Large scale modelling of salmon lice (*Lepeophtheirus salmonis*) infection pressure based on lice monitoring data from Norwegian salmonid farms

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ABSTRACT

Infection by parasitic sea lice is a substantial problem in industrial scale salmon farming. To control the problem, Norwegian salmonid farms are not permitted to exceed a threshold level of infection on their fish, and farms are required to monitor and report lice levels on a weekly basis to ensure compliance with the regulation. In the present study, we combine the monitoring data with a deterministic model for salmon lice population dynamics to estimate farm production of infectious lice stages. Furthermore, we use an empirical estimate of the relative risk of salmon lice transmission between farms, that depend on inter-farm distances, to estimate the external infection pressure at a farm site, *i.e.* the infection pressure from infective salmon lice of neighbouring farm origin. Finally, we test whether our estimates of infection pressure from neighbouring farms as well as internal within farm infection pressure, predicts subsequent development of infection in cohorts of farmed salmonids in their initial phase of marine production. We find that estimated external infection pressure is a main predictor of salmon lice population dynamics in newly stocked cohorts of salmonids. Our results emphasize the importance of keeping the production of infectious lice stages at low levels within local networks of salmon farms. Our model can easily be implemented for real time estimation of infection pressure at the national scale, utilizing the masses of data generated through the compulsory lice monitoring in salmon farms. The implementation of such a system should give the salmon industry greater predictability with respect to salmon lice infection levels, and aid the decision making process when the development of new farm sites are planned.

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Introduction

Infection by parasitic sea lice is a substantial problem in salmon farming and the negative impacts of sea lice of farm origin on wild salmonid populations cause environmental concerns (Costello, 2009; Krkosek et al., 2013; Vollset et al., 2014). Control of sea lice infections on farmed fish is largely by treatment with antiparasitic drugs, but this has lead to development of resistance in parasitic lice to these drugs (Lees et al., 2008; Espedal et al., 2013; Helgesen et al., 2014). Spatio-temporal variation in the intensity of infections, as well as efforts to control infections, are positively associated with the density of farmed salmon (Jansen et al., 2012) and transmission between farm sites is a key factor in the population dynamics of sea lice in areas with large scale industrialized salmon farming (Aldrin et al., 2013).

Norwegian salmon farming is highly industrialized (Bostock et al., 2010). In 2012, 40% of farmed salmon produced in the world were from the coasts of Norway (1.23 million tonnes in 2012, FAO, 2014). This high production volume implies high densities of farmed salmon in parts of the coastal areas. To limit the impact of sea lice of salmon farm origin on wild Atlantic salmon and sea trout (*Salmo trutta*), responsible authorities have implemented strict regulations on allowable sea lice levels in farms. From 2012, a key regulation states that farms are not permitted to exceed a threshold level of infection of on average 0.5 mature female salmon lice (*Lepeophtheirus salmonis*) per fish at any time. Furthermore, to monitor infection levels, farmers are required to count salmon lice on representative samples of fish every week, with reporting

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mandatory within the following Tuesday (The Ministry of Trade, Industry and Fisheries, 2012). To be able to comply with these regulations there is increasing demand for predictive models that allow farmers to plan their effort with respect to salmon lice control. While internal infection pressure can be evaluated based on the locally obtained monitoring data, external infection pressure is considerably more difficult to estimate as it depends on salmon lice infection levels and demography in the surrounding sites. In this paper we explore information contained in the data generated through the nationwide salmon lice monitoring of fish farms, especially focusing on modelling and estimating the external infection pressure on individual salmon farms.

The nationwide salmon lice monitoring of fish farms contains weekly data on the abundance of adult female salmon lice in all active fish farms along the coast of Norway. We combine these data with a simple model for female temperature-dependent fecundity and the demographic rates of their offsprings (Stien et al., 2005), as well as a model for the relative risk of infection between neighbouring farms (Aldrin et al., 2013). To evaluate the model, we use data on lice abundances from the first 16 weeks of the production cycle at 363 farm sites in 2012–2013. In our evaluation we choose to focus on the first weeks at sea to limit confounding effects of internal infection processes, as farmed salmon are free of salmon lice when moved from freshwater hatcheries to marine environment farm sites.

Methods

Host–parasite system

Farming of salmonids in marine environment cages was initiated in the early 1970s in Norway. Salmonid farming has since developed into an intensive food production industry with harvested quantums of about 1.23 million tonnes in 2012 (FAO, 2014). Operators of salmonid farms are required to have a legal concession authorized by the Directorate of Fisheries and all legal consessions are featured in the aquaculture register with a geo-reference (Directorate of Fisheries, 2014). The marine phase of salmonid production is typically initiated by stocking juvenile smolts to net-pens on the farm in spring or in autumn. The net-pens openly exchange water with the surroundings. After stocking, the fish are on-grown for a period of roughly 18 months, after which they are slaughtered. Only fish of the same yearclass of age are produced in a given farm and we term a given farm stock of fish for a cohort in this paper. After slaughtering, the farm must be fallowed for a shorter period of time before a new cohort can be stocked. A more detailed description of salmonid farming in Norway is given by Kristoffersen et al. (2009).

Salmon lice are marine ectoparasitic copepods of salmonids, with 8 morphologically distinct stages (Maran et al., 2013; Hamre et al., 2014). The adult female salmon louse produces eggs that are aligned in two eggstrings, attched to the genital complex (Schram, 2000). The eggs hatch into planktonic nauplii. After developing through a second nauplius stage, the salmon louse develops into a planktonic infectious copepodid. If the copepodid comes into contact with a host it may attach and develop through two sessile chalimus stages, then through two mobile preadult stages and finally to adult males and adult females. Demographic rates and reproduction are highly dependend on temperatures (Stien et al., 2005).

Data

Kristoffersen et al. (2009) and Jansen et al. (2012) give detailed descriptions of the requirements for reporting key production statistics from marine salmonid farms. In the present paper, we use the same datasources for geographic location of marine fish farms and seaway distances between farms, as well as statistics on the stocks of farmed salmonids. Fig. 1 shows the distribution of all salmonid farms included in the present study. Estimates of lice development times and infection pressure (see definition below) are presented seperately for farms in the North-, Mid- and South regions (Fig. 1).

The datasource used by Jansen et al. (2012) was also used for salmon lice (*Lepeophtheirus salmonis*) infections in this study. However, one important change in the regulations aimed at salmon lice control was implemented from January 2012 when the mandatory requirements changed from monthly to weekly salmon lice monitoring and reporting. The weekly reports cover abundances of the lice stage-categories chalimus, pre adults and adult males (PAAM) and adult females (AF). According to regulations, lice must be counted on a minimum of 10 fish in half of the cages on a farm every week and reported as the mean of cage mean numbers of lice per fish. Counts are alternated biweekly so all cages on a given farm are counted within a two week period.

In addition to lice abundances, the weekly reports cover water temperatures at 3 m depth and the use of drug treatments to control lice. Infections by other sea lice species, *e.g. Caligus elongatus*, are not required to be reported, but may be misidentified especially at the chalimus stage. We ignore this here and term all reported infections as salmon lice.

Estimation of infection pressure

We assume that exposure to salmon lice infection depends on the number of infective copepodids in the aquatic environment. We use data on numbers of salmonids in the farms, farm reports of adult female lice abundances, water temperatures and a simplified version of the models in Stien et al. (2005) to quantify the production of infective copepodids in all activ farm-populations of salmonids along the coast of Norway. Furthermore, we use a simple deterministic model on the relative risk of infection as a function of distance to copepodid producing farms (Aldrin et al., 2013). To test this simple model of infection pressure, we relate estimates of infection pressure to time series of observed PAAM abundance in a sample of fish farms. We focus on the population dynamics of salmon lice of the PAAM stage category since lice in this category generally are reported with higher abundances than the AF stages, giving a better resolution in the data analyses. Furthermore, the small size of the chalimus stages makes precise counts difficult, causing larger measurement errors and negatively biased estimates of their abundance. The expected time from salmon lice eggs hatch in one farm until they appear as PAAM stage lice at a neighbouring farm, depend on development times thgrough the pre-infective developmental stages. We use a simple demographic model to match these events in our evaluation of our estimates of infection pressure. We divide estimates of infection pressure into internal infection pressure (IIP), representing within-farm produced infections; and external infection pressure pressure (EIP), representing infections produced in neighbourhood farms.

Farm numbers of fish are reported monthly, whereas lice data are reported weekly. Each week in the lice data are assigned to a given callendar month. The same assignement of weeks to callendar month was used for the farm numbers of fish data, with the weekly numbers of fish set equal to the assigned callendar month. To obtain a daily resolution in the model, each weekly farm observation was designated to Wednesday and observations were linearly interpolated between Wednesdays.

The total population of adult female lice on a given farm in a given week was calculated as: $n_{AF} = A_{AF} * n_{fish}$, where n_{AF} is the total
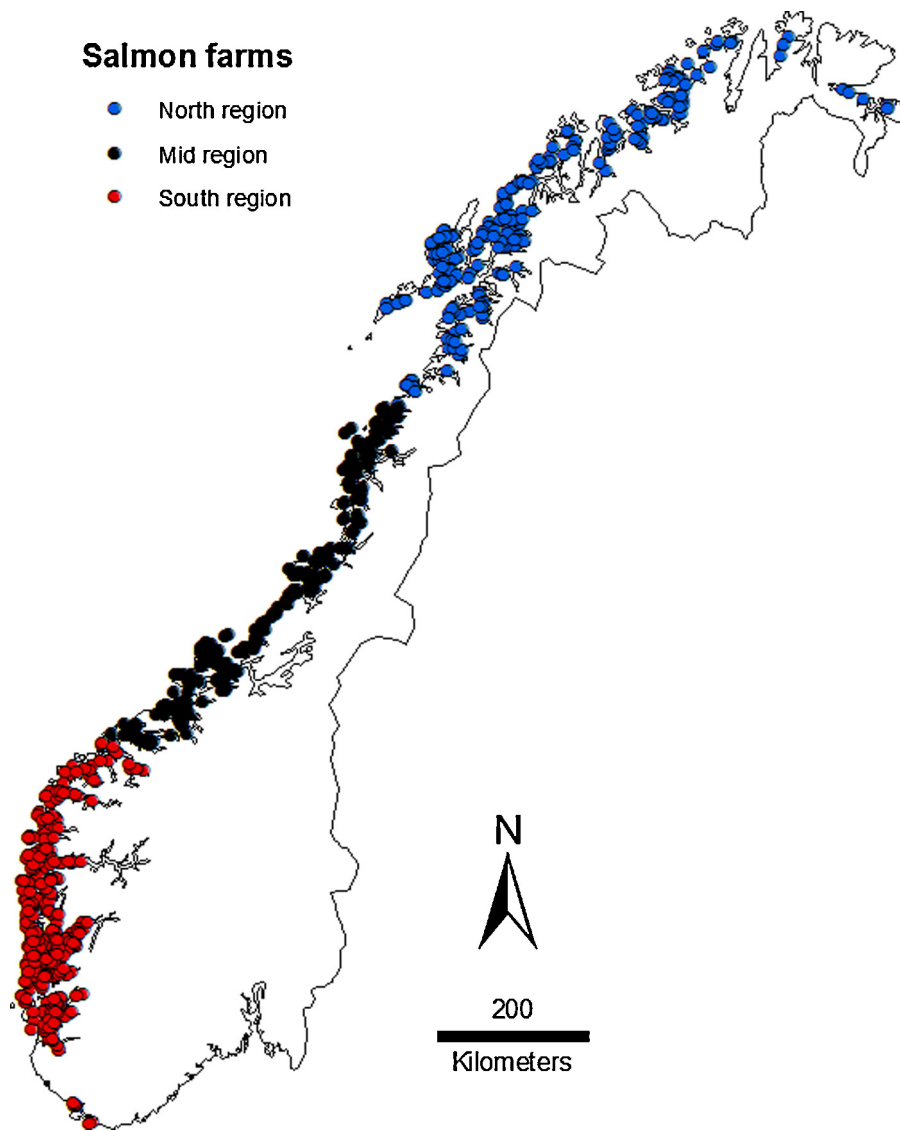
Fig. 1. Salmon farms that reported salmon lice abundances in any week during 2012–2013. The farms are assigned to a North- (blue circles), Mid- (black circles) or a South-region (red circles) along the Norwegian coast. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

population of adult female salmon lice, A_{AF} is the reported adult female lice abundance on the farm and n_{fish} is the number of fish on the farm.

The fecundity (F), defined as the daily production of newly hatched salmon lice larvae from an adult female lice, was calculated as the number of eggs per two eggstrings devided by the development time of the eggstrings. We assume that each eggstring consists of 150 eggs, and model F as:

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

where T is temperature (°C) (Stien et al., 2005). The total daily production of hatched larvae at a farm site is then given by $F_{tot} = F * n_{AF}$.

For hatching eggs to appear as PAAM stage lice, they must develop and survive through preinfective stages, settle as infective copepodids and develop through the chalimus stages. We estimated the time from egg hatching to PAAM stage lice appearance using a degree-days approach, with degree days needed for development based on the temperature-dependent demography reported in Stien et al. (2005). Development was devided into: (i) development from egg hatching to infective stage, which was set to 35 degree-days; (ii) the average time delay from developed into

the infective stage to successful infection of a host, which was set to the average survival time of infective copepodids: $1/0.22 \approx 4$ days irrespective of temperature; and (iii) the development through the chalimus stages into the PAAM stage, which was set to 155 degree-days.

During the period of development through pre-infective stages we assumed a daily mortality rate of 0.17 per individual (Stien et al., 2005), giving the proportion of hatched eggs that survive this development period: $s_{PI} = (1-0.17)^{\Delta t_{PI}}$, where Δt_{PI} is the number of days it takes to accumulate 35 degree-days.

During the period of development through chalimus stages we assumed a daily mortality of 0.05 per individual (Stien et al., 2005), giving a proportion of successfully infecting copepodids that survive this development period: $S_{CH} = (1-0.05)^{\Delta t_{CH}}$, where Δt_{CH} is the number of days it takes to accumulate 155 degree-days with the given temperatures.

The relative risk for infective copepodids produced at farm j to contribute to infection pressure at farm i was assumed to follow:

$$RR_{ij} = \frac{\exp(-1.444 - (d_{ij}^{0.57} - 1)/0.57)}{\exp(-1.444 - (d_{jj}^{0.57} - 1)/0.57)}$$

where RR_{ij} denotes the relative risk of infection between farms i and j as a function of the inter-farm seaway distance, d_{ij} (km), and the distance $d_{jj} = 0$ (Aldrin et al., 2013).

To model our estimates of infection pressure on variations in PAAM abundance, internal infection pressure on a daily level is defined by combining the submodels above as:

$$IIP_{i,day} = \sum_{\Delta t^*} A_{AF,i,(day-\Delta t_{PI,i}-\Delta t_{CH,i}-4)} n_{fish,i,(day-\Delta t_{PI,i}-\Delta t_{CH,i}-4)} F_i,$$

$$(day - \Delta t_{PI,i} - \Delta t_{CH,i} - 4) S_{PI,\Delta t_{PI,i}} S_{CH,\Delta t_{CH,i}}$$

where Δt^* represents all timepoints $\Delta t_{PI,i} + \Delta t_{CH,i} + 4$ that contributes with copepodids to the given day. To obtain IIP on a weekly basis the daily IIPs were summed for all weekdays t:

$$IIP_{i,t} = \sum_{day \in t} IIP_{i,day}$$

The total infection pressure (IP) on site j is then found by weighting all internal infection pressures from all farms within 100 km by the formula:

$$IP_{j,t} = \sum_{\forall i} IIP_{i,t} RR_{i,j}$$

External infection pressure is then defined as:

$$EIP_{j,t} = IP_{j,t} - IIP_{j,t}$$

To investigate whether the demographic detail included in the above model improves model performance, we estimated a simpler alternative measure of exposure to infection pressure called contributing adult females (CAF), directly from the reported number of AF lice on neighbourhood farms. The internal contributing adult females ($CAF_{internal}$) were adjusted with respect to development time as IIP on a daily basis, but temperature dependence in salmon lice fecundity and mortality was not accounted for:

$$CAF_{internal,i,day} = \sum_{\Delta t^*} A_{AF,i,(day-\Delta t_{PI,i}-\Delta t_{CH,i}-4)} n_{fish,i,(day-\Delta t_{PI,i}-\Delta t_{CH,i}-4)}$$

Then the daily numbers were added up to weekly estimates

$$CAF_{internal,i,t} = \sum_{day \in t} CAF_{internal,i,day}$$

The external CAF on farm j at time t was then weighted with the relative risk between farms.

$$CAF_{external,j,t} = \sum_{i \neq j} CAF_{internal,i,t} RR_{i,j}$$

Statistical modelling

A main goal of the present study is to evaluate whether the estimated production of infective copepodids of salmon lice in salmon farms and the simple assumptions regardig the planktonic spread of the copepodids can be used to predict the development of infections on farmed salmon. In order to test this idea, we selected cohorts of farmed salmonids that were newly stocked to marine farms, and followed the development of infections in their initial phase of marine production. The reason for selecting newly stocked cohorts of fish is that they are free of salmon lice when stocked from freshwater to marine environment net pens. Hence, these cohorts will only be exposed to externally produced infective stages until adult female lice appear and start reproducing. The criteria for including a cohort of fish was that the farm holding the stock of fish had not reported stock statistics or reported lice counts for a period of

at least a month, followed by a first report of fish with a reported mean weight of less than 250 g.

The development of PAAM stage lice abundance was followed weekly for a period of 16 weeks from the first reported counts of salmon lice in a given cohort of fish. Only cohorts that reported lice counts each week for at least 19 consecutive weeks were included in the study, while farms that reported to have treated their cohorts of fish with antiparasitic drugs during this period were discarded from the data. Extending the period for discarding cohorts from 16 to 19 week was done to ensure that antiparasitic treatment did not affect lice abundances in the data. We chose 19 weeks as a compromise between that of following groups of fish for an extended period of time and whithout discarding to many cohorts of fish from the dataset. The choise of 19 weeks resulted in discarding 205 out of 575 identified cohorts of fish. The discarded cohorts had higher on average PAAM stage lice abundance and higher estimates of exposure to EIP than the included cohorts. Hence, we present a suplementary analysis extending only over 8 weeks from the first reported counts of salmon lice in a given cohort of fish (Supplementary material). The final dataset in the present paper consisted of a total of 370 cohorts of fish from 363 farm sites, while in the supplementary analysis the dataset consited of 506 cohorts from 493 farms sites.

As a simple graphical approach we first investigated the relationship between the 16 week average external infection pressure of cohorts and their time series of average PAAM abundances. We grouped cohorts that were exposed on average to low (lower 33% quantile of EIP, $n = 123$), intermediate (middle 33% quantile of EIP, $n = 126$) and high (highest 33% quantile of EIP, $n = 123$) external infection pressure, and calculated the within group mean abundance of PAAM for each week at sea.

In more formal statistical models, we modelled the association between PAAM abundance and possible predictors using the package glmmADMB in R (Fournier et al., 2012) for general linear modelling with a zero-inflated negative binomial variance structure and a log link function. The model had the general form:

$$E(y) = \begin{cases} e^{\alpha + \sum_{\forall j} \beta_j x_j} & p = 1 - p_{zi} \\ 0 & p = p_{zi} \end{cases}$$

where p_{zi} is the probability of being zero inflated, x_j is the different explanatory variables and α and β_j the estimated parameters. Since this is a model for integer counts, we transformed PAAM abundance by multiplying with 30 and rounding off this number. The predictor variables being tested in the model are tabulated in Table 1, except for the temporal seasonal trend that was modelled according to Jansen et al. (2012). All variables were scaled, *i.e.* to mean = zero and variance = 1, to simplify comparisons of parameters for different variables. Models were compared using the Akaike information criteria (AIC). Model selection and residual diagnostics followed the principles outlined in Jansen et al. (2012) and Kristoffersen et al. (2013).

To emphasize the contribution of EIP to predicting PAAM abundance and to mimic a situation where lice monitoring data for a given location is not accessible, we also present a simplified model where PAAM abundance is modelled as a function of EIP and time after initial lice monitoring only (Fig. 5).

Potential predictors

Since we expected high temporal correlation in lice abundances with weekly counts, we entered the natural logarithm of the abundance of PAAM stage lice + 1 in the previous week as a predictor denoted $PAAM_{t-1}$. Furthermore, since the abundance of PAAM stage lice was zero for more than 50% of the data, we also entered

Table 1
Descriptive statistics for the variables potentially predicting the outcome variable defined as counts of stage category pre-adults and adult males of salmon lice (PAAM) on 30 fish (PAAM$_{t-1}$ is PAAM in the previous week; EIP is external infection pressure; IIP is internal infection pressure). Percentile levels (<33%; 33–66%; >66%) of the predictor variables are related to means of the outcome variable. Results of univariate zero inflated negative binomial regression analyses are summarized by Akaike's information criterion (AIC; the null model had an AIC of 23486).

	Mean value or True/False distribution for variables	80% Range for continuous variables	Percentile levels for continuous variables	Mean counts of PAAM on 30 fish for variable levels	AIC for univariate linear regression
log (PAAM$_{t-1}$)	0.083	0.0–0.25	0–0 0–0.03 >0.03	0.60 1.28 11.41	21360
PAAM$_{t-1}$ = 0	T: 3489 F: 2431			0.60 9.27	20065
log (EIP + 1)	13.0	9.61–16.09	0–12.2 12.2–14.5 >14.5	0.45 2.55 9.47	21935
IIP = 0	T: 5426 F: 494			3.06 16.27	22856
Temperature (°C)	9.81	5.3–14.0	<8.2 8.2–11.5 >11.5	2.56 4.30 5.64	22858
Count week	8.5	2–15	<6 6–11 >11	0.89 3.85 8.09	21880
Cleaner fish = 0	T: 4427 F: 1493			2.83 8.09	22701

a dichotomous variable representing zero infection or non-zero infection in the week prior to that of the dependent variable.

Infection pressure was estimated both as that produced within farms as internal infection pressure, IIP, and as that produced on external farms, EIP. Since we only used data from the first marine phase of production, adult female lice had little time to develop and reproduce on the cohorts of fish and IIP was estimated to above zero for less than 10% of the data. We therefore entered IIP only as a dichotomous variable, representing IIP = 0 or IIP > 0, in the analyses (Table 1). EIP was entered on the logarithmic scale as a continous variable.

Water temperature (T °C) at 3 m depth was included in the analyses as a continuous variable.

The week number, denoted count week, of the time series of lice counts from the first count at week 1 after stocking in the sea to week 16 was entered in the analyses as a continuous variable.

The use of cleaner fish to control lice infections was entered as a dichotomous variable being true when farmers reported such use, and false otherwise.

In preliminary analyses, the use of cleaner fish was found to be significantly positively related to PAAM abundance. Since this is counter-intuitive to expected effects, but probably reflects a positive association between the use of cleaner fish and experienced problems with lice infection, we excluded this variable in our final analyses.

To ensure that possible effects of predictors in the model were not merely due to seasonal correlations, we entered week number in the year (1–52) and a set of 6 seasonal trend variables as predictors in the model. The seasonal trend variables were entered in the same way as was done in Jansen et al. (2012). We do not present statistics for the seasonal variable other than ΔAIC values for comparable models with and without this set of variables.

Summary statistics for the predictor variables are given in Table 1.

Results

Estimates of development times and infection pressure

Estimated mean development times from the week of reporting AF lice abundance to next generation PAAM stage lice was generally longest in the north and shortest in the south due to a gradient in

water temperature but with a similar seasonal timing of maximum and minimum development times (Fig. 2a). The seasonal fluctuations in the internal infection pressure (Fig. 2b), adjusted by the PAAM development time, showed a similar pattern between years, with high IIP around the same time as PAAM development time was short and low IIP in the period February–May when development
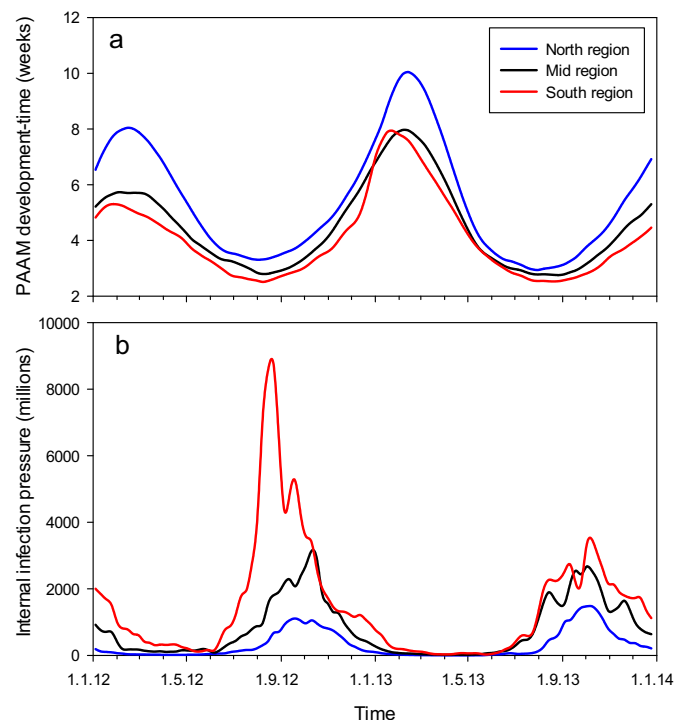

Fig. 2. (a–b). Mean estimated development times of preadult and adult male (PAAM) stage salmon lice (a) and and estimated internal infection pressure (IIP) in the North- (blue line), Mid- (black line) and South (red line) regions of Norway (b). Development times are from the week of reporting of adult female lice (AF) abundance until next generation PAAM lice are expected to appear in subsequent reports on lice abundance. IIP represents the the total accumulated over each week for the three regions and is adjusted to PAAM development time (see methods). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Estimated internal infestation pressure
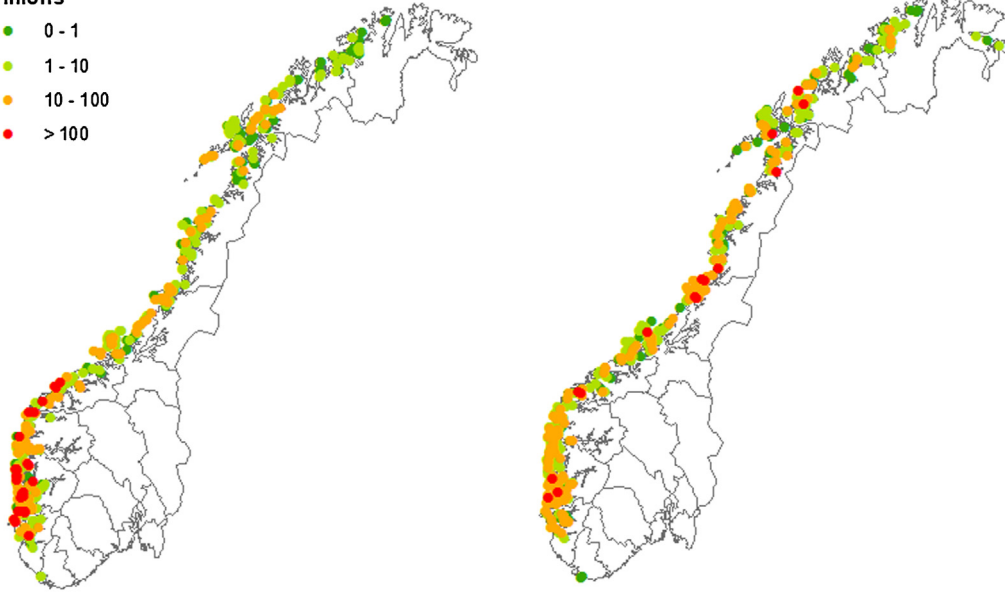
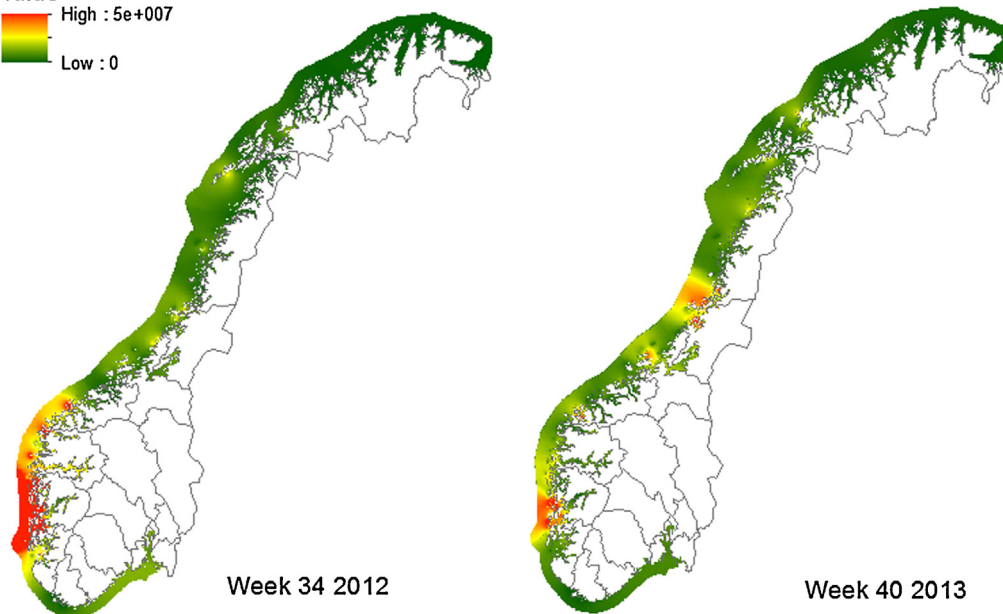**Estimated external infestation pressure**

Fig. 3. Estimated internal infection pressure (IIP, upper panel) and inverse distance weighted interpolations of external infection preassure (EIP) along the Norwegian coast. The maps correspond in time to peaks in IIP in Fig. 2, which was in week 34 in 2012 and week 40 in 2013. Quantities of IIP are given as geometrically increasing intervals (in millions) and where the higher symbol levels are given priority over lower symbol levels. Interpolations were done by accounting for the estimated exposure to EIP in the 50 nearest neighbourhood farms using ArcGIS Spatial Analyst.

times were high. Still, the timing of peak IIP differed somewhat between the two years. IIP showed a distinct peak in the south in week 34 in 2012, while differences between regions were less pronounced in 2013 when an overall peak in IIP was seen in week 40.

In addition to these regional trends, our model enables detection of substantial spatial and temporal variation in farm level estimates of IIP and EIP along the Norwegian coast (Fig. 3), *e.g.* high estimates of IIP and EIP were found locally in all three North–South regions along the coast in week 40 in 2013.

Analyses PAAM-stage salmon lice abundance

There was a strong positive relationship between the estimated 16 week average external infection pressure and PAAM abundance (Fig. 4). PAAM infections in cohorts exposed to high EIP increased at higher rates than in intermediate and low exposure cohorts. Notably, low exposure cohorts report near zero PAAM infections during the first 10–12 weeks of marine production.
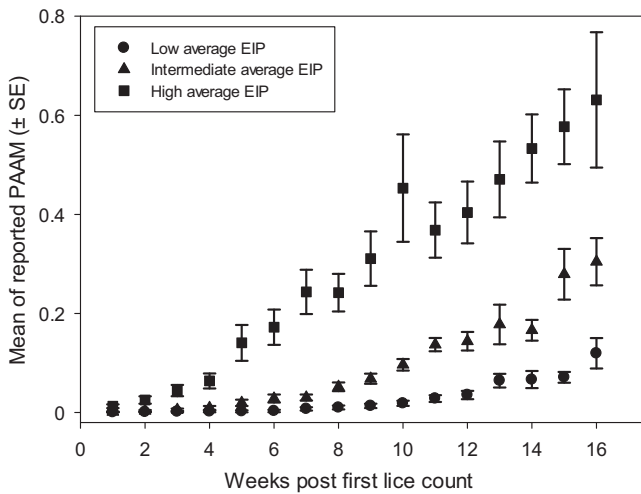
Fig. 4. Mean (±SE) of reports of PAAM stage salmon lice on cohorts of salmonids during their initial period of 16 weeks of marine production. Cohorts are divided into low, intermediate and high average external infection pressure (EIP) according to percentiles (<33%; 33–66%; >66%) of average exposure to EIP over the 16 week period.

Regression analyses of PAAM stage lice abundances resulted in a top ranked model that included a positive effect of log ($PAAM_{t-1} + 1$), Countweek and log (EIP + 1), and a negative effect of no PAAM infection the previous week ($PAAM_{t-1} = 0$, Table 2). The zero-inflated component of the distribution was estimated to include 0.53% of the data. According to ΔAIC, $PAAM_{t-1}$ was the most important predictor variable, followed by EIP (Table 3). Exchanging EIP with the simpler measure of external infection pressure, $CAF_{external}$, resulted in a poorer model fit (ΔAIC = 114). Also, standardized regression coefficients in the comparable models were reduced from 0.48 for EIP to 0.15 for $CAF_{external}$. Hence, EIP was a substantially better predictor of PAAM infections than $CAF_{external}$.

The supplementary analysis restricted to only 8 weeks of PAAM development did not alter the set of predictors in the top ranked regression model, but tended to increase the effects of EIP (Supplementary material).

Table 2

Parameter coefficient estimates and standard errors for the scaled predictor variables in the AIC top ranked model for abundance of PAAM stage salmon lice on cohorts of salmonids during their initial period of 16 weeks of marine production (AIC: 18433). All coefficients were highly significant ($p < 0.001$) predictors of PAAM abundance. Coefficients of the seasonal trends are not given in the table ($PAAM_{t-1}$ is PAAM in the previous week; EIP is external infection pressure).

Variable name	Coefficient estimate	Standard error
Intercept	0.081	0.040
log ($PAAM_{t-1} + 1$)	0.363	0.008
$PAAM_{t-1} = 0$	−0.861	0.029
log (EIP + 1)	0.480	0.036
Count week	0.167	0.023

Table 3

Differences in the AIC, ΔAIC, between the top ranked model in Table 2 and models excluding predictory variables ($PAAM_{t-1}$ is PAAM in the previous week; EIP is external infection pressure).

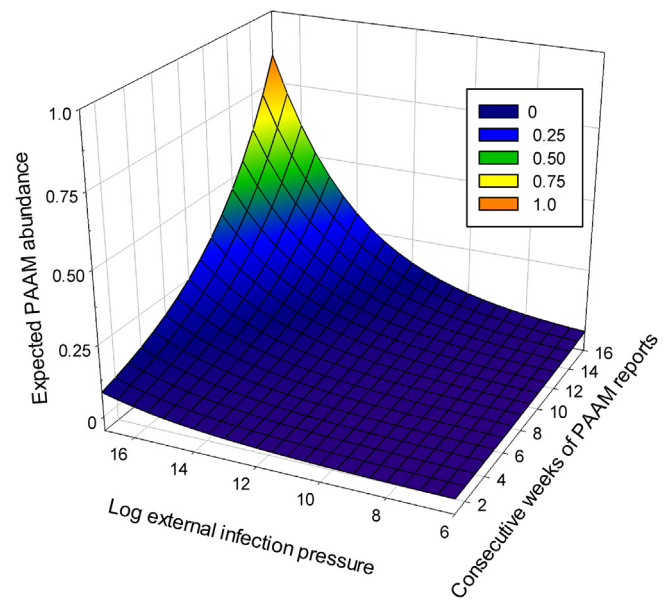| Variables	No. variables	ΔAIC
$PAAM_{t-1}$	2	2047
EIP	1	205
Count week	1	55
Seasonal trend	7	96
Zero inflation	1	214

Fig. 5. Expected report on abundance of PAAM stage salmon lice on cohorts of salmonids during their initial period of marine production as a function of weeks following the first reported lice count and external infection pressure (EIP) on a log scale. The plot is reproduced from predictions using a simplified version of the model presented in Tables 2 and 3, including only EIP and Count Week as predictors. Coefficient estimates (scaled) were 0.75 (±0.04 SE); 0.99 (±0.03 SE) and 0.70 (±0.02 SE) for the intercept; log (EIP + 1) and Count week (AIC: 20716), respectively.

Predictions from the simplified model for the expected abundance of PAAM stage salmon lice, including only the predictory variables count week and EIP are presented in Fig. 5. The model emphasizes the low rate of expected increase of PAAM infections at low exposure to EIP, as opposed to that expected at high EIP exposure.

Discussion

In the present paper we use lice monitoring data along with previously published models on salmon lice population dynamics, to calculate the internal infection pressure (IIP) and development times from egg hatching to next generation preadults and adult male lice (PAAM stage category). Futhermore, we use an empirically derived model on the relative risk of transmission between farms as a function of inter-farm seaway distance (Aldrin et al., 2013), to estimate the external infection pressure originating from neighbouring farms (EIP). Finally, we test if estimated EIP and IIP predict the development of salmon lice infection levels in cohorts of salmonids the first 16 weeks after being stocked in marine environment cages. We find that exposure to EIP contributes significantly to predict the development of salmon lice infections on these cohorts. Exposure to IIP was zero for most cohorts in most weeks and did not affect the population dynamics of salmon lice significantly because of the restricted time available for development into reproducing adult female lice during this initial phase of marine production.

We show here that the abundance of salmon lice is strongly associated with our estimates of EIP. We interpret this pattern as evidence for EIP to be proportional to the force of infection from external farm sources. For the fish farms, salmon lice transmission rates from external sources will determine the initial seeding and increase in lice infections, but is also expected to be important for parasite population growth rates in the period after effective drug treatments have been applied to farmed fish. Hence, lice transmission from external sources will be a prime determinant of the efforts needed to control lice levels within legal limits. Bearing in mind that

lice control is costly to the farmer and that frequent drug treatment increases the risk of development of resistance in the lice, estimates of EIP are likely to be positively associated with both aspects of modern salmonid farming. As such, our results pinpoint the importance of keeping the production of infective salmon lice low at local to regional spatial scales.

When farmed salmonids are moved from a juvenile production phase in freshwater and into marine environment cages as smolts, they are free of salmon lice infections. Hence, transmission of salmon lice to such newly stocked cohorts of fish must be by infectious copepodids that are produced on external salmonid hosts and have drifted with the water currents into the smolt cages. Theoretically, the external salmonid hosts could be of both wild and farmed origin. The present results, however, emphasize effects of infection of neighbourhood farm origin. This effect of external infection pressure, we will argue, is a manifestation of the fundamental host density effects that are at play in the parasite–host population dynamics of salmon louse and farmed salmonids (Anderson and May, 1991). Areas of intense salmonid production have high densities of salmonid hosts with high on average levels of lice infection (Jansen et al., 2012), implying high production of salmon lice infective stages and high infection pressure. A similar conclusion was arrived at for neighbourhood farm densities of *Caligus rogercressey*, a caligid copepod parasitizing farmed salmonids in Chile (Kristoffersen et al., 2013). The observed host–parasite density effects corroborate predictions from theoretical models for sealice epidemics, which conclude that lice transmission rates are highly sensitive to increasing host densities above critical thresholds (Frazer et al., 2012). Hence, the corroborative theoretical and empirical evidence emphasizing density dependent effects in the farmed salmonid–salmon lice associations suggest that host–parasite density considerations should be an integral part of management plans aimed at controlling salmon lice. Any management measure that would act to reduce the effective salmonid host density in an area, *e.g.* reducing the marine net-pen production time, is expected to reduce infection pressure.

The effect of EIP on the development of salmon lice populations on farmed fish implies that information on neighbourhood levels of infection is informative for farm level predictions of future lice abundances. Nevertheless, in the present multivariable model, the information contained in the autoregressive term representing lice counts in the previous week, contributes more to predicting PAAM abundance than the external infection pressure. The strength of this autoregressive term probably depends on the interval between counts. In the present data, lice counts are very frequent (weekly) in relation to the development times and the population dynamics of the salmon louse (Stien et al., 2005). It is thus not surprising that the autoregressive term is an important predictor in the model. It is worth noting, however, that also the lice counts backward in time are a result of exposure to infective lice stages. The lesson learned from this is that the most important information a farmer has with respect to predicting future infection on the farm comes from lice monitoring on the farm. However, knowing lice infection levels on neighbourhood farms adds to this information. Also, when you do not have information from lice monitoring, *e.g.* if you are interested in evaluating the prospects for lice transmission in a potential farm location or for local wild stocks of salmonids, information on infection levels in the surrounding area contains important information (Serra-Llinares et al., 2014).

The main goal in the present study was to merge the temperature-dependent development and reproduction part of the salmon lice model of Stien et al. (2005) with the lice dispersal model by Aldrin et al. (2013) in a national scale transmission network model, and to evaluate whether this resulted in improved predictions of salmon lice abundances in Norwegian salmon farms.

We fixed model parameters according to Stien et al. (2005) and Aldrin et al. (2013) without explicitly addressing the sensitivity of varying model parameters. The parameter estimates used are the best available at present and form a baseline which can be used to evaluate further developments of the model. Of special interest in this regard, are the mortality and dispersal processes of the planktonic lice stages. We assume mortality in the planktonic lice stages to be constant and independent of temperature in the present model (Stien et al., 2005). However, if the duration of infectiousness is temperature dependent, then this will affect the relative risk function given by Aldrin et al. (2013). Furthermore, a better description of the salmon lice dispersal process by including hydrodynamic processes (Salama et al., 2013; Asplin et al., 2014), may be needed to obtain high quality predictions of the infection dynamics at the local farm level scale.

Salmon lice on farmed salmonids in Norway are regulated by a system allowing a threshold maximum abundance of 0.5 adult female salmon lice per fish. Extensive counting and reporting of lice abundances are required to control these regulations. This threshold regulation is not optimal since it does not account for the number of fish on the farm, nor does it account for the density of fish or parasites at local to regional spatial scales. We show here that the use of models on salmon lice reproduction, together with the substantial body of data generated weekly on lice infections and fish numbers on farms, can be used to estimate the infection pressure farms experience along the coast. This approach, could be used in novel management systems that aim at improving the predictability and management of the salmon lice problem. Different models to spread the planktonic stages of the salmon louse, either simple deterministic models as in the present or more complex hydrodynamic models, can be used to extrapolate the estimates to maps showing estimates of local infection pressure. Calculations of expected development times into infectious copepodids according to temperatures would additionally inform about when to expect exposure to copepodid-stages. Such a system would greatly improve the information value of the large efforts spent on counting and reporting lice counts in Norway, both for the salmon farming industry, but also through improved insights into interactions between farmed and wild salmonids with respect to salmon lice infections. Such an information system could also lay the foundations for new ways of managing the salmon louse problem, accounting for farm production of infective copepodites and local infection pressure.

Conclusions

Estimates of exposure to infection by salmon lice infective stages produced on external farms was found to be a main predictor of salmon lice population dynamics during the initial phase of marine production of farmed salmon. We therefore argue that the external infection pressure will be a prime determinant of efforts needed to be spent on lice control in farms, emphasizing the importance of keeping the production of salmon lice infective stages low at local to regional spatial scales.

The results corroborate theoretical and empirical studies that show that density dependent effects shape farmed salmonid–salmon lice associations. We argue that farmed salmonid–salmon lice density considerations should be an integral part of any management plan aimed at controlling salmon lice infections in salmon farming. A system showing local infection pressure in real time based on demographic models of lice population dynamics and utilizing the masses of data generated through the compulsory lice monitoring in salmon farms, is proposed as an aid to increase the predictability of the development of salmon louse infections on farm, local and regional spatial scales.

Conflict of interest

None declared.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.epidem.2014.09.007.

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Appendix A

Large scale modelling of salmon lice (*Lepeophtheirus salmonis*) infection pressure based on lice monitoring data from Norwegian salmonid farms: Supplementary material

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Introduction and methods

Treatment with antiparasitic drugs reduces sea lice levels and thereby may obscure the relationship between model based estimates of infection pressure and observed sea lice abundances in cohorts of farmed salmon. In the main text of the article, we handled this problem by removing all cohorts that were treated in the course of their first 19 weeks of marine production. This approach may cause a bias in that the dataset as cohorts that develop high sea lice abundances are more likely to be treated within the first 19 weeks than cohorts slower development of infection. To evaluate the impact of the large number of discarded cohorts on our analysis and conclusions we present here an analysis on the development of PAAM infections over the initial 8 weeks in marine environments. Hence, only cohorts that reported salmon lice counts each week for at least 11 consecutive were included in the analyses and cohorts treated with antiparasitic drugs within the 11 weeks were discarded from the analysis. This resulted in a 69 cohorts discarded and 506 cohorts included in the analysis while the analysis in the main text resulted in 205 discarded cohorts and 370 cohorts included in the analysis. In both analyses (8 and 16 weeks) we use data from the initial infection process subsequent to the release of farmed salmon in the marine environment. Therefore, when compared to the dataset for 16 weeks, the restriction of the dataset to only the first 8 weeks in the marine environment reduced the average PAAM abundance in the dataset, increased the proportion of observations with no PAAM abundance observed the previous week, and decreased the proportion of observations with cleaner fish present (Supplementary table 1, Table 1). Due to the lower abundance of sea lice infection, also the proportion of observations with internal infection pressure greater than zero was lower, while the estimates and variability of external infection pressure was similar in the 8 week dataset when compared to the 16 week dataset (Supplementary table 1, Table 1). The analysis of the relationship between the model estimates of external infection

pressure and PAAM abundances was done exactly the same way on the 8 week dataset as the analysis extending over 16 weeks reported in the main paper (see Methods, Statistical modelling).

Supplementary table 1. Descriptive statistics for the variables potentially predicting the outcome variable defined as counts of stage category pre-adults and adult males of salmon lice (PAAM) on 30 fish ($PAAM_{t-1}$ is PAAM in the previous week; EIP is external infection pressure; IIP is internal infection pressure). Percentile levels (<33%; 33 – 66%; > 66%) of the predictor variables are related to means of the outcome variable. Results of univariate zero inflated negative binomial regression analyses are summarized by Akaike's information criterion (AIC ; the null model had an AIC of 10789).

	Mean value or True/False distribution for variables	80 % range for continuous variables	Percentile levels for continuous variables	Mean counts of PAAM on 30 fish for variable levels	AIC for univariate linear regression
log ($PAAM_{t-1}$)	0.055	0.0 – 0.11	0 – 0 0 – 0 > 0.01	0.49 8.63	9801
$PAAM_{t-1}$ == 0	T: 3150 F: 894			0.49 8.63	8771
log (EIP +1)	13.1	9.45 – 16.50	0 – 12.1 12.1 – 14.8 > 14.8	0.19 1.16 5.51	9915
IIP == 0	T: 3980 F: 64			2.11 13.31	10661
Temperature (˚C)	9.60	4.9 – 11.6	< 7.5 7.5 – 11.6 >11.6	0.58 2.87 3.42	10431
Count Week	4.5	1-8	<3 3 – 6 >6	0.61 1.93 4.61	10422
Cleaner fish == 0	T: 3402 F: 642			1.74 5.22	10538

Results and discussion

The analysis of the dataset from salmon the first 8 weeks after release in the marine environment reinforce the conclusion that model estimates of external infection pressure (EIP) is a reliable predictor of PAAM abundance. As for the 16 week dataset, PAAM infections in cohorts exposed to high EIP increased at higher rates than in intermediate and low exposure cohorts (Supplementary figure 1). Furthermore, the difference between low exposure cohorts and intermediate and high exposure cohorts became larger, as there was little change in the abundance of PAAM stage lice in low exposure cohorts, while the abundance off PAAM stage salmon lice was higher in the

intermediate and high exposure cohorts, when compared with the estimates from the 16 week dataset. This difference between the 8 and 16 weeks datasets is due to the exclusion of many of the most infected cohort in the 16 weeks dataset, which were subjected to early antiparasitic treatment.

Reducing the time-series from 16 to 8 weeks also led to an increase in the standardised estimate of the effect of EIP on observed abundances of PAAM stage salmon lice in the regression analysis (Supplementary table 2, Table 2). In comparison, there was less change in coefficient estimates for the other predictors. However, the carry over effect of previous week PAAM abundance continued to be the dominant predictor of current week PAAM abundance in the 8 week dataset (Supplementary table 3).

Supplementary table 2. Parameter coefficient estimates and standard errors for the scaled predictor variables in the AIC top ranked model for abundance of PAAM stage salmon lice on cohorts of salmonids during their initial period of 8 weeks of marine production (AIC: 8063). All coefficients were highly significant ($p < 0.005$) predictors of PAAM abundance and scaled according to mean and standard deviations in the full 16 week dataset (Table 2; main paper). Coefficients of the seasonal trends are not given in the table ($PAAM_{t-1}$ is PAAM in the previous week; EIP is external infection pressure).

Variable name	Coefficient estimate	Standard error
Intercept	- 0.236	0.107
log ($PAAM_{t-1}$ +1)	0.338	0.017
$PAAM_{t-1}$ == 0	- 1.088	0.039
log (EIP + 1)	0.729	0.068
Count Week	0.203	0.073

Supplementary table 3. Differences in the AIC, ΔAIC, between the top ranked model in Table 2 and models excluding predictory variables ($PAAM_{t-1}$ is PAAM in the previous week; EIP is external infection pressure).

Variables	No. variables	ΔAIC
PAAM t-1	2	1322
EIP	1	128
Count Week	1	6
Seasonal trend	7	47
Zero inflation	1	15
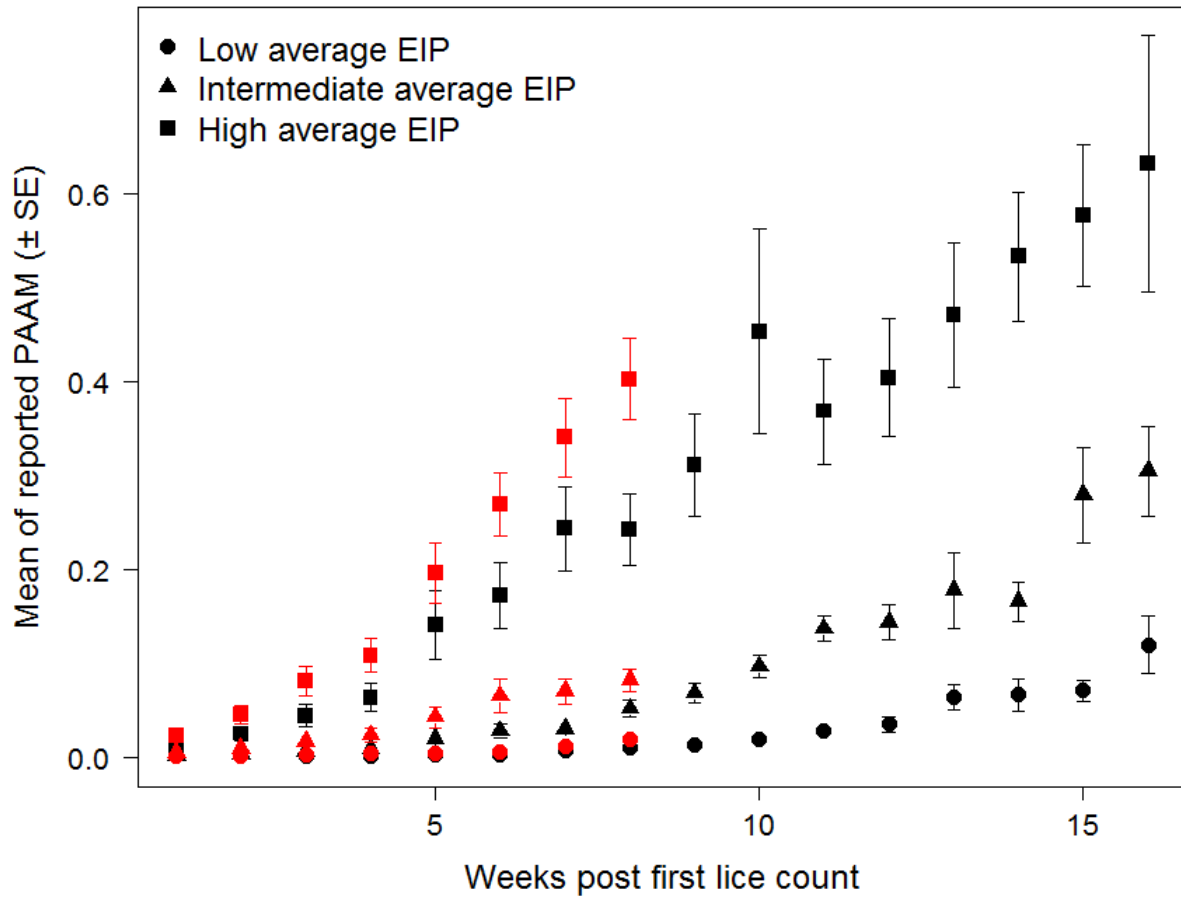
Supplementary figure 1. Mean (±SE) of reports of PAAM stage salmon lice on cohorts of salmonids during their initial period of 8 weeks of marine production (red symbols), compared to the full dataset covering the initial period of 16 weeks (black symbols, Figure 4 in the main paper). Cohorts are divided into low (circles), intermediate (triangels) and high (squares) average external infection pressure (EIP) according to percentiles (< 33%; 33 – 66%; > 66%) of average exposure to EIP over the 8 and 16 week period.