in the temporal distribution of start migration. At present, we lack general models to predict such variation, but studies have shown that the interannual variability of start migration is about 20–30 d in Norwegian rivers (Hvidsten *et al.*, 1995; Jensen *et al.*, 2012; Jonsson and Jonsson 2014; Vollset *et al.*, 2016a; Skaala *et al.*, 2019).

To evaluate the effect of the temporal distribution of the start migration for the 401 rivers, the average prevalence and intensity across all rivers for each MA was calculated for different assumed distributions for start migration. The altered timing of start migration influenced the estimated lice level on the VPS, where simulations with earlier skewed migrations gave lower mean intensity on the VPS. As the abundance of lice typically increases during the spring, the earlier migration of VPS decreased both prevalence and mean intensity of salmon lice infestation. In addition, the number of adult female salmon lice permitted on farmed salmon in open net-pens is decreased from an average of 0.5 lice per fish to 0.2 lice per fish during 6 weeks in the spring in order to help protect wild salmonids. Therefore, both prevalence and mean intensity increased in the simulation of skewed late migrating VPS. The increase is an effect of the increasing lice concentration in the

migration route. This is to our understanding most likely the result of the altered management regime as well as the nonlinear temperature-dependent development of salmon lice (Samsing *et al.*, 2016).

In accordance with the expectations, and as indicated in a previous study (Kristoffersen *et al.*, 2018), the estimated mortality of VPS was highly sensitive to alterations in the assumed tolerance limits to salmon lice. In 2019, the mean estimated mortality for MA2-6 was decreased ~20% using the higher tolerance limits and increased ~40% using the lower tolerance. The percentage difference was larger in the northern MAs.

Future model developments

Although the simulated concentration of salmon lice is shown to be in accordance with the observed levels of lice on salmonid fish, there are uncertainties and possible room for improvement in the parameterization of the salmon lice distribution model (Sandvik *et al.*, 2016; Myksvoll *et al.*, 2018; Sandvik *et al.*, 2020). Due to lack of better information, the model today includes a fixed mortality. In high latitude spring bloom systems, we expect seasonal variability in the salmon lice mortality. Also, as the salmon post-smolts migrate to sea in a limited period during spring (here assumed to be 40 d), information of the lice release with a higher resolution than weekly data would be highly valuable.

Both the exact timing of post-smolt migration and the routes travelled are not yet fully understood. The assumed migration dates and the parameterization of smolt migration in the model (swimming speed and direction) are based upon published studies (Økland *et al.*, 2006; Davidsen *et al.*, 2009; Thorstad *et al.*, 2004; 2007; 2012; Urke *et al.*, 2013; Halttunen *et al.*, 2018). As the model system calculates the temperature, salinity, and current conditions along the entire Norwegian coast, it is possible to implement individual behavioural cues depending on the surrounding environmental conditions for the VPS. The current velocity, in particular, may be of similar magnitude to the swimming velocity of a post-smolt and has therefore a direct influence on the migration speed and route.

The sensitivity tests conducted here illustrate that the estimated mortality of salmon post-smolts is more sensitive to the assumed tolerance limits than the timing of the start migration. The tolerance limits are based upon published results (Taranger *et al.*, 2015), which again is based on a report reviewing all relevant literature. These limits are largely based upon laboratory experiments using farmed or cultivated salmon. These limits need verification, not at least since there are major differences between laboratory conditions (for instance no predators, no feed competition or limitations, stable environmental conditions) and nature. Verification of these limits from wild fish residing in its natural habitat would be highly valuable.

More complex migration timing and swimming routes may be implemented in the model system in the future; however, the present parameterization makes the model fast and efficient to run for all rivers and reflects both the rivers' different exposure period as a function of the distance between river and ocean and the concentration of infective salmon lice in the area between river and ocean.

Concluding remarks

Salmon lice-induced mortality has a negative effect on wild Atlantic salmon post-smolts, and is documented in areas of

intensive salmonid aquaculture (Skilbrei *et al.*, 2013; Vollset *et al.*, 2016b). However, it can be hard to evaluate for all rivers in Norway and on an annual basis based upon observations. Here, we developed a unique VPS model that estimates the lice-induced mortality of out-migrating salmon post-smolts.

The distribution of infectious agents in the marine environment is highly influenced by the surrounding conditions. Salmon lice are known to avoid water masses with low salinity by adjusting their vertical position in the water column (Heuch, 1995; Heuch *et al.*, 1995; Bricknell *et al.*, 2006; Crosbie *et al.*, 2019). As post-smolts migrate in the surface-layers, and the timing of migration into the ocean often coincides with high river discharges during spring with maximum stratification of the fjords, inclusion of environmental conditions is essential in order to realistically calculate the interaction and level of contact between host and agent. As the VPS model system uses the salmon lice distribution from a hydrodynamic model system, which already takes key environmental parameters including current, salinity, and temperature into consideration, this has been achieved in the current work.

The estimated lice level on modelled post-smolts is shown to coincide with the level observed on captured wild post-smolts. The concentration of salmon lice rapidly increases with the ambient temperatures and altered farm regulations during spring and early summer when post-smolts start their oceanic migration. Hence, the number of lice on a post-smolt is dependent on the timing of migration. As the exact timing of migration is unknown for most rivers, we have assumed a likely migration window based upon available knowledge. The estimated mortality from the VPS model can therefore deviate from the actual mortality of wild fish. However, the VPS model provides the regulatory authorities with an objective measure of the influence salmon lice have on wild fish in a time period and area that the post-smolts are likely to migrate.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

Acknowledgements

The simulations with the hydrodynamic model were performed on resources provided by UNINETT Sigma2—the National Infrastructure for High Performance Computing and Data Storage in Norway. The manuscript was improved due to constructive comments from two anonymous reviewers, thank you for your effort.

Funding

This work was financed by the Norwegian Department of Trade, Industry and Fisheries in its funding to the Institute of Marine Research (internal project no. 14650).

Data availability

The model data results obtained in this study are published at the Norwegian Marine Data Centre (Johnsen *et al.*, 2020). This data set includes lice infestation number and corresponding estimated mortalities for all 401 rivers included in this study.

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Handling editor: Carrie Byron