



Salmon lice dispersal and population model for management strategy evaluation

Tróndur J. Kragestein^{a,*}, Tróndur T. Johannesen^a, Anne Sandvik^c, Ken H. Andersen^b, Ingrid Askeland Johnsen^c

^a Fiskaaling - Aquaculture Research Station of the Faroes, við Áir, 430 Hvalvík, Faroe Islands

^b VKR Centre for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark, Bygning 202, 2800 Kgs. Lyngby, Denmark

^c Havforskningsinstituttet, 1870 Nordnes Bergen, Norway

ARTICLE INFO

Keywords:

Disease management
Treatment threshold
Sustainable food production

ABSTRACT

Modern marine salmon aquaculture includes management of salmon lice (*Lepeophtheirus salmonis*) infestations. Moving from a reactive delousing treatment effort to a proactive preventive strategy requires a simulation tool integrating salmon lice spread between farms with a population dynamic model at individual farms. However, such predictions have proven challenging. Here, we propose a mechanistic cohort-based model of salmon lice that explicitly accounts for the development of lice in relation to temperature coupled with hydrodynamic particle simulations of lice infections between farms. The model was validated against observed salmon lice counts and is able to produce realistic patterns of salmon lice epidemic development, but has a limited ability to resolve realistic temporal salmon lice dynamics on a per-farm basis. The model can, however, be used to evaluate general regional and national management strategies e.g. level of treatment threshold. Results shown that decreasing the treatment threshold has no significant impact the total number of treatments indicating that there is no argument against lowering the treatment threshold in a connected farm network which will eventually benefit the wild salmonid populations.

1. Introduction

A fundamental aspect of modern marine salmonid aquaculture is managing salmon lice (*Lepeophtheirus salmonis*) infestations. At elevated levels salmon lice will harm farmed fish both directly (Taranger et al., 2014) and indirectly (Pike and Wadsworth, 1999; Barker et al., 2019). In addition, salmon lice on farmed fish have been shown to negatively impact wild salmonid stocks (Krkošek et al., 2013; Kristoffersen et al., 2018; Serra-Llinares et al., 2020). Farmers currently manage this notorious exodermic parasite using various treatment methods, cleaner fish and to some extent preventive measures including spatial and temporal planning.

A significant challenge for farmers is predicting lice population dynamics in a production cycle which is crucial for estimating the optimal time to stock fish, treatment administration, lice development post-treatment or determining farm positioning. Further, it is difficult for regulators to evaluate the effects of different treatment strategies on a regional or national scale e.g. the level of lice before intervention is

required also referred to as a treatment threshold.

Numerical models attempt to capture the population dynamics in different areas of the salmon lice life cycle and previous studies on salmon lice dynamics on a per-farm basis have used different modelling approaches ranging from delayed differential equations (Adams et al., 2015), a Bayesian approach (Aldrin et al., 2017), a partly stage structured approach (Aldrin et al., 2019) to a matrix population model (Toorians and Adams, 2020). Aldrin et al. (2017, 2019) re-model in situ salmon lice counts of a production cycle taking a statistical approach and use the model to predict up to 8 weeks ahead. They included lice counts on other farms in the region using seaway distance and treatment events. Adams et al. (2015); Toorians and Adams (2020) use a more mechanistic approach and include connectivity between farms based on hydrodynamic simulations. They do not attempt to integrate in situ lice counts but try to identify general key population dynamic parameters.

The hydrodynamic environment where pelagic lice stages disperse is dynamic, leading to a highly variable infection rates between farms and between production cycles. Temperature has a strong effect on salmon

* Corresponding author.

E-mail address: trondurk@fiskaaling.dk (T.J. Kragestein).

<https://doi.org/10.1016/j.aquaculture.2023.739759>

Received 23 January 2023; Received in revised form 26 May 2023; Accepted 4 June 2023

Available online 8 June 2023

0044-8486/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

lice dynamics as it determines the egg production rate, development rate of the pelagic stages, attachment success and development rate of the attached stages (Hamre et al., 2019; Sandvik et al., 2021). In addition, salinity plays a significant role in lice dispersion and lice population dynamics as low salinity water effects both lice mortality (Groner et al., 2016) and their vertical swimming behaviour, consequently affecting horizontal dispersion (Heuch, 1995; Bricknell et al., 2006; Crosbie et al., 2019; Sandvik et al., 2020). A realistic description of the hydrodynamic environment (including 3D information on both temperature and salinity) is therefore crucial in order to reproduce realistic lice dispersal and population dynamics.

A regional or national treatment thresholds is common in salmon aquaculture (Kragestein et al., 2019). E.g. in Norwegian regulation for salmon lice allow a limit of 0.5 adult female lice salmon⁻¹ in general and 0.2 in the salmonid migrations periods before intervention is mandated (Anon, 2012). Lowering the treatment threshold decreases the number of salmon lice in the management area, benefiting wild salmonid stocks. The intuitive argument against lowering the treatment threshold is it leads to a significantly higher number of treatments decreasing fish health and economic output. However, in an idealised farm network the number of treatment remained the same or decreased by lowering the treatment threshold (Kragestein et al., 2019).

Existing models lack the comprehensive factors required to simulate an entire production cycle in a network of farms and mechanistically explain lice dynamics after e.g. a treatment or input of cleaner fish. The main objective of this work is to:

i) develop a holistic mechanistic cohort-based lice model capable of simulating salmon lice population dynamics on a per-farm basis within a connected farm network. The model explicitly accounts for temperature dependency at all stages i.e. egg production rate and, development of pelagic stages, attachment rate and development time from copepodis to adult lice on the farmed fish. Hence, a new method is established to couple hydrodynamic connectivity between farms and parameterization of the transition from lice larvae in the water masses to the number of lice per fish.

ii) Validate the model effort by comparing simulated results with reported lice counts from production zone 2 in Norway (Ådlandsvik, 2015) using a hydrodynamic model run from production zone 2 as input (Dalsøren et al., 2020). Number of lice larvae released from each farm was computed using two scenarios: temperature reported from farm sites at 3 m depth and simulated temperature based on where salmon are assumed to reside (Johnsen et al., 2020).

iii) Finally, in order to test the models ability to evaluate management strategies on a regional scale we investigated how different treatment threshold and treatment efficiency impacted the total number of treatments required to comply with that threshold within production zone 2.

2. Method

2.1. Study area

Production zone 2 (PZ2) was used as the study area which is located at the southern part of the coast of Norway (Fig. 1). This area was selected as it holds one of the highest density of farmed salmonid fish globally with a annual production of over 162,000 t on around 49 unique aquaculture farms between year 2016–2019 (Anon, 2022). PZ2 consists of a great ocean bay with islands, narrows straits and several smaller fjords. The environment in PZ2 is highly dynamic, with strong vertical shear in both temperature, salinity and velocity. In addition, environmental conditions can also have rapid temporal alterations. Normally the temperature at 3 m depth, reported by the farms, varies between 4 and 6°C during winter to 15–18°C during summer. Freshwater input from the rivers in the area contribute the low salinity surface water, but it is only the innermost part of the fjord-arms which have surface salinity below 20‰ in the long term. The vertical gradient in the

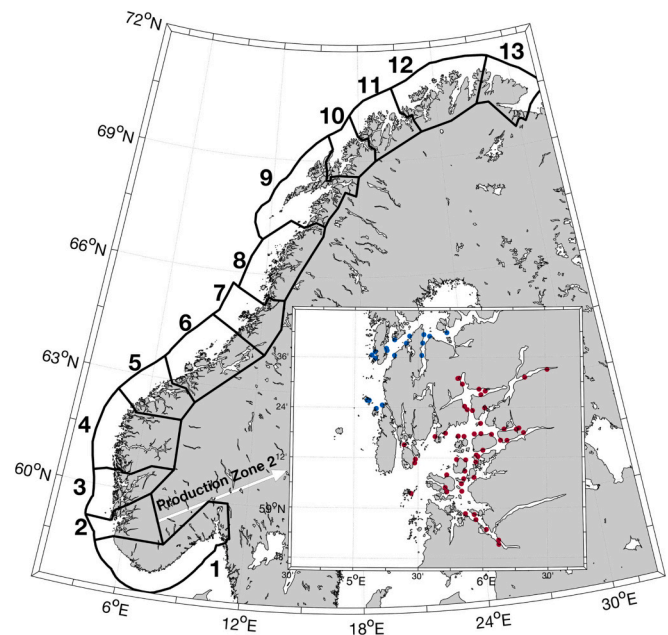


Fig. 1. Map of Norway showing the 13 defined aquaculture production zones. Farms in production zone 2 are highlighted as red dots. Some farms form production zone 3 which are included in this study are marked as blue dots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

salinity is also large, and at 5 m depth the salinity is normally well above 20‰ (Dalsøren et al., 2020). Thus, the fish in the approximately 30 m deep cages will experience different conditions depending on their individual residence depth during the production cycle. Physical parameters were obtained through the NorFjords-160 model, a numerical model set up with a horizontal resolution of 160 × 160 m, described in detail in (Albretsen, 2011; Dalsøren et al., 2020). A detailed description of the fjord physics (currents, temperature, and salinity) and dispersion mechanisms in Norwegian fjords can be found in Asplin et al. (2014); Johnsen et al. (2014); Asplin et al. (2020).

2.2. The salmon lice population model

The salmon lice population model is based on previous work (Revie et al., 2005; Stien et al., 2005; Adams et al., 2015; Kragestein et al., 2019, 2021) and tracks the development of all 8 lice life stages (Hamre et al., 2013) and distinguishes between male and female lice. The 3 first planktonic stages (nauplii I & II and copepodids) are tracked in a hydrodynamic particle model where the development of the planktonic stages is dependant on temperature (Samsing et al., 2016) and where only copepodids can infected a new farm (Johnsen et al., 2016). The additional 5 attached stages (chalimus I & II, pre-adult I & II and adult) are tracked in a cohort-based model (Fig. 2). Further, there is a period from when the adult female is fertilised until it starts releasing larvae (Hamre et al., 2019). This period is defined in the model by distinguishing between adult females and gravid adult females. The larvae production l can be calculated as:

$$l_i(t) = AG_i(t) \cdot E(T_i(t)) \Delta t. \quad (1)$$

where larvae production is based on the amount of gravid adult females AG , egg production E , and temperature T , at farm site i and time t . Δt was set to 0.5 d. Egg production is a linear interpolation of results from literature (Stien et al., 2005; Samsing et al., 2016; Hamre et al., 2019). Hamre et al. (2019) is used between 6 and 18 degrees, while Stien et al. (2005); Samsing et al. (2016) is used for 3 and 5 °C. 20 °C was estimated to be 90.8 eggs $AG^{-1} d^{-1}$ same as for 18 °C (Table 1). Temperature data

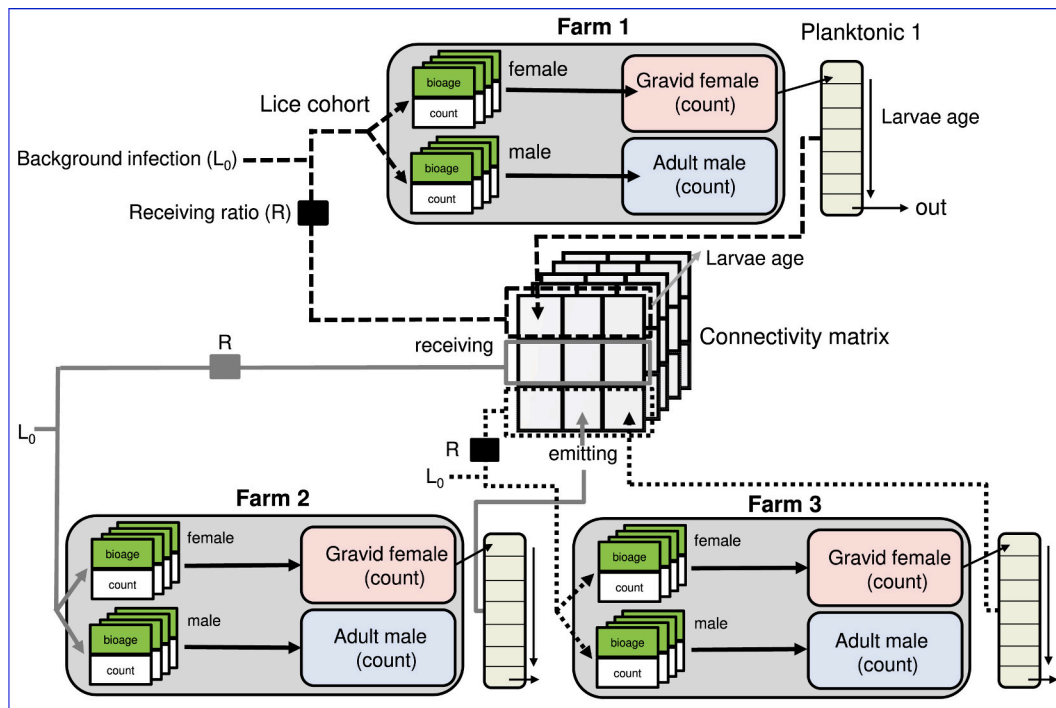


Fig. 2. Model Diagram.

Table 1
Estimated egg production E per gravid adult female per day.

Egg production (eggs d^{-1} AG^{-1}):	Temp	source
8.4	3	(Samsing et al., 2016; Stien et al., 2005)
26.6	5	(Samsing et al., 2016; Stien et al., 2005)
28.6	6	(Hamre et al., 2019)
80.9	12	(Hamre et al., 2019)
90.8	18	(Hamre et al., 2019)
90.8	20	same as for 18 °C

was reported from all farm sites and is included in the dataset provided in this study. Further, a temperature dataset based on model temperature (Johnsen et al., 2020) was also tested against reported temperature. (See Fig. 6.)

A farm site will hold a collection of female and male lice cohorts, keeping track of the amount of lice A and the biological age B . New lice-cohort's are created every time step. The initial amount of lice, which start by being in the chalimus 1 stage, in a new cohort q is defined as:

$$A_{i,q}(t_0) = R(W_i) \left(L_{0,i}(t) + \sum_j \sum_d C_{i,j,d}(t) \cdot I_j(t-d) \right). \quad (2)$$

where C is the connectivity expressing the proportion of lice coming from farm j to farm i with a time delay d . R is the receiving area ratio as function of fish biomass W . L_0 refers to the background infection which is the amount of larvae coming from wild salmonid stocks while external and internal infection pressure refers to the influx of larvae from other farm sites and own larvae production, respectively. Background infection is hard to estimate but generally believed to be very low compared to external pressure as the population of wild salmon in Norway is estimated to be around 0.5 million (Anon, 2019) in contrast to the standing stock 436 million salmon in 2022 (Anon, 2022).

There are essentially two ways to start the model: either with some value of L_0 or start with a given number and age of attached lice. In this

study simulations always started with some value of L_0 . For practical reasons L_0 can be assigned a high value in order to start the model faster. After a spin-up period farms predominantly (depending of the level of connectivity) receive larvae from farms within the network e.i. the sum of larvae l and connectivity C at and between external and internal sources.

The change in biological age for each cohort is dependant on temperature and is calculated based on Hamre et al. (2019) growth model:

$$B(t + \Delta t) = B(t) + \frac{bT_i^2 + cT_i + d}{5H_s} \Delta t \quad (3)$$

where parameters b , c , d are fitted constants (Table 2) and H_s represents the stage fraction (Table 3). Which stage s a given cohort is in is determined by the value of B (Table 2). Number of lice in a cohort is updated by the stage mortality, μ_s , given in Table 2 and any potential treatment events $\psi_{i,s}(t)$:

$$A_{i,q}(t + \Delta t) = A_{i,q}(t) \cdot e^{-\mu_s \Delta t} \psi_{i,s}(t). \quad (4)$$

2.2.1. Treatments

There are a wide range of lice treatments and prevention strategies. Treatments can be divided into 3 groups: in-feed (SLICE and Diflubenzuron), bath (Hydrogen peroxide, Salmosan, Alphamax, Betamax, Pyrethroid and Azametiphos) and non-medical (freshwater bath, hydrolicer, optilicer, termolicer or flushing). Treatments are implemented in two different ways and are dependant of lice stage s . Bath and non-medical treatments are considered instant treatments as they both are assumed to have an instant one-off effect $\tau_{\alpha,s}$. In-feed treatments work over a longer period and are implemented as a daily effect $\tau_{\beta,s}$ over a time period: For a given time t the delouse effect can be the product of several instant treatments $\Omega_{\alpha}(t)$ with the efficiency $\tau_{\alpha,s}$, and in-feed treatments $\Omega_{\beta}(t)$ with efficiency $\tau_{\beta,s}$. From here, the effect of a treatment effect is $\psi_{i,s}(t)$ from Eq. 4:

$$\psi_{i,s}(t) = \prod_{\tau_{\alpha,s} \in \Omega_{\alpha}(t)} (1 - \tau_{\alpha,s}) \prod_{\tau_{\beta,s} \in \Omega_{\beta}(t)} (1 - \tau_{\beta,s})^{\Delta t} \quad (5)$$

Determining an appropriate standard treatment efficiency can be

Table 2Table of stage, bioage, stage fraction H_s and mortality μ_s for female and male lice.

stage (s)	bio-age(female)	H_s (female)	μ_s (female)	bio-age(male)	H_s (male)	μ_s (male)
ch1	$0 \leq B < 1$	0.36	$0.005d^{-1}$	$0 \leq B < 1$	0.40	$0.005d^{-1}$
ch2	$1 \leq B < 2$	0.20	$0.005d^{-1}$	$1 \leq B < 2$	0.20	$0.005d^{-1}$
pa1	$2 \leq B < 3$	0.20	$0.01d^{-1}$	$2 \leq B < 3$	0.20	$0.01d^{-1}$
pa2	$3 \leq B < 4$	0.24	$0.01d^{-1}$	$3 \leq B < 4$	0.20	$0.01d^{-1}$
adult	$4 \leq B < 5$	0.30	$0.01d^{-1}$	$4 \leq B$	0.30	$0.01d^{-1}$
adult _{egg}	$5 \leq B$	0.30	$0.01d^{-1}$	–	–	–

Table 3

Fitted parameters for Eq. 3 from Hamre et al. (2019).

Parameter	male (m)	female (f)
$b \frac{1}{\sigma C^2}$	0.000677	0.000485
$c \frac{1}{\sigma C}$	0.010294	0.008667
d	0.005729	0.003750

challenging as it will vary both in time and space. When validating the model against reported lice counts the in-feed treatments are, for simplicity, assumed to be SLICE or emamectin benzoate and set to be constant with 5% d^{-1} efficacy on chalimus and pre-adults stages and 2% d^{-1} efficacy on adult stages 40 days post-treatment (Lees et al., 2008; Krkošek et al., 2010). Note lice resistance has developed over the years and therefore the assumed efficacy may currently lower. Bath-treatments and non-medical treatments are set to have a 70% efficiency if nothing else is stated. This is within the range reported by previous studies (Gislason, 2018; Overton et al., 2019).

In addition to the treatments described above, many farmers deploy cleaner fish in their farms, which continuously delouse the farmed fish. The effect of cleaner fish is implemented by estimating the number of lice a cleaner fish can eat per day. Cleaner fish efficiency varies highly both within a year and between years (Eliassen et al., 2018). For simplicity, cleaner fish are assumed to eat on average 0.1 lice fish $^{-1} d^{-1}$ which is within a realistic range (Boissonnot et al., 2022; Engebretsen et al., 2023) although in the lower end if lice digestion is 2–3 days. Cleaner fish are assumed to primarily eat pre-adult and adult stages. The number of cleaner fish stocked is reported for each farm site. A source of uncertainty is cleaner fish mortality which varies greatly, and is not included in the available data set and caution should therefore be exercised when interpreting cleaner fish data.

2.2.2. Connectivity

Connectivity is estimated from a particle tracking simulation based on hydrodynamic forcing with NorFjords 160 (Dalsoren et al., 2020) in the period 01-sep-2016 to 05-dec-2019. 5 particles were released every hour from all active farms in production zone 2 and from 50 farms in production zone 3, where the size of the particles are given by Eq. 1. Particles were given vertical behaviour in accordance to observed lice response (Johnsen et al., 2016; Sandvik et al., 2020). Mortality during the lice pelagic stages is assumed to be constant in time and space at $0.17d^{-1}$ (Stien et al., 2005). Connectivity $C_{ij,d}$ can be expressed in a variety of ways e.g. total number of particles or some probability. Here, connectivity is expressed as the total number of particles entering a 3 by 3 grid (each grid is 160 m \times 160 m) area around a farm in a day divided by the number of particles released by a farm in a day. Particles were not allowed to re-infect a given farm. The particle age in days, i.e., the number of days it takes for the particle to travel from the transmitting to the receiving farm, d , was recorded. This means that a farm can have an internal connectivity up to 1 or 100% if all particles re-infect the source farm and there is no mortality. But the same farm can (in theory) have an external infection of 1 (number of farms in the network – 1) if all particles from other farms enter the farm and with no mortality.

2.2.3. Farm and receiving area ratio

In order to estimate how many lice actually attach on a farm the ratio, R_i , between the receiving area and farm area was estimated. We explored 3 methods to estimate the ratio (Fig. 3): i) a constant ratio r of lice attach to a farm independent on farm size, temperature and season:

$$R(W_i) = r. \quad (6)$$

ii) a type II functional response where lice attachment was dependant on biomass, W and max biomass, W_{max} , on the farm:

$$R(W_i) = r \frac{\frac{W}{W_{max}} - a}{1 + \frac{W}{W_{max}} a}, \quad (7)$$

where a is a scaling parameter and set to 100 and r is the maximum surface ratio and set to 0.15. iii) Farm area depends on farm biomass:

$$R(W_i) = \sqrt{\frac{W}{DV_r}}, \quad (8)$$

where V_r is the estimated volume of the receiving area. E.g., a farm with 1 million salmon having a weight of 3 kg have a total biomass W of 3000 t, stocked with density, D , of 20 kg/m^3 , and with a volume of the receiving areas V_r of 3,456,000 m^3 (480m \cdot 480m \cdot 15m), will receive 20.8% of the incoming lice (see Appendix A).

2.3. Validation

2.3.1. Correlation and difference

Validation of the conceptual framework of our modelling approach was done by comparing official reported lice counts to model results. External and internal infection pressure was computed based on reported lice counts, number of fish, temperature and connectivity. Lice populations on farm-sites were therefore not able to run freely and potentially grow exponentially. Because treatments, cleaner fish, and preventive measures distort lice populations dynamics, two different periods in a production cycle were investigated: i) From first stocking date until first treatment was reported (not considering cleaner fish) and ii) from first stocking date until first reported treatment or use of cleaner fish. Period 1 was on average 153.5 days with a minimum and maximum length of 35.0 and 546.0 days, respectively, while period 2 was on average 52.7 days with a minimum and maximum length of 7 and 322 days, respectively. 73 production cycles were included and no treatments were reported for 18 production cycles in period 1 and no treatments or cleaner fish were reported for 3 production cycles in period 2. In these cases counts until 250 days after production start were included.

2.3.2. Treatment threshold

The total amount of adult female lice and number of treatments reported in PZ2 was compared to the corresponding model results. Model-farms had the same amount of fish in the same period as reported. Model-farms were set to perform a treatment if lice levels reached 0.5 adult female lice fish $^{-1}$ with a treatment efficiency of 50, 70 and 90% for all attached stages. The number of treatments needed to keep a treatment threshold ranging from 0.005 to 3 adult female lice fish $^{-1}$ was investigated. Simulation spin-up was done by setting L_0 or background infection of all active farms within the first 200 days of the simulation

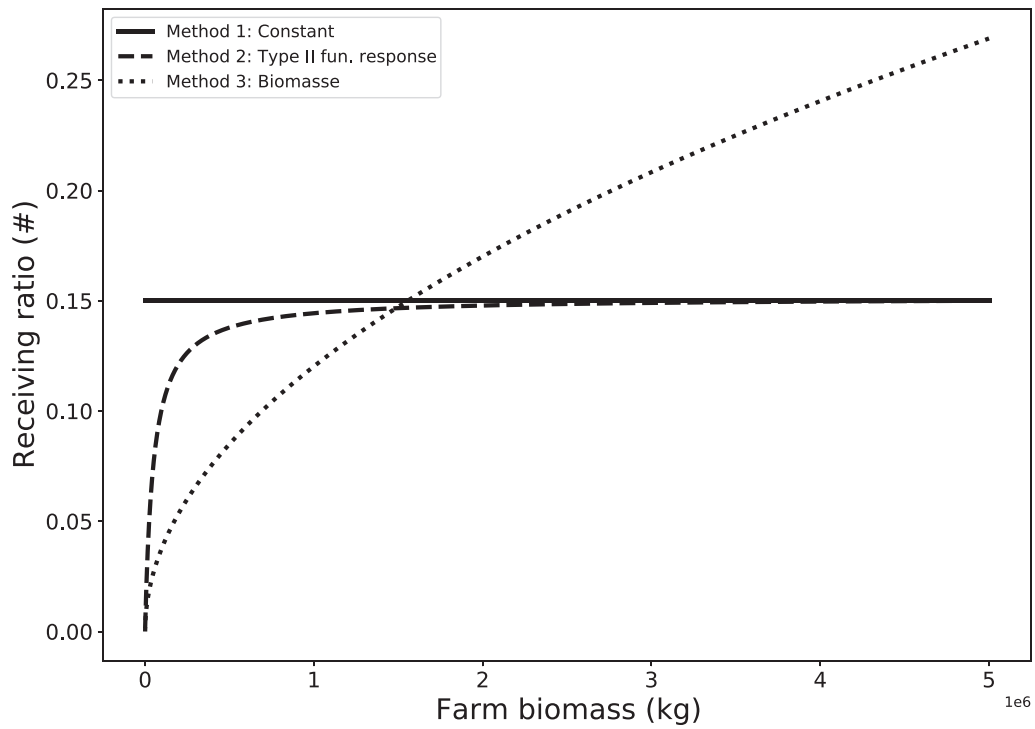


Fig. 3. The three receiving ratio methods as a function of biomass; see text for details.

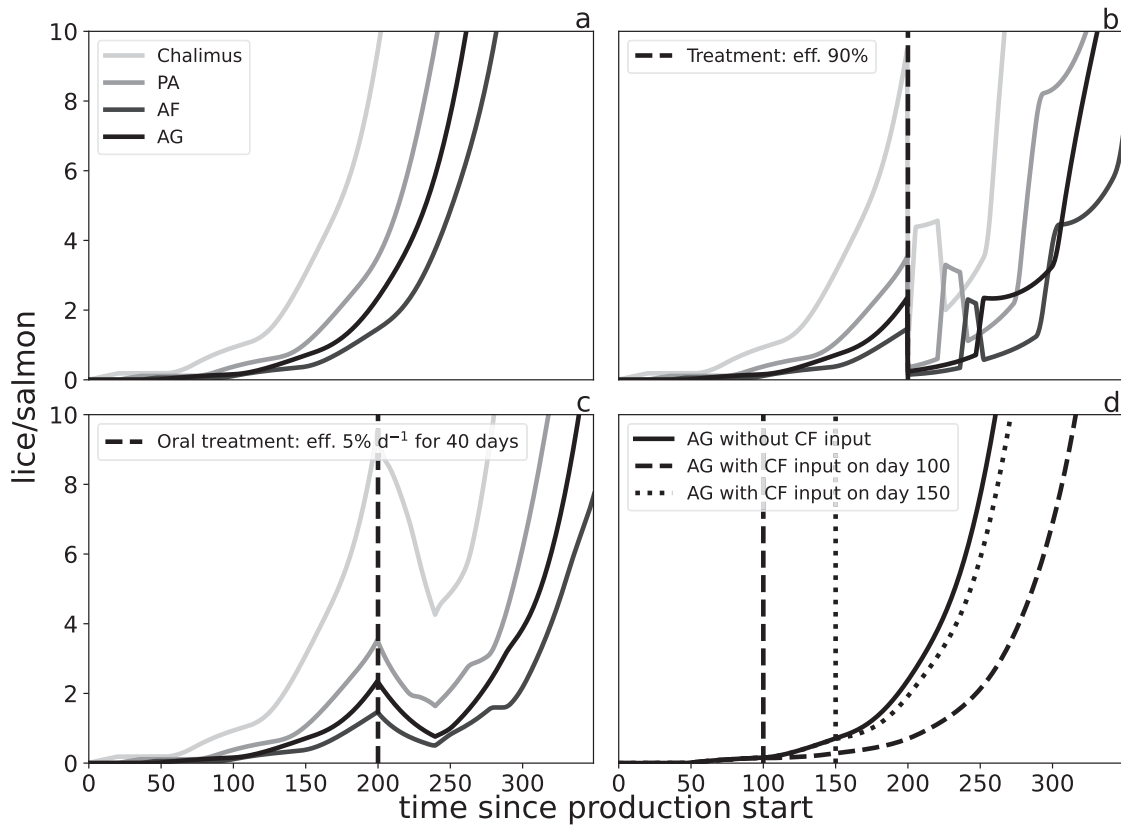


Fig. 4. Modelled salmon lice population over a 350 day period on a idealised single farm site. Lice stages shown are female chalimus, pre-adult (PA), adult female (AF), and gravid adult females (AG), coloured light grey to black. a) No treatments b) a 90% effective treatment, c) an oral treatment killing 5% d^{-1} of all stages over a period of 40 days and d) three different simulations with no cleaner fish input, cleaner fish input at day 100 and at day 150. Cleaner fish input is 20% of salmon number and they eat 0.1 pre-adults and adult lice $fish^{-1} d^{-1}$. Treatments and cleaner fish stocking is indicated as vertical lines.

period to 30,000 lice d^{-1} . After the initial 200 days period L_0 was set to 0.

2.4. Reported lice and fish data - used for model validation

Lice counts and temperature at 3 m depth are reported weekly for each farm site. Lice counts are normally performed by designated staff at the farming company counting at least 20 fish per cage in all cages. Further, the weight and total amount of fish at each farm site is reported every month. Lice stages are divided into three groups: sessile, mobile, and adult female. Sessile counts contain chalimus I and II which can be up to 1.5 mm in length (Hamre et al., 2013) and generally more difficult to see compare to the pre-adult and adult stages. We decided to exclude sessile counts as we are unsure of the data quality. Mobile lice counts include pre-adult I and II stages of both male and female and the adult male stage. Mobile and adult female lice will also be referred to as PAAM and AF, respectively. AF includes gravid lice (AG) if nothing else is stated or no information is given for AG.

3. Results

3.1. Model mechanics - idealised examples

3.1.1. Treatment dynamics

For the purpose of demonstrating the population dynamics of salmon lice a series of simulations were performed with a simple idealised case containing a single isolated farm with 500 thousand fish. Temperature was assumed to be constant at 10°C , with a background infection (L_0) of 5000 lice $\text{farm}^{-1} \text{d}^{-1}$, an internal connectivity C_{ii} of $1\% \text{d}^{-1}$, and a delay from larvae release to attachment of 5 days (Fig. 4a). When fish are stocked into sea cages copepodid larvae attach and the chalimus stages start to increase linearly in numbers until 20.2 days where they moult into pre-adult I. Because the background infection is constant, the number of chalimus, in new cohorts, is constant until internally produced larvae start to re-attach. 36 days after fish are stocked (model started) the pre-adult II lice moult into adult lice and after 46.8 days

adult lice have developed their first egg strings and start releasing planktonic larvae. With a constant temperature of 10°C , then after almost 100 days the first internally produced adult females start releasing planktonic larvae. After this point and with a internal connectivity C_{ii} of $1\% \text{d}^{-1}$ and the given mortality (Table 2) population growth becomes exponential.

Instant treatments kill attached lice, here set to 90% of all attached stages. The chalimus stage, however, first increased rapidly after a treatment because planktonic larvae are not killed and are free to infect the salmon farm. 5 days after a instant treatment chalimus stages stop increasing rapidly as new cohorts have lower number of larvae. Eventually the chalimus stages decrease in numbers when the high abundance cohorts have reached the pre-adult stages (Fig. 4b).

Oral treatments have a longer effect and, here, set to kill $5\% \text{d}^{-1}$ of all attached stages for a period of 40 days hereafter attached stages again start to increase (Fig. 4c).

The effect of cleaner fish is sensitive to timing (Fig. 4d). If cleaner fish are stocked at day 100 there is over a 50 days delay in the exponential growth whereas stocking cleaner fish at day 150 has a very small delay on the exponential growth.

3.1.2. Temperature and lice dynamics

Temperature has a significant effect on lice pressure, both in terms of development time, egg production and infectivity. E.g a farm with no internal dynamics, meaning produces no larvae to it-self and is solely driven by lice from elsewhere will eventually reach an equilibrium point dependant on mortality and temperature and independent of the stocking date (Fig. 5a). For illustrative purposes, very high constant background infection of 50,000 lice $\text{farm}^{-1} \text{d}^{-1}$ was assumed on a farm with 500 thousand fish. Meanwhile, if a farm has internal production the infection trajectory will depend on the stocking date because temperature varies during the season (Fig. 5b). In this example internal connectivity is set to $1\% \text{d}^{-1}$ and external infection is set 2500 lice $\text{farm}^{-1} \text{d}^{-1}$ with a fish number of 500 thousand. If farms start production January 1st they will have most adult and gravid female lice after 1 year of production compared to starting April, June or October 1st. A farm

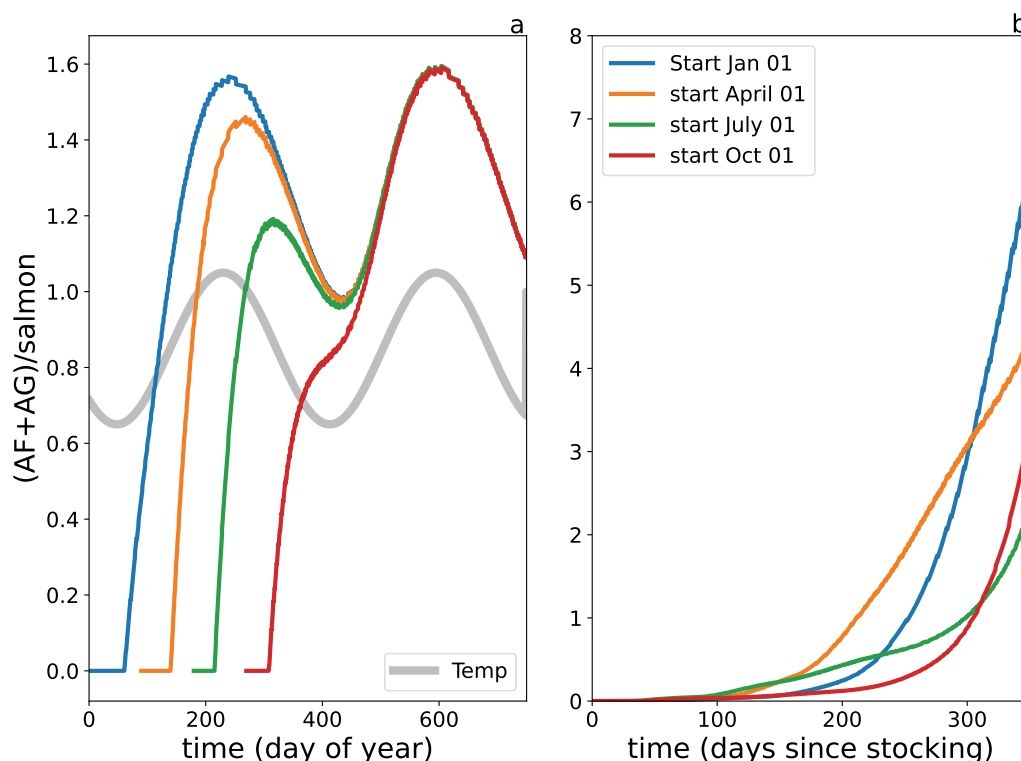


Fig. 5. Effects of seasonal temperature in two different scenarios: a) adult female development with an external infection pressure of 50,000 lice $\text{farm}^{-1} \text{d}^{-1}$, fish number of 500 thousand and no internal infection over a period of two years, and: b) development of adult female with external infection of 2500 lice $\text{farm}^{-1} \text{d}^{-1}$ fish number of 500 thousand and internal infection of $1\% \text{d}^{-1}$. The scenarios are run in 4 different farms with production cycles starting in January, April, July, and October. Note different x- and y-axes in the two panels are not equal.

will have least adult and gravid female lice after 1 year of production if production starts June 1st.

3.2. The salmon lice model and production zone 2

3.2.1. Connectivity

The salmon lice model was used to simulated all farm sites in PZ2 using hydrodynamic connectivity, production data and reported lice counts from the above mentioned period. The overall connectivity varies significantly over time and between seasons (Fig. 6a). Connectivity, here expressed as percentage of incoming particles standardised with the amount of particles released at the farm itself. The average internal infection pressure in PZ2 varies from 0 to close to 10%, while external infection pressure varies from 0 to 15%. Average external infection pressure is generally significantly higher than internal infection pressure.

The mean age of successful infectious lice copepodides over the simulation period varies seasonally from 3 to over 20 days (Fig. 6b). Lice from internal infections are generally older in winter and younger in summer compared to external lice (larvae from other farms). Lice dispersing from PZ3 to PZ2, although very few, have an average age from 5 to 17 days.

3.2.2. Validation

A significant correlation was found between lice counts and the salmon lice model when looking at AF, PAAM and AF + PAAM lice counts until first treatment or stocking of cleaner fish (Fig. 7, red). In this period 388 lice counts across 32 unique farms were compared. Highest correlation, r -value = 0.7, is between AF + PAAM, and when surface to area ratio follows method 3 where the receiving area is a function of the biomass (Fig. 7i).

When including lice counts until first treatment or period 1 (excluding the stocking of cleaner fish) the number of comparable lice counts increases to 1319 across 45 unique farms, but the correlation

decreased. Again, method 3 and AF + PAAM lice gave the highest correlation of r -value = 0.53. (Fig. 7i black). Correlation between model and observed lice counts over the whole production cycle gave a low correlation (0.34, data not shown) assuming a treatment efficiency of 70% and cleaner fish efficiency of 0.1 lice fish⁻¹ day⁻¹.

Running the model with temperature based on Johnsen et al. (2020) gave almost identical results as running the model with reported temperature (Appendix, Fig. D.14).

Few farms captured lice dynamics confidently and often the model overestimated the first periods (Appendix, Fig.B.13).

The correlation (r -value) between reported and modelled lice per fish (AF + PAAM stages) for individual farms ranged from -0.6 to 1.0 where 20% of the farms had a correlation of <0.4, 18% of the farms had a correlation from 0.4 to 0.7, and 62% of the farms had a correlation of >0.7 (Fig. 9a).

When looking at the reported and modelled number of AF fish⁻¹ the correlation was lower with an average of 0.4 between all farms. 44% of the farms had a correlation <0.4, 20% of the farms had a correlation from 0.4 to 0.7, and 36% of the farms had a correlation >0.7.

The absolute difference in reported and modelled number of AF lice at the farms, 71% of the farms had a deviation <0.1 AF fish⁻¹, 20% 0.1–0.5 difference, 9% of the farms (4 farms) had a difference > 0.5 modelled and reported female lice. These 4 farms were located in relatively open parts of the fjord in the middle of production zone 2 (Fig. 9b).

3.2.3. Treatments and treatment threshold

When considering the entire time series of all farms, we found good agreement between total number of AF lice and treatments reported and the corresponding model predictions. 70% treatment efficiency resulted in 400 treatments compared to 396 reported by the farm companies (Fig. 10a-b). Further, the total number of treatments needed in order to keep a threshold remained between 370 and 380 from a threshold of 3 to 0.005 AF fish⁻¹ (Fig. 11a) when excluding the first 365 days of the

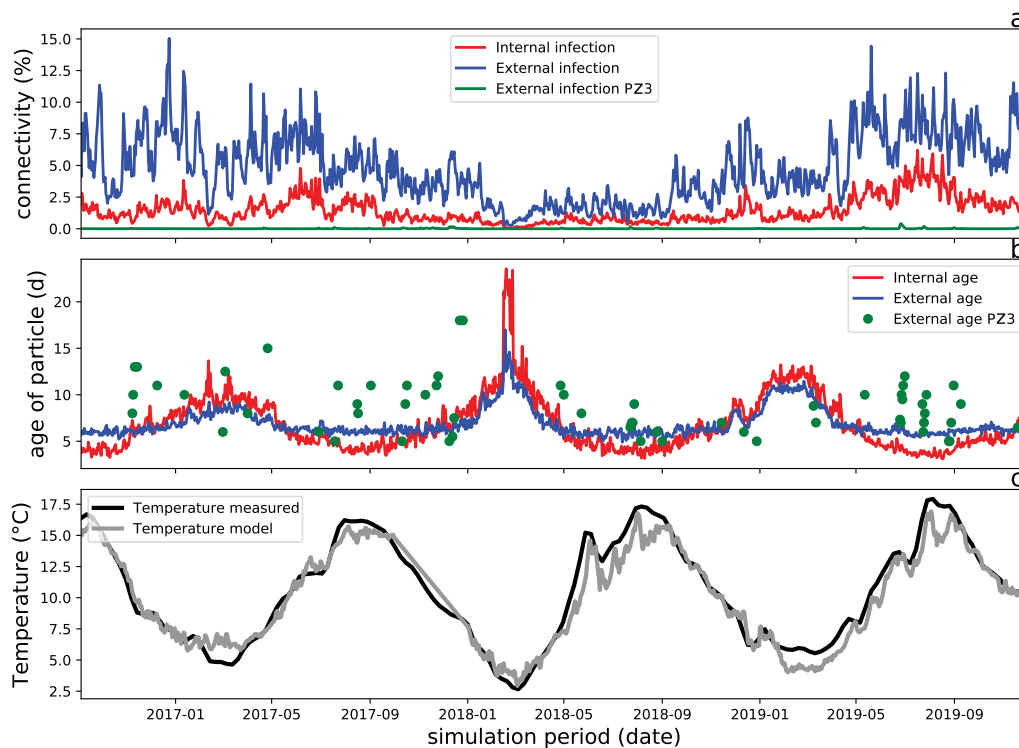


Fig. 6. a) average connectivity of PZ2 measured as % of incoming particles divided by out going particles per farm. Green line indicates particles coming from PZ3. b) average age in days of lice originated from internal and external sources. Green dots indicate particles originating from PZ3. c) Model and measured temperature throughout the simulation period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

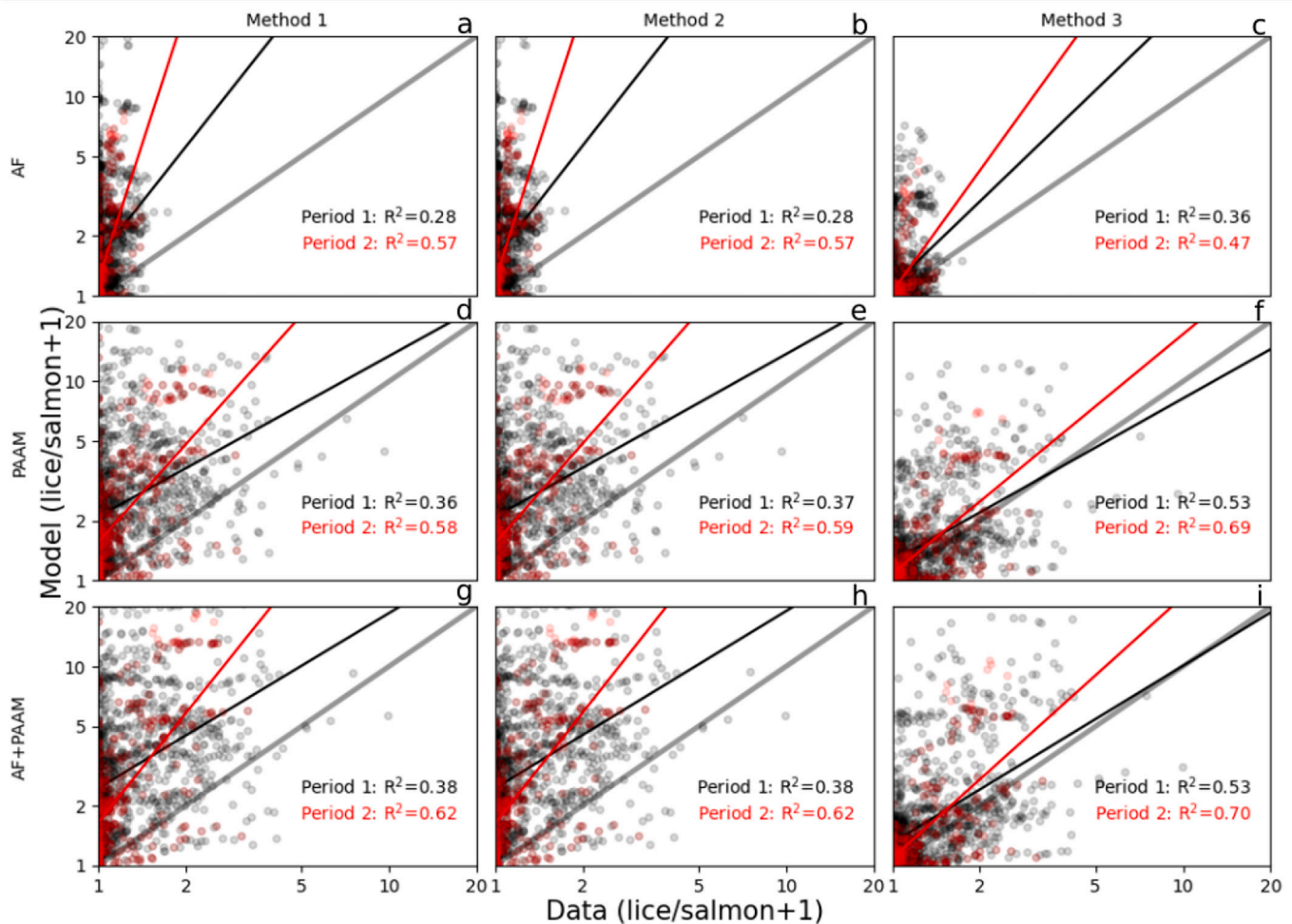


Fig. 7. Data vs model of AF, PAAM and AF + PAAM. a,d,g) method 1: constant receiving ratio of 0.15. b,e,h) method 2: Type II functional response receiving ratio with a r of 0.15. c,f,i) receiving area ratio follows biomass. a,b,c) are AF, d,e,f) are mobile lice and g,h,i) are AF + PAAM. Period 1 consists of 387 data points and period 2 consists of 1319 data points. Linear regression trend lines are shown for period 1 and 2 as black and red, respectively. 1:1 line shown as grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

simulation. And treatment frequency is also almost identical from start of 2018 and to simulation end (Fig. 11b) indicating that decreasing the treatment threshold does not necessarily mean increasing number of treatments in the long term.

4. Discussion

In this study we have developed a fully mechanistic salmon lice model accounting for all life cycle stages. The model was validated against lice counts from production zone 2 in Norway. At some farm sites the model simulated the dynamics on a per-farm basis fairly well compared to the reported lice counts, while other farms were in less agreement with the reported numbers (Appendix, Fig. B.13). The model tends to overestimate farm lice levels, in particular in warmer periods (Fig. 8). Note that the difference is shown as absolute difference and therefore colder periods will have lower lice levels and subsequently a lower absolute difference. Despite the discrepancy on single farms the overall dynamics in the production zone and the number of salmon lice on the farms until first treatment or cleaner fish use were captured well, with a r -value up to 0.7 between model results and observed lice counts (Fig. 7).

4.1. Reported lice levels at farms

It should be noted that the reported lice levels are known to be uncertain, both due to the number of fish needed to resolve low lice numbers (Heuch et al., 2011) and due to expressed doubts concerning the veracity of these numbers used for regulative purposes (Jeong et al., 2022).

Another issue when comparing model results to the reported lice counts is that lice counts are required weekly, but the day of the count is not specified in the regulation. Hence, the data can include temporal mismatch between the farms. Prior comparison between model results and reported lice counts increased in agreement when averaging over weeks (Samsing et al., 2016). Averaging over time would likely also give a higher correlation in the effort here, but also make the validation less transparent. In addition, the farms may delouse single pens or the whole site before counting lice: Hence, it is unknown if the reported value is representative for the lice level that week, or if it is an underestimation of the weeks condition. Finally, farm sites do not report the amount of lice during slaughter. Farms can be large with a lot of fish and therefore there may be a periods lasting week with no data. Therefore, it can be speculated that the level of lice may be higher at the end of a production cycle.

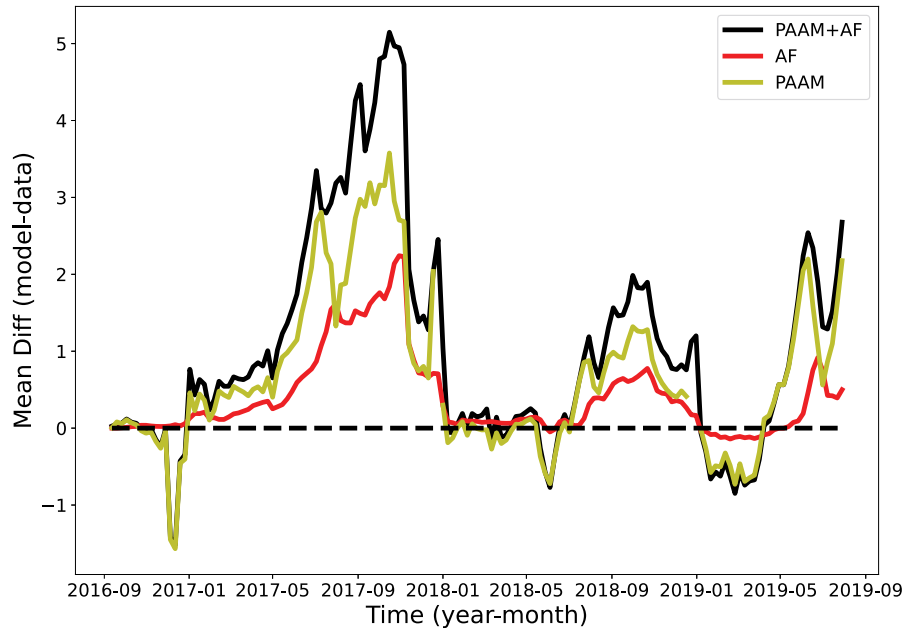


Fig. 8. Absolute difference between modelled and observed lice counts averaged across all farms throughout the simulation period for AF, PAAM and AF + PAAM lice.

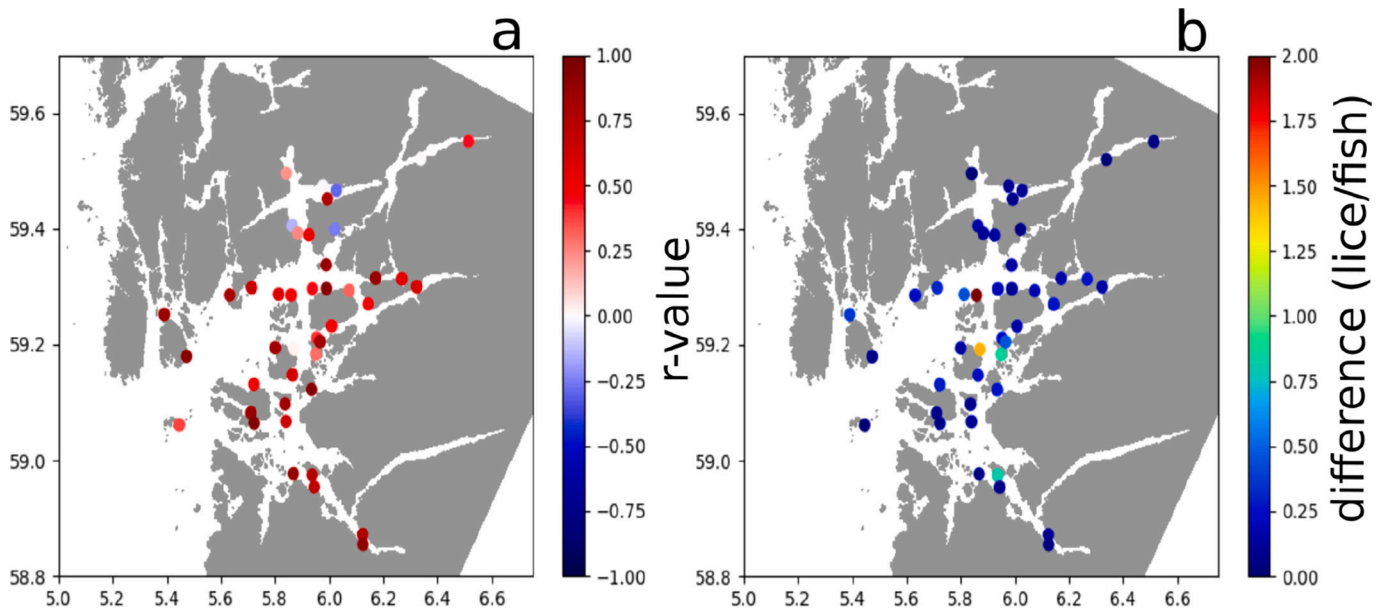


Fig. 9. a) r-value and average absolute difference of mobile stages (AF + PAAM) individual farms in production zone 2.

4.2. Model potential and limitations

The salmon lice population model has a flexible setup, however, development rates of lice stages are equal for each individual lice cohort. In reality there is a distribution of development rates with some lice developing faster than others. This issue could be addressed by creating additional lice cohorts each time step with different development rates, e.g., 15% of lice could be represented in a fast developing lice cohort.

Treatment efficiency varies a lot depending on the location, crew, equipment, resistance and environmental conditions on the day of treatment. This makes it challenging to re-model past production cycles as treatment efficiency for the same type of treatment at the same farm

can vary significantly for each time it is used. By fitting the efficiency of each individual treatment it could be possible to more accurately re-model past production cycles. Another challenging aspect is that treatments are sometimes only preformed on a single or just a few cages and this information is not always available. Therefore, estimating treatment efficiency for the whole farm site becomes difficult. This issue can be addressed by modelling lice on a cage level, this would, however, require a much higher data resolution.

The model integrates the impact of cleaner fish and results highlight the importance of when farmer stock them. Presently, the model does not contain a lower limit at which cleaner fish cease to eat lice, although it is likely that at some level cleaner fish cease to search and feed on lice.

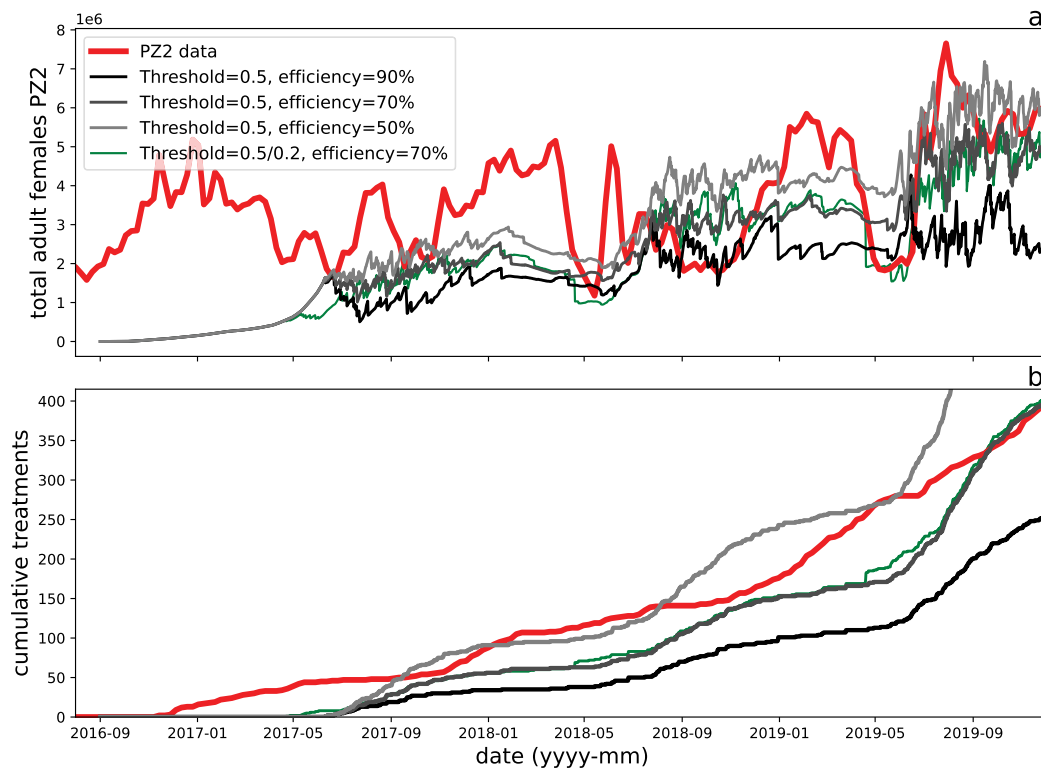


Fig. 10. a) Total AF lice in PZ2 and b) accumulative treatments with treatment threshold of 0.5 AF fish⁻¹ and treatment efficiency of 50, 70 and 90% d⁻¹. In addition, seasonal treatment thresholds of 0.2 in week 16–21 and else 0.5 AF fish⁻¹ shown in green. Official reported AF lice and accumulative treatments shown as red lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Another source of uncertainty is cleaner fish mortality which varies greatly, and is not included in the available data set. Caution should therefore be exercised when interpreting cleaner fish data.

Estimating how many lice actually attach to a farm is hard as attachment success is dependant on several factors (Dalvin et al., 2020). The hydrodynamic simulation used in this study estimates how many lice larvae disperse from one farm site back to the source farm or another farm. We assumed all viable lice dispersing through one or several farm cages attached to a host leading to an attachment rate proportional to the number of copepodids through a linear relationship. Not surprisingly, the attachment ratio following biomass had the highest correlation between model and observed data. However, attachment ratio following biomass is a very coarse estimate and does not account for the potential importance of local currents in relation to the shape of the farm cages or any attachment success due other environmental factors such as temperature (Skern-Mauritzen et al., 2020) or preventive measures like lice skirts or snorkel (Barrett et al., 2020). The presented model could be improved by incorporating these factors.

The number of particles used in the connectivity simulations is likely on the lower limit when the resolution is lice d⁻¹ and the receiving area is 3 × 3 grid square. Nevertheless, it is sufficient in order to validate the proposed conceptual model framework.

Population dynamics on individual farms is based on lice coming from other farms and internal production. Therefore, in order to accurately model a farm other farms must also be accurately modelled. To overcome this problem, we based the dynamics on model connectivity and reported lice counts. Alternately, internal dynamics could be based on modelled lice while keeping the external pressure based on reported lice counts.

When testing the model on PZ2 the initial infection pressure was 30,000 lice d⁻¹ per receiving area the first 200 days. This value was chosen with a trial and error method and 30,000 lice d⁻¹ was estimated

to be sufficient. However, treatments are reported >6 months before any model treatments are observed. This could be improved by having a longer simulation period or developing a more detailed initial infection protocol. A significant unknown in lice population dynamics is mortality of both planktonic stages and attached stages. Most models use a planktonic mortality estimated by (Stien et al., 2005) where mortality of the nauplii and copepodid was calculated to be 0.17 and 0.22d⁻¹, respectively, based on (Johnson and Albright, 1991). However, Gillibrand and Willis (2007) adopted a mortality of 0.1d⁻¹ based on typical copepodid mortality (Hirst and Kjørboe, 2002). This highly uncertain parameter should be explored further e.g. exploring how salmon lice populations models respond to seasonal varying mortality due to environmental cues like salinity and temperature (Groner et al., 2016). Mortality of attached stages has been more studied than planktonic stages but the results vary significantly, from close to 0 mortality (Dalvin et al., 2020) to as high as 0.18d⁻¹ (Stien et al., 2005). Mortality of attached lice is not effected by temperature, except with <3 and > 24 °C (Dalvin et al., 2020). Here, we adopted a relatively low mortality estimates of 1% d⁻¹ for pre-adult and adult stages and 0.5% d⁻¹ for the chalimus stages. These mortality parameters have a significant effect on the populations dynamics and should be further investigated.

4.3. Connectivity between farms in production area 2

The connectivity between farms in a given area is tightly linked to the present site-structure and local flow patterns. In our study area, both the internal and external connectivity was found to be generally higher than those found in Adams et al. (2015); Samsing et al. (2017) and more similar to Skarðhamar et al. (2018). Samsing et al. (2017) found internal infection on average to be 0.18% and external infection to account for 71% of farm site infection for the Norwegian coast. Skarðhamar et al. (2018) found internal connectivity could be as high as 9–10% based on a

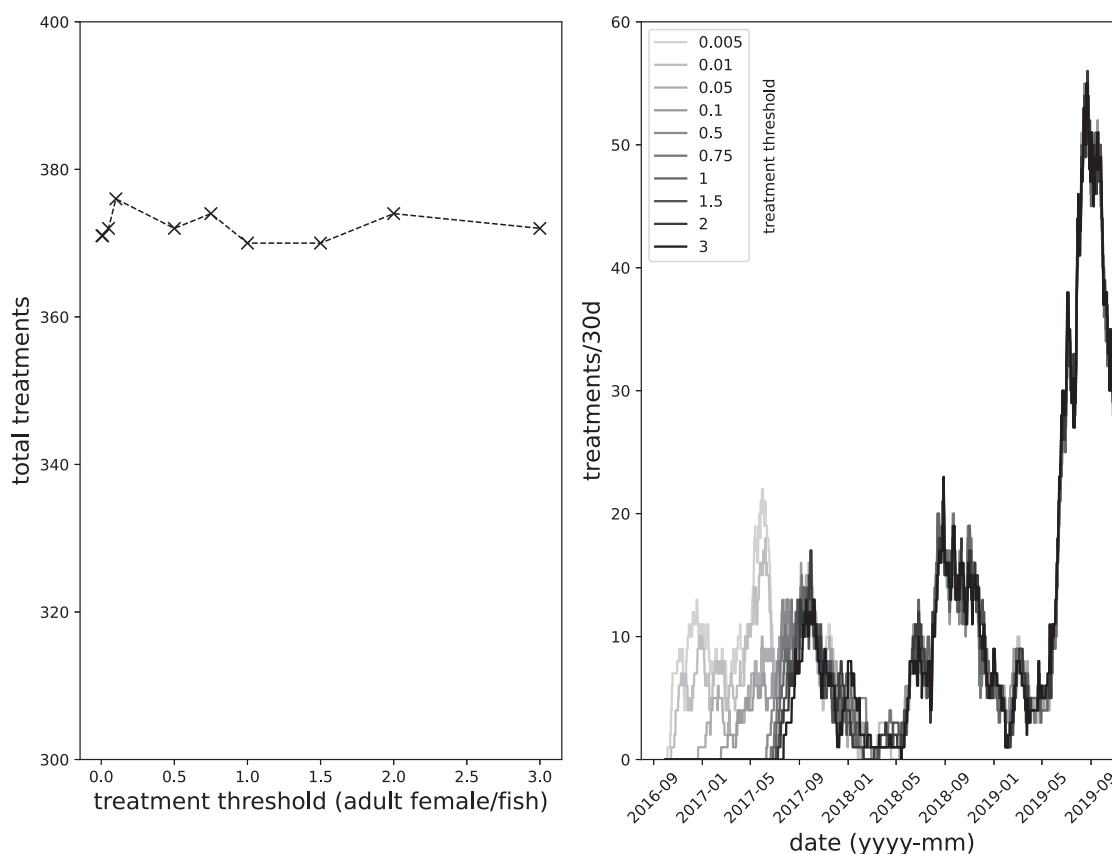


Fig. 11. a) Total number of treatments when excluding the first 365 days of the simulation. b) Treatment frequency (treatment/30d) throughout the simulation period. Treatment efficiency is set to 70%.

160 m hydrodynamic simulation and 1 grid cell receiving area. Here, connectivity was shown over time and there is no clear seasonal signal in the overall connectivity level. This may be counter-intuitive as we would expect connectivity to decrease with water temperature, as lice larvae take longer to develop to copepodids and therefore less would be alive to infect. On the other hand, there is a clear signal of the average age of connected infectious copepodids where they were younger during summer with higher temperatures. The highest average lice age was seen in 2018 which also was the year with lowest temperatures. Hence, the calculated connectivity here, confirms the pattern found in [Samsing et al. \(2016\)](#); [Huserbråten and Johnsen \(2022\)](#) where lice were mapped to disperse over large areas during winter with the low temperatures and connecting farms in the networks over a larger area. On the contrary, at higher water temperatures the farm or lice network was more fragmented and divided in smaller clusters, but with stronger connectivity within the clusters.

4.4. Management implications

Despite its uncertainty, the reported lice numbers from the aquaculture sites are used for validation purposes in this effort. While the model is currently unable to reproduce the reported lice level at specific farms, its ability to simulate overall infections dynamics and number of treatments makes the model useful as a simulation tool to evaluate delousing and management strategies for an entire salmon farm area. The model roughly captured the observed number of treatment events assuming a treatment efficiency of 70%. The results illustrate that treatment threshold has a limited effect on number of treatments ([Fig. 11](#)). Treatment efficiency, had on the other hand, a significant

effect on total number of the treatments reducing the number of treatments by 37% when increasing the treatment efficiency from 70 to 90% ([Fig. 10](#)). Overall the treatment threshold results indicate that there is no argument against lowering the treatment threshold in a connected farm network in order to benefit the wild salmonid populations. Further, the potential presence of a mate limitation effect ([Stormoen et al., 2013](#); [Krkošek et al., 2012](#)) will make it more beneficial to lower the treatment threshold, which further can turn out in a looping positive feedback with gradually fewer lice larvae in the water masses. Further, our results show that having a seasonal treatment threshold decreases the total amount of adult female lice but does not increase total number of treatments. In practise, applying a low treatment threshold (<0.1 adult female fish⁻¹) is challenging as current regulation requires lice count on 20 fish per cage. However, with the emerging advancement in automatic counting it should become feasible to obtain reliable data even at low lice numbers.

5. Conclusions

Here, we have developed a general model of lice infection dynamics accounting for varying temperature in a network of connected farms, where the connections are modelled with detailed hydrodynamic simulations. The model is unable to reproduce the reported lice dynamics on individual farms, however, it recaptured the overall dynamics of infections and treatments in the farm network and was used for management strategy evaluation. Simulations of production zone 2, showed that the treatment threshold level effects the total number of lice but did not impact the total number of treatments significantly. This implies that the industry should strive for a lower treatment threshold which would

eventually benefit wild salmonid populations without increasing the number of treatments. Further, the results showed that treatment efficiency is the relevant factor to consider in order to decrease the number of delouse treatments. By increasing the delouse efficiency from 70 to 90%, the number of treatments was reduced by about 37%.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Attachment ratio

In order to simulate realistic salmon lice dynamics it is crucial to estimate how many lice disperse between farms. Comparing the surface area of the fish farm and receiving area is therefore arguably relevant. The 3 by 3 grid receiving area used in the simulations has the depth of the water column, however, we can comfortably assume that most infectious copepodids and farmed fish are found in the upper 15 m of the water column (Á Norði et al., 2015). The receiving area can therefore be converted to a 3 dimensional box with a depth, d , of 15 m and width and length, l , of 3·160m or 460 m. The receiving volume V_r is therefore:

$$V_r = l^2 d \quad (\text{A.1})$$

The practical volume of a fish farm, V_f can be estimated as:

$$V_f = \frac{W}{D} \quad (\text{A.2})$$

where the fish farm biomass, W , is found in the Norwegian lice database. Schooling density, D of farmed fish can range anywhere between 20 kg/m³ to 400–500 kg/m³ (Oppedal et al., 2011). For simplicity a 20 kg/m³ was adopted which is a restrictive estimate. Further, we assume that the farm volume also has a depth of 15 m.

The relevant surface area, A , of these boxes with equal width and length, excluding the top and bottom, can be defined as:

$$A = 4ld \quad (\text{A.3})$$

the length, l , can be found from the depth and volume (Eq. A.1):

$$l = \sqrt{\frac{V}{d}} \quad (\text{A.4})$$

eq. 11 can therefore be rewritten as:

$$\Rightarrow A = 4d \sqrt{\frac{V}{d}} \quad (\text{A.5})$$

$$\Rightarrow A = 4\sqrt{dV} \quad (\text{A.6})$$

The ratio between, $R_i(W)$ the vertical area of the fish farm, A_f , and receiving area, A_r , was therefore calculated as:

$$R_i(W) = \frac{A_f}{A_r} = \frac{4\sqrt{dV_f}}{4\sqrt{dV_r}} = \frac{\sqrt{\frac{W}{D}}}{\sqrt{V_r}} = \sqrt{\frac{W}{DV_r}} \quad (\text{A.7})$$

For example, if a farm has 1 million salmon with a total weight of 3 kg having a total biomass of 3000 t. If the stocked density, D , is 20 kg/m³ and the volume of the receiving area is 3,456,000 m³ (480m·480m·15m), the farm will receive 20.8% of the incoming lice.

Appendix B. Connectivity

Connectivity within production zone 2 and 3 is magnitudes higher than connectivity between the two production zones (Fig. B.12). This is expected as the production zones are based upon an analysis calculating areas of minimal lice transport (Samsing et al., 2017). Considerable more lice disperse from PZ2 to PZ3 than from PZ3 to PZ2 (Fig. B.12) due to the northwards coastal current along the Norwegian coastline.

Data availability

The data that has been used is confidential.

Acknowledgements

This study was financially supported by Granskingarráðið - Research Council Faroe Islands (Grant No. 0456) and the Institute of Marine Research internal project number 15696. We would like to thank Ása Johannesen for help with the statistical analysis.

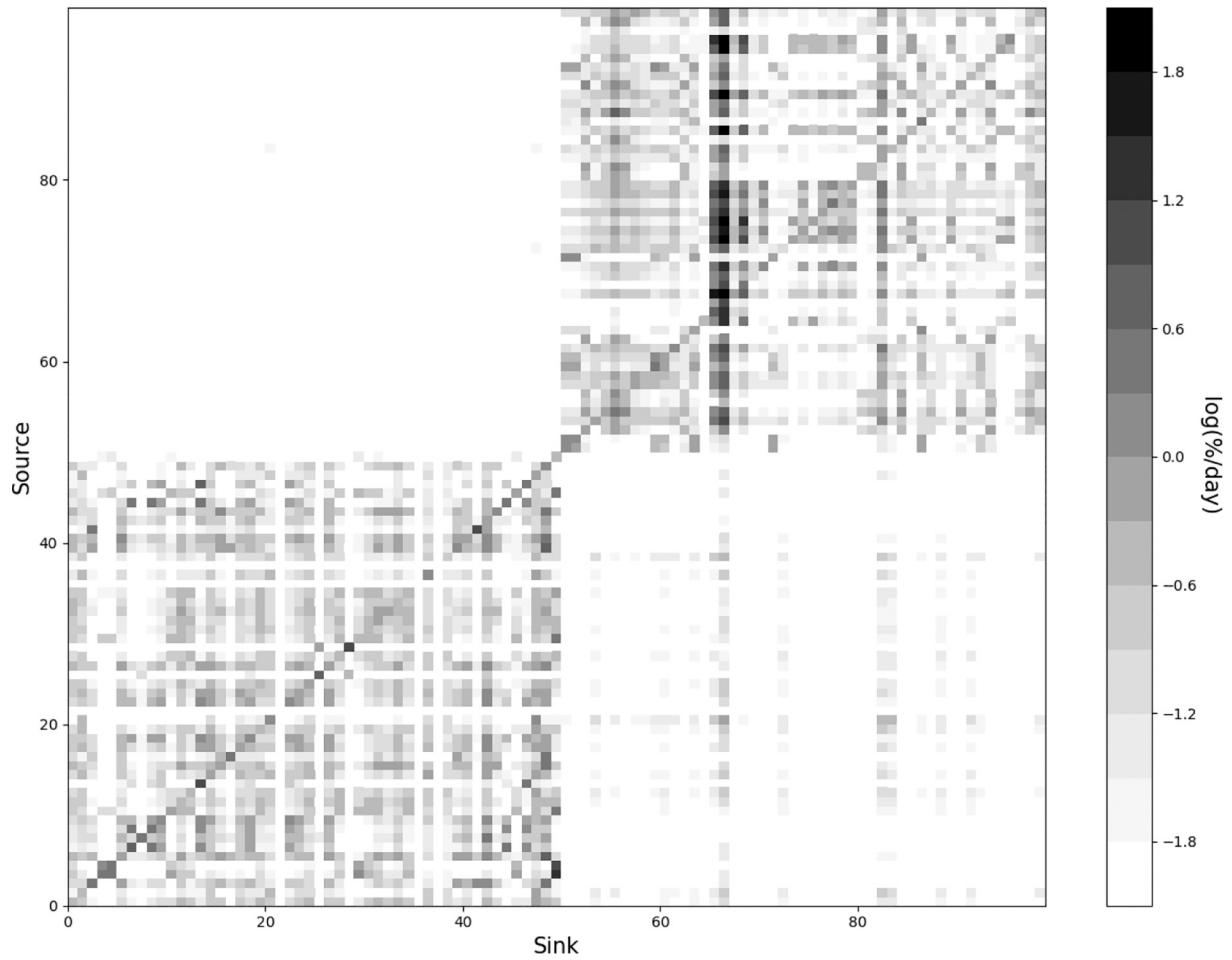


Fig. B.12. Source farms on the y-axis and sink farms on the x-axis. Farms 1–50 are in production zone 2 and farms 51–99 are in production zone 3. % particles in/particle out is log scaled.

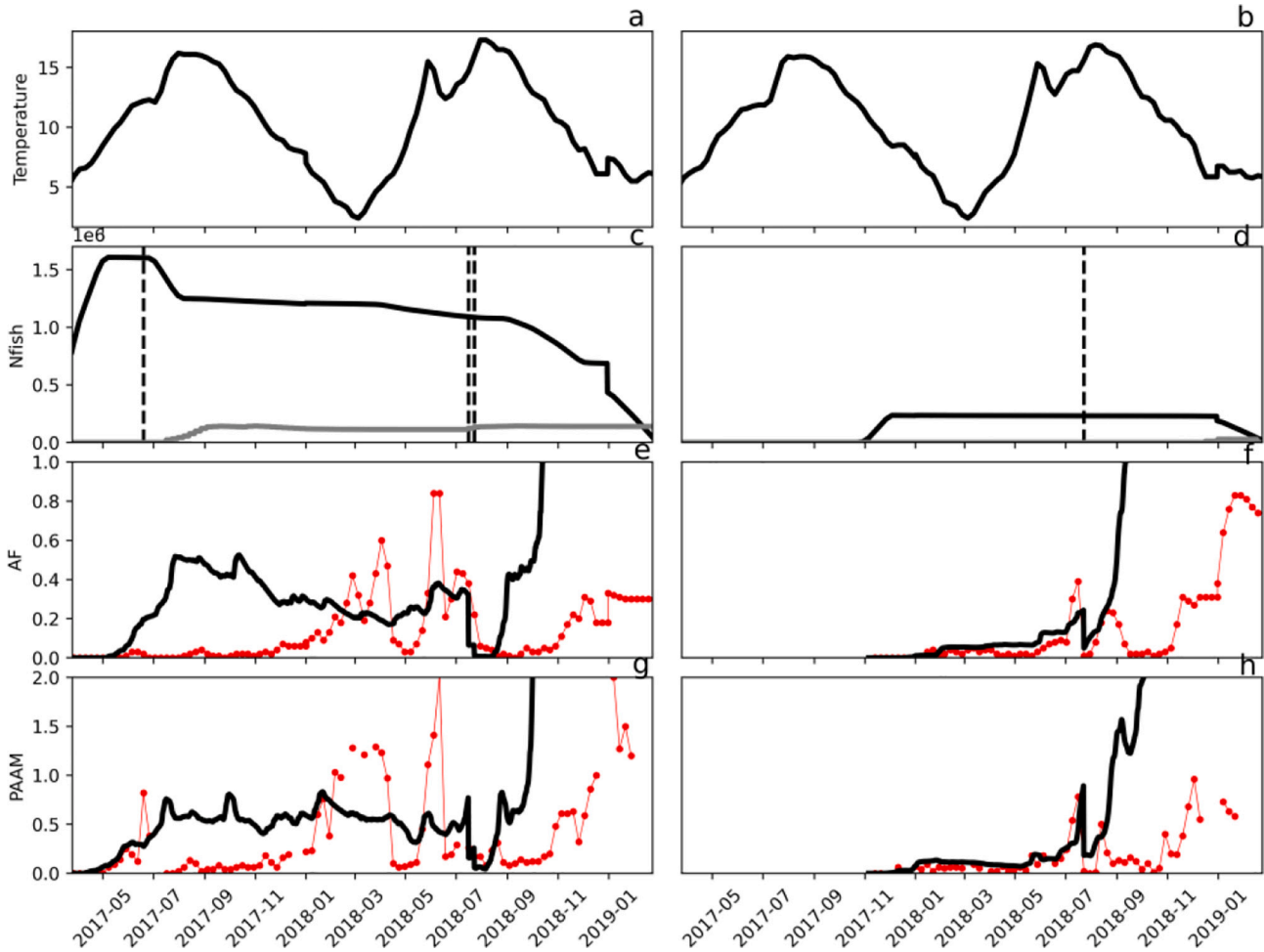


Fig. B.13. Examples of lice dynamics in two farms in PZ2, which capture the lice dynamics poorly (left) and well (at least the first 8 months) (right). a-b temperature. c-d) Number of salmon (black) and cleaner fish (grey). Vertical lines indicate treatments. e-f) Lice counts of AF/fish (red) and model output black line. g-h) Lice counts of PAAM/fish (red) and model output (black line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix C. Lice dynamics per farm

Model validation was as mentioned done by comparing the reported lice counts with corresponding model output from each individual farms that was active in the simulation period. Examples from two farms are showcased here to illustrate how the validation process works and highlight some of the challenges with the current approach. In both examples the model captures dynamics relatively well when we can expect to see pre-adult and adult stages on the fish farm. The model highly overestimates the salmon lice counts on farm A after day 100 and where after it generally poorly captures the lice dynamics. The model fairly accurately captures the lice dynamics on Farm b until day 350 where it seems like a treatment is preformed but it is not reported. This shows why is it difficult to accurately simulate dynamics on a per farms basis.

Appendix D. Modelled temperature

Temperature as a significant effect on lice dynamics. In our study we used the reported temperature on the farms. However, we compared the results with simulations based on temperature from hydrodynamic simulations and found virtually no difference (Fig. D.14).

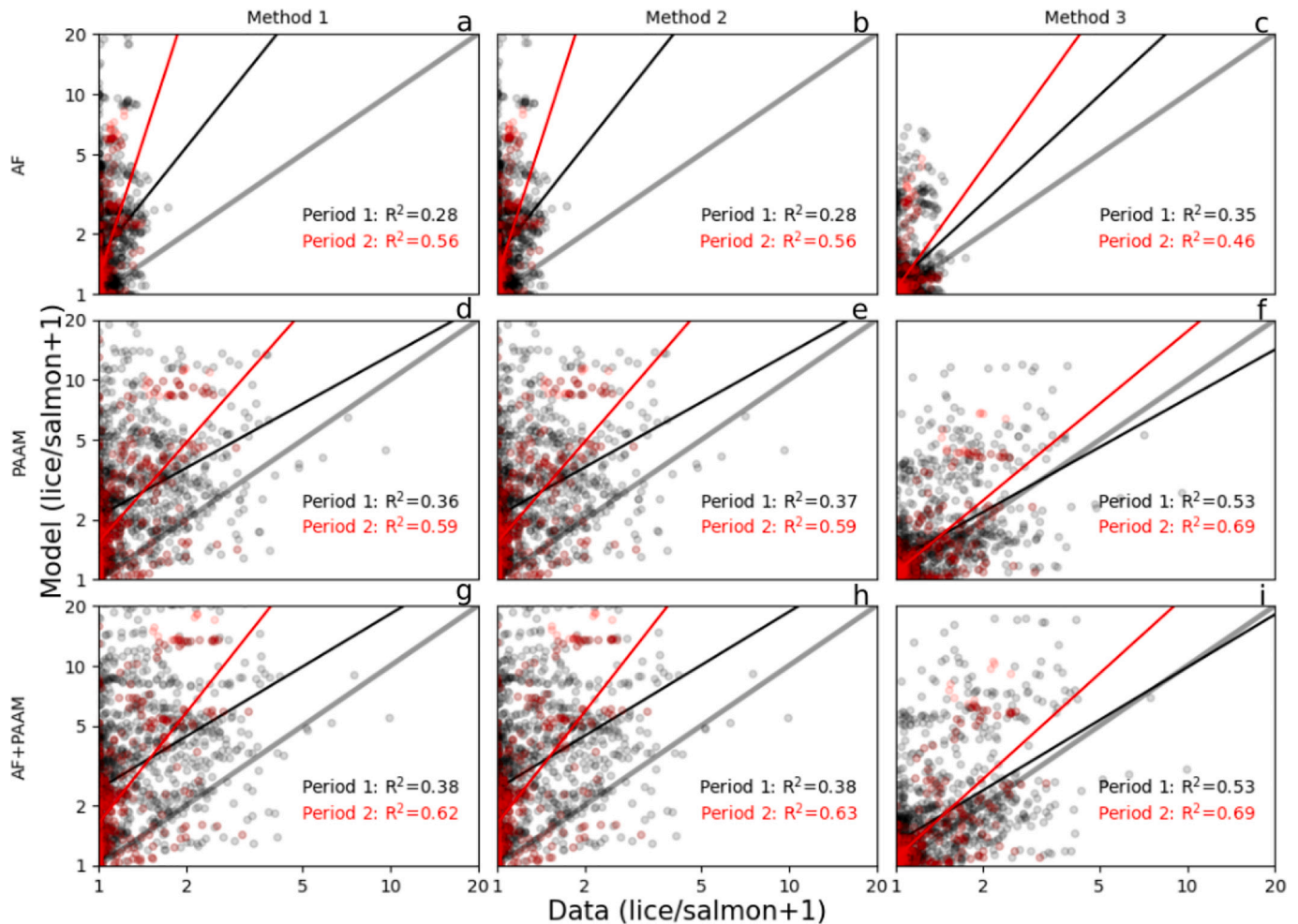


Fig. D.14. Data vs model of AF, PAAM and AF + PAAM lice with temperature from a,d,g) method 1: constant receiving ratio of 0.15. b,e,h) method 2: Type II functional response with a 0.15 constant receiving ratio. c,f,i) receiving area ratio follows biomass. a,b,c) are adult female, d,e,f) are mobile lice and g,h,i) are adult female + mobile lice. Period 1 covers the period from stocking until first treatment or input of cleaner fish and consists of 387 data points. Period 2 consists of 1319 data points and covers the periods from stocking until first treatment and not taking cleaner fish into consideration. Linear regression trend lines are shown for period 1 and 2 as black and red, respectively. 1:1 line show as grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

References

- á Norði, G., Simonsen, K., Danielsen, E., Eliassen, K., Mols-Mortensen, A., Christiansen, D., Steingrund, P., Galbraith, M., Patursson, Ø., 2015. Abundance and distribution of planktonic lepeophtheirus salmonis and caligus elongatus in a fish farming region in the Faroe Islands. *Aquac. Environ. Interact.* 7, 15–27.
- Adams, T., Proud, R., Black, K.D., 2015. Connected networks of sea lice populations: dynamics and implications for control. *Aquac. Environ. Interact.* 6, 273–284.
- Ådlandsvik, B., 2015. Forslag til produksjonsområder i norsk lakse-og ørretoppdrett.
- Albretsen, J., 2011. Norkyst-800 report no. 1: user manual and technical descriptions. *Fisken og havet*.
- Aldrin, M., Huseby, R.B., Stien, A., Grøntvedt, R.N., Viljgrein, H., Jansen, P.A., 2017. A stage-structured bayesian hierarchical model for salmon lice populations at individual salmon farms—estimated from multiple farm data sets. *Ecol. Model.* 359, 333–348.
- Aldrin, M., Jansen, P., Stryhn, H., 2019. A partly stage-structured model for the abundance of salmon lice in salmonid farms. *Epidemics* 26, 9–22.
- Anon, 2012. Forskrift om bekjempelse av lakselus i akvakulturanlegg. URL: https://lovdata.no/dokument/SF/forskrift/2012-12-05-1140#KAPITTEL_1.
- Anon, 2019. Status for norske laksebestander i 2018. URL: <http://hdl.handle.net/11250/2619889>.
- Anon, 2022. Norwegian Fisheries Directorate. URL: <https://www.fiskeridir.no/Akvakultur/Tall-og-analyse/Biomassestatistikk/Biomassestatistikk-etter-produksjonsomraade>.
- Asplin, L., Johnsen, I.A., Sandvik, A.D., Albretsen, J., Sundfjord, V., Aure, J., Boxaspen, K.K., 2014. Dispersion of salmon lice in the hardangerfjord. *Mar. Biol.* 10, 216–225.
- Asplin, L., Albretsen, J., Johnsen, I.A., Sandvik, A.D., 2020. The hydrodynamic foundation for salmon lice dispersion modeling along the norwegian coast. *Ocean Dyn.* 70, 1151–1167.
- Barker, S.E., Bricknell, I.R., Covelto, J., Purcell, S., Fast, M.D., Wolters, W., Bouchard, D.A., 2019. Sea lice, lepeophtheirus salmonis (krøyer 1837), infected Atlantic salmon (salmo salar l.) are more susceptible to infectious salmon anemia virus. *PLoS One* 14, e0209178.
- Barrett, L.T., Oppedal, F., Robinson, N., Dempster, T., 2020. Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. *Rev. Aquac.* 12, 2527–2543.
- Boissonnot, L., Kharlova, I., Iversen, N.S., Staven, F.R., Austad, M., 2022. Characteristics of lumpfish (cyclopterus lumpus) with high cleaning efficacy in commercial Atlantic salmon (salmo salar) production. *Aquaculture* 560, 738544.
- Bricknell, I.R., Dalesman, S.J., O'Shea, B., Pert, C.C., Luntz, A.J.M., 2006. Effect of environmental salinity on sea lice lepeophtheirus salmonis settlement success. *Dis. Aquat. Org.* 71, 201–212.

- Crosbie, T., Wright, D.W., Oppedal, F., Johnsen, I.A., Samsing, F., Dempster, T., 2019. Effects of step salinity gradients on salmon lice larvae behaviour and dispersal. *Aquac. Environ. Interact.* 11, 181–190.
- Dalsøren, S.B., Albretsen, J., Asplin, L., 2020. New validation method for hydrodynamic fjord models applied in the hardangerfjord, Norway. *Estuar. Coast. Shelf Sci.* 246, 107028.
- Dalvin, S., Are Hamre, L., Skern-Mauritzen, R., Vågseth, T., Stien, L., Oppedal, F., Bui, S., 2020. The effect of temperature on ability of lepeophtheirus salmonis to infect and persist on Atlantic salmon. *J. Fish Dis.* 43, 1519–1529.
- Eliassen, K., Danielsen, E., Johannesen, A., Joensen, L.L., Patursson, E.J., 2018. The cleaning efficacy of lumpfish (*Cyclopterus lumpus* L.) in faroese salmon (*Salmo Salar* L.) farming pens in relation to lumpfish size and seasonality. *Aquaculture* 488, 61–65.
- Engelbreten, S., Aldrin, M., Qviller, L., Stige, L.C., Rafoss, T., Danielsen, O.R., Lindholm, A., Jansen, P.A., 2023. Salmon lice (*lepeophtheirus salmonis*) in the stomach contents of lumpfish (*Cyclopterus lumpus*) sampled from norwegian fish farms: relationship between lice grazing and operational conditions. *Aquaculture* 563, 738967.
- Gillibrand, P.A., Willis, K.J., 2007. Dispersal of sea louse larvae from salmon farms: modelling the influence of environmental conditions and larval behaviour. *Aquat. Biol.* 1, 63–75.
- Gislason, H., 2018. Statistical modelling of sea lice count data from salmon farms in the Faroe Islands. *J. Fish Dis.* 41, 973–993.
- Groner, M.L., McEwan, G.F., Rees, E.E., Gettinby, G., Revie, C.W., 2016. Quantifying the influence of salinity and temperature on the population dynamics of a marine ectoparasite. *Can. J. Fish. Aquat. Sci.* 73, 1281–1291.
- Hamre, L.A., Eichner, C., Caipang, C.M.A., Dalvin, S.T., Bron, J.E., Nilsen, F., Boxshall, G., Skern-Mauritzen, R., 2013. The salmon louse *lepeophtheirus salmonis* (copepoda: Caligidae) life cycle has only two chalimus stages. *PLoS One* 8, e73539.
- Hamre, L.A., Bui, S., Oppedal, F., Skern-Mauritzen, R., Dalvin, S., 2019. Development of the salmon louse *lepeophtheirus salmonis* parasitic stages in temperatures ranging from 3 to 24 °C. *Aquac. Environ. Interact.* 11, 429–443.
- Heuch, P.A., 1995. Experimental evidence for aggregation of salmon louse copepodids (*lepeophtheirus salmonis*) in step salinity gradients. *J. Mar. Biol. Assoc. U. K.* 75, 927–939.
- Heuch, P.A., Gettinby, G., Revie, C.W., 2011. Counting sea lice on Atlantic salmon farms—empirical and theoretical observations. *Aquaculture* 320, 149–153.
- Hirst, A., Kjørboe, T., 2002. Mortality of marine planktonic copepods: global rates and patterns. *Mar. Ecol. Prog. Ser.* 230, 195–209.
- Huserbråten, M., Johnsen, I., 2022. Seasonal temperature regulates network connectivity of salmon louse. *ICES J. Mar. Sci.* 79, 1075–1082.
- Jeong, J., Arriagada, G., Revie, C.W., 2022. Targets and measures: challenges associated with reporting low sea lice levels on Atlantic salmon farms. *Aquaculture* 738865.
- Johnsen, I.A., Fiksen, Ø., Sandvik, A.D., Asplin, L., 2014. Vertical salmon lice behaviour as a response to environmental conditions and its influence on regional dispersion in a fjord system. *Aquac. Environ. Interact.* 5, 127–141.
- Johnsen, I.A., Asplin, L., Sandvik, A.D., Serra-Llinares, R.M., 2016. Salmon lice dispersion in a northern norwegian fjord system and the impact of vertical movements. *Aquac. Environ. Interact.* 8, 99–116.
- Johnsen, I.A., Stien, L.H., Sandvik, A.D., Asplin, L., Oppedal, F., 2020. Optimal estimation of lice release from aquaculture based on ambient temperatures. *Aquac. Environ. Interact.* 12, 179–191.
- Johnson, S., Albright, L., 1991. Development, growth, and survival of *lepeophtheirus salmonis* (copepoda: Caligidae) under laboratory conditions. *J. Mar. Biol. Assoc. U. K.* 71, 425–436.
- Kragestein, T.J., Simonsen, K., Visser, A.W., Andersen, K.H., 2019. Optimal salmon lice treatment threshold and tragedy of the commons in salmon farm networks. *Aquaculture* 512, 734329.
- Kragestein, T.J., Simonsen, K., Visser, A.W., Andersen, K.H., 2021. Estimation of external infection pressure and salmon-lice population growth rate in faroese salmon farms. *Aquac. Environ. Interact.* 13, 21–32.
- Kristoffersen, A.B., Qviller, L., Helgesen, K.O., Vollset, K.W., Viljugrein, H., Jansen, P.A., 2018. Quantitative risk assessment of salmon louse-induced mortality of seaward-migrating post-smolt Atlantic salmon. *Epidemics* 23, 19–33.
- Krkošek, M., Bateman, A., Proboyszcz, S., Orr, C., 2010. Dynamics of outbreak and control of salmon lice on two salmon farms in the broughton archipelago, British Columbia. *Aquac. Environ. Interact.* 1, 137–146.
- Krkošek, M., Connors, B.M., Lewis, M.A., Poulin, R., 2012. Allee effects may slow the spread of parasites in a coastal marine ecosystem. *Am. Nat.* 179, 401–412.
- Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B., Todd, C.D., 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. *Proc. R. Soc. B* 280, 20122359.
- Lees, F., Baillie, M., Gettinby, G., Revie, C.W., 2008. The efficacy of emamectin benzoate against infestations of *lepeophtheirus salmonis* on farmed Atlantic salmon (*Salmo Salar* L.) in Scotland, 2002–2006. *PLoS One* 3, e1549.
- Oppedal, F., Dempster, T., Stien, L.H., 2011. Environmental drivers of Atlantic salmon behaviour in sea-cages: a review. *Aquaculture* 311, 1–18.
- Overton, K., Dempster, T., Oppedal, F., Kristiansen, T.S., Gismervik, K., Stien, L.H., 2019. Salmon lice treatments and salmon mortality in norwegian aquaculture: a review. *Rev. Aquac.* 11, 1398–1417.
- Pike, A., Wadsworth, S., 1999. Sealice on salmonids: their biology and control. *Adv. Parasitol.* 44, 233–337.
- Revie, C.W., Robbins, C., Gettinby, G., Kelly, L., Treasurer, J., 2005. A mathematical model of the growth of sea lice, *lepeophtheirus salmonis*, populations on farmed Atlantic salmon, *Salmo Salar* L., in Scotland and its use in the assessment of treatment strategies. *J. Fish Dis.* 28, 603–613.
- Samsing, F., Oppedal, F., Dalvin, S., Johnsen, I., Vågseth, T., Dempster, T., 2016. Salmon lice (*lepeophtheirus salmonis*) development times, body size and reproductive outputs follow universal models of temperature dependence. *Can. J. Fish. Aquat. Sci.* 73.
- Samsing, F., Johnsen, I., Dempster, T., Oppedal, F., Tremblay, E.A., 2017. Network analysis reveals strong seasonality in the dispersal of a marine parasite and identifies areas for coordinated management. *Landsc. Ecol.* 32, 1–15.
- Sandvik, A.D., Johnsen, I.A., Mykssvoll, M.S., Sævik, P.N., Skogen, M.D., 2020. Prediction of the salmon lice infestation pressure in a norwegian fjord. *ICES J. Mar. Sci.* 77, 746–756.
- Sandvik, A.D., Dalvin, S., Skern-Mauritzen, R., Skogen, M.D., 2021. The effect of a warmer climate on the salmon lice infection pressure from norwegian aquaculture. *ICES J. Mar. Sci.* 78, 1849–1859.
- Serra-Llinares, R.M., Bøhn, T., Karlsen, Ø., Nilsen, R., Freitas, C., Albretsen, J., Haraldstad, T., Thorstad, E.B., Elvik, K.M.S., Bjørn, P.A., 2020. Impacts of salmon lice on mortality, marine migration distance and premature return in sea trout. *Mar. Ecol. Prog. Ser.* 635, 151–168.
- Skarøhamar, J., Albretsen, J., Sandvik, A.D., Lien, V.S., Mykssvoll, M.S., Johnsen, I.A., Asplin, L., Ådlandsvik, B., Halttunen, E., Bjørn, P.A., et al., 2018. Modelled salmon lice dispersion and infestation patterns in a sub-arctic fjord. *ICES J. Mar. Sci.* 75, 1733–1747.
- Skern-Mauritzen, R., Sissener, N.H., Sandvik, A.D., Meier, S., Sævik, P.N., Skogen, M.D., Vågseth, T., Dalvin, S., Skern-Mauritzen, M., Bui, S., 2020. Parasite development affect dispersal dynamics; infectivity, activity and energetic status in cohorts of salmon louse copepodids. *J. Exp. Mar. Biol. Ecol.* 530, 151429.
- Stien, A., Bjørn, P.A., Heuch, P.A., Elston, D.A., 2005. Population dynamics of salmon lice *lepeophtheirus salmonis* on Atlantic salmon and sea trout. *Mar. Ecol. Prog. Ser.* 290, 263–275.
- Stormoen, M., Skjerve, E., Aunsmo, A., 2013. Modelling salmon lice, *lepeophtheirus salmonis*, reproduction on farmed Atlantic salmon, *Salmo Salar* L. *J. Fish Dis.* 36, 25–33.
- Taranger, G.L., Karlsen, Ø., Bannister, R.J., Glover, K.A., Husa, V., Karlsbakk, E., Kvamme, B.O., Boxaspen, K.K., Bjørn, P.A., Finstad, B., et al., 2014. Risk assessment of the environmental impact of norwegian Atlantic salmon farming. *ICES J. Mar. Sci.* 72, 997–1021.
- Toorians, M.E., Adams, T.P., 2020. Critical connectivity thresholds and the role of temperature in parasite metapopulations. *Ecol. Model.* 435, 109258.