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Article *in* Epidemics · December 2017

DOI: 10.1016/j.epidem.2017.11.001

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ARTICLE INFO

Keywords:
Density dependent
Sea lice
Transmission
Farmed salmon
Migration pathway
Migration time

ABSTRACT

The Norwegian government recently implemented a new management system to regulate salmon farming in Norway, aiming to promote environmentally sustainable growth in the aquaculture industry. The Norwegian coast has been divided into 13 production zones and the volume of salmonid production in the zones will be regulated based on salmon lice effects on wild salmonids. Here we present a model for assessing salmon louse-induced mortality of seaward-migrating post-smolts of Atlantic salmon. The model quantifies expected salmon lice infestations and louse-induced mortality of migrating post-smolt salmon from 401 salmon rivers draining into Norwegian coastal waters. It is assumed that migrating post-smolts follow the shortest path from river outlets to the high seas, at constant progression rates. During this migration, fish are infested by salmon lice of farm origin according to an empirical infestation model. Furthermore, louse-induced mortality is estimated from the estimated louse infestations. Rivers draining into production zones on the West Coast of Norway were at the highest risk of adverse lice effects. In comparison, rivers draining into northerly production zones, along with the southernmost production zone, were at lower risk. After adjusting for standing stock biomass, estimates of louse-egg output varied by factors of up to 8 between production zones. Correlation between biomass adjusted output of louse infestation and densities of farmed salmon in the production zones suggests that a large-scale density-dependent host-parasite effect is a major driver of louse infestation rates and parasite-induced mortality. The estimates are sensitive to many of the processes in the chain of events in the model. Nevertheless, we argue that the model is suited to assess spatial and temporal risks associated with farm-origin salmon lice.

1. Introduction

The Norwegian government recently produced a white paper on “Predictable and environmentally sustainable growth in Norwegian salmon and trout farming” (Anon, 2014 − 2015). A main goal for the government was to promote growth in the aquaculture industry by restricting regulations to focus primarily on environmental sustainability. The white paper suggested implementing a new system for regulating the volume of production of farmed salmonids by dividing the Norwegian coast into separate production zones. The production zones were constructed based on large-scale cluster analyses using hydrodynamic models to analyse water current connectivity between farms, aiming to minimize connectivity between zones (Ådlandsvik, 2015). Hence, the Norwegian coast was recently divided into 13 production zones for farming salmonids (Fig. 1), *i.e.* Atlantic salmon (*Salmo salar,* Salmonidae) and rainbow trout (*Onchorhyncus mykiss*, Onchorhyncus), in a separate regulation (Anon, 2017a). This new management system is referred to as “the traffic light system” (Vollset et al., 2017).

The white paper also presented a discussion on what indicators that should be subjects for evaluating future adjustments in the production capacity within production zones (Anon, 2014 − 2015). Only indicators of environmental concern and for which effects depend on the intensity of production, *i.e.* density-dependent environmental effects of production, were to be considered. In accordance with this premise, the government suggested that the salmon louse (*Lepeophtheirus salmonis*, Caligidae) for the time being should be the first and only indicator for evaluating future growth in the production capacity of the various production zones (Anon, 2014 − 2015). Sea lice control is recognised as a top priority subject in need of more insight to facilitate expansion of sustainable aquaculture also on a global scale (Jones et al., 2015). In the recently implemented Norwegian regulation, it is further specified

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https://doi.org/10.1016/j.epidem.2017.11.001
Received 16 August 2017; Received in revised form 26 October 2017; Accepted 29 November 2017

Please cite this article as: Kristoffersen, A.B., Epidemics (2017), https://doi.org/10.1016/j.epidem.2017.11.001

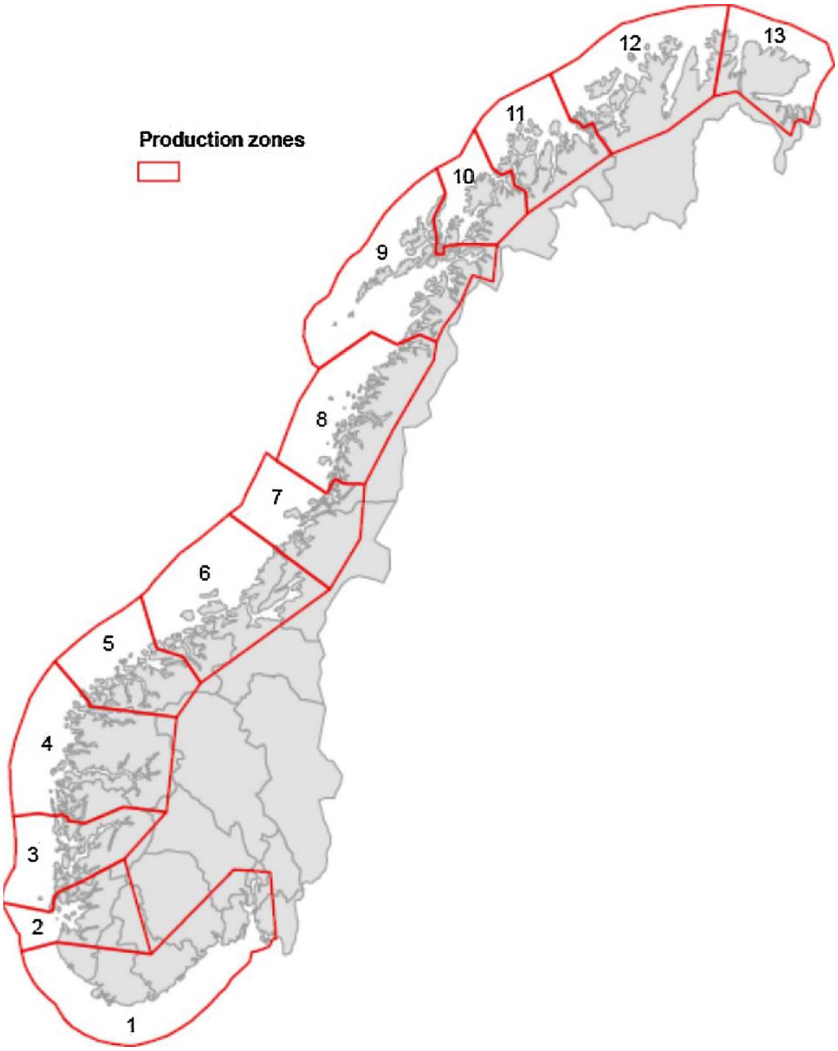

Fig. 1. Production zones 1–13 along the Norwegian coast.

that effects of salmon lice on wild salmonids should be the environmental indicator for the new management system and that the authorities are obligated to evaluate such effects every other year, in order to adjust the production volume within production zones (Anon, 2017a).

Norway holds more than 400 rivers producing Atlantic salmon (Hindar et al., 2011). The total abundance of wild Atlantic salmon, however, has declined over the last decades, both in terms of the number of populations and the productivity in freshwater and marine environments (Chaput 2012; Windsor et al., 2012). The total annual return of Atlantic salmon spawners to Norwegian rivers was recently estimated to about 522 thousand fish in 2015, which represents an estimated decline of 55% in returning salmon from around 1985 (Anon, 2016). At the same time, salmon farming in Norway has increased massively. The total sale of Atlantic salmon was estimated to be 1.30 million metric tonnes round weight in 2015, with an additional sale of 72.9 thousand tonnes of rainbow trout. Comparable figures in 1994 were 0.2 million metric tonnes of Atlantic salmon and 14.5 thousand tonnes of rainbow trout (Fiskeridirektoratet, 2017a). The present day production implies a standing stock of about 350–450 million farmed Atlantic salmon in marine farms along the Norwegian coast at all times (Fig. 2).

Effects of aquaculture on pathogen transmission to wild stocks of fish have received a lot of focus in different salmon-producing areas around the world (Johansen et al., 2011; Marra, 2005; Naylor et al., 2009). Discussions regarding effects of spill over of salmon lice from farms to wild salmonids have been especially controversial (Krkosek et al., 2007; Krkosek et al., 2006; Marty et al., 2010; Shepard et al., 2016). In Norway, effects of the massive numbers of farmed compared to wild salmon has been of special concern (Glover et al., 2017; Heuch and Mo 2001; Taranger et al., 2015; Torrissen et al., 2013). In a recent review of the major threats to Atlantic salmon in Norway, escaped farmed salmon was classified as the highest ranked threat, followed by the salmon louse (Forseth et al., 2017). The political dilemma in this situation is to balance the interests of a prospering salmon farming industry, while also ensuring the conservation of a large number of wild Atlantic salmon populations along the Norwegian coast. Many of the salmon-producing rivers are locally of economic and cultural importance due to angling and many are also threatened by other anthropogenic impacts, *e.g.* hydropower regulation and habitat alterations (Forseth et al., 2017).

To facilitate political decision-making concerning regulation of the production capacity within production zones, we developed a model for quantitative risk assessment of salmon louse-induced mortality of seaward-migrating post-smolts of Atlantic salmon. Louse infestations and louse-induced mortality are modeled for 401 salmon-producing rivers with marine outlets within specific production zones (Forseth et al., 2017). The expected timeframe for seaward migration of smolts is estimated for each river. Migrating post-smolt salmon are assumed to follow the shortest path from the river outlets in marine environments to the high seas, at a constant progression rate. During this seaward migration, salmon are exposed to salmon lice infestations. Louse infestation rates are modeled using a spatio-temporal model for louse

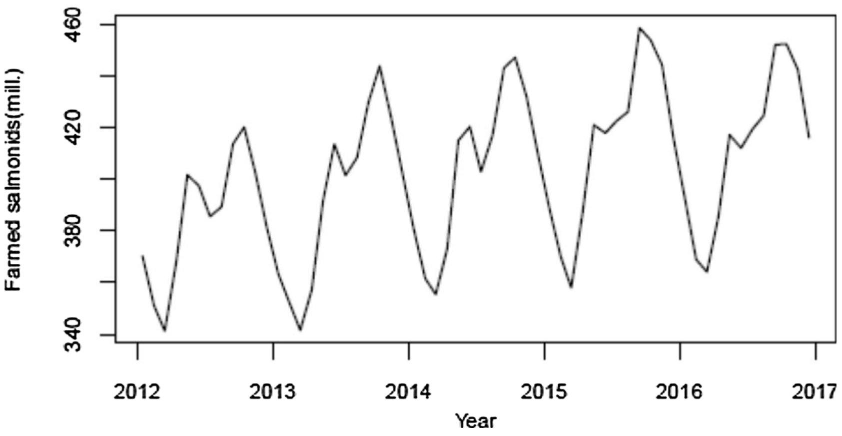

Fig. 2. The standing stock, i.e. the sum of monthly reported numbers, of farmed salmonids (in millions) in Norwegian marine waters over the years 2012–2016.

transmission. This spatio-temporal model was derived from reported numbers of reproductive female lice in farms and reported water temperatures (Kristoffersen et al., 2014; Stien et al., 2005), and calibrated according to rates of infestation of fish in sentinel cages (Bjørn et al., 2011; Sandvik et al., 2016). Finally, the modeled distribution of the number of infesting lice per seaward-migrating post-smolt, covering the total predicted migration period for each river, was used to model parasite-induced mortality. For this we assume that post-smolts weigh 20 g and that parasite-induced mortality of migrating salmon follow the weight-dependent figures suggested by Taranger et al. (2015). Accumulated parasite-induced mortality is calculated for the entire migration period of all rivers, the years 2014–2016 and for best- and worst-case scenarios with respect to empirical infestation rates derived from the louse transmission model.

Many processes in the chain of events depicted by the risk model are poorly documented. Accordingly, we present sensitivity analyses focusing on the processes we regard to potentially be critical to the outcome of the risk calculations. We discuss uncertainties associated with some of the underlying assumptions for the chain of events, and their possible contribution to biases in the model output. The main conclusions from these discussions are that a large-scale density-dependent host-parasite effect is a major driver of the spatially variable estimates of expected lice infestation rates and parasite-induced mortality. There are large uncertainties in the estimations of both the rate of infestations and parasite-induced mortality. However, all processes in the chain of events are modeled transparently and with reproducible output. Hence, we argue the output from the risk model is well suited to assess relative spatial and temporal risks associated with farm-origin salmon lice.

2. Methods

The risk model covers a chain of events or processes starting with (1) the modeled production of pelagic nauplii larvae of salmon lice on salmon farmed in open net pen cages along the Norwegian coast. (2) Exposure of post-smolt wild salmon depend on the production of lice larvae in nearby farms. Salmon lice larvae are spread locally with the water current while they develop through the second nauplius stage and into infestive copepodids (Hamre et al., 2013; Johnson and Albright 1991). To model this we use a spatio-temporal model that estimates the local infestation pressure (Kristoffersen et al., 2014), taking into account the temperature-dependent development rates of salmon lice (Aldrin et al., 2017; Samsing et al., 2016; Stien et al., 2005). To translate the local infestation pressure to infestation rates on migrating salmon, we use a functional relationship between the two, derived from empirical data of salmon smolts in sentinel cages. (3) Seaward-migrating wild salmon post-smolts from salmon rivers are exposed to salmon lice according to this model as they migrate from the river through the fjords and outer coastal areas. This is described with a directional migration route from each river to the coast taking the shortest path to sea. Finally, (4) infestation rates are related to an additive mortality of the seaward-migrating post-smolts based on threshold values currently being used in Norwegian management (Taranger et al., 2015). In the following, the consecutive parts of the risk model are described in more detail.

2.1. Farm-origin infestation pressure

Norwegian salmon farms are registered with an identifying number along with a geo-reference in the Aquaculture Register, operated by The Directorate of Fisheries (Fiskeridirektoratet, 2017b). Marine salmon farms are required to count and report salmon louse infestations on a weekly basis, along with reporting farm numbers of fish and water temperature at a depth of 3 m (Anon., 2017b). For every week, the total numbers of reproductive female salmon lice are calculated as the reported mean number multiplied by the number of fish. The numbers of reproductive female lice and reported water temperatures are used to estimate the daily production of salmon louse eggs in farms. It is assumed that each of two egg strings contain 150 eggs, and that new egg strings containing 150 eggs each are extruded post hatching at a rate (Stien et al., 2005),

$$E = \frac{300\text{eggs}}{(41.98/[T - 10 + (41.98^{*}0.338)])^{2}}$$

where E is the number of eggs per female lice, T is the seawater temperature measured at 3 m depth at the farm. E is then multiplied by the number of female lice per fish and number of fish per farm.

In order to relate the production of louse eggs on farms and exposure to infestation of next generation lice on the fish in the given farms, we estimated internal infestation pressure, IIP. Internal infestation pressure is defined by the farm production of salmon louse eggs adjusted in time according to development time (in absolute days) through to the next generation chalimus stages, using temperature and time in degree days (Kristoffersen et al., 2014; Stien et al., 2005),

$$IIP_{i,d} = \sum AF_{i,d-\Delta t} E_{i,d-\Delta t} S_{\Delta t}$$

where $AF_{i,d-\Delta t}$ is the number of female salmon lice at farm i at day $d - \Delta t$. This number is calculated from the weekly reported mean abundance of adult female lice per fish and numbers of fish on the farm, and linearly adjusted to a number of females per day. Δt is the time it takes from the minimum development time for an adult female and until this female on average has produced eggs, and for the eggs to have developed into next generation chalimus stage lice. Chalimus stage I or II is not specified (Stien et al., 2005). Δt is here assumed to be 126°-days. During the development time, lice are assumed to experience mortality of 0.17 per day, *i.e.* the numbers of lice are reduced by this factor for each development day, $S_{\Delta t} = (1 - 0.17)^{\Delta t}$.

To model spatial infestation pressure, the farm-specific estimates of infestation pressure are interpolated in coastal waters from the farm of origin, using an empirical kernel density function (Aldrin et al., 2013). Infestation pressure at any point is thus expressed as the distance-adjusted sum of contributions from all farms within 100 km seaway distance,

$$RR_{ij} = \frac{e^{-1.444-0.351\left(d_{ij}^{0.57}-1\right)/0.57}}{e^{-1.444-0.351(0-1)/0.57}}$$

where d_{ij} is the seaway distance from farm *i* to location *j* along the coast. Infestation pressure from farms more distant than 100 km was set to 0, since they by definition are ~ 0.

To obtain coast-wide quantitative maps expressing infestation pressure, raster maps (Datum WGS84, zone 33N) with 100 m^2 resolution were first generated for all farms and each week, by extrapolation of farm-specific infestation pressure with the empirical kernel density function. Final raster maps were then generated by summing every pixel for all farms in a given week (Veterinærinstituttet, 2017). All calculations were done using the R statistical software (R Development Coar Team, 2017). Seaway distances were calculated using the extension package “gdistance” (van Etten 2017), while all raster map calculations used the extension package “raster” (Hijmans et al., 2016).

Table 1 summarizes key statistics on Norwegian salmon farming along with estimates of salmon louse-egg production per production zone. The local biomass density (LBD; Table 1) represents a measure of the kernel density of farmed fish biomass in the surrounding neighborhood of each farm. LBD is calculated as a Gaussian kernel density with a standard deviation of 20.25 km and truncated at 40 km, for each farm and each reporting month (Jansen et al., 2012 p. 3).

2.2. Infestation model

In order to assess the risk of infestation of wild salmon post-smolts, we needed to establish a functional relationship between farm-origin infestation pressure and the post-smolt infestation rates. This was performed by modeling counts of salmon lice, both sessile and motile stages, on individual fish from sentinel cages. The sentinel cage trials have been described in Bjørn et al. (2011) and aggregated infestation data from such trials have been used in validations of a hydrodynamic model for the spread of salmon lice (Sandvik et al., 2016). Here we have analyzed lice numbers counted on altogether 7911 individual fish from 329 individual sentinel cage trials (Table 2).

The cage trials were conducted over the years 2013–2016, in 4 different areas along the coast (Fig. 3), and in up to 3 different periods per area. These area-period-year combinations, comprising of altogether 17 groups, were used to group the data into a random effects variable to be accounted for in mixed model regressions. All cage trials were performed between the earliest start date, May 8th, and the latest end date, June 29th.

Table 1
The number of actively reporting farms and farm weeks of production for each production zone in 2016. The mean biomass (Mean bio., metric tonnes) refers to the mean standing stock of farmed salmonids per month. LBD refers to the mean local biomass density of salmonids per farm and month of 2016 (10^6 kg). Louse eggs are the estimated accumulated number of salmon louse eggs produced (in billions, 10^9) in 2016. Eggs per biomass expresses the number of louse eggs divided by the mean biomass (in millions, 10^6).

M. zone	Farms	Farm weeks	Mean bio. (t)	LBD	Louse eggs	Eggs per bio.
1	13	546	11874	97	4.0	0.34
2	46	1882	40560	333	35.2	0.87
3	133	5096	106165	391	121.9	1.15
4	123	4617	92389	239	112.6	1.22
5	36	1407	37894	118	45.9	1.21
6	115	4098	126743	352	153.3	1.21
7	45	1296	43795	223	31.8	0.73
8	74	2523	63715	162	55.7	0.87
9	71	2129	52818	72	28.6	0.54
10	54	1851	63888	209	33.6	0.53
11	30	1049	35121	111	8.1	0.23
12	50	1778	50657	130	10.7	0.21
13	4	146	4047	18	0.6	0.15

Table 2
The numbers of fish and duration of sentinel cage trials.

	Numbers of fish	Duration (days)
Median	25	16
Interquartile range	22–29	14–21
Range	2 − 38	12 − 27

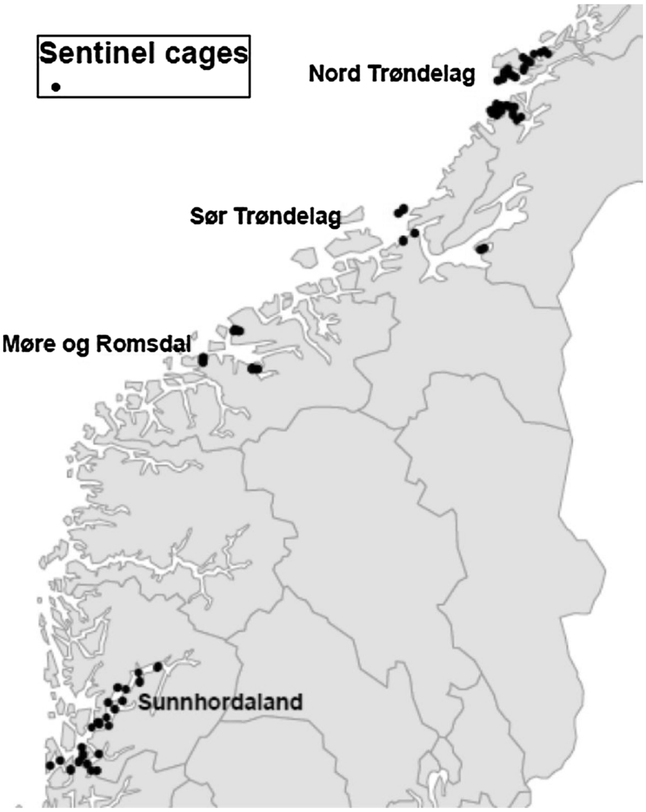

Fig. 3. Locations for sentinel cage-experiments in four coastal areas in Norway.

Lice counts were modeled in a mixed model regression with a negative binomial variance structure using the R-package lme4 (Bates et al., 2015), as:

$$Licecounts_{i,c,t} \sim e^{intercept+\log(IP_{c,t})+\text{offset}(\log(duration_{c,t}))+area\_year\_period_{c,t}}$$

where $Licecounts_{i,c,t}$ is the number of lice per fish *i* in cage *c* at time t given by year and period. $IP_{c,t}$ is the mean infestation pressure over the last two weeks before the end date of each cage trial. The mean of the last two weeks was chosen because two weeks are as close as we could get to the median duration of experiments of 16 days, with a weekly resolution in the lice data. The $duration_{c,t}$ of each cage trial is accounted for by the offset variable. Finally, the area_year_$period_{c,t}$ variable is entered as a random effect. We also tested an alternative model where $\log(IP_{c,t})$ was replaced by temperature, which was entered as a spline function with 5 degrees of freedom.

The capability of the infestation model to predict the observed abundance of lice per fish in the sentinel cage experiments, was tested by least squares linear regression,

$$\log(obs_{c,t} + 0.033) \sim intercept + \log(predicted_{c,t} + 0.033)$$

where $obs_{c,t}$ is the observed mean abundance of lice in cage *c* at time *t*, 0.033 was added being the lowest nonzero observation of lice abundance, and $predicted_{c,t}$ is the expected mean abundance from the infestation model.

2.3. Data on wild smolts and timing of smolt migration

The present risk model includes data from 401 Norwegian rivers producing Atlantic salmon. The rivers are compiled from the table Appendix A (Vedlegg 1) in a recent report from the Norwegian Scientific Advisory Committee for Atlantic Salmon Management (Anon, 2016). In this table, rivers are identified by unique codes ("Vassdrags nr.") from the database Regine, which is supported by The Norwegian Water Resources and Energy Directorate (NVE 2017). The rivers and their catchment areas are geo-referenced in this database, and the outlet of each watercourse into the marine environment was identified from the Regine database. For each watercourse in Appendix A, advisory production goals have been estimated in the form of the total number of eggs to be spawned annually and the total weight of spawning adult female salmon (Anon, 2016). These estimates are derived from studies of the total area accessible to spawning Atlantic salmon in rivers (Hindar et al., 2007). Based on the egg-production goal, estimates of theoretical smolt production have also been calculated, by combining knowledge on smolt age with standardized survival figures (Hindar et al., 2007). These authors listed estimates of survival from eggs to smolt and theoretical smolt production in 80 Norwegian watercourses. The present data was compiled from Hindar and co-authors for the 80 watercourses. For the remaining watercourses, theoretical smolt production was estimated by assuming equal survival from eggs to smolt to the nearest of the 80 pre-estimated rivers presented in (Hindar et al., 2007). The nearest river was defined by the least difference between the numbers constituted by the first three digits of the river id (see Supplemenatry Table 1), which defines the water system area in the Regine database (NVE, 2017).

The timing of outward migration of post-smolt salmon is critical, due to the pronounced seasonal population dynamics of the salmon louse on farmed salmon (Aldrin et al., 2013; Jansen et al., 2012). Smolt migration time for a given watercourse can be characterized by a distribution of the proportion of outward migrating smolts over time, from the annual onset of migration to the end of migration. Otero et al. (2014) presented a model on the timing of the onset of outward migration of Atlantic salmon, defined as the day of the year when 25% of the smolt had descended from a given river in a given year. The effect of latitude and longitude was included as a nonlinear function. To set rough dates for the day corresponding to 25% of post-smolt migration from rivers within production zones, we used the 10-day resolution isoclines depicted in Fig. 3 (a) in Otero et al. (2014), with May 18 representing the 0 isocline from the intercept in their model. The resulting times for 25% post-smolt migration within production zones (25% SMT), are tabulated in Table 3.

Smolt migration times can vary considerably from year to year within and between rivers (Vollset et al., 2016). Attempts have been made to create models that link watershed characteristics and environmental factors for predicting smolt migration (Hvidsten et al., 1995). As of now, however, such models are only river specific and cannot be used to predict the smolt migration times in other rivers with a precision that would be useful in the present context. Variation in the timing of migration may occur due to factors that are specific to the region (such as climate and weather), and may occur due to river specific configurations such as river and catchment area morphology (e.g. river length, presence of glacier or lakes) or river regulation. Also, genetic variation in life history strategy will interact with different environmental factors and may potentially augment or reduce this variation. Similarly, the duration of smolt migration may also vary considerably due to the above mentioned factors.

Between-year variations in median run time have been reported to be up to 25 days in the river Dale in western Norway (Vollset et al., 2016). In the same publication, the between-river migration within the same fjord was up to 27 days. Similarly, Jonsson and Jonsson (2014) reported a range of 29 days in the date for 5% descent in the smaller river Imsa. In mid Norway, Hvidsten et al. (1995) reported a range in median smolt migration time of 22 days between the dates with the highest catch in the river Orkla, while in northern Norway, Jensen et al. (2012) reported a range in median migration time of 28 days in the river Halselv. Concerning the duration of smolt migration, smaller rivers have been found to have a short and more truncated period of migration, while the larger rivers have longer and more protracted migration periods (Vollset et al., 2016). Examples of inter-annual variation and interquartile range in duration of migration periods from Norwegian rivers are given in Table 4.

Due to the fragmented information on river-specific migration times, we opted for fixing migration times within production zones, but keeping between-zone differences roughly according to the model by Otero et al. (2014) (Table 3). We have no information that would indicate that ranges in smolt migration time, neither the timing nor the duration of smolt migration, would change with latitude. Hence, for all calculations of the risk model, the timing of smolt migration was set equal for all rivers within production zones and the duration of smolt migration was set equal for all production zones. The duration of migration periods was set to 40 days, where the start-time of migration is set 10 days prior to the 25% migration time; the median (50%) migration time is set to 10 days post the 25% migration time; and the end-time of migration is set 40 days post the start-time. These settings are roughly in accordance with data presented for the rivers Vosso and Ekso (see Fig. S2 in Vollset et al., 2016).

Table 3
The number of rivers, their estimated potential for production of salmon smolts (in millions, 10^6); smolt migration time corresponding to 25% of smolt migrated, start and end of migration; mean (range) of shortest migration distances for rivers (km); and mean migration time (range) in days for rivers within production zones.

Prod. zone	Rivers	Prod. potential	SMT 25%	SMT start	SMT end	Migration distance	Migration time
1	38	2.18	08 May	28 April	07 June	63 (23–145)	9 (4–21)
2	18	0.44	08 May	28 April	07 June	104 (27–150)	15 (4–21)
3	12	0.19	10 May	30 April	09 June	140 (59–233)	20 (9–33)
4	40	0.75	13 May	03 May	12 June	122 (35–264)	18 (5–37)
5	44	0.53	15 May	05 May	14 June	103 (46–158)	15 (7–23)
6	62	2.39	18 May	08 May	17 June	141 (62–272)	20 (9–39)
7	22	0.90	23 May	13 May	22 June	120 (82–166)	17 (12–24)
8	30	0.36	28 May	18 May	27 June	137 (79–222)	20 (12–32)
9	54	0.19	02 June	23 May	02 July	131 (37–225)	19 (6–32)
10	28	0.33	07 June	28 May	07 July	90 (32–155)	13 (5–22)
11	17	0.14	12 June	02 June	12 July	120 (53–190)	17 (8–27)
12	18	0.59	17 June	07 June	17 July	120 (25–173)	17 (4–25)
13	18	1.11	27 June	17 June	27 July	89 (26–140)	13 (4–20)

Table 4
Examples of inter-annual variation in smolt migration times (SMT, days) and distributions in migration periods (defined as interquartile ranges in days) from regions in Norway. Method refers to different sampling for migrating smolts.

River	Method	Inter-annual variation in SMT	Interquartile range in miration period	Reference
Imsa	River trap	29 [1]	16	Jonsson and Jonsson (2004)
Dale	Wolf trap	25 [2]	42	Vollset et al. (2016)
Vosso	Smoltscrew and trapnets	NA	27	Vollset et al. (2016)
Orkla	Trap	28 [3]	NA	Hvidsten et al. (1995)
Halselv	Wolf trap	22 [2]	25 ± 13	Jensen et al. (2012)
Lone	Video	NA	6	Vollset et al. (2016)
Arna	Video	NA	4	Vollset et al. (2016)

[1]Based on 5 percentile; [2]Based on median date; [3]Based on highest catch.

2.4. Post-smolt marine migration

Thorstad et al. (2012) review Atlantic salmon post-smolt migration behavior. Movement patterns during the first phase of the coastal migration are described as complex, with some post-smolts taking a direct route towards the sea while others move in different directions over short temporal and spatial scales (Hedger et al., 2008; Okland et al., 2006). In addition, swimming speeds are reported to be highly variable (Thorstad et al., 2012). For the present modeling system, we assumed that post-smolts migrate following the shortest path from the river outlets to the high seas feeding grounds. This shortest path was calculated for each river using the R Package gdistance (van Etten, 2017). From each outlet, the shortest path through a 100 m^2 coastal raster map, delimited by the 12 M offshore border, was estimated (Fig. 4). While model fish traversed the coastal raster grid, it was not accounted for directions in crossing pixels, implying that the distance accounted for by crossing a pixel was 100 m in either the south – north axis or the east – west axis. The migration distance for any river is therefor given by the number of pixels crossed * 0.1 km (Table 3).

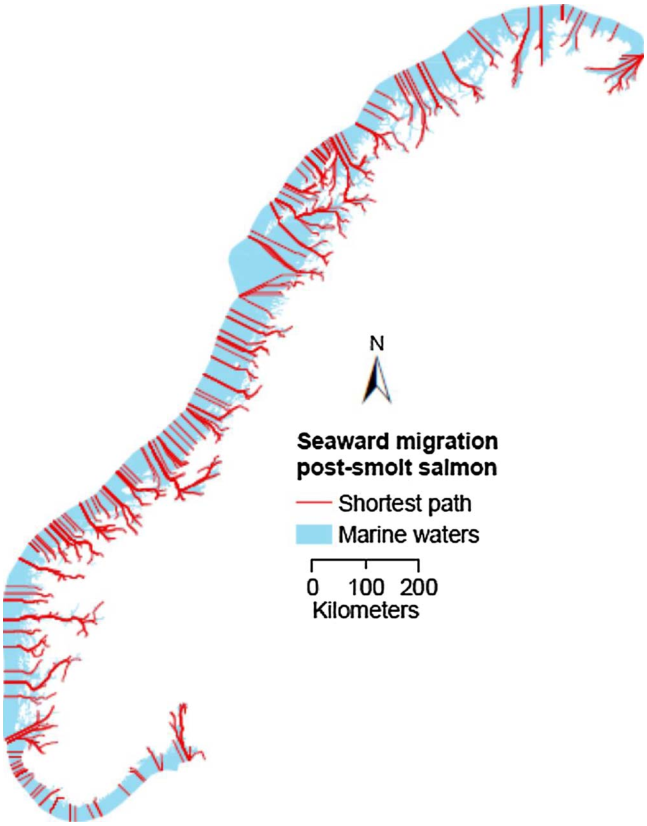

Fig. 4. Shortest paths for 401 rivers (red lines) through a costal grid (blue) from the river outlet to the 12 neutical mile offshore border. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We define the speed of migration along the given pathways as a rate of progression from the river outlet to the high seas (the 12 mile offshore border). A rather slow rate of migratory progression of 8.2 cm s^{-1}, corresponding to a migration distance of ~200 km over 4 weeks (Thorstad et al., 2012), was chosen.

To estimate infestation rates on migrating salmon post-smolts, we used the infestation model and raster maps of infestation pressure, and assigned the shortest migration pathways and the given rate of migratory progression to the post-smolts from each river. For each of the three given migration weeks, post-smolt migration was initiated at the river outlet. Then, following the shortest path, fish were exposed to an infestation pressure corresponding to the given week of migration. The first and last weeks of migration, the fish migrated the number of days left in the week* 500 pixels/7 along their route. For the next 500 pixels' distance, the fish were exposed to infestation pressure corresponding to the week following that of the given migration week. Continuing, through the following 500 pixels, the fish were exposed to infestation pressure from the subsequent week, and so on. Finally, infestations according to the infestation model were summed up for each pixel along the shortest migration path, yielding an expected mean number of infesting salmon lice for the whole pathway.

For all the various migration times and scenarios, we used the full negative binomial probability distribution for the expected mean infestation to model the distribution of parasites per fish. This was performed by simulating the distribution of the number of parasites on 10^5 fish using a theta (distribution parameter) of 2.733 from the infestation model.

Fig. 5 is a graphic representation of the model where the shortest migration pathways for rivers draining into Production zones 2–8 traverse coast-wide transmission pressures. Transmission pressure ($TP_{p,t}$) is rescaled from infestation pressure (IP) to express the expected accumulated abundance of salmon lice on migrating fish after one week of exposure in a given pixel (p) of the coast-wide raster grid. The rescaling was done by:

$$TP_{p,t} \sim e^{-14.603+\log(7)+0.843IP_{p,t}}$$

where the addition of log(7) rescales the infestation model (log link) to a 7 day period.

2.5. Parasite-induced mortality

A number of studies document increased marine survival of salmon that are chemically protected against salmon lice infestations (Gargan et al., 2012; Jackson et al., 2013; Krkosek et al., 2013; Skilbrei et al., 2013; Vollset et al., 2015), suggesting that salmon lice decrease the marine survival of Atlantic salmon. Also, physiological and pathological effects of salmon lice on salmonids have been thoroughly described in laboratory experiments (Finstad and Bjørn 2011; Grimnes and Jakobsen 1996; Wagner et al., 2008). However, the parasite burdens post-smolt salmon may tolerate are uncertain and probably vary individually, *e.g.* related to the size of the fish. Taranger et al. (2015) reviewed studies on

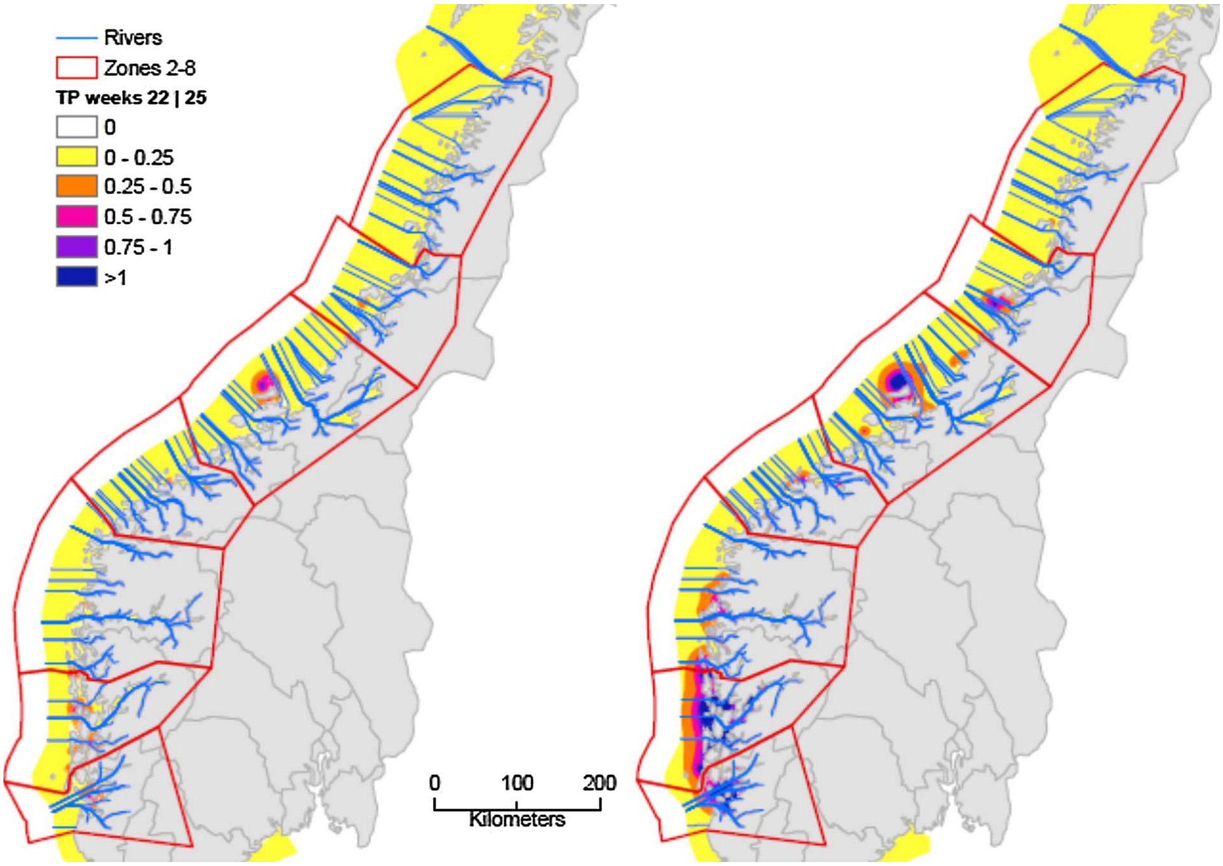

Fig. 5. Transmission pressure (TP) for week 22 (left panel) and week 25 (right panel) showing the expected abundance of lice after one week's positioning of fish in a given location along the coast, productions zones 2–8 and the shortest seaward migration paths for rivers draining into these production zones.

Table 5
The percentage of fish assumed to die from parasite-induced mortality according to the number of infesting lice, following the risk index for small sized salmon in Taranger et al. (2015). Low and high mortality schemes were also implemented in the calculations, for sensitivity testing.

Normal mortality		Low mortality		High mortality	
Lice per fish	Mortality (%)	Lice per fish	Mortality (%)	Lice per fish	Mortality (%)
< 2	0	< 2	0	0 − 1	0
2–3	20	2–3	10	2–3	40
4–6	50	4–6	25	> 3	100
> 6	100	7–10	50		
		> 10	100		

Table 6
Regression statistics for the infestation model. The estimated dispersion parameter (theta) of the negative binomial family was 2.733, and the random effect variance was 1.116.

	Estimate	Std. error	p-value
Intercept	− 14.603	0.327	< 0.001
log(IP)	0.843	0.015	< 0.001

louse-induced mortality of salmon smolt and suggested a risk index to be used to estimate additional smolt mortality due to louse infestation. In the present risk model, we adopted the schematic mortality figures given by this risk index (Taranger et al., 2015). Furthermore, we assumed that migrating post-smolts weighed 20 g and that all infesting lice would live to develop into pathogenic pre-adult and adult stages. Table 5 lists percentage additive mortality according to the number of infesting lice per migrating fish.

For river-wise parasite-induced mortality estimations, the start, median and end-point in time for migration were fitted to a beta-pert distribution (Vose 2000), thus covering the total migration period for each river. Irrespective of the timeframe of the migration periods, the beta-pert distribution was divided into 1000 evenly distributed time-points. The height under the curve at each of the 1000 time-points then represents the relative proportion of the river population migrating at a given time point, $h_j/\sum_i h_i$, where h_j is the height under the curve at time point j and $\sum_i h_i$ is the height under the curve summed for all 1000 time points. The proportional mortality for each time point was subsequently calculated according to Table 6, by linear interpolation for the 1000 time points, from the start of migration to median migration time, and then from median migration time to the end-time of migration. The estimated proportional parasite-induced mortality for each river was then calculated as the sum of the proportion of post-smolts dying at each time point, relative to the proportion migrating at each time point.

The potential for smolt production varies markedly between production zones (Table 3). To emphasize the risk potential between production zones (z), we also calculated the proportion of the potential smolt production capacity estimated to suffer from parasite-induced mortality attributed to the different zones, $Prop_z$,

$$Prop_z = \frac{\sum_{i\in z} p_i \cdot SPP_i}{\sum_i p_i \cdot SPP_i}$$

where p_i is the proportional mortality of river I and SPP_i is the smolt production potential of river i.

2.6. Sensitivity testing

Sensitivity analyses focusing on the processes we regard to potentially be critical to the outcome of the risk model were conducted by varying model parameters one-at-a-time. Calculations of the risk model were performed by: 1) infestation rates were varied by a best and worst case scenario in which the random effect of the infestation model was varied according to the 5th and 95th percentiles of the standard deviation; 2) varying the fixed migration times to migration periods moved two and four weeks pre and post the migration dates given in Table 3; 3) varying the extension of migration periods, either reduced to 20 days, or prolonged to 80 days, symmetrically around the median migration date (Table 3); 4) varying the mortality schemes by approximately halving or doubling the mortality percentages for the various levels of infestation (Table 5); 5) varying the rate of migratory progression for smolts between low (4.25 cm s^{-1}) and high (12.75 cm s^{-1}) progression rates; and 6) varying the dispersion parameter of the negative binomial distribution, theta, to 1.367 and 4.100.

3. Results

Farm production of fish and the accompanying production of salmon louse eggs vary extensively between production zones (Table 1). The estimated production of salmon louse eggs per mean standing stock of farmed salmonids (Eggs per bio.; Table 1) varied by a factor of 1.22/0.15 = 8.1 and was significantly correlated to LBD (Pearson r = 0.70, df = 11, p = 0.008). This suggests that the output of louse infestation from farms, per unit of farm biomass, is dependent on the density of farmed salmonids in the neighborhood (Jansen et al., 2012). Accordingly, areas of high densities of farmed fish will have very high infestation pressures, because of the combined effect of host density and the increased per unit host contribution to the output of infestive louse larvae. In other words, there is evidently a large-scale nonlinear host-parasite interaction in the salmon farming production systems (Anderson and May 1991; Frazer 2009; Frazer et al., 2012).

There was a significant effect of infestation pressure (log (IP)) on lice counts in the sentinel cage-experiments (Table 6). The random effect in the mixed model gave an intraclass correlation coefficient (ICC, (Dohoo et al., 2003)) equal to 0.551. The mixed effect negative binomial dispersion parameter theta was estimated to 2.733, yielding quantiles of the distribution of lice numbers as in Fig. 6.

Table 7
Regression statistics for the relationship between the observed and predicted lice abundance in sentinel cage experiments. The regression model had an adjusted R-squared of 0.39 on 327 degrees of freedom.

	Estimate	Std.Erros	T value	Pr(> |t|)
intercept	−0.168	0.067	−2.49	0.013
coeff	0.927	0.064	14.56	< 0.001

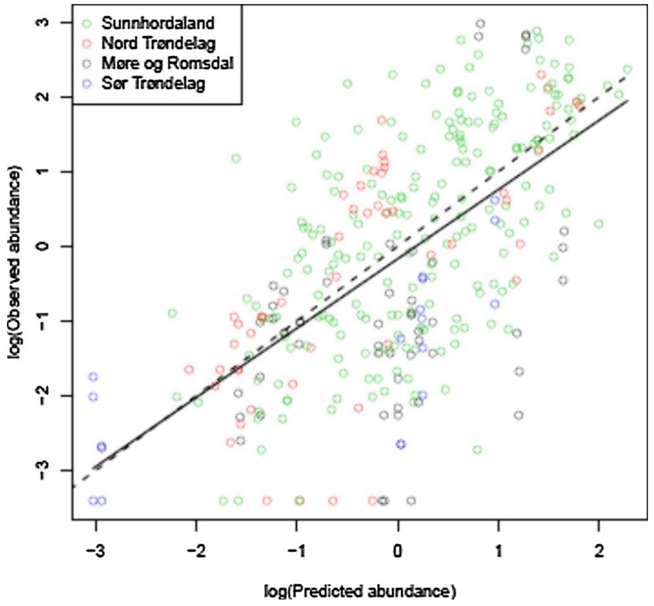

Fig. 7. Log of the observed lice abundance (+0.033) plotted against log of the expected lice abundance (+0.033) predicted by the infestation model. The black line is the best fit linear relationship between the variables and the hatched line shows an x = y plotted line.

The diagnostic model of the observed versus the predicted lice abundance, suggests that the infestation model explains 39% of the variation in the observed lice abundances in the sentinel cages, on the log scale (Table 7). The compliance between the x = y line and the

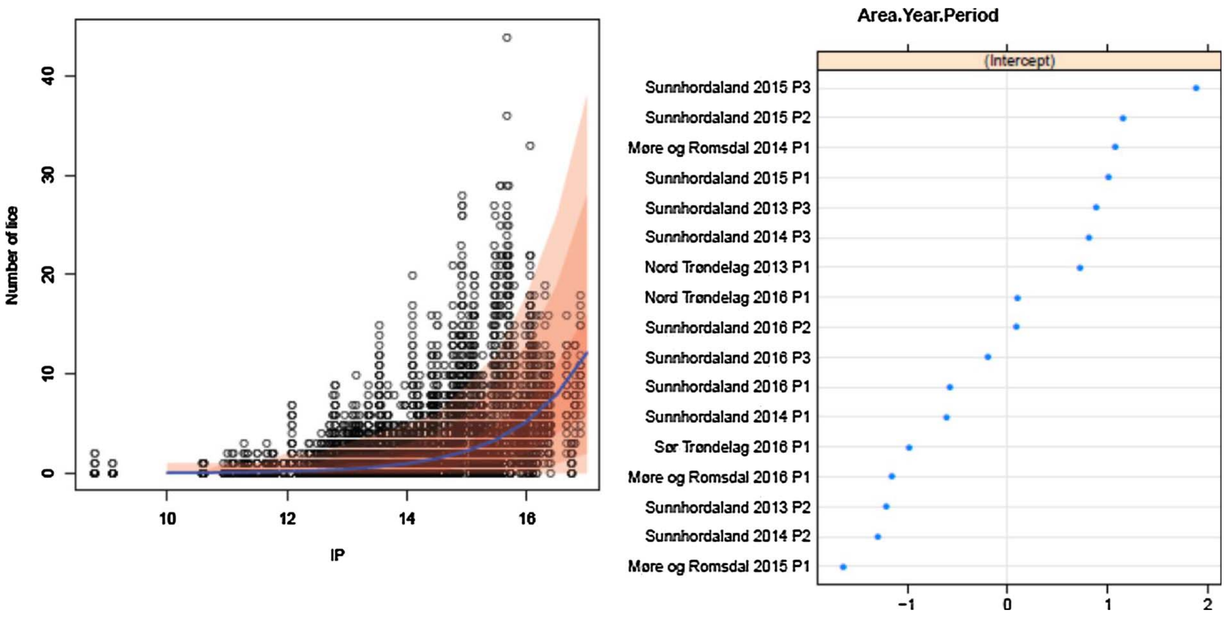

Fig. 6. The left panel show the expected abundance of lice scaled to a median of 16 days duration of sentinel cage experiments (blue line) and the observed numbers of lice per fish (black circles) plotted against the natural logarithm of infestations pressure. The red transparent bands represent quantiles (1–99%, lightest color; 5–95%, medium dark color; 25–75%, darkest color) from simulations of lice on 10^5 fish using the negative binomial distribution. The right panel shows the estimates of the random effect attributed to the area_year_period hierarchic level in the data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

linear model in Fig. 7, indicates that the infestation model is unbiased in its predictions over the range of infestation pressures. This figure, however, also illustrates that the precision of predicted lice infestations is variable.

When *predicted* $_{c,t}$ was based on the alternative model, with a spline function (d.f. = 5) for temperature entered as a predictor instead of infestation pressure, the random effects variance and Aikaike Information Criterion (AIC) increased markedly (Supplementary Figure 1a,b). The model using infestation pressure was thus a better predictor of observed lice numbers on the fish in the sentinel cages, compared to the model using temperature.

Exposure of salmon post-smolts to transmission pressure is clearly sensitive to the timing of the seaward migration (Fig. 5). Exposure also seems to be sensitive to the actual migration pathways that post-smolts follow, although the model for transmission pressure is relatively smooth in space compared to models using hydrodynamics to distribute lice larvae (Johnsen et al., 2016; Samsing et al., 2016; Sandvik et al., 2016).

Expected lice abundance on post-smolts was substantially higher for rivers draining into production zone 3 than for any other of the production zones (Fig. 8). Post-smolts from rivers draining into zones 1 and 9–13 were exposed to low infestation, and thus results from these zones are not shown in figures 8 and 9 (but see the Supplementary Figure 2). Post-smolts from zones 2 and 4–8 were exposed to intermediate infestation. There were large differences in the estimated infestations for the best and worst case scenarios (Supplementary Figures 3 and 4), reflecting large uncertainties in terms of area_period_year effects in the infestation model.

Rivers draining into production zone 3 also had a comparably large variance in the expected abundance of lice infecting post-smolts (Fig. 8). With regard to exposure to infestation, much of the same pattern between production zones is seen in different years. The expected abundance of infesting lice increased from the start to the end of the migration period. The magnitude of infestations, however, was substantially higher for 2016 compared to 2015 and 2014 (Fig. 8).

The estimated proportional louse-induced mortality was highest in production zone 3, with the basic scenario varying from 2–17% and the worst case scenario varying between 10–72%, between rivers in 2016 (Fig. 9). Mortality-estimates were substantially higher in 2016 than in 2014 and 2015. Data for production zone 1 and 9–13, as well as for the best-case scenario, were omitted from Fig. 9, due to low numbers (see Supplementary Fig. 5).

The second highest median estimate of louse-induced mortality in 2016 was for rivers in production zone 6 (Fig. 9). This production zone

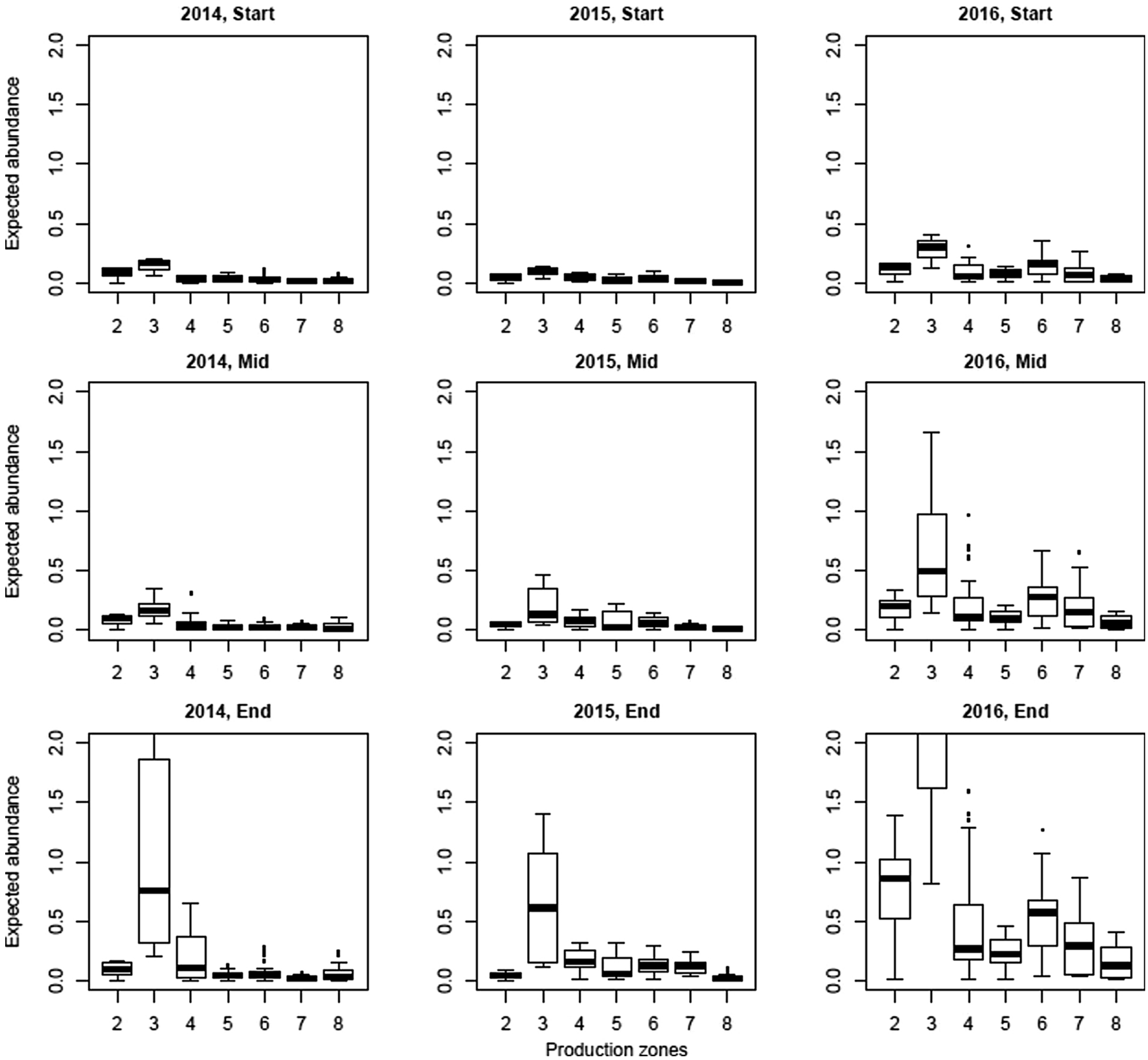

Fig. 8. Boxplot showing the expected abundance of lice on migrating smolt for rivers within production zones 2 − 8 for 2016, 2015 and 2014. The timing of migration corresponds with the start-time (upper panel), median-time (mid panel) and end-time (lower panel). (The estimated median and max for zone 3 in 2016 were 2.6 and 4.2; and max in 2014 was 2.3).

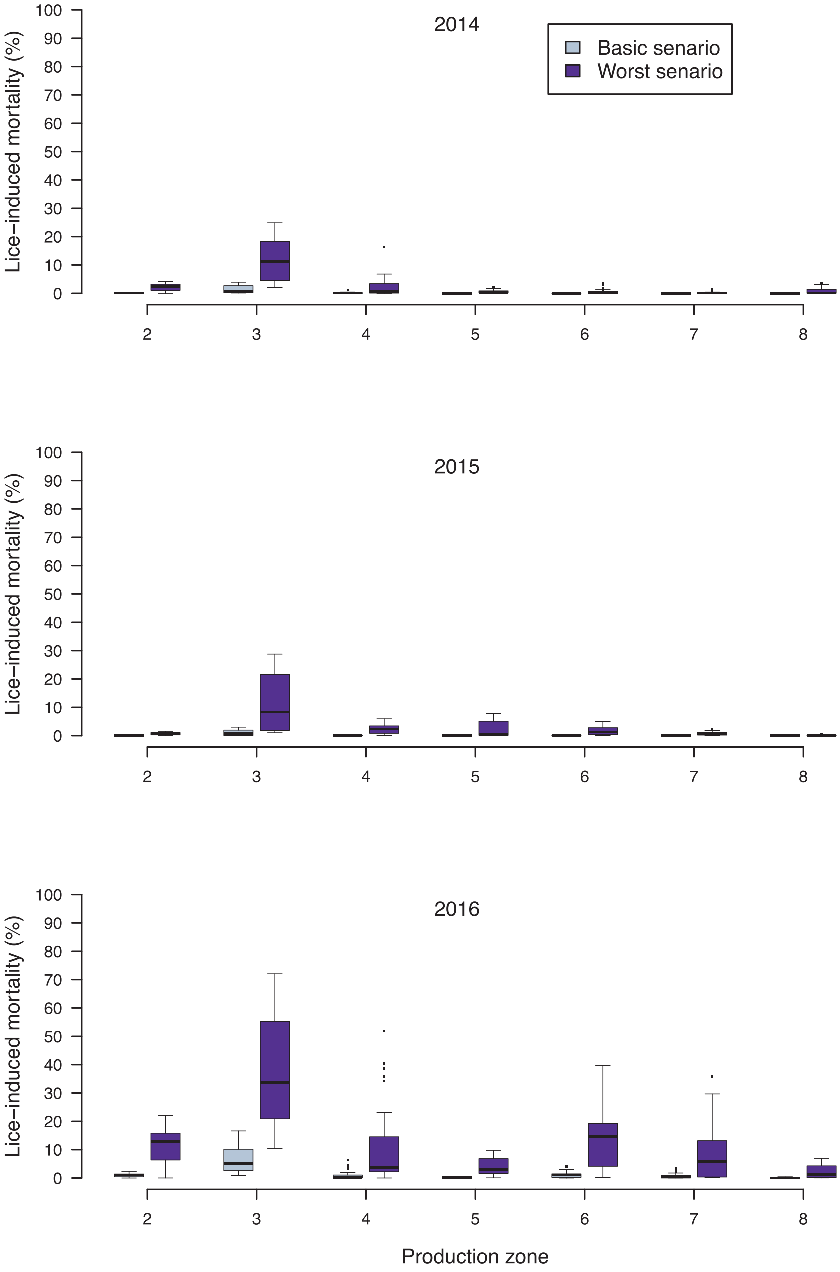

Fig. 9. Boxplot showing the estimated proportion (%) of fish dying from lice-induced mortality for rivers within production zones 2–8 for 2014, 2015 and 2016. Mortality estimates are shown for both the basic scenario and the worst-case scenario.

also has the highest potential for smolt production of all zones, which for comparison is rather low in production zone 3 (Table 5). The calculated potential for parasite-induced mortality was thus substantially higher for production zone 6 than for the other zones (Fig. 10).

The risk calculations are highly sensitive to migratory progression rates and the timing of migration, as depicted by production zones 3 and 6 (Fig. 11). The large effect of reducing migratory progression is partly due to the prolonged time of exposure of migrating fish to infestation and partly that low progression rates delay the timing of exposure. The timing of exposure is critical since the infestation pressure increases as the summer progresses, due to the repetitive seasonal dynamics of the salmon louse in Norwegian salmon farms (Aldrin et al., 2013; Jansen et al., 2012). This is also illustrated by prolonging the migration period, which increases the parasite-induced mortality estimates. Prolonging the migration period implies that parts of the salmon migrate earlier and parts later. The increasing mortality estimates thus arise from a nonlinear increase in the transmission pressure as the migration time progresses, further emphasizing the critical importance of migration timing. Varying mortality schemes also had a large impact on the output from the risk model. These mortality schemes are critical since there is limited knowledge on detrimental effects relative to intensities of infestation of salmon lice on salmonid hosts in the wild (Vollset et al., 2017). Finally, the risk model was highly sensitive to the infestation rates derived from the infestation model. This latter sensitivity may be argued to be especially critical, since (1) the worst-case scenario actually is within the empirical infestation rates in the cage-experiments; and (2) that the cage experiments may underestimate the exposure of an actively migrating post-smolt salmon.

Varying the distribution parameter theta of the negative binomial distribution had only minor effects on the risk model calculations and is therefore not shown (but see Supplementary Fig. 6).

4. Discussion

The present paper presents a complete model for risk assessment of salmon louse-induced mortality in seaward-migrating wild salmon from altogether 401 salmon-producing rivers draining into 13 production zones for salmon farming in Norway. The system accounts only for

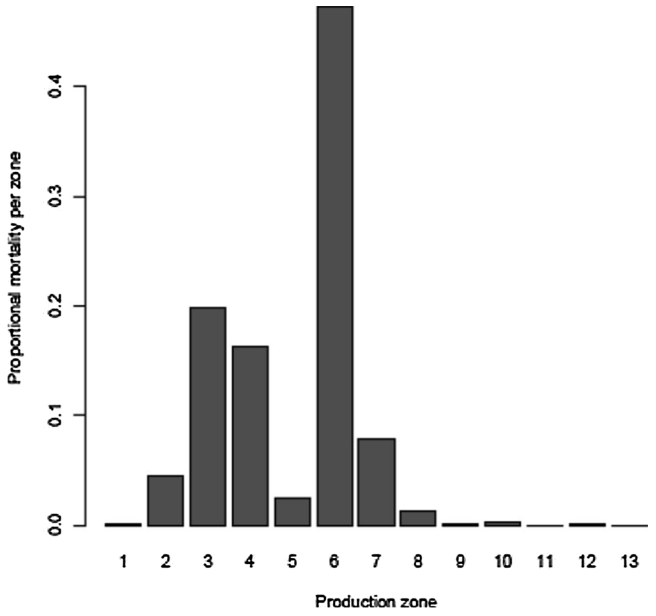

Fig. 10. Estimated parasite-induced mortality attributed to production zones, given as the proportion of the total smolt production potential. The estimates are based on the basic scenario in 2016.

infestation by salmon lice originating from farmed salmonids, but we assume that lice of farm origin generally will dominate due to the massive outnumbering of farmed versus wild salmonids (Heuch and Mo 2001; Jansen et al., 2012). Notable quantitative results from calculating the risk model are: 1) large differences between production zones with respect to the output of infestive lice larvae relative to standing stocks of farmed salmonids; 2) production zone three, followed by other production zones on the West Coast of Norway are at the highest risk of experiencing detrimental effects of farm-origin salmon lice; and 3) there are large uncertainties in the exact estimates of infestation rates and salmon louse-induced mortality of salmon post-smolts from the risk model. Nevertheless, we argue that the model captures the main spatio-temporal trends in the risks of infestation and parasite-induced mortality, e.g. that these risks were comparably higher in 2016 than in 2014 or 2015 and that there is a general decreasing spatial trend in risks in the northerly production zones. In the following we discuss these main findings along with uncertainties that we regard to be potentially critical to the outcome of the risk calculations.

4.1. Why does the production of infestive lice larvae relative to the standing stock of farmed fish vary between production zones?

The accumulated production of salmon louse eggs per mean standing stock biomass of farmed salmonids in the production zones varied by a factor of 8.1. Louse-egg production per unit of biomass was also significantly correlated with local biomass density (LBD). This comparison suggests massive differences in infestation pressures between areas of low and high farm production of salmon. In a high fish density area, there will be many hosts for the lice and each host will on average contribute more to the local infestation pressure. Thus, local infestation pressure will be expected to increase exponentially with linear increases in the local density of farmed hosts. We believe that this large-scale density-dependent host-parasite interaction is a major driver of the spatially variable estimates of expected louse infestation rates and parasite-induced mortality from the present risk model (Anderson and May (1991), Frazer (2009), Frazer et al., (2012)).

Clearly, the relatively large management zones in the north, where both temperatures and the local biomass density of famed salmonids are comparatively low, manage to produce fish with a low output of salmon louse infestation. This is partly due to the low temperatures in the north, which have direct bearings on the louse-egg production figures (Stien et al., 2005). However, also the southernmost production zone 1 had a low production of louse eggs per standing stock biomass of farmed salmonids. Production zone 1 has relatively low local densities of farmed salmon, which is in common with the northerly production zones. Zone 1, however, generally has higher water temperatures due to the more southerly location. This temperature discrepancy forms part of the support for the large-scale host density effects, which have been reported for salmon farming areas in Norway as well as in Chile and Scotland (Jansen et al., 2012; Kristoffersen et al., 2013; Murray and Hall 2014). The variable output of louse eggs and the dependency of this output on the local densities of farmed fish suggest that spatial densities of farmed salmonids should be a focus on its own merit, when evaluating future production volumes within production zones.

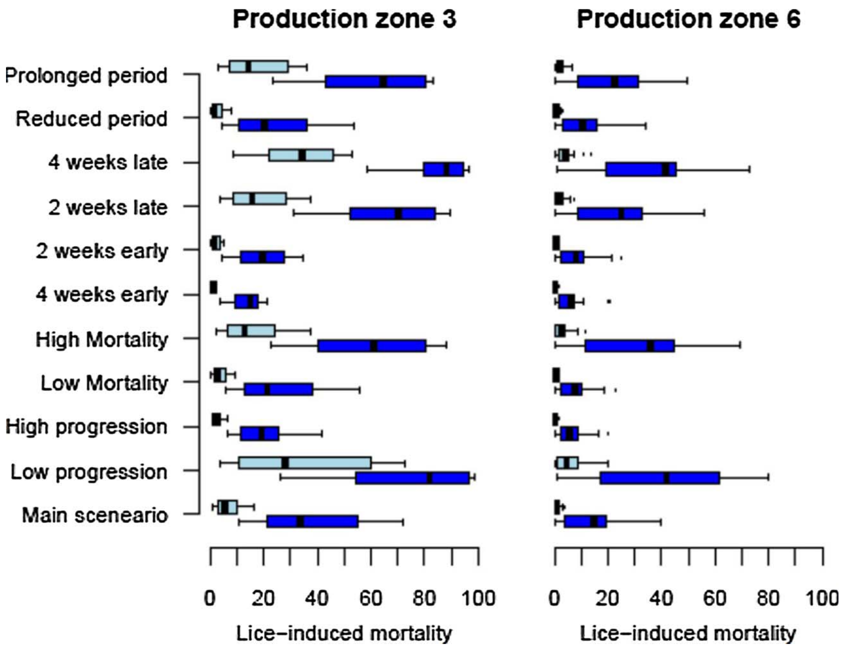

Fig. 11. Boxplots showing the estimated proportion of fish dying in rivers within productions zones 3 and 6, for the main scenario, compared to various settings of smolt migration times (SMT's), lice-induced mortality levels and smolt migratory progression rates (speed). Dark blue boxes are for the worst case scenario, whereas light blue boxes represent the basic scenario (Prolonged period = 80 day migration time; reduced period = 20 days migration time; 2–4 weeks early or late timing of SMT; low and high mortality schemes; and low and high migratory speed). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Where and when are seaward-migrating post-smolt salmon at risk of detrimental lice effects?

It follows from above that migrating smolts are at comparably high risk of louse infestation in areas of intense salmon farming. Furthermore, the present risk estimates suggest that salmon migrating relatively late within a given year are at higher risk than early migrating fish. Norwegian salmon farms are predominantly located in the outer coastal areas and less so in the inner fjords. In the present risk model, the timing of outward migration of salmon was set equal for all rivers draining into the same production zone. Accordingly, rivers with long migration distances will migrate through the outer coastal farming areas comparably late in time and will therefore be exposed to higher transmission pressures (see Supplementary Table 1). This will render long distance migration pathways at a comparably high risk of infestation, probably more due to late exposure than exposure to louse transmission in the inner fjords. It is also worth noting that rivers that drain into the inner fjords often have large catchment areas and large potential smolt production capacity.

4.3. What are the critical uncertainties in the risk model?

The present risk calculations were highly sensitive to varying infestation rates, as manifested by the best- and worst-case scenarios. It is noteworthy that the profound differences in risk estimates from these scenarios arise from the empirical area_year_period random effects in the infestation model. We do not know what generates this systematic effect related to area_year_period, but it suggests that transmission within the specter of the worst- and best-case scenarios for a given infestation pressure can be expected. A different question is whether infestation rates in the stationary cage-experiments are a good model for infestation of actively migrating smolt. A salmon smolt in a stationary cage will not experience the same physical surroundings and most likely interact somewhat differently with infestive larvae of salmon lice. For example, the volume of water moving past a sentinel cage may be much lower than the amount of water sampled by a smolt swimming unidirectional towards the open ocean. In addition, the cage itself may interfere with the behavior of salmon lice, which are known to locate their host by vision, olfactory cues and sensitivity to water movement from swimming fish (Browman et al., 2004; Heuch and Karlsen 1997). Experiments where cages with salmon smolt that are towed through fjords to mimic the behavior of a wild swimming salmon smolt are presently being conducted (Knut Wiik Vollset, personal communication), and preliminary results suggest that the infestations rates of fish in these experiments may be somewhat higher than what is estimated from sentinel cages. To date, however, the sentinel cages, and to a lesser extent plankton trawls as shown by Salama et al. (2013), provide the best empirical data to link modeled infestation pressure to infestation rates on fish. Uncertainties with regard to how the infestation pressure model scales to infestation rates on migrating salmon smolts, stress the need for more research to gather more and better data for validation of these models.

The timing of smolt migration was also critical to the risk calculations. This is due to the pronounced seasonal population dynamics of the salmon louse and the resulting estimates of the production of louse eggs in salmon farms (Fig. 12). This seasonal dynamics, with low lice abundances in the spring time and high abundance in the autumn, has been reported from wild sea trout in areas without salmon farming (Schram et al., 1998), indicating that this is a natural phenomenon for salmon louse population dynamics. In salmon farms, however, pronounced seasonal dynamics have been observed consistently over many years (Aldrin et al., 2013; Jansen et al., 2012). The spring troughs of farm lice abundance are probably also augmented by Norwegian louse regulations, requiring low maximum abundance of adult female lice in the period when post-smolt Atlantic salmon migrate (Anon, 2017b). Following the troughs in louse abundance, louse numbers increase more than linearly through the summer and until peak abundances are reached sometime in autumn. These peaks, and louse abundances in individual farms in this period, are also affected by antiparasitic treatments (Jansen et al., 2016) and other control methods, *e.g.* cleaner fish (Aldrin et al., 2017). The seasonal population dynamics seen for salmon lice in farms, with pronounced increases in transmission pressure as time progresses in summer, emphasize the critical importance of smolt migration times for the risk of louse infestations. Nevertheless, the present calculations from the scenario model do indicate that Atlantic salmon smolts migrate in periods of low transmission pressure and that the strategies for keeping louse abundances at low levels during salmon migration have been successful in most regions in the period 2012 − 2016 (Fig. 12). It is worth noting, however, that the results from 2016 were worse than for 2014 and 2015, which we suspect could be because of a general loss of medicinal treatment effects (Jansen et al., 2016). This has resulted in a pronounced shift in salmon louse control methods applied in Norwegian salmon farms (Helgesen and Jansen 2017).

The louse-induced mortality scheme used in the present risk model was adopted from the risk assessment by Taranger et al. (2015). This was primarily motivated by operating in consensus with other risk assessment approaches, more so than empirical support for this parasite-induced mortality scheme. In laboratory experiments, lice have been shown to have adverse effects on smolt growth and survival at infestation levels that are comparable with the present schemes, e.g. (Finstad et al., 2000; Wagner et al., 2008). However, effects in the lab may not be valid for effects experienced in the wild and studying parasite-induced mortality related to infestation levels in the wild is notoriously complicated (Costello 2006; Vollset et al., 2017). Nevertheless, effects of louse infestations on survival and growth of wild salmon during the marine ongrowing phase of their life cycle have been demonstrated (Krkosek et al., 2013; Vollset et al., 2014; Vollset et al., 2015). Also returns of salmon have been associated with salmon louse abundance in farms (Krkosek et al., 2007; Shepard and Gargan 2017), although the causal relationship of such associations have been questioned (Marty et al., 2010). The actual levels of infestation that would lead to significant adverse effects, however, is uncertain and the sensitivity of varying the mortality scheme has large effects on the outcome of the present risk calculations (Vollset et al., 2017).

We assumed that smolts follow the shortest path while migrating from the river outlets and through the coastal areas to the sea. This could be fundamentally wrong, for example if migrating fish followed paths along the coast before heading out to the sea, in which case the present migration model would be fundamentally misleading. Existing evidence, however limited, suggest that Atlantic salmon post smolts orient rather directionally towards the sea during migration (Davidsen et al., 2009; Thorstad et al., 2012; Urke et al., 2013). Nevertheless, any deviation from the shortest path towards the sea would affect the risk estimates. In some areas, e.g. production area 6 (Fig. 5), altering paths could have large effects on the estimates. The spatial model of infestation pressure used for estimating infestation rates, however, is relatively smooth, at least when compared to hydrodynamic models for the spread of salmon lice (Asplin et al., 2014; Sandvik et al., 2016). Furthermore, knowledge on migration pathways for salmon from different rivers are limited (Thorstad et al., 2012). Finally, the large number of rivers incorporated into the present risk model demonstrates the spatially varying infestation pressure (see Supplementary Table 1). On this background, effects of varying migration-pathways were not explored in the present risk model. Nevertheless, assumptions regarding migration pathways could be critical for the present risk calculations, emphasizing the need for more research in this area.

A key physical parameter that is not taken into account in our model is salinity. Salmon lice are known to avoid low salinity and salinity effects are emphasized in many studies of salmon louse population dynamics (Heuch 1995; Heuch et al., 2009; Rittenhouse et al., 2016). Similarly, Helland et al. (2015) included precipitation as a significant

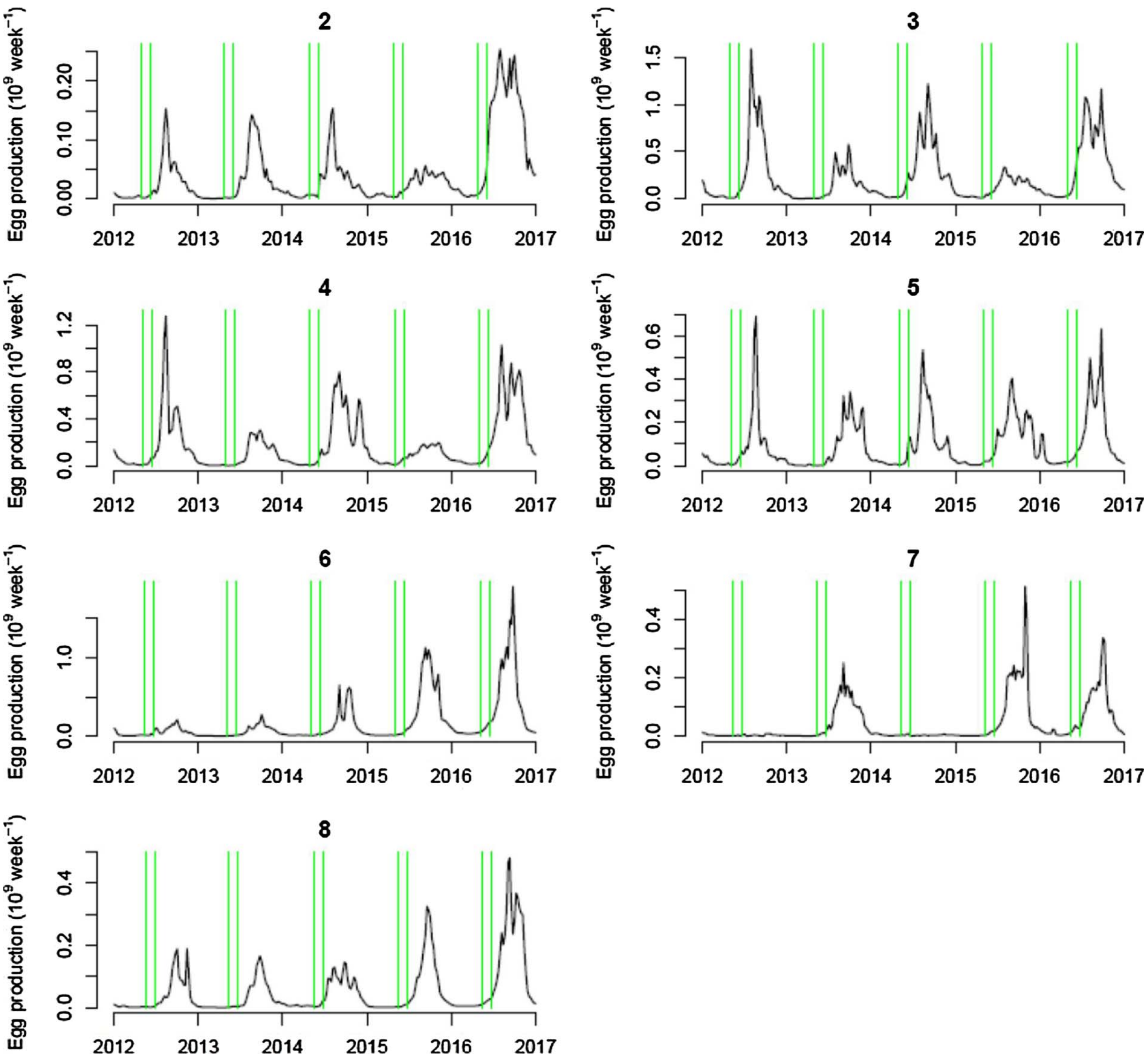

Fig. 12. The weekly estimated sum of eggs produced and the extension of the onset of post-smolt migration (vertical lines) in production zones 2–8 over the period 2012–2017.

predictor in a model attempting to model the infestation rates on sea trout, showing that high discharge from rivers was associated with lower lice levels. Also, salmon lice levels on escaped rainbow trout have been reported to be high during the winter months when discharge from rivers are low and the salinity gradient becomes less pronounced (Skilbrei 2012). Salmon smolts are known to migrate during peak discharge during the spring (Thorstad et al., 2012; Urke et al., 2013). During this time, salinities in surface layers in the inner fjords are usually low. Consequently, we would also expect infestation rates to be low during early migration through the inner fjords and higher during the later migration in the outer fjords and coastal areas. The areas influenced by freshwater would be expected to vary with precipitation and discharge patterns. To date we do not have salinity measurements that we can use to tease out such patterns.

5. Conclusions

We present a risk model for quantitative assessment of farm-origin salmon louse effects on migrating wild salmon from 401 rivers draining into 13 production zones for farmed salmon in Norway. Rivers draining into production zones on the west coast of Norway were at the highest risk of adverse lice effects, whereas northerly production zones were at comparably low risk, along with the southernmost production zone where there are few salmon farms. Estimation of louse-egg output from the production zones suggest that a large-scale density-dependent host-parasite effect is a major driver of the spatially variable estimates of expected lice infestation rates and parasite-induced mortality between rivers and production zones in the present risk model. The present risk estimates are sensitive to many of the processes depicted by the chain of events, from farm contribution of infestive lice larvae to adverse effects on river populations of wild salmon. Nevertheless, we argue that the output from the risk model is well suited to assess relative spatial and temporal risks associated with farm-origin salmon lice.

Conflict of interest

The authors have no conflicts of interest to declare.

Acknowledgements

This work forms part of the contributions from an expert group with the agenda to evaluate the risk of salmon lice effects on wild stocks of salmonid in Norway. We appreciate the contributions of the members of this group, including Ingrid Ellingsen, Bengt Finstad, Ørjan Karlsen, Mari Skuggedal Myksvoll, Frank Nilsen, Anne Dagrun Sandvik and Harald Sægrov. We also acknowledge all those who have participated in performing the sentinel cage experiments, as well as all those who have worked with compiling data for salmon-producing rivers.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.epidem.2017.11.001.

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