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Estimation of external infection pressure and salmon-louse population growth rate in Faroese salmon farms

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Abstract

Managing salmon lice (*Lepeophtheirus salmonis*) outbreaks is a crucial part of salmon aquaculture in sea cages. Treatment management strategies can be optimized with the aid of salmon-louse population dynamic models. These models, however, need to be calibrated and validated with biological meaningful parameters. Here, based on a time-series of lice data, we estimated two essential model parameters: The external infection pressure and the salmon-louse population growth rate for each active salmon farm site in the period 2011 to 2018 in the Faroe Islands. External infection pressure was found to vary between farm sites and ranged on average from 0.002 to 0.1 lice salmon^{-1} d^{-1}. Further, external infection was significantly correlated with the total number of gravid lice in the Faroese farm network. Salmon-louse population growth rates were found to vary between farm sites and ranged on average from 1.7 to 5.4 % d^{-1}. These model parameter estimates are crucial in developing a salmon-louse population dynamic model for the Faroe Islands and the method to estimate these parameters may be applicable in other aquaculture regions.

Keywords: Salmon Aquaculture, Salmon lice, Modelling

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1. Introduction

Managing sea lice on a regional or national scale is a crucial part of modern sea-based salmon aquaculture. In the northern hemisphere the most important sea lice impacting salmon aquaculture is the ectoparasite *Lepeophtheirus salmonis*, also know as salmon louse. The salmon louse is a naturally occurring parasite on salmonid fish and feeds on the mucus, skin and blood of it's host (Pike & Wadsworth 1999). At high densities, lice can cause physical damage to their host and expose them to secondary infections as well as causing stress and osmotic regulatory imbalance (Pike & Wadsworth 1999).

As the salmon farming industry has grown, so has the number of salmon-louse host's providing favourable conditions for the parasite. At sufficiently high host densities salmon lice can develop into an epidemic (Frazer et al. 2012) negatively affecting both salmon farms and wild salmonid stocks (Krkošek et al. 2006, Kristoffersen et al. 2018). Understanding the dynamics of louse population growth and outbreaks and how lice disperse has obvious potential to reduce treatment frequency and fish mortality on both farmed and wild salmon stocks, increasing economic output and decreasing ecological impact.

Numerical models describing salmon-louse population growth have been developed based on Anderson et al. (1979) type host-parasite models (Krkošek et al. 2010, Frazer et al. 2012) and delayed stage structured models (Revie et al. 2005, Stien et al. 2005, Robbins et al. 2010, Gettinby et al. 2011, Adams et al. 2015, Kragesteen et al. 2019). Louse population growth rate is determined by two processes: external and internal infection. The external infection pressure is determent by lice arriving from other salmon farms and wild salmonid stocks. The internal infection pressure is determent by the production of lice on the farm. If internal infection is high enough it will eventually lead to a exponentially growing salmon lice population. In the initial phase of salmon production, the external infection pressure is the dominating process of the population growth rate (Kristoffersen et al. 2014). Internal infection becomes the dominating process as the lice population increases (Krkošek et al. 2010).

The external infection pressure has been estimated using sentinel cages in Norway, Scotland and Iceland (Bjørn et al. 2011, Pert et al. 2014, Sandvik et al. 2016, Karbowski et al. 2019). A sentinel cage is typically deployed 2-3 weeks at a time over a period of months and for each deployment lice are recorded. External infection pressure reported in these studies was found to vary significantly depending on the level of gravid lice in the area. Bjørn et al. (2011) found the external infection to be up to 2.3 lice salmon^{-1} in the Romsdalsfjord system, Norway, with a 14 days deployment time. Sandvik et al. (2016) found up to 20 lice salmon^{-1} in Hardangerfjord, Norway, with 14-21 days deployment time and Pert et al. (2014) found close to 15 lice salmon^{-1} in Loch Shieldaig, Scotland with 7 days deployment time. In Arnarfjörður, Iceland, which only contained 2 salmon farms Karbowski et al. (2019) found only 0.022 lice salmon^{-1} when sampling for $\approx$ 21 days.

Salmon-louse population growth rates have been reported for salmon farms in the Broughton Archipelago, Canada and the Faroe Islands (Krkošek et al. 2010, Patursson et al. 2017). These estimates assume exponential growth and Krkošek et al. (2010) reported two farms having 0.9 and 4.8 %/d while Patursson et al. (2017) reported growth rates to range from 0.9 to 4.1 % d^{-1} for several Faroese farms.

Here, we describe the general development of salmon lice abundance in Faroe Islands from 2011 to 2018 based on an extensive time series of sea lice counts. Further, we estimated external infection pressure and salmon-louse population growth rate on a per-farm basis using an alternative approach described in the method section. These parameter estimates are essential for the development of a salmon-louse population dynamic models which can aid in salmon lice management strategies.

2. Methods

2.1. Lice data and salmon number

Lice data is based on a the Faroese lice count program which started in 2009 where the Faroese government mandated farmers to count lice every 14 days from 1 May to 31 December and once a month from 1 January to 30 April. However, lice counts were not performed on all farms until after 2012. From 2009 to 2016 a minimum of 10 fish were counted from 4 cages. The farmer choose 2 cages where one being the first stocked cage and the second cage was, based on prior experience, estimated to have the highest sea lice load. The two other cages were chosen at random between cages which had not been counted previously. After 2016 a minimum of 10 fish were counted for all cages at each farm site every 14 days all year (Anon 2016). In year 2011 counting was not performed at 3 farms and at 3 farms lice counts started 3-6 months into the year 2011. In addition aily salmon numbers for each farm site was provided by the Faroese aquaculture companies for the period between 2011 and 2018.

Both *L. salmonis* and *Caligus elongatus* have been recorded, however, we will exclusively focus on salmon louse as they have by far the largest economic impact on the salmon industry (Boxaspen 2006). The life cycle of *L. salmonis* consists 8 stages (Schram 1993, Hamre et al. 2013). Non-feeding planktonic nauplii larvae hatch from gravid female egg strings and moults into nauplius II, and subsequently, into the third, and infective, stage, as a copepodite. After attachment, copepodites moult into immobile chalimus I and start feeding. The chalimus phase consists of 2 stages (chalimus I and II), where the latter moults into the first mobile pre-adult stage. After the pre-adult stages (pre-adult I and II), the louse moults into the adult and final stage.

Salmon louse counts categorise these life-stages into three groups: immobile (chalimus I and II), mobile, and gravid female. *L. salmonis* and *C. elongatus* are not distinguished from each other in the immobile group and these counts are therefore discarded and only mobile and gravid female lice are considered. Mobile lice counts include the pre-adult stages (male and female) and adult male stage while gravid lice only include this stage.

2.2. Treatments

Treatment data was gathered from the active Faroese farming companies since 2011. There have been several kinds of treatments performed, which here are organized into four groups: Medical oral (SLICE and Diflubenzuron), medicinal bath (Hydrogen peroxide, Salmosan, Alpbamax, Betamax, Pyretroid and Azametiphos) and mechanical (freshwater bath, hydrolicer, optilicer, termolicer or flushing). A "treatment event" was defined as a given kind of treatment performed at a given farm which had not been performed within the previous 7 days. Number of treated cages was not resolved.

2.3. Sea Water Temperature

Sea water temperature was measured by the Faroe Marine Research Institute and available at the online data service, www.envofar.fo. Sea water temperature is measured at 3 m depth at Oyrargjógv (62°07'N, 7°10'W) which is located in a tidally well mixed strait, and thus representative for a relative large geographical region (Fig. 1).

2.4. Calculating total lice

The total number of gravid and mobile lice was estimated for each farm i by linear interpolating between the day of the counts to obtain the daily values $l_i(t)$. Knowing the number of salmon in each farm per day $F_i(t)$ the total number of lice in the region on a given day, t, is obtained from:

$$L_{\text{tot}}(t) = \sum_{i=1}^{n} l_i(t) F_i(t). \tag{1}$$

where n is number of farms in the system.

2.5. The Salmon-louse Model

To estimate the external infection pressure and salmon-louse population growth rate, we used a series of delay differential equations (Revie et al. 2005):

$$\frac{\mathrm{d}\rho_1(t)}{\mathrm{d}t} = \beta(t) - \beta(t-t_1)e^{-\mu_1 t_1} - \mu_1 \rho_1(t) \tag{2}$$

$$\frac{\mathrm{d}\rho_2(t)}{\mathrm{d}t} = \beta(t-t_1)e^{-\mu_1 t_1} - \beta(t-t_1-t_2)e^{-\mu_1 t_1 - \mu_2 t_2} - \mu_2 \rho_2(t) \tag{3}$$

$$\begin{aligned}\frac{\mathrm{d}\rho_3}{\mathrm{d}t}(t) = \beta(t-t_1-t_2)&e^{-\mu_1 t_1 - \mu_2 t_2} \\ &- \beta(t-t_1-t_2-t_3)e^{-\mu_1 t_1 - \mu_2 t_2 - \mu_3 t_3} - \mu_3 \rho_3(t)\end{aligned} \tag{4}$$

$$\frac{\mathrm{d}\rho_4(t)}{\mathrm{d}t} = \beta(t-t_1-t_2-t_3)e^{-\mu_1 t_1 - \mu_2 t_2 - \mu_3 t_3} - \mu_4, \rho_4(t), \tag{5}$$

where ρ_{1-4} represent the male and female lice at the chalimus, pre-adult, adult and sexually mature stages, respectively, and μ_{1-4} and t_{1-4} represent mortality and development times. The amount of attached larvae $\beta(t)$ is defined in Kragesteen et al. (2019) as:

$$\beta(t) = q\eta\rho_4(t-t_e)s(\rho_4(t-t_e)) + L_0, \tag{6}$$

where q is the amount of viable larvae per day per sexually mature lice which includes connectivity and larvae production rate and η is the proportion of female lice. L_0 is the external infection pressure and t_e is the time it takes larvae to reinfect a host and is assumed to be 5 days (Stien et al. 2005). $s(\rho_4(t))$ is mate limitation or an Allee effect which states that fertilisation success is close to zero at near zero lice abundances and close to 100 % at around 2 gravid lice salmon^{-1} (Krkošek et al. 2012, Stormoen et al. 2013, Kragesteen et al. 2019). The initial conditions are given by:

$$\rho_1(0) = 0 \text{ for } t = 0 \tag{7}$$

$$\rho_{j+1}(t) = 0 \text{ for } t \leq t_j \text{ where } j \in \{1, 2, 3\}. \tag{8}$$

where t_j is the development time for each stage and salmon are stocked in sea cages at $t = 0$.

2.6. External infection

The external infection pressure in this study includes, as mentioned, salmon louse larvae from other farms and from the environment or natural background infection. To calculate external infection pressure we rewrite Eqs. 2-6 by summing all mobile stages ($\rho_2(t)+\rho_3(t)+\rho_4(t)$), which corresponds to the mobile and gravid lice counts, ρ_m. Therefore:

$$\begin{aligned}\frac{\mathrm{d}\rho_m(t)}{\mathrm{d}t} &= \frac{\mathrm{d}\rho_2(t)}{\mathrm{d}t} + \frac{\mathrm{d}\rho_3(t)}{\mathrm{d}t} + \frac{\mathrm{d}\rho_4(t)}{\mathrm{d}t} \\ &= \beta(t - t_1)e^{-\mu_1 t_1} - \mu_2\rho_2(t) - \mu_3\rho_3(t) - \mu_4\rho_4(t).\end{aligned} \tag{9}$$

If we assume that $\mu_m \approx \mu_2 \approx \mu_3 \approx \mu_4$ and the practical implementation of this assumption is $\mu_m = \frac{(\mu_2+\mu_3+\mu_4)}{3}$ Eq. 9 can be written as:

$$\frac{\mathrm{d}\rho_m(t)}{dt} = \beta(t - t_1)e^{-\mu_1 t_1} - \mu_m\rho_m(t). \tag{10}$$

We argue that in the first 150 days of the production cycle there is virtually no internal dynamics, meaning we assume no internal viable larvae and/or no females are fertilized and set $q \cdot s$ in Eq. 6 to zero. There are two reasons for assuming this: First, at 11 °C (maximum Faroese shelf water temperature) the first attached lice start releasing larvae after ≈ 50 d ($= t_1 + t_2 + t_3$) and it takes another ≈ 20 days ($= t_e + t_1$) until these lice appear in the lice counts (Table 1, Stien et al. (2005)). Second, due to the Allee effect, where few female lice get fertilized at low lice abundances (Krkošek et al. 2012, Stormoen et al. 2013), s is close to zero. Further, gravid lice have been shown to produce fewer eggs in their first pair of egg strings (Heuch et al. 2000). With the approximation that $q \cdot s$ is zero, Eq. 10 can be written as:

$$\frac{\mathrm{d}\rho_m(t)}{\mathrm{d}t} = L_0 e^{-\mu_1 t_1} - \mu_m\rho_t(t), \quad \text{for } t < 150 \text{ days} \tag{11}$$

which with the initial conditions ($\rho_m(t_1) = 0$) has the analytical solution:

$$\rho_m(t) = L_0 \frac{e^{-\mu_1 t_1}}{\mu_m} \left(1 - e^{-\mu_m (t - t_1)}\right) \tag{12}$$

for $t \geq t_1$. From here the external infection pressure, L_0, may be isolated to:

$$L_0 = \frac{\mu_m \rho_m(t)}{e^{-\mu_1 t_1} \left(1 - e^{-\mu_m (t - t_1)}\right)}. \tag{13}$$

The stage duration and mortality are based on the estimates by Stien et al. (2005) (Table 1), where μ_m is the average of the minimum mortalities.

2.7. Salmon-louse population growth rate

Salmon-louse population growth rates can be calculated using Eq. 10 and dividing with $\rho_m(t)$:

$$\frac{1}{\rho_m(t)} \frac{\mathrm{d}\rho_m(t)}{\mathrm{d}t} = \frac{\beta_i(t - t_1)}{\rho_m(t)} e^{-\mu_1 t_1} - \mu_m. \tag{14}$$

Writing Eq. 6 for $\beta(t)$ we get:

$$\frac{\mathrm{d} \ln\left(\rho_m(t)\right)}{\mathrm{d}t} = \left[q\eta s(\rho_4(t - t_e - t_1)) \frac{\rho_4(t - t_e - t_1)}{\rho_m(t)} + \frac{L_0}{\rho_m(t)} \right] e^{-\mu_1 t_1} - \mu_m. \tag{15}$$

All lice counts 150 days after production start are included. The growth rate is calculated by taking the log of salmon lice counts ($\rho_m(t)$) and estimating the slope of a fitted line with 5 consecutive points or counts using a linear regression model MATLAB (2020) with random slope and intercept. Unfortunately, lice counts are affected by treatments events and/or cleaner fish. To omit these periods we have discarded periods where the slope is negative or has an adjusted $R^2 < 0.6$. See Appendix, Fig. A1 for an example of how external infection pressure and population growth rate was estimated at one farm site.

3. Results

3.1. Total lice

The total number of gravid and mobile lice in the Faroese aquaculture has fluctuated a lot since 2011. The highest number of gravid and mobile lice was in December 2015 with over 35 million and 129 million, respectively (Fig. 2). The lowest number of gravid lice was under 5 million and recorded in June 2013 and the lowest for mobile lice was under 5 million in March 2011. The total number of gravid lice has generally been below 20 million except in the winter of 2011, 2014, 2015 and 2016. Lice numbers in year 2011 may be underestimated as 6 farms were not counted regularly or not at all.

Number of salmon in Faroese waters has been relatively stable and close to 20 million since 2011, while production has increased significantly from $50{\cdot}10^3$ tonnes in 2011 to $71{\cdot}10^3$ tonnes in 2014 (www.hagstovan.fo), indicating a general increase in harvest or stocking fish size. The maximum recorded number of salmon was 23.4 million in November of 2017 and the minimum was 16.8 million in February 2011 (Fig. 2a).

Number of treatments events per year has steadily increased since 2011 and was over 90 treatment events per year in years 2016-2018. There is no consistent seasonal treatment pattern. Treatment type shifted from chemical to mechanical starting in 2016 and was almost exclusively mechanical in 2018 (Fig. 2b).

Average shelf sea temperature varies consistently between 10-11 °C in September to 6 °C in March (Fig. 2c). There is a significant correlation between temperature and total gravid and mobile lice with a lag of -95 and -74 days having a correlation of 0.49 and 0.32, respectively. In addition, a high correlation (0.95) was found between average annual gravid lice population growth rate and temperature (see Fig. 6).

Overall the total amount of gravid and mobile lice steadily increased from 2011 to 2015 where after it has steadily decreased. This is consistent with changes in regulation in 2016 where treatment threshold was decreased from 2 gravid lice salmon^{-1} to 1.5 (Faroese Ministry of Foreign Affairs and Trade 2016). We also see a shift from chemical to mechanical treatments and increased treatment frequency in this period. Total lice numbers are generally lowest between May and August and highest in December and January. Number of salmon (Table 2) and average temperature in the period 2011 to 2018 have stayed relatively constant (Fig. 2) and therefore the total number of lice between years is likely tied to treatment frequency and efficiency.

3.2. External Infection Pressure

Based on all lice counts in the first 150 days in all production cycles at each farm from 2010-2018 the external infection pressure is estimated on average to range from 0.002 to 0.1 lice salmon^{-1} d^{-1}. This corresponds to 1 lice per salmon for every 500 to 10 days (Fig. 3). A total of 30 farms were investigated (Fig. 1). Farm 28 is an outlier and has the highest average external infection pressure, however this estimate is only based on one production cycle in 2015. Farm 30 has clearly the lowest average external infection pressure with 0.002 lice salmon^{-1} d^{-1}. In addition to the period of no internal dynamics of 150 days (discussed in section 2.6), the external infection is estimated using periods of 75, 100, and 125 days. For many farms the external infection pressure increases with number of days included while for other farms it decreases and for a few farms external infection pressure stays constant, but generally the effect is not significant (Fig. 3).

In highly connected farm networks such as Faroe Islands (Kragesteen et al. 2018) we expect external infection pressure to increase with the total amount of gravid lice within the farm network. Therefore, the relationship between external infection pressure and the total number of gravid lice was investigated by performing a linear regression model fit with random slope and intercept for the estimated external infection pressure as a function of the total gravid lice (MATLAB 2020). The mean level of gravid lice was estimated from 15 to 45 days prior to each lice count. The results show that an increase in total gravid lice significantly increased external infection pressure ($F_{29,844} = 12.7$, $p < 0.001$), however, the R^2 was low (0.312) indicating that total number of gravid lice does not explain the variability well (Fig. 4). In addition, for the majority of farms, external infection pressure increases roughly between 0.001 to 0.004 lice salmon^{-1} d^{-1} for every million gravid lice in the farm network (Fig 4). Farm no. 30 is an exception having a significant lower external infection pressure likely due to it's isolated location.

3.3. Population growth rate

Growth rates of lice per salmon was estimated to be between 1.7 and 5.4 % d^{-1} on average for all farms (Fig. 5). These estimates are slightly higher but comparable to what Patursson et al. (2017) and Krkošek et al. (2010) found. The estimated growth rates do not separate between internal and external dynamics (Eq. 15), however, we expect that highly self-infectious farms will have a higher growth rate and vise versa. For example, farm 4, 23 and 24 all have relatively low population growth rates, which is expected because they are located in areas with high ventilation due to the tidal currents. Farm 28 has the highest measured growth rate likely because the estimate is based on only one production cycle between years 2015-2016 where the total number of gravid lice also was high and/or the growth rate is positively influenced by treatment events as growth rate is typically high for a period right after a treatment.

We also explored the average annual population growth rate of the total number of gravid lice in Faroe Islands from 2011 to 2018 (Fig. 6). This was done by calculating per day population growth rate by log transforming the total number of gravid lice (Eq. 14) and finding the slope of a straight line fitted with 14 and 90 consecutive days. Each calculated growth rate was sorted into day of year and averaged between all years. We see that average population growth rate is negative approximately the first 160-170 days of the year where after the average growth rate turns positive until approximately day 350 in the year. The average annual lice population growth rate over 90 d is highly correlated (0.95) with average annual temperature. The average annual lice population growth rate over 14 d oscillates consistently and no clear correlation with temperature is found.

4. Discussion

From an extensive time-series of lice counts we show how salmon louse have developed in Faroese aquaculture from 2011 to 2018. Further, the average external infection pressure and salmon lice growth rate for each active farm site since 2009 was estimated. External infection pressure varies greatly between farms (Fig. 3) which is also expected due to differences in hydrodynamic conditions (Patursson et al. 2017) and connectivity between farm sites (Kragesteen et al. 2018). The external infection pressure within farms depends on the total amount of gravid lice present in the farm network (Fig. 4).

The total number of gravid and mobile lice in Faroe Islands is significantly higher compared to a similar salmon aquaculture area (15-18 million salmon) off the coast of mid-Norway (Jevne & Reitan 2019). This coastal area has 18 farm sites located between a group of islands and has a similar water temperature range to the Faroe Islands. One difference is that this Norwegian aquaculture region has synchronized production cycles and the level of salmon lice is therefore effectively reset between each cycle. Comparing the number of treatments between these two areas is not straightforward as treatments are reported differently (number of cages treated in Norway and number of treatment events in the Faroe Islands). However, if we assume that a treatment event on average represents 5 treated cages then about 450 cages are treated per year (90·5) in Faroe Islands in the period from year 2016 to 2018 (Table 2). Jevne & Reitan (2019) reported 262, 550 and 102 cages being treated in the 1, 2 and 3 production cycle, respectively, where a production cycle is almost 2 years long. Production cycle 2 had the highest levels of lice and also the highest number of cages treated but this is still a factor lower 2 compared to the Faroe Islands. A reason for the higher treatment frequency in the Faroe Islands may be the overlapping production in contrast to synchronized production in the Norwegian area. This would contradict claims that coordinated fallowing is ineffective (Guarracino et al. 2018). Another reason could be the relatively low treatment threshold of 0.2 to 0.5 gravid lice salmon^{-1} in Norway (Anon 2012) in contrast to 1.5 to 2 gravid lice salmon^{-1} in the Faroe Islands which may seem counter-intuitive. However, farms in Norway are forced to treat early to keep lice levels relatively low and thereby earn the benefit of the Allee effect resulting in a overall lower larvae production rate and consequently a lower lice population growth rate (Krkošek et al. 2012, Stormoen et al. 2013, Kragesteen et al. 2019). Third, there is a mean current flow through the Norwegian area and therefore lice may be less retained in contrast to Faroe Islands where shelf water is relatively retained (Kragesteen et al. 2018). Last, we currently have insufficient data for cleaner fish, which may be more widely used in the Norwegian island group resulting in fewer treatments.

Salmon-louse levels are typically highest in December/January (Fig. 2). This is likely because the population growth rate of salmon-louse in Faroe Islands is positive until approximately 90 days after the highest sea temperature (September). Highest lice abundance is observed right before the net growth rate turns negative (Fig. 6).

We also speculate that chlorophyll could be a good indicator of lice population growth rate and lice levels. Because high levels of chlorophyll will subsequently lead to high levels of zooplankton which may lead to a higher mortality of planktonic lice larvae. However, we found no clear correlation, maybe due chlorophyll and zooplankton being out of phase or that the chlorophyll samples are from a single location not representative of the general chlorophyll concentration in the Faroe Islands.

If the sentinel cage external infection estimates are converted to lice salmon^{-1} d^{-1} using Eq. 2, we find up to 0.17 (Bjørn et al. 2011), 1.16 (Sandvik et al. 2016), 2.16 (Pert et al. 2014) and 0.001 lice salmon^{-1} d^{-1} (Karbowski et al. 2019), when minimum mortality of the chalimus stage is assumed (Table 1). The external infection pressure estimates in this study are therefore considerably lower compared to the sentinel cage estimates in Norway and Scotland (Bjørn et al. 2011, Pert et al. 2014, Sandvik et al. 2016) and while slightly higher than estimates form Iceland in a fjord containing only two salmon farms (Karbowski et al. 2019). One reason for the observed difference could be the dilution effect reported by Samsing et al. (2014), because there are relatively few salmon in the sentinel cages there are potentially a lot more lice per salmon compared to a fully operational high salmon density farm cage. External infection pressure estimates from sentinel cages may as a result be much higher compared to our estimates. This dilution effect should be investigated further.

External infection pressure was estimated based on the first 150 days of a production cycle as we assume effects of salmon-louse internal dynamics to be low or non-existing in this period. This assumption can be debated in particular when water temperature is high (i.e. >11 °C). If internal dynamics are significant in this period there will be an overestimation of the external infection pressure. However, the difference between including the first 75, 100, 125 and 150 days does not significantly affect the average estimated external infection pressure (Fig. 3). An explanation for increasing external infection pressure could be that the self-infection or internal dynamics starts before the 150 days which would cause the estimated external infection pressure to increase with time. Another explanation could be the increased surface area of salmon e.g. if a salmon weighs 200 g when put out to sea, they will increase their weight to about 900 g the first 150 days (Austreng et al. 1987). This increase in weight will increase the salmon surface area from approximately 335 cm^2 to 810 cm^2 (O'Shea et al. 2006). Consequently infectious lice larvae will have 2.4 time more area to attach on 150 day after sea stocking. Therefore, external infection pressure should be standardized with salmon size, however, these data were not available. An issue with the external infection pressure estimates is that treatments do occur in the first 150 days period and in many farms especially after 2015 had cleaner fish present in their sea cages. This would lead to an underestimation of the external infection parameter L_0 and could cause the external infection pressure to decrease in the 150 day period. In summary the external infection pressure estimates are quite uncertain. Nevertheless, these estimates have a high applied value as they are based on *in situ* lice counts from commercial farms reflecting the actual infection pressure at a operational salmon farm.

Here we do not distinguish between external infection pressure caused by larvae production from neighboring farms and the natural background infection from wild salmonid stocks. There is a small wild salmon stock which was introduced and has been maintained since 1940's in four Faroese rivers (www.laks.fo). The population size and level of infection of other salmon-louse hosts like sea trout and Arctic charr are unknown. In Norway the wild salmon stock is estimated to about 550.000 fish (Anon 2019), and the Faroese wild stock is likely only a small fraction of this and consequently the ratio between the wild stock and the 20 million salmon in the cages is likely small, and therefore it seems reasonable to assume that the infection load from the wild salmonids is low. As a result external infection should predominately be determined by the total number of gravid lice in Faroese salmon farms. Our study shows a significant but low R^2 although varying highly between farms (Fig. 4). The reason for the relatively low correlation could be the stochastic nature of the lice counts procedure, where only 10 fish per cage are counted. In addition, treatments and cleaner fish will also negatively influence the correlation. Further, some farms may be strongly connected to only a few farms and therefore the total amount of Faroese gravid lice may not be representative of the external pressure at these farms (Kragesteen et al. 2018).

The principles of measuring salmon-louse population growth rates are relatively simple as we assume exponential growth (Eq. 15) and fit a straight line with a number of consecutive log transformed lice counts. Here, we have decreased the effects of treatments by excluding negative growth rates and badly correlated data ($R^2 < 0.6$, Fig. A1c). This approach differs from that by Patursson et al. (2017) as we here consider all lice counts after 150 days into a production cycle, while Patursson et al. (2017) discarded an initial period until the first treatment occurred. Population growth rates include both internal and external dynamics and at low lice abundances external dynamics are more dominant ($\frac{L_0 e^{-\mu_1 t_1}}{\rho_m(t)}$), while at higher lice abundances the internal dynamics will dominate the growth rate both due to decreased contribution of external dynamics and low or absent Allee effect. A problem with this method is that population growth rate is very high right after a treatment event and may lead to an overestimation of the growth rate. Nevertheless, we estimated the growth rate for each production cycle and each active farm site with a relatively high number of growth rate estimates which makes the estimates altogether robust and illustrates the variability between farm sites.

5. Concluding remarks

In conclusion, our results provide estimates of vital salmon-louse population dynamic parameters based on biweekly monitoring lice counts. External infection was found to vary between farm sites from 0.002 to 0.1 lice salmon^{-1}d^{-1} (Fig. 3). Because of the likely small ratio between wild and farm salmon we believe there is a negligible contribution from wild salmonid stocks on external infection pressure compared to the infection within the Faroese farm network. And we show an overall significant relationship between external infection pressure and total number of gravid lice, which generally increases around 0.001 to 0.004 lice salmon^{-1}d^{-1} for every million gravid lice (Fig. 4). The salmon-louse population growth rate was found to vary between farms ranging from 1.7 - 5.4% d^{-1} (Fig. 6). These growth rates are comparable to other estimates (Krkošek et al. 2010, Patursson et al. 2017).

The estimated parameters can be used to fit a salmon-louse population dynamic model allowing for robust predictions of salmon-louse development on a per farm basis. Further, such estimates can be used to calibrate and validate a bio-economic lice model (Kragesteen et al. 2019) forced by connectivity between farms based on hydrodynamic modelling, which could substantially improve lice management by identifying the most cost effective approach.

6. Acknowledgements

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Table 1: Development and mortality for attached mobile lice stages (Stien et al. 2005). Development or stage length was calculated using: $\tau(T) = [\beta_1/(T - 10 + \beta_1\beta_2)]^2$.

Stage	β_1	β_2	μ (d^{-1})	$\tau[11°C]$ (d)
(ρ_1)	74.70 (±33.64)	0.246 (±0.007)	0.002-0.01	14.9 (t_1)
(ρ_2)	67.47 (±20.36)	0.177 (±0.006)	0.025-0.18	27.2 (t_2)
(ρ_3&ρ_4)	41.98 (±2.85)	0.338 (±0.012)	0.025-0.06	7.6 (t_3)

Table 2: Number of salmons and treatments per year, and average number of gravid and mobile lice per year in the Faroe Islands for years 2011-2018.

	2011	2012	2013	2014	2015	2016	2017	2018
Salmon·10^7	1.81	1.87	1.98	1.94	2.01	2.16	2.02	1.92
Gravid lice·10^7	0.97	1.23	0.83	1.15	1.78	1.54	1.26	0.68
Mobile lice·10^7	1.92	4.93	3.52	4.10	5.80	4.81	3.57	2.03
Treatments (#)	12	26	66	71	70	94	98	93

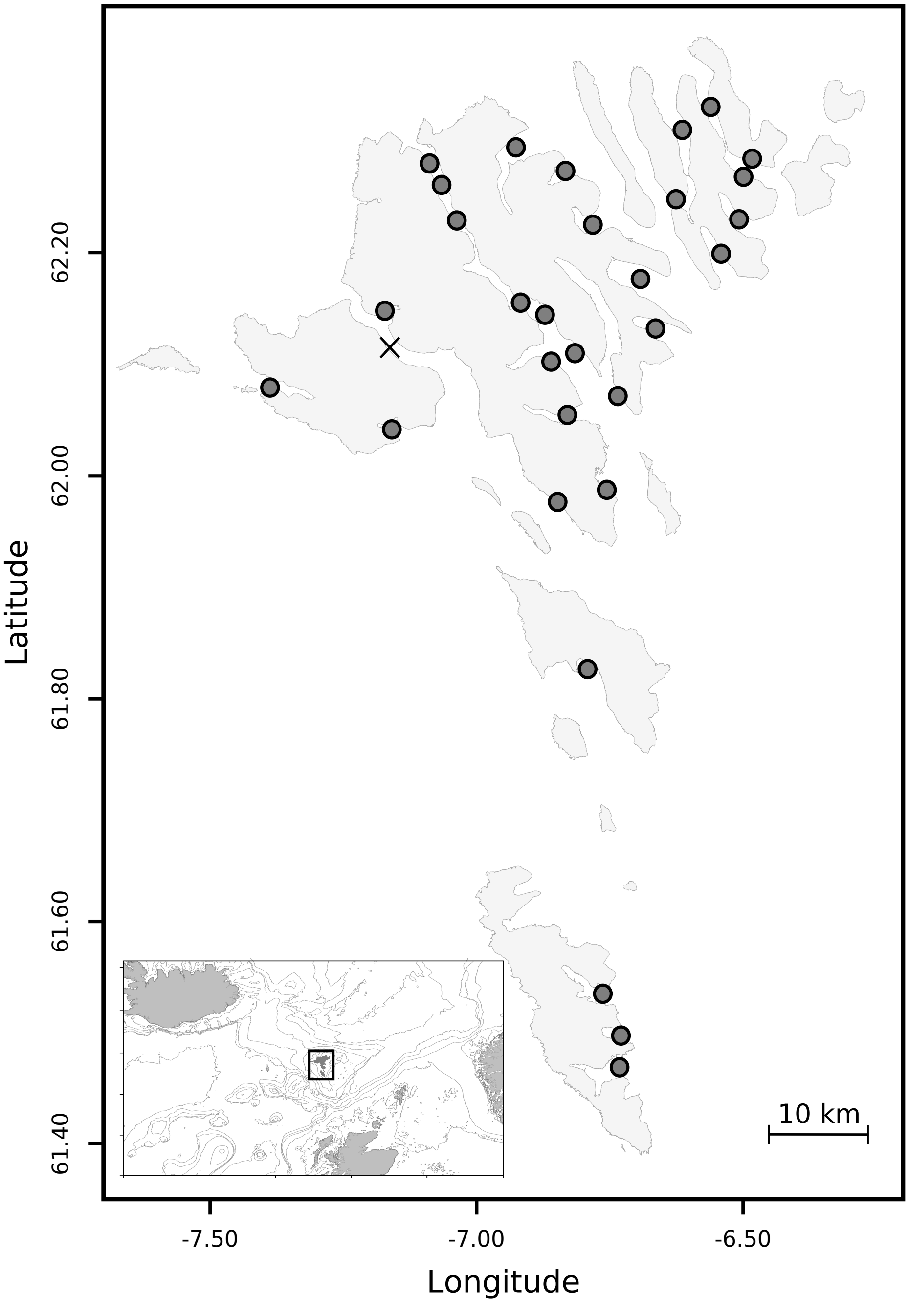

Figure 1: Faroese farm areas (black circles) and location of temperature measurements (black cross).

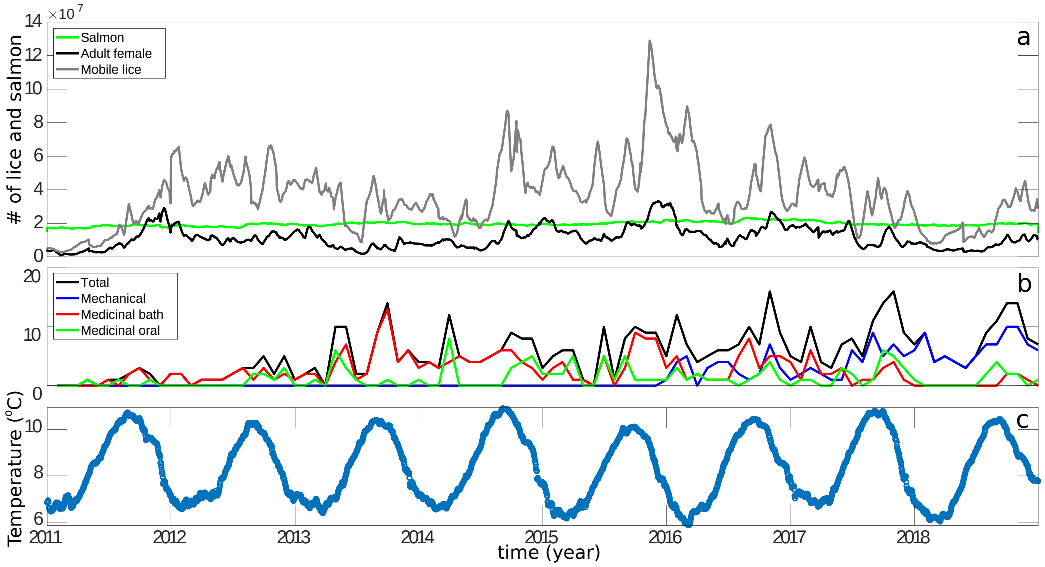

Figure 2: a) Total number of gravid lice (black line), other mobile lice (gray line) and salmon (green line) in Faroe Islands. b) Number of treatments in Faroe Islands per month shown as total (black line), mechanical (blue line), bath treatments (red line) and medicinal oral (green line). c) The Faroese shelf temperature (blue). Data is shown of the period from 2011 to 2018.

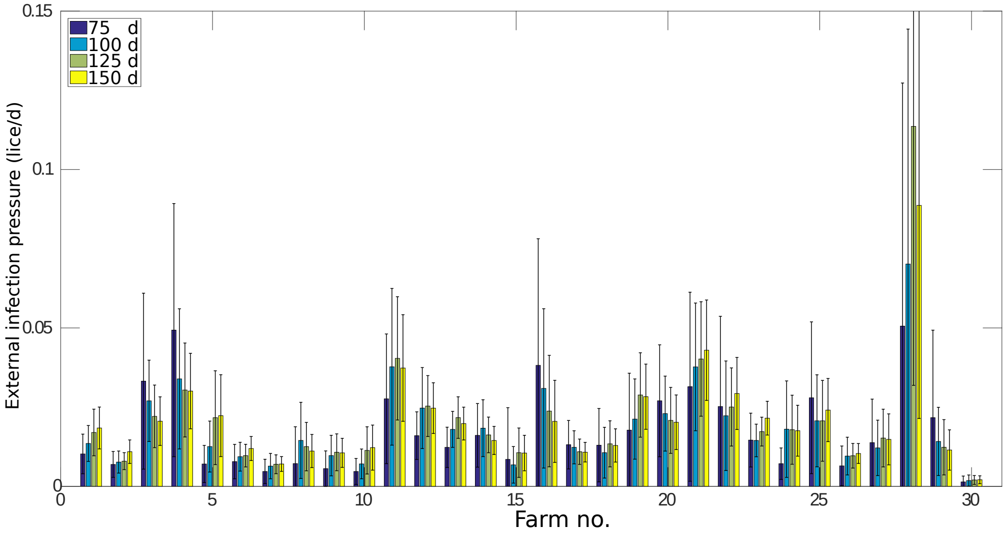

Figure 3: Average external infection pressure including first 75, 100, 125 and 150 days with 95 % CI error-bars for each farm site in the Faroe Islands.

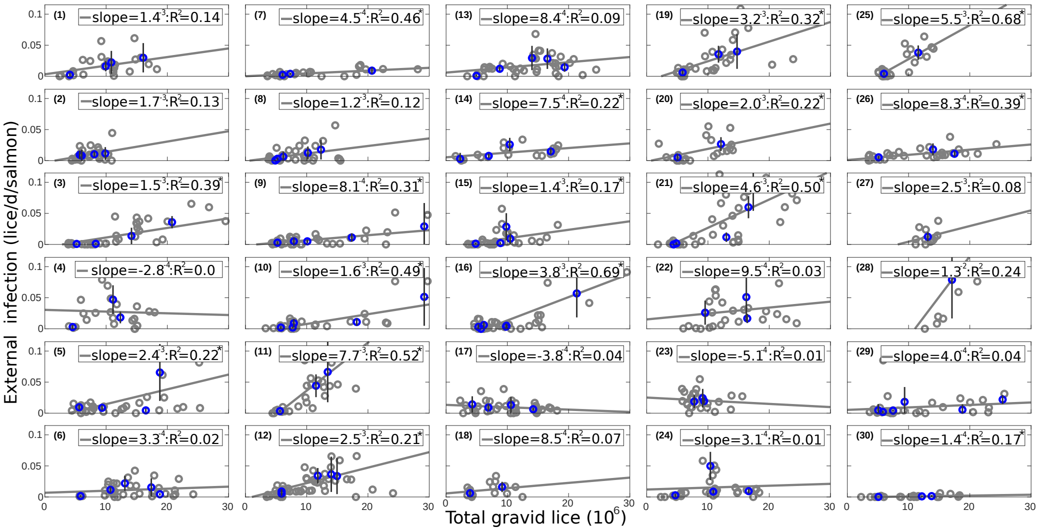

Figure 4: External infection pressure estimates as a function of total number of gravid lice. Each panel is a farm site and the blue circles are averaged external infection pressures of each production cycle. Black error bars show 95 % confidence interval. Line ($y = ax + b$; gray line) is linear regression model fit on all data points (gray circle) with random slope and intercept. Bold number in the legend indicates farm number and * indicates $p < 0.05$. Overall linear regression model fit by farm: $\mathrm{R}^2 = 0.312$ and $\mathrm{F}_{29,844} = 12.7$ with a $p < 0.001$.

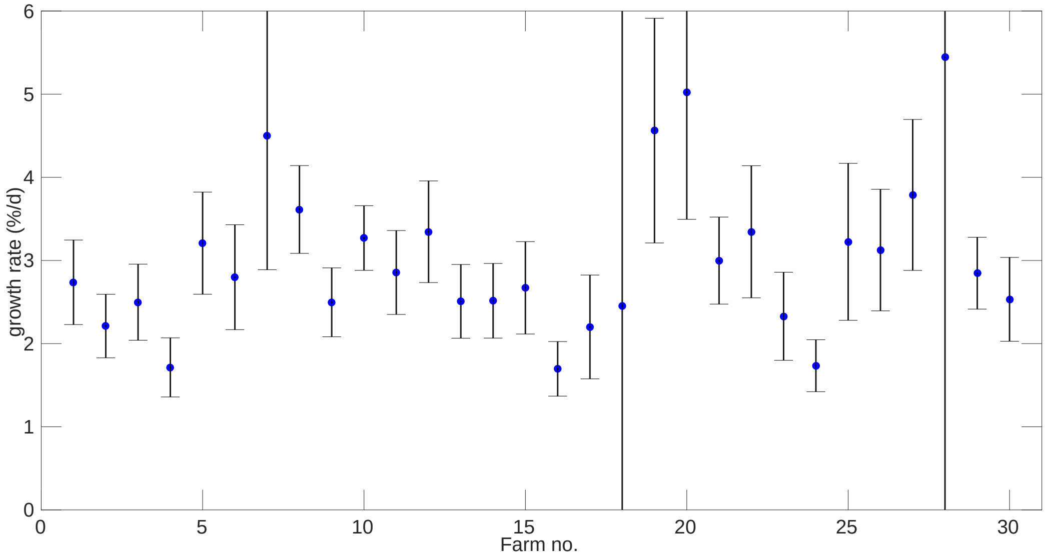

Figure 5: Average growth rate for each farm site in Faroe Island with 95 % confidence interval.

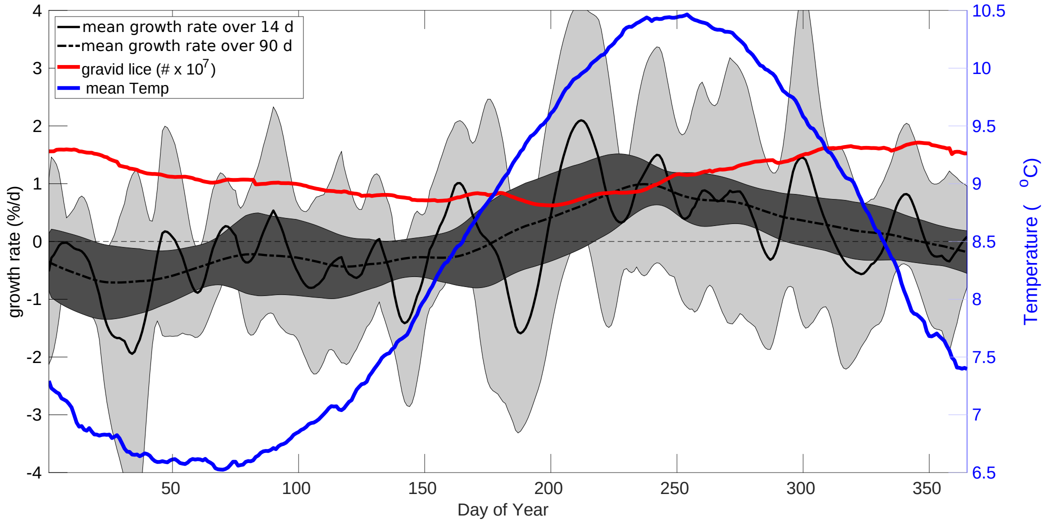

Figure 6: Salmon-louse growth rate in day of the year of total Faroese gravid lice averaged over 14 d (black line) and 90 d (black dotted line) from 2011 to 2018 and total gravid lice $\cdot 10^7$ (red line). Light gray and dark gray color indicate 95% confidence interval for population growth rate averaged over 14 and 90 days, respectively. Average annual temperature (blue line) shown on the right y-axis in day of year from 2011 to 2018.

Appendix

External infection pressure and salmon-louse population growth rate was estimated for each active Faroese farm site and each production cycle since 2009. Calculation is exemplified with Fig. A1. External infection (L_0) pressure was estimated for each lice count performed the first 150 days after sea-stocking (Fig. A1b) using Equation 13. Example: The third lice count at 58 days after sea-stocking has 0.45 gravid lice salmon^{-1} and 1.25 mobile lice salmon^{-1} where the mean sea temperature the previous 30 days was 10.4 °C (Fig. A1a). Using equation $t_1(T) = [\beta_1/(T - 10 + \beta_1\beta_2)]^2$ from (Stien et al. 2005) and Table 1. Then we find that $t_1(10.4°C) = 14.8$d. When calculating L_0 we use equation 13:

$$L_0 = \frac{0.025\mathrm{d}^{-1}(0.45 + 1.25 \text{ lice salmon}^{-1})}{e^{-0.002d^{-1}\cdot 14.8d}\left(1 - e^{-0.025\mathrm{d}^{-1}(58\mathrm{d}-14.8\mathrm{d})}\right)} = 0.066 \text{ lice salmon}^{-1}\mathrm{d}^{-1} \quad (16)$$

Doing this calculation for all lice counts the first 150 days we get a mean $L_0 = 0.06$ lice salmon^{-1} d^{-1}.

Salmon-louse population growth rate (Eq. 15) was estimated by fitting a straight line between 5 consecutive lice counts 150 days after sea-stocking and excluding all lines with a negative slope and/or R^2 less than 0.6 (Fig. A1c). Using the salmon-louse population model (Eq. 2-6) to simulate population growth we find that the growth rate is relatively high for a short period after a treatment, because a treatment only kills attached stages and therefore all larvae produced before a treatment can re-infect the farm site resulting in a higher percentage growth.

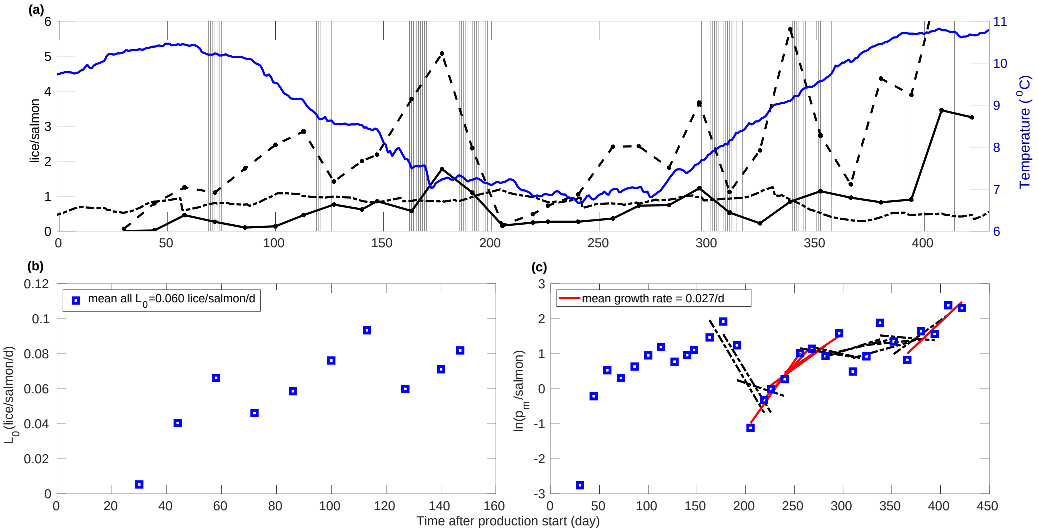

Figure A 1: Example of calculation of external infection pressure and population growth rate. a) Gravid and mobile lice shown as solid and dashed line, respectively. Dashed dotted line is the mean gravid lice salmon^{-1} in farm network. Vertical lines indicate treatment events and blue line is temperature (right y-axis). b) External infection pressure, L_0, (blue square) calculated for lice counts before 150 after sea-stocking. c) natural log of ρ_m where lines are fitted with 5 consecutive lice counts after 150 days after sea stocking. Red lines indicate positive slopes and/or R^2 > 0.6 and the legend is the average slope of all red lines.