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Estimation of external infection pressure and salmon-lice 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-lice 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-lice 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-lice 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-lice 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 known as salmon louse. The salmon louse is a naturally occurring parasite on salmonid fish and feeds on the mucus, skin and blood of its 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-lice 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-lice 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 determined by lice arriving from other salmon farms and wild salmonid stocks. The internal infection pressure is determined by the production of lice on the farm. If internal infection is high enough it will eventually lead to an 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

36 recorded. External infection pressure reported in these studies was found to
37 vary significantly depending on the level of gravid lice in the area. Bjørn
38 et al. (2011) found the external infection to be up to 2.3 lice salmon⁻¹ in the
39 Romsdalsfjord system, Norway, with a 14 days deployment time. Sandvik
40 et al. (2016) found up to 20 lice salmon⁻¹ in Hardangerfjord, Norway, with 14-
41 21 days deployment time and Pert et al. (2014) found close to 15 lice salmon⁻¹
42 in Loch Shiel, Scotland with 7 days deployment time. In Arnarfjörður,
43 Iceland, which only contained 2 salmon farms Karbowski et al. (2019) found
44 only 0.022 lice salmon⁻¹ when sampling for \approx 21 days.

45 Salmon-lice population growth rates have been reported for salmon
46 farms in the Broughton Archipelago, Canada and the Faroe Islands (Krkošek
47 et al. 2010, Patursson et al. 2017). These estimates assume exponential
48 growth and Krkošek et al. (2010) reported two farms having 0.9 and 4.8 %/d
49 while Patursson et al. (2017) reported growth rates to range from 0.9 to 4.1
50 % d⁻¹ for several Faroese farms.

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

58 **2. Methods**

59 *2.1. Lice data and salmon number*

60 Lice data is based on a the Faroese lice count program which started in
61 2009 where the Faroese government mandated farmers to count lice every
62 14 days from 1 May to 31 December and once a month from 1 January to
63 30 April. However, lice counts were not performed on all farms until after
64 2012. From 2009 to 2016 a minimum of 10 fish were counted from 4 cages.
65 The farmer choose 2 cages where one being the first stocked cage and the
66 second cage was, based on prior experience, estimated to have the highest sea
67 lice load. The two other cages were chosen at random between cages which
68 had not been counted previously. After 2016 a minimum of 10 fish were
69 counted for all cages at each farm site every 14 days all year (Anon 2016). In
70 year 2011 counting was not performed at 3 farms and at 3 farms lice counts
71 started 3-6 months into the year 2011. In addition aily salmon numbers for

72 each farm site was provided by the Faroese aquaculture companies for the
73 period between 2011 and 2018.

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

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

91 2.2. Treatments

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

100 2.3. Sea Water Temperature

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

106 *2.4. Calculating total lice*

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

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

111 where n is number of farms in the system.

112 *2.5. The Salmon-louse Model*

113 To estimate the external infection pressure and salmon-louse population
 114 growth rate, we used a series of delay differential equations (Revie et al.
 115 2005):

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

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

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

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

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

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

120 where q is the amount of viable larvae per day per sexually mature lice which
 121 includes connectivity and larvae production rate and η is the proportion of
 122 female lice. L_0 is the external infection pressure and t_e is the time it takes
 123 larvae to reinfect a host and is assumed to be 5 days (Stien et al. 2005).
 124 $s(\rho_4(t))$ is mate limitation or an Allee effect which states that fertilisation
 125 success is close to zero at near zero lice abundances and close to 100 % at

126 around 2 gravid lice salmon⁻¹ (Krkošek et al. 2012, Stormoen et al. 2013,
127 Kragestein et al. 2019). The initial conditions are given by:

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

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

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

130 2.6. External infection

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

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

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

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

138 We argue that in the first 150 days of the production cycle there is virtually
139 no internal dynamics, meaning we assume no internal viable larvae and/or no
140 females are fertilized and set $q \cdot s$ in Eq. 6 to zero. There are two reasons for
141 assuming this: First, at 11 °C (maximum Faroese shelf water temperature)
142 the first attached lice start releasing larvae after ≈ 50 d ($= t_1 + t_2 + t_3$)
143 and it takes another ≈ 20 days ($= t_e + t_1$) until these lice appear in the
144 lice counts (Table 1, Stien et al. (2005)). Second, due to the Allee effect,
145 where few female lice get fertilized at low lice abundances (Krkošek et al.
146 2012, Stormoen et al. 2013), s is close to zero. Further, gravid lice have been
147 shown to produce fewer eggs in their first pair of egg strings (Heuch et al.
148 2000). With the approximation that $q \cdot s$ is zero, Eq. 10 can be written as:

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

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

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

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

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

151 The stage duration and mortality are based on the estimates by Stien et al.
152 (2005) (Table 1), where μ_m is the average of the minimum mortalities.

153 2.7. Salmon-lice population growth rate

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

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

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

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

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

166 3. Results

167 3.1. Total lice

168 The total number of gravid and mobile lice in the Faroese aquaculture
169 has fluctuated a lot since 2011. The highest number of gravid and mobile

170 lice was in December 2015 with over 35 million and 129 million, respectively
171 (Fig. 2). The lowest number of gravid lice was under 5 million and recorded
172 in June 2013 and the lowest for mobile lice was under 5 million in March
173 2011. The total number of gravid lice has generally been below 20 million
174 except in the winter of 2011, 2014, 2015 and 2016. Lice numbers in year 2011
175 may be underestimated as 6 farms were not counted regularly or not at all.

176 Number of salmon in Faroese waters has been relatively stable and close
177 to 20 million since 2011, while production has increased significantly from
178 $50 \cdot 10^3$ tonnes in 2011 to $71 \cdot 10^3$ tonnes in 2014 (www.hagstovan.fo), indicating
179 a general increase in harvest or stocking fish size. The maximum recorded
180 number of salmon was 23.4 million in November of 2017 and the minimum
181 was 16.8 million in February 2011 (Fig. 2a).

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

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

193 Overall the total amount of gravid and mobile lice steadily increased
194 from 2011 to 2015 where after it has steadily decreased. This is consistent
195 with changes in regulation in 2016 where treatment threshold was decreased
196 from 2 gravid lice salmon⁻¹ to 1.5 (Faroese Ministry of Foreign Affairs and
197 Trade 2016). We also see a shift from chemical to mechanical treatments and
198 increased treatment frequency in this period. Total lice numbers are gener-
199 ally lowest between May and August and highest in December and January.
200 Number of salmon (Table 2) and average temperature in the period 2011 to
201 2018 have stayed relatively constant (Fig. 2) and therefore the total number
202 of lice between years is likely tied to treatment frequency and efficiency.

203 3.2. External Infection Pressure

204 Based on all lice counts in the first 150 days in all production cycles at each
205 farm from 2010-2018 the external infection pressure is estimated on average
206 to range from 0.002 to 0.1 lice salmon⁻¹ d⁻¹. This corresponds to 1 lice per

207 salmon for every 500 to 10 days (Fig. 3). A total of 30 farms were investigated
208 (Fig. 1). Farm 28 is an outlier and has the highest average external infection
209 pressure, however this estimate is only based on one production cycle in
210 2015. Farm 30 has clearly the lowest average external infection pressure with
211 0.002 lice salmon⁻¹ d⁻¹. In addition to the period of no internal dynamics of
212 150 days (discussed in section 2.6), the external infection is estimated using
213 periods of 75, 100, and 125 days. For many farms the external infection
214 pressure increases with number of days included while for other farms it
215 decreases and for a few farms external infection pressure stays constant, but
216 generally the effect is not significant (Fig. 3).

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

232 3.3. Population growth rate

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

244 by treatment events as growth rate is typically high for a period right after
245 a treatment.

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

258 4. Discussion

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

267 The total number of gravid and mobile lice in Faroe Islands is significantly
268 higher compared to a similar salmon aquaculture area (15-18 million salmon)
269 off the coast of mid-Norway (Jevne & Reitan 2019). This coastal area has
270 18 farm sites located between a group of islands and has a similar water
271 temperature range to the Faroe Islands. One difference is that this Nor-
272 wegian aquaculture region has synchronized production cycles and the level
273 of salmon lice is therefore effectively reset between each cycle. Comparing
274 the number of treatments between these two areas is not straightforward as
275 treatments are reported differently (number of cages treated in Norway and
276 number of treatment events in the Faroe Islands). However, if we assume that
277 a treatment event on average represents 5 treated cages then about 450 cages
278 are treated per year ($90 \cdot 5$) in Faroe Islands in the period from year 2016 to
279 2018 (Table 2). Jevne & Reitan (2019) reported 262, 550 and 102 cages being

280 treated in the 1, 2 and 3 production cycle, respectively, where a production
281 cycle is almost 2 years long. Production cycle 2 had the highest levels of lice
282 and also the highest number of cages treated but this is still a factor lower 2
283 compared to the Faroe Islands. A reason for the higher treatment frequency
284 in the Faroe Islands may be the overlapping production in contrast to syn-
285 chronized production in the Norwegian area. This would contradict claims
286 that coordinated fallowing is ineffective (Guarracino et al. 2018). Another
287 reason could be the relatively low treatment threshold of 0.2 to 0.5 gravid lice salmon⁻¹
288 in Norway (Anon 2012) in contrast to 1.5 to 2 gravid lice salmon⁻¹
289 in the Faroe Islands which may seem counter-intuitive. However, farms in
290 Norway are forced to treat early to keep lice levels relatively low and thereby
291 earn the benefit of the Allee effect resulting in a overall lower larvae pro-
292 duction rate and consequently a lower lice population growth rate (Krkošek
293 et al. 2012, Stormoen et al. 2013, Kragesteen et al. 2019). Third, there is a
294 mean current flow through the Norwegian area and therefore lice may be less
295 retained in contrast to Faroe Islands where shelf water is relatively retained
296 (Kragesteen et al. 2018). Last, we currently have insufficient data for cleaner
297 fish, which may be more widely used in the Norwegian island group resulting
298 in fewer treatments.

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

304 We also speculate that chlorophyll could be a good indicator of lice pop-
305 ulation growth rate and lice levels. Because high levels of chlorophyll will
306 subsequently lead to high levels of zooplankton which may lead to a higher
307 mortality of planktonic lice larvae. However, we found no clear correla-
308 tion, maybe due chlorophyll and zooplankton being out of phase or that
309 the chlorophyll samples are from a single location not representative of the
310 general chlorophyll concentration in the Faroe Islands.

311 If the sentinel cage external infection estimates are converted to lice
312 salmon⁻¹ d⁻¹ using Eq. 2, we find up to 0.17 (Bjørn et al. 2011), 1.16 (Sandvik
313 et al. 2016), 2.16 (Pert et al. 2014) and 0.001 lice salmon⁻¹ d⁻¹ (Karbowski
314 et al. 2019), when minimum mortality of the chalimus stage is assumed (Ta-
315 ble 1). The external infection pressure estimates in this study are therefore
316 considerably lower compared to the sentinel cage estimates in Norway and
317 Scotland (Bjørn et al. 2011, Pert et al. 2014, Sandvik et al. 2016) and while

318 slightly higher than estimates from Iceland in a fjord containing only two
319 salmon farms (Karbowski et al. 2019). One reason for the observed differ-
320 ence could be the dilution effect reported by Samsing et al. (2014), because
321 there are relatively few salmon in the sentinel cages there are potentially a
322 lot more lice per salmon compared to a fully operational high salmon density
323 farm cage. External infection pressure estimates from sentinel cages may as a
324 result be much higher compared to our estimates. This dilution effect should
325 be investigated further.

326 External infection pressure was estimated based on the first 150 days of
327 a production cycle as we assume effects of salmon-lice internal dynamics to
328 be low or non-existing in this period. This assumption can be debated in par-
329 ticular when water temperature is high (i.e. >11 °C). If internal dynamics are
330 significant in this period there will be an overestimation of the external in-
331 fection pressure. However, the difference between including the first 75, 100,
332 125 and 150 days does not significantly affect the average estimated external
333 infection pressure (Fig. 3). An explanation for increasing external infection
334 pressure could be that the self-infection or internal dynamics starts before
335 the 150 days which would cause the estimated external infection pressure to
336 increase with time. Another explanation could be the increased surface area
337 of salmon e.g. if a salmon weighs 200 g when put out to sea, they will increase
338 their weight to about 900 g the first 150 days (Austreng et al. 1987). This
339 increase in weight will increase the salmon surface area from approximately
340 335 cm^2 to 810 cm^2 (O’Shea et al. 2006). Consequently infectious lice larvae
341 will have 2.4 time more area to attach on 150 day after sea stocking. There-
342 fore, external infection pressure should be standardized with salmon size,
343 however, these data were not available. An issue with the external infection
344 pressure estimates is that treatments do occur in the first 150 days period
345 and in many farms especially after 2015 had cleaner fish present in their
346 sea cages. This would lead to an underestimation of the external infection
347 parameter L_0 and could cause the external infection pressure to decrease in
348 the 150 day period. In summary the external infection pressure estimates
349 are quite uncertain. Nevertheless, these estimates have a high applied value
350 as they are based on *in situ* lice counts from commercial farms reflecting the
351 actual infection pressure at a operational salmon farm.

352 Here we do not distinguish between external infection pressure caused
353 by larvae production from neighboring farms and the natural background
354 infection from wild salmonid stocks. There is a small wild salmon stock
355 which was introduced and has been maintained since 1940’s in four Faroese

356 rivers (www.laks.fo). The population size and level of infection of other
357 salmon-lice hosts like sea trout and Arctic charr are unknown. In Norway
358 the wild salmon stock is estimated to about 550.000 fish (Anon 2019), and
359 the Faroese wild stock is likely only a small fraction of this and consequently
360 the ratio between the wild stock and the 20 million salmon in the cages is
361 likely small, and therefore it seems reasonable to assume that the infection
362 load from the wild salmonids is low. As a result external infection should
363 predominately be determined by the total number of gravid lice in Faroese
364 salmon farms. Our study shows a significant but low R^2 although varying
365 highly between farms (Fig. 4). The reason for the relatively low correlation
366 could be the stochastic nature of the lice counts procedure, where only 10
367 fish per cage are counted. In addition, treatments and cleaner fish will also
368 negatively influence the correlation. Further, some farms may be strongly
369 connected to only a few farms and therefore the total amount of Faroese
370 gravid lice may not be representative of the external pressure at these farms
371 (Kragesteen et al. 2018).

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

389 5. Concluding remarks

390 In conclusion, our results provide estimates of vital salmon-lice popu-
391 lation dynamic parameters based on biweekly monitoring lice counts. Ex-

392 ternal infection was found to vary between farm sites from 0.002 to 0.1 lice
393 salmon⁻¹d⁻¹ (Fig. 3). Because of the likely small ratio between wild and farm
394 salmon we believe there is a negligible contribution from wild salmonid stocks
395 on external infection pressure compared to the infection within the Faroese
396 farm network. And we show an overall significant relationship between ex-
397 ternal infection pressure and total number of gravid lice, which generally
398 increases around 0.001 to 0.004 lice salmon⁻¹d⁻¹ for every million gravid lice
399 (Fig. 4). The salmon-lice population growth rate was found to vary be-
400 tween farms ranging from 1.7 - 5.4% d⁻¹ (Fig. 6). These growth rates are
401 comparable to other estimates (Krkošek et al. 2010, Patursson et al. 2017).

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

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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)	$\tau[11^\circ\text{C}]$ (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 salmon 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

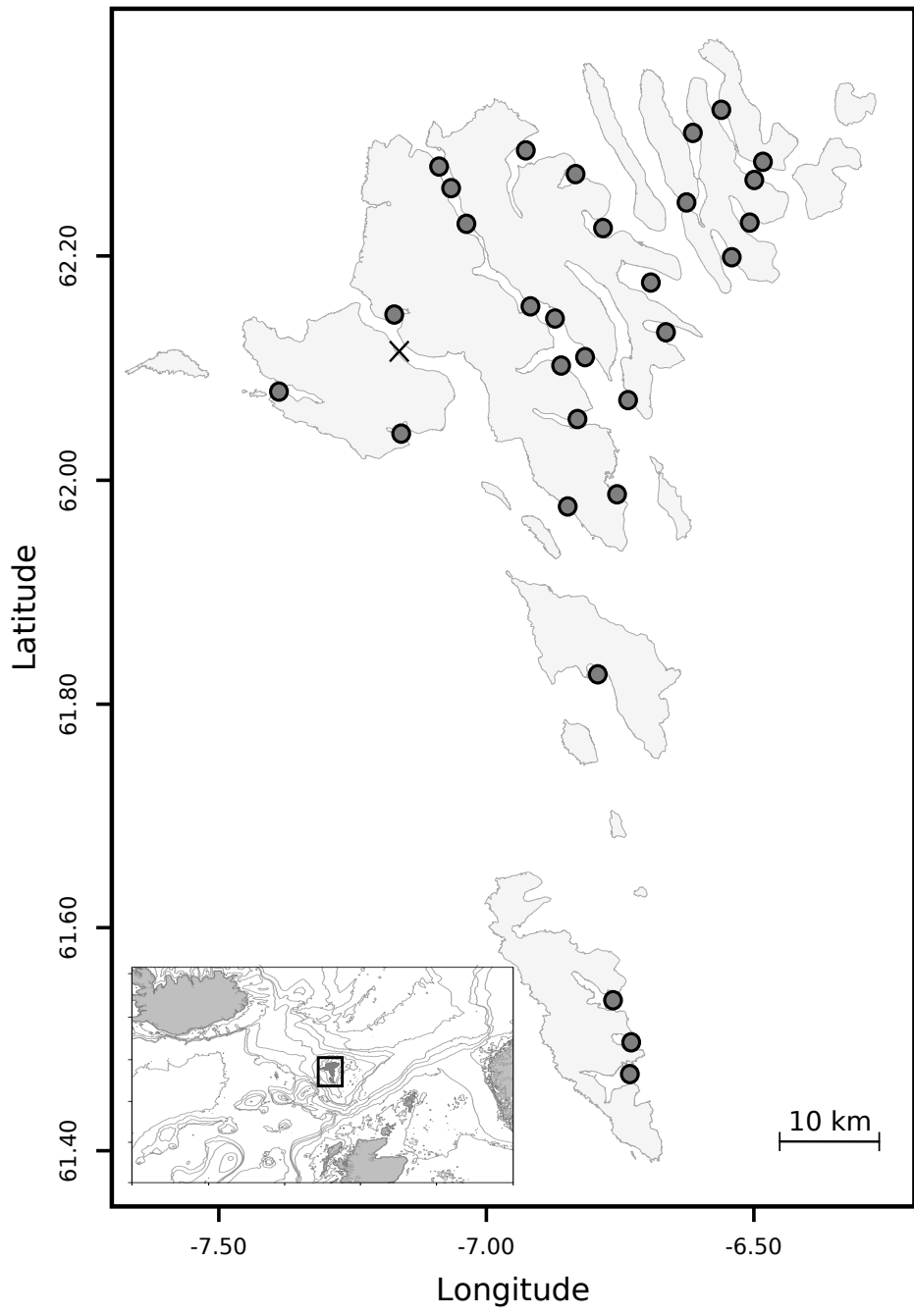


Figure 1: Faroese farm areas (black circles) and location of temperature measurements (black cross).

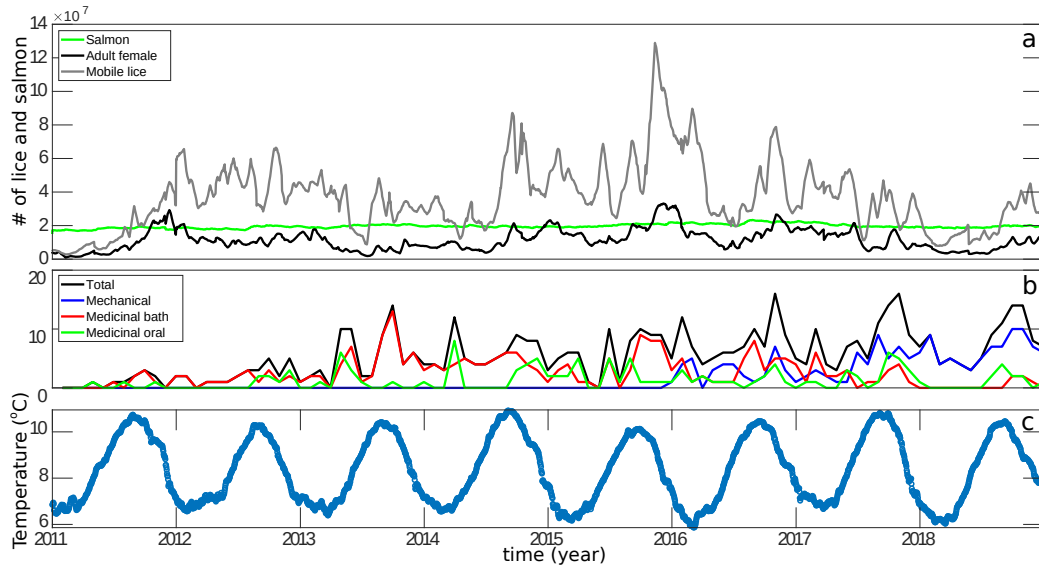


Figure 2: a) Total number of gravid lice (black line), other mobile lice (gray line) and salmon (green line) in Faroe Islands. b) Number of treatments in Faroe Islands per month shown as total (black line), mechanical (blue line), bath treatments (red line) and medicinal oral (green line). c) The Faroese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

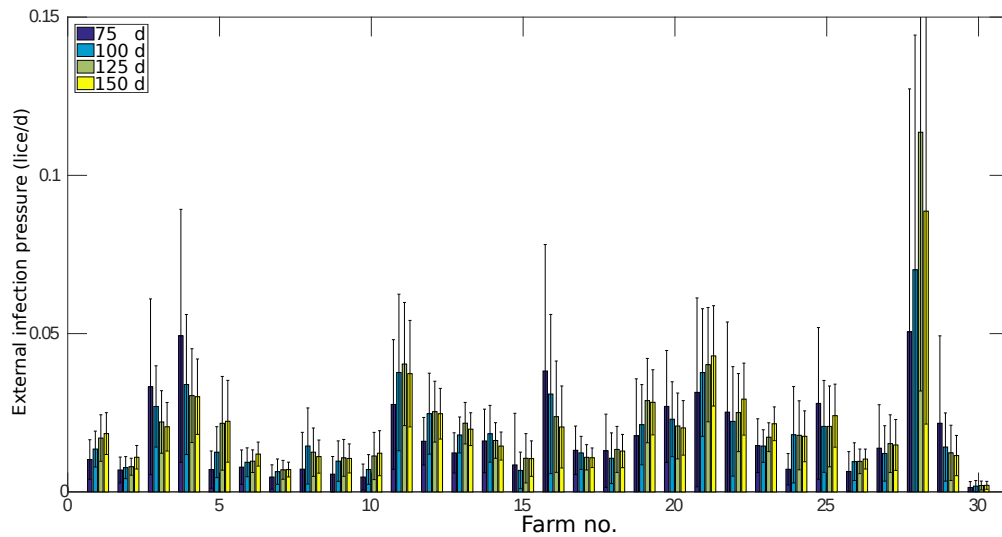


Figure 3: Average external infection pressure including first 75, 100, 125 and 150 days with 95 % CI error-bars for each farm site in the Faroe Islands.

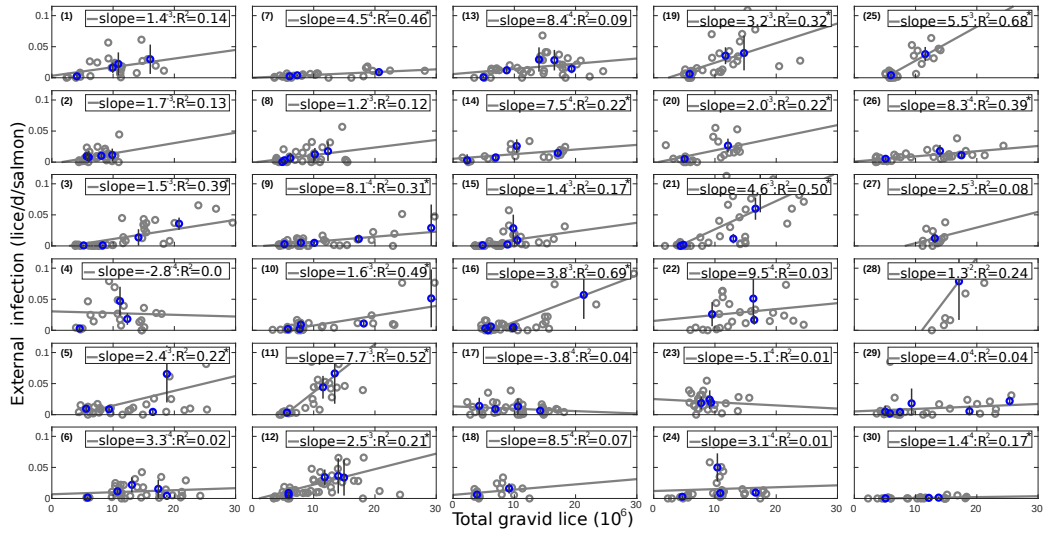


Figure 4: External infection pressure estimates as a function of total number of gravid lice. Each panel is a farm site and the blue circles are averaged external infection pressures of each production cycle. Black error bars show 95 % confidence interval. Line ($y = ax + b$; gray line) is linear regression 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: $R^2 = 0.312$ and $F_{29,844} = 12.7$ with a $p < 0.001$.

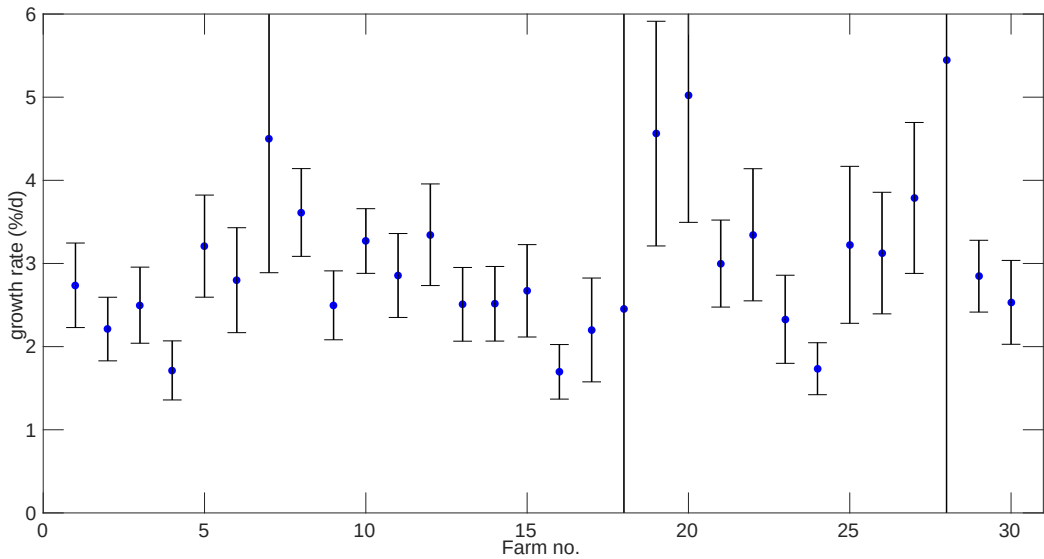


Figure 5: Average growth rate for each farm site in Faroe Island with 95 % confidence interval.

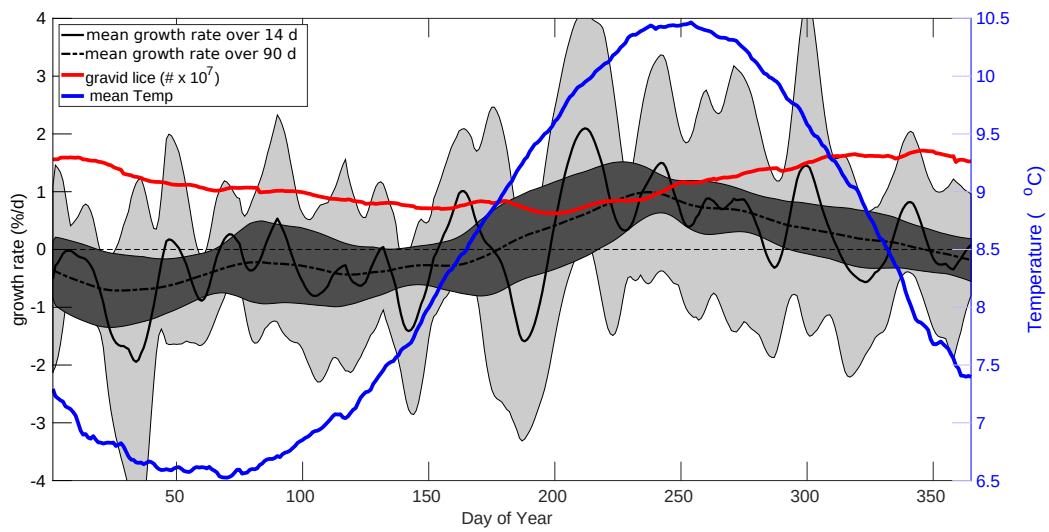


Figure 6: Salmon-lice growth rate in day of the year of total Faroese gravid lice averaged over 14 d (black line) and 90 d (black dotted line) from 2011 to 2018 and total gravid lice $\cdot 10^7$ (red line). Light gray and dark gray color indicate 95% confidence interval for population growth rate averaged 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.

523 **Appendix**

524 External infection pressure and salmon-lice population growth rate was
 525 estimated for each active Faroese farm site and each production cycle since
 526 2009. Calculation is exemplified with Fig. A1. External infection (L_0) pres-
 527 sure was estimated for each lice count performed the first 150 days after
 528 sea-stocking (Fig. A1b) using Equation 13. Example: The third lice count at
 529 58 days after sea-stocking has 0.45 gravid lice salmon⁻¹ and 1.25 mobile lice
 530 salmon⁻¹ where the mean sea temperature the previous 30 days was 10.4 °C
 531 (Fig. A1a). Using equation $t_1(T) = [\beta_1/(T - 10 + \beta_1\beta_2)]^2$ from (Stien et al.
 532 2005) and Table 1. Then we find that $t_1(10.4^\circ C) = 14.8d$. When calculating
 533 L_0 we use equation 13:

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

534 Doing this calculation for all lice counts the first 150 days we get a mean
 535 $L_0 = 0.06 \text{ lice salmon}^{-1} d^{-1}$.

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

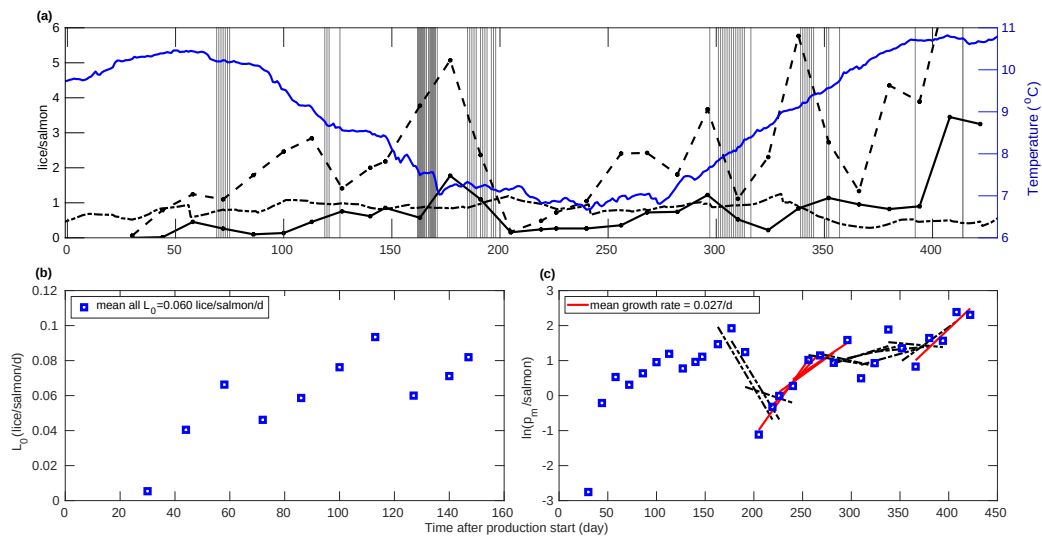


Figure A 1: Example of calculation of external infection pressure and population growth rate. a) Gravid and mobile lice shown as solid and dashed line, respectively. Dashed dotted line is the mean gravid lice salmon $^{-1}$ in farm network. Vertical lines indicate treatment events and blue line is temperature (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.