

## Identifying salmon lice transmission characteristics between Faroese salmon farms

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1     **Identifying Salmon Lice Transmission Characteristics**  
2                     **between Faroese Salmon Farms**

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9                     **Abstract**

10            Sea lice infestations are an increasing challenge in the ever-growing salmon aquaculture sector  
11            and cause large economic losses. The high salmon production in a small area creates a perfect  
12            habitat for parasites. Knowledge of how salmon lice planktonic larvae disperse and spread the  
13            infection between farms is of vital importance in developing treatment management plans to  
14            combat salmon lice infestations. Using a particle tracking model forced by tidal currents, we  
15            show that Faroese aquaculture farms form a complex network. In some cases as high as 10%  
16            of infectious salmon lice released at one farm site enter a neighboring fjord containing another  
17            farm site. Farms were characterize as emitters, receivers or isolated, and we could identify  
18            two clusters of farms that were largely isolated from each other. The farm characteristics are  
19            a valuable input for the development of management plans for the entire Faroese salmon industry.

20  
21            Running page head: Salmon Lice Transmission Characteristics between Faroese Salmon Farms

22            KEY WORDS: Connectivity, Dispersal, Tidal Forcing, Particle Tracking, Salmon lice.

## 23 INTRODUCTION

24 In salmonid aquaculture, the infestation of parasitic organisms is a major challenge and causing  
25 significantly economic losses in the aquaculture industry. The treatment cost are estimated to be  
26 around € 0.25/kg (Costello 2009) and applied on the global salmon production in 2015 of 2.3 million  
27 tonnes (FAO 2017) the sea lice management cost translates to roughly € 575 million. The estimated  
28 treatment cost per kg, although widely used may be outdated (Shinn et al. 2015). In addition, the  
29 parasites impacts the global aquaculture industry with negative publicity (Adams et al. 2015) due  
30 to the possible damage the parasite has on the environment as a result of chemical treatments and  
31 it's influence on local wild life (Ford & Myers 2008). Consequently, salmon lice are a major obstacle  
32 in any further expansion of the salmon aquaculture industry.

33 As in other temperate coastal areas, the production of Atlantic salmon in the Faroe Islands has  
34 expanded to become a major activity. With an annual production now exceeding 80,000 ton the  
35 Faroe Islands is currently the fifth largest salmon producing country, and the aquaculture industry  
36 has become a major economic player locally as it accounts for 46% of the Faroese export value in  
37 2016 (SFI 2017). In 2014 the cost of drugs to combat sea lice used by the Faroese salmon farming  
38 industry exceeded € 18 million, or roughly € 0.22/kg. Introduction of cleaner fish and mechanical  
39 treatments has however reduced the expenses of chemoterapeutants to less than € 13 million in 2016  
40 (SFI 2017).

41 Sea lice is a common name for a range of marine ectoparasitic copepods belonging to the family  
42 Caligidae. Two sea lice species cause by far the greatest challenge in salmonid aquaculture in the  
43 northern hemisphere: *Lepeophtheirus salmonis* and *Caligus elongatus*. *L. salmonis* is a parasite only  
44 found on salmonids, often referred to as salmon lice, while *C. elongatus* is a more opportunistic  
45 parasite, and has been found on 80 different fish species (Kabata 1979). Of the two species *L.*  
46 *salmonis* has by far the largest economic impact on the salmonid aquaculture industry due to its  
47 damaging effect on its host (Boxaspen 2006).

48 The increased salmon production has elevated the density of the naturally occurring salmon lice  
49 in the water column primarily due to the large growth in the number of hosts. The high density  
50 further increases the chances of transmitting salmon lice between hydrodynamically connected farms.  
51 Additionally, experience shows that sporadic uncontrolled treatment of salmon lice in an area yields  
52 a resistant salmon lice population over time (Murray 2011, Aaen et al. 2015). Farms with intense

53 treatment might quickly develop resistant salmon lice strains. In inter-connected farm networks the  
54 resistant strains spread out to the whole network after a given period. Therefore, in connected farm  
55 networks, there may be a point when the external infection pressure reaches a stage when, from  
56 a farmers perspective, treatment becomes virtually pointless. Coordinated treatment management  
57 plans are thus essential to achieve long term sustainable control of salmon lice. Achieving control  
58 requires a thorough understanding of the sea lice dispersion patterns, a factor highly dependent on  
59 regional and local hydrography (Adams et al. 2015).

60 Dispersion of salmon lice larvae has been studied using numerical models in Scotland (Amundrud  
61 & Murray 2009, Adams et al. 2012, Salama et al. 2013, Adams et al. 2015), Canada (Stucchi et al.  
62 2011) and Norway (Asplin et al. 2014, Johnsen et al. 2014, 2016, Samsing et al. 2017). For a more  
63 comprehensive overview, see Salama & Rabe (2013). In some fjord systems farms were found to  
64 be inter-connected (Adams et al. 2012, Johnsen et al. 2016), while in other cases several clusters of  
65 connected farms could be identified (Salama et al. 2013, 2017). Samsing et al., (2017) investigated the  
66 connectivity between most farms on the Norwegian coast and found seasonal variations to influence  
67 the connectivity. These cases needs different management strategies, emphasizing the importance of  
68 knowing the specific farm network. This study presents a first attempt to investigate the dispersion  
69 of salmon lice and connectivity between aquaculture farms in the Faroe Islands. While earlier studies  
70 have either been on farms located in a restricted area mainly enclosed by land (Adams et al. 2012,  
71 Salama et al. 2013, 2017) or along a long coast with complicated fjord systems (Stucchi et al. 2011,  
72 Asplin et al. 2014, Johnsen et al. 2014, 2016, Samsing et al. 2017), this study is of a spatially  
73 limited archipelago with a relatively high farm density in a tidal energetic area surrounded by open  
74 ocean. The limited number of farms in a nearly isolated system makes Faroe Islands an ideal area  
75 to investigate the interaction and population dynamics of salmon lice.

## 76 METHODS

### 77 Study Area

78 The Faroe Islands is an archipelago in the Atlantic ocean containing complicated coastlines, multiple  
79 fjords and connecting straits (Fig. 1). The distance from the northernmost to the southernmost  
80 point is about 110 km. Due to its location in the path of the North Atlantic Current the sea around  
81 Faroe Island is dominated by relatively warm and saline waters with fairly stable conditions. The  
82 temperature varies from 6°C in February to approximately 10°C in August and September and the  
83 variation in salinity is confined to 35.05–35.25 ‰ on the shelf (Larsen et al. 2008, Gaard et al. 2011),  
84 but is seen reduced towards 32‰ in the fjords due to freshwater runoff (Gaard et al. 2011).

85 The waters on the Faroe Shelf can be characterized as a tidal energetic system, although the tidal  
86 elevation amplitude is quite modest. The amplitude of the dominating  $M_2$ -constituent varies from  
87 some 60 cm in the westernmost islands to less than 10 cm at the central eastern coast (Simonsen  
88 & Niclasen 2011), which may be characterized as a semi-amphidromic point. This relatively large  
89 gradient towards the central east coast creates strong currents with maximum speeds up to 3.6 m/s  
90 (Fig. 1) in some straits (Larsen et al. 2008, Simonsen & Niclasen 2011). Further, Larsen et al.,  
91 (2008) shows that the tides through rectification are the main driver of a steady current clockwise  
92 around the islands (Fig. 2).

93 In some of the fjords, and in the strait between the two biggest islands (white arrowhead, Fig. 1),  
94 the tides has less influence on the circulation (Fig. 1) and stratification may occur mainly due to  
95 the freshwater runoff (Gaard et al. 2011). In these areas, estuarine and wind driven circulation is of  
96 significant importance.

97 Outside the fjords, however, the water masses are quite homogeneous due to the intense mixing  
98 caused mainly by tidal currents (Larsen et al. 2008). We therefore focus on the tidal component  
99 in the model due to the dominating influence it has on water movement around the Faroe Islands.  
100 Including only the tidal component simplifies the model, but still reveals the general background  
101 dispersion pattern.

102 **Model Overview**

103 The underlying tidal circulation model is an implementation of the barotropic mode of the Regional  
 104 Ocean Model System (ROMS) (Shchepetkin & McWilliams 2005) on a half nautical mile grid res-  
 105 olution covering a larger area, and on a 100 m resolution grid for the coastal region (Simonsen &  
 106 Niclasen 2011). The higher resolution model was forced by the solution from a coarser model, which  
 107 applied altimetry generated data by Egbert et al., (1994) along its open sea boundaries. After a  
 108 spin-up period, data were stored at one hour intervals in every grid point in 30 days for tidal anal-  
 109 ysis using the Ttide software (Pawlowicz et al. 2002). Validation of the derived harmonic constants  
 110 towards similar data derived from observed timeseries from tidal gauges and current measurement  
 111 showed a general good agreement (Simonsen & Niclasen 2011). Here the current is estimated from  
 112 the dominating constituents and the residual current obtained from the 100 m resolution tidal model.

113 **Tidal Current**

114 We included three semi diurnal constituents:  $M_2$ ,  $S_2$  and  $N_2$ , two diurnal constituents:  $K_1$  and  $O_1$ ,  
 115 one over-tide constituent  $M_4$ , and the residual current. The east ( $u$ ) and north ( $v$ ) component of  
 116 the forcing current at a given time ( $t$ ) is obtained by summing up the contribution from the six ( $n$ )  
 117 tidal constituents and residual current ( $u_r, v_r$ ) at each horizontal position ( $x, y$ ):

$$u(t, x, y) = u_r(x, y) + \sum_i^n a_i(x, y) \cos(\omega_i t - \varphi(x, y)) \cos(\theta(x, y)) - b_i(x, y) \sin(\omega_i t - \varphi(x, y)) \sin(\theta(x, y)) \quad (1)$$

$$v(t, x, y) = v_r(x, y) + \sum_i^n a_i(x, y) \cos(\omega_i t - \varphi(x, y)) \sin(\theta(x, y)) - b_i(x, y) \sin(\omega_i t - \varphi(x, y)) \cos(\theta(x, y)) \quad (2)$$

$$\omega_i t = 2\frac{\pi}{T_i} t \quad (3)$$

118 where  $\varphi_i$  is the Greenwich phase lag,  $\theta_i$  the inclination and  $a_i$  and  $b_i$  are the major and minor semi-  
 119 axis, respectively, defining the tidal ellipse at a given geographical location of the  $i$ 'th constituent  
 120 with frequency  $\omega_i(t)$  and corresponding period  $T_i$ .

## 121 Particle Tracking Model

122 Salmon lice are represented as passive particles, each representing an arbitrary but uniform number  
123 of salmon lice. Because the tidal current model is barotropic, the current is assumed to be vertically  
124 uniform, and the vertical movement of the salmon lice is omitted. Turbulent diffusion was included  
125 with a horizontal random walk component (Visser 1997). The trajectories of each particle is calcu-  
126 lated with an Euler scheme where the position  $(x, y)$  of particle  $q$  at the next time step,  $t + \Delta t$ , is  
127 calculated from the velocity,  $u$  and  $v$ :

$$x_q(t + \Delta t) = x_q(t) + u(x, y, t)\Delta t + R\sqrt{6D_h\Delta t} \quad (4)$$

$$y_q(t + \Delta t) = y_q(t) + v(x, y, t)\Delta t + R\sqrt{6D_h\Delta t}, \quad (5)$$

128 where  $R$  is a uniformly distributed random number between  $[-1, 1]$ .  $D_h$  is the diffusion coefficient  
129 and set to  $0.1 \text{ m}^2/\text{s}$  (Gillibrand & Willis 2007). The computational cheap and easily implemented  
130 Euler scheme was chosen instead of a more accurate higher order scheme. This loss of numerical  
131 accuracy is justified by the inclusion of the turbulent diffusion term, which anyway leads to diffusion.  
132 A sensitivity analysis of the time step was conducted (not shown) and satisfying convergence was  
133 obtained with a time step of  $0.005 \text{ h}$  (18 sec), which is used in the present simulations. Particles  
134 crossing the outer boundary are considered lost and removed from the simulation. At the shoreline  
135 a no flux reflective boundary condition is applied (Brickman et al. 2009). For the particle tracking  
136 simulation the  $100 \text{ m}$  resolution grid of the tidal model is adopted. The number of particles released  
137 was tested and the mean trajectory of the particle cluster between identical simulations was found  
138 to be reasonably converged when releasing 900 particles every hour.

## 139 Biological Parameters

140 When modeling the dispersion of salmon lice the three non-feeding planktonic stages, nauplii I,  
141 nauplii II and copepodid are relevant. The non-infectious *L. salmonis* nauplii larvae hatch from the  
142 adult female egg strings and are released into the planktonic environment where they moult into  
143 a second nauplii stage and further into the infectious copepodid larvae (Pike & Wadsworth 1999).  
144 Being non-feeding, the planktonic larvae have only the energy from their internal yolk reserves for  
145 survival and therefore need to locate and infect a host within a limited life span. Infection of a

146 new host is determined by the survival of the larvae and the likelihood of a infectious larvae making  
147 contact with a new host. The infection rate is a function of attachment success, water currents,  
148 temperature, salinity, grazing, etc..

149 In our model salmon lice larva biology is represented by three processes: The duration of the  
150 nauplii and copepodid stages and the mortality. The development time of the planktonic phases are  
151 primarily determined by the water temperature at salinity above 30 ‰ (Samsing et al. 2016). Here  
152 we assume a summer scenario with sea temperature of 10°C. The duration and longevity in these  
153 first phases decreases with increasing temperature. Both Johnson & Albright (1991) and Samsing  
154 et al. (2016) found a similar development time for *L. salmonis* naupulii, and at 10 °C they spend  
155  $\approx 3.7$  days to develop into a infectious copepodid, while the longevity of the copepodid at the same  
156 temperature is approximately 13 days (Gravil 1996, Samsing et al. 2016).

157 Determining mortality is harder because studies of *L. salmonis* larvae in their natural environ-  
158 ment are scarce. Stien et al., (2005) studied population dynamics of *L. salmonis* and estimated  
159 a mortality rate of napulii to be  $\approx 0.17 \text{ d}^{-1}$  and copepodid to be  $\approx 0.22 \text{ d}^{-1}$ , based on laboratory  
160 experiments. The survival probability over time is:

$$p(t) = e^{-\mu t} \tag{6}$$

161 where  $p$  is the survival probability at time  $t$ . Mortality ( $\mu$ ) was assumed to be  $0.17 \text{ d}^{-1}$  for both  
162 planktonic phases.

163 Naupulii and copepodid larvae have been shown to be photo-tactic as well as having the ability  
164 to migrate away from low salinity and seek higher temperature in the upper layers (Johnsen et  
165 al. 2014, á Norði et al. 2015, Johnsen et al. 2016). Gillibrand & Willis (2007) and Johnson et  
166 al. (2014) showed that relative small vertical movement behaviors had a significant effect on the  
167 dispersion pattern in stratified waters emphasizing the need for a more comprehensive model in  
168 estuarine driven areas. However, outside the Faroese fjords where the circulation is dominated by  
169 the tides (Larsen et al. 2008), the connectivity between the salmon farming locations will those also  
170 be dominated by tides.



## 171 Simulations and Connectivity Matrices

172 Based on the existing farm locations as listed by the authorities, 24 farm sites were defined, to which  
173 a receiving and an emitting area was assigned (Fig. 3). The emitting area corresponds to the actual  
174 farm site locations. In those cases where several farms are located in a fjord only the farm site closest  
175 to the fjord opening is included (Fig. 3). The model is barotropic, and thus no attempt is made  
176 to simulate the estuarine circulation which may appear in fjords with little tidal influence (Fig. 1).  
177 The neglected estuarine circulation is, however, of importance for the dispersion within these fjords,  
178 and consequently the receiving farm area (or "hit area") is subjectively defined as the entire fjord if  
179 the farm is located inside a fjord or the long narrow strait between the two largest islands (Fig. 3).  
180 A copepodid larvae entering these areas is considered an infection risk to the whole area. Farms  
181 located in more open and tidal dominated areas (farm 5, 9 and 13, Fig. 3) are assigned a receiving  
182 area which corresponds to the farming site. This is different from other connectivity studies where  
183 a fixed area around the farm is considered to pose an infectious risk to the farm ranging between  
184 a 500 m radius (Adams et al. 2012, Salama et al. 2017) to a 600x600m (Johnsen et al. 2016) and  
185 800x800m area around the farm (Samsing et al. 2017).

186 The connectivity matrices were generated by releasing 900 particles every hour from each defined  
187 farm site emitting area (1.8 million particles) over a period of 2000 hours (83.3 days). The simulation  
188 period includes several spring-neap tide cycles and gives the system sufficient time to converge and  
189 therefore reflects a long term dispersion trend. All farms are evenly weighted assuming this is a  
190 linear process and therefore the exact number of salmon lice a particle represents becomes irrelevant  
191 in this context. We adopted a similar approach as described by Adams et al., (2012) where particles  
192 can infect any farm, including its initial release farm, when they are older than 3.7 days. Further,  
193 the particles have an infections window of 13 days, assuming a typical Faroese summer scenario with  
194 10°C water temperature. A particle was only allowed to infect a given farm site once, meaning that  
195 if they re-enter the same farm site the particles were not recorded. However the particle was allowed  
196 to continue in the simulation and potentially infect a new farm site, which is different from Adams  
197 et al., (2012) where particles were taken out of the simulation when the first connection was made.  
198 Particles were taken out of the simulation when they become older than 16.7 days. The connection  
199 probability between two farms is calculated as the ratio between infectious particles entering one  
200 farm's receiving area from another farm and the total amount of released particles from the emitting

201 farm. An average age of the infectious particles in a connection is estimated using the age at their  
202 entry into a receiving area. The connection probability between two farms including mortality is  
203 found by weighing the infectious particles with the survival probability using Eq. 6.

## 204 RESULTS

### 205 Dispersion

206 Examples of particle dispersion patterns are illustrated in dispersion maps showing the mean age  
207 over the simulation period of particles released from farms 2, 5 and 21 (Fig. 4) in every 100x100m  
208 grid cell. The three locations were chosen by their geographic location and because they are placed  
209 in tidally relatively exposed areas allowing larvae to escape their initial release site, but at different  
210 rates.

211 Particles disperse rapidly from farm 5 (Fig. 4b), which is located in the energetic strait on the  
212 west side of the largest island in the center. In contrast, the particle dispersion from the other two  
213 farm sites (Fig. 4a and c) is slow the first couple of days, as seen by the limited dispersal area of  
214 the youngest particles (red color). However, once particles escape their initial fjord, they enter what  
215 might be called a "dispersion highway", that goes clockwise around the Faroe Islands. Here, they  
216 quickly disperse around the archipelago. These results illustrate that larvae are capable of travelling  
217 to almost any location around the Faroe Islands, some more likely than others, within their  $\approx 2$   
218 week lifespan, provided that they manage to escape their release area. Further, the clockwise residual  
219 current also implies that only few particles are lost from the system.

220 The maximum Euclidean distance traveled by a particle varies greatly between farms. Particles  
221 can easily travel more than 20 km during the nauplii phase (3.7 days in Faroese summer conditions;  
222 Fig. 6a). In three farms, one being farm 5 (dash line with cross), over half of the particles travel  
223 over 40 km. On the other hand particles older than 3.7 days generally travel, not surprisingly,  
224 significantly longer distances than their nauplii counterparts (Fig. 6b). Here over 50% of particles  
225 from most farms travel over 50 km. In several farms, including farms 5 and 21, approximately 10%  
226 of the particles travel at least 80 km. It may be noted that the particles are not weighted with  
227 mortality here.

228 The relative distribution of nauplii and copepodid particles in each 100x100m grid cell over the  
229 whole simulation period, including mortality, is shown with a heat map (Fig. 5). Here, particles  
230 are recorded every time step and weighed with survival probability. Particles released from many  
231 farms (10-11 and 22-23) have a very limited dispersion range both in the nauplii and copepodid  
232 stage. On the other hand particles released from farms in more exposed areas as farms 5 and 9 have

233 relativity low densities at their initial release sites, indicating the quick dispersion away from these  
234 areas after being released. No clear "cold" spots, i.e. areas with relatively low density of copepodids,  
235 are in the coastal regions. The exception is some of the fjords with little tidal influence where  
236 estuarine circulation, which is neglected in the present simulation, must be expected to dominate  
237 the dispersion (Fig. 5b). The highest density is found around the northern group of islands, which  
238 is also where the majority of the farms are located.

## 239 **Connectivity**

240 The proportion and mean age of infectious salmon lice larvae that disperse between Faroese salmon  
241 farms is summarized in three connectivity matrices (Fig. 7). The connectivity matrices reveal gen-  
242 erally a high connection between farms although the range of connectivity is quite diverse. The  
243 diagonal line indicates the degree of self-infection and is dependant on the strength of exposure in  
244 the area. Farm 5, 9, and 13, which are located in tidally exposed areas (Fig. 3), are clearly not  
245 self-infectious (Fig. 7a and c). The farms 10-12, 20, 22, and 23 are close to 100% self-infectious and  
246 emit very few larvae to other farms, while also having a relatively (to the amount emitted) high  
247 infection rate from other farms.

248 The mean age in the highly self-infectious connections is close to 3.7 days, the time when larvae  
249 become infectious, while the mean age for non-self-infectious farms is much higher, between 8-14  
250 days (Fig. 7b). Larvae from farm 5 infecting farm 9 are very old (14-16 days) and vice versa, even  
251 though they are very close geographically implying that the particles have traveled a long distance  
252 before they enter the neighbour site. Interestingly, however, larvae from these farms infect nearby  
253 farms (4, 6, 7 and 8) with younger larvae.

254 Figure 7c illustrates how infectious a connection is by accounting for mortality. Here the defined  
255 receiving area around farm 15 receives over 10% of infectious particles from farm 16, which is the  
256 strongest connection in the network. The matrices in figure 7, reveal at least two clusters of farms in  
257 the Faroe Islands. One includes farms 1-3, which appear to be internally well connected with quite  
258 limited interaction with the other farms. With the exception of a few isolated farms, the rest of the  
259 network comprises a large connected cluster.

260 Farms are characterized as emitters, receivers, and/or isolated by looking at how many infectious  
261 larvae they emit and receive to and from other farms, excluding self-infection, expressed as % of

262 particles corresponding to the amount released from one farm site (Fig. 8). Farms 16, 18, 21 and 14  
263 are the highest emitting, while farm 15 is by far the highest receiving farm followed by farms 5, 9  
264 and 2. Three farms are virtually isolated (10, 12 and 20, Fig. 8), as they are neither receivers nor  
265 emitters.

## 266 DISCUSSION

267 Our results demonstrate that Faroese salmon farms form a complex network with a wide range  
268 of connectivity strengths. The overall connectivity appears to be much higher than other studies  
269 (Adams et al. 2012, 2015, Salama et al. 2013, Johnsen et al. 2016, Salama et al. 2017, Samsing  
270 et al. 2017), although a direct comparison is problematic due to the difference in how connectivity  
271 is defined. Particles quickly disperse far and wide once outside a fjord and inside the "dispersion  
272 highway" which runs clockwise around the Faroe Islands. For the most dynamic sites there is a high  
273 probability that the particles reach more than a 20 km distance from their origin, while in the most  
274 isolated fjords there is less than 10% probability that the particles travel longer than 20 km before  
275 they become infectious. The maximum expected distance in the non-infectious stage is about 60  
276 km for a few sites (Fig. 6a). Including the life span of the copepodid stage there is a fairly high  
277 probability for the majority of the sites that the maximum distance is beyond 50 km and some few  
278 sites there is up 10% probability that they even reach beyond 80 km (Fig. 6b), which are distances  
279 comparable with the geographical size of the archipelago. Note that these distances are maximum  
280 Euclidean distances, however, the actually traveled sea distance may be considerable longer as they  
281 travel around the islands. Consequently, particles have the potential not only to infect the other  
282 farms, but also a potential risk of a delayed self-infection. The presented dispersion distances are  
283 comparable with maximum distances found along the Norwegian coast, but considerable longer than  
284 the typical 20-40 km found in Norwegian fjords (Asplin et al. 2014) and the median distances of 6  
285 km with maximum distances around 36 km in a Scottish Loch (Salama & Rabe 2013, Salama et al.  
286 2016).

287 The self-infection in a number of farms is quite high, as seen by the low mean age and small  
288 dispersion range in these connections (Fig.'s 7 and 5). The high self-infection is partly caused by the  
289 low water fluxes in and out of these fjords, which may be underestimated due to the omission of the  
290 estuarine and wind driven circulation, and that the particles stay within the initial receiving area  
291 when becoming infections and therefore recorded the moment they become infectious (3.7 days).

292 Identifying critical nodes in the farm network is highly valuable information when developing  
293 a management plan. We were able to identify farms either as emitters, receivers, or isolated. The  
294 highest emitting farms (16, 18, 21 and 14, descending order, Fig. 8) are all located in the northern  
295 part of the Faroe Islands. They all emit the highest proportion of their infectious salmon lice particles

296 to the close neighbour, farm 15, which is the highest receiving farm (Fig. 3). Farm 16 emits over  
297 10% of its infectious salmon lice to farm 15, which must be considered a very strong connection.  
298 One reason farm 15 is the highest receiver is that the defined receiving area is quite large as this  
299 fjord is relatively wide. In addition, the connection to the strait outside this fjord includes a tidally  
300 rectified eddy at the fjord mouth, which transports particles into the area. The connection decreases  
301 significantly if the receiving line at the fjord mouth is moved further into the fjord. Therefore, care  
302 should be taken in drawing too bold conclusions on this relatively strong connection, but still it  
303 indicates that the infection risk in this fjord is noticeable. The situation is quite different for the  
304 two following farms in the receiving rank list. They both have a modest receiving area, but have a  
305 large tidal through-flow resulting in a high particle flux from other farms.

306 The connectivity matrices suggest that the three farms at the southernmost islands (farms 1-3)  
307 are largely separated from the other islands, but are internally well connected. The rest of the farm  
308 network seems to be one cluster with negligible contribution from the three isolated farms (10, 12  
309 and 20) and the three relatively isolated farms (11 and 22-23) (Fig. 8). These isolated farms are  
310 in the narrow strait between the two main islands and in fjords in the northeast group of islands,  
311 which all are characterized by weak tidal currents (Fig. 1). Likely the dispersion within these areas  
312 is dominated by estuarine and/or wind driven circulation (Gaard et al. 2011), which is not included  
313 in the present model.

314 Recently, Paturson et al., (2017) assessed variations in salmon lice population dynamics in  
315 Faroese farms in relation to the physical exposure to the local circulation patterns and flushing  
316 with adjacent waters expressed through an exposure index, and found that up to 65% of the varia-  
317 tions in the sea lice dynamics was related to the freshwater input and tides. In the fjords with farms  
318 20 and 22-23, they found a generally low exposure, of which 60-70% was explained by the fresh  
319 water runoff, and a general higher exposure index for the fjord hosting farm 10 where nearly 90% of  
320 the sea lice variance could be related to the freshwater runoff. A study conducted in Kaldbaks fjord  
321 (farm 10, Fig. 3) indicated an average exchange rate of approximately 10 days (Gaard et al. 2011),  
322 in contrast to virtually no exchange found in our simulations. Including wind and freshwater forces  
323 will increase the interaction with the other farms in the northern cluster as well as the rest of the  
324 farm network. However in calm and dry periods, when the tides are the primary forcing mechanism,  
325 these farms must be considered as isolated and highly self-infectious.

326 The connectivity in this study was measured as the number of infectious particles (older than  
327 3.7 days) released at one farm entering the defined receiving area of another farm or its own. Adams  
328 et al., (2012) took particles out of the simulation after the first connection. In many cases particles  
329 in our simulations did not leave their own receiving area before becoming infectious because we  
330 defined the whole fjord to be a potential infectious risk. This is evident when looking at the mean  
331 age in most of the self-infection connections (Fig 7b). It would be unpractical in our setup to  
332 take most particles out of the simulation after one connection as we would then in most cases  
333 only observe self-infection. Therefore particles were allowed to continue in the simulation but they  
334 were only allowed to infect once in any given connection. One downside with this method is that  
335 relevant information is lost, such as the amount of time an infectious salmon louse spends in a farm  
336 area. Johnson et al., (2016) and Samsing et al., (2017) partially solved this by letting salmon lice  
337 reinfect a farm site multiple times. Some studies include the biomass and/or salmon lice counts into  
338 the farm connectivity (Salama et al. 2017, Samsing et al. 2017). This is especially relevant when  
339 studying specific time periods and verifying towards salmon lice counts, which however is not the  
340 case in our simulations. Here all farms release an equal amount of particles, which can represent any  
341 arbitrary uniform number of salmon lice, which provides the option to include number of salmon  
342 lice in a future expansion of the model when number of fish and salmon lice counts data at farm  
343 level become available. As mentioned, the connectivity probabilities found in this study are high  
344 compared to other studies. This is in part due to the way we define our receiving area, but likely  
345 also due to salmon lice having a very high dispersion range in Faroe Islands, in contrast to other  
346 areas.

347 Averaged over several spring-neap tide cycles the only parameters that can change the connec-  
348 tivity are the length of the planktonic phases and the mortality. This study assumed typical Faroese  
349 summer conditions. We also ran some simulations in winter conditions where the planktonic phases  
350 become longer and observed difference in the connectivity, although the overall connectivity pattern  
351 look very similar compared to summer conditions.

352 The Faroe Islands are notoriously windy, especially in the winter months. The dominating wind  
353 direction is southwest, while the less frequent direction is east, but the wind direction and strength is  
354 highly variable due to the geographical location of the Faroe Islands in the path of the low pressures  
355 crossing the Atlantic (Cappelen & Laursen 1998, Larsen et al. 2008). In the fjords and straits the



356 wind strength and direction is highly influenced by the surrounding mountains, but currently there  
357 is no meteorological data with sufficient high spatial resolution available for the area. Most likely  
358 wind affects the dispersion dynamics, especially on short time scales forcing salmon lice larvae out of  
359 or into a fjord and outside the fjords wind affects the drifting path. However, due to the variability  
360 in the wind forcing it is likely that the overall distribution will be even more smeared out than  
361 obtained here from the underlying tidal forcing only, but this still remains to be investigated.

362 The results presented have many implications which can benefit the Faroese aquaculture industry,  
363 where at the moment there is no coordinated treatment management plan based on the underlying  
364 hydrographic connectivity between the sites. As mentioned, all farms are weighted equally as we  
365 assumed a linear process. The connectivity matrices may therefore be seen as a background or  
366 underlying connectivity providing options to include the individual farms sea lice pressure when this  
367 information is lifted from its confidentiality.

368 Our results clearly demonstrate that a holistic treatment plan should be developed as salmon  
369 farms are not isolated but connected to each other. Intuitively we would strictly manage the farms  
370 that are characterized as emitters to prevent unnecessary external infection pressure on other farms  
371 e.g. farms 16, 18 and 21 (if all farms contribute equally). On the contrary, Adams (2015) combined  
372 connectivity estimates with a salmon lice population dynamic model by Reive et al., (2005) and  
373 found that management was most effective when targeting the highest receiving or influx farms,  
374 which is somewhat counter-intuitive. This finding suggests the need to include population dynamics,  
375 specifically to examine the network response to different treatment strategies.

376 In addition to treatment strategies, the approach described here can also aid in the planning of  
377 farm locations. For instance salmon farmers can decide to place their farms further out or into the  
378 fjord. The trend in the Faroe Islands in recent years has been to place farms further out in the fjord  
379 to obtain better growth condition due to higher water exchange, less local bed load and less sea  
380 lice self infection. By placing farms further out, as recommended by e.g. Samsing et al. (2015), the  
381 connectivity between farms increases. In this way, the benefit to the individual farm increases the  
382 challenge for the entire farm network. Also the placement of potential new farm sites is problematic  
383 as there are no obvious salmon lice "cold spots" close to Faroese coast (Fig. 5), emphasizing the  
384 need for a holistic management approach.

## 385 CONCLUSION

386 In the last decade there has been a gradual increase in the use of numerical models to study the  
387 dispersion of *L. salmonis* in all leading Atlantic salmon producing countries and they are now at  
388 a state where fairly realistic results can be obtained (Stucchi et al. 2011, Salama & Rabe 2013,  
389 Asplin et al. 2014, Johnsen et al. 2016, Samsing et al. 2017, Salama et al. 2017). This study presents  
390 the first model which can to a certain degree, realistically simulate the mean dispersion patterns in  
391 an archipelago with a circulation dominated by tidal currents. The tidal currents and the residual  
392 current due to their highly dominating influence on water currents on the Faroe shelf are the main  
393 responsible for the connectivity between farms sites as well as acting as a retention mechanism for  
394 the resident sea lice population.

395 We acknowledge that wind and freshwater forcing, which are not included in the present study,  
396 will influence the dispersion dynamics, especially on shorter time scales in the more sheltered fjords.  
397 However on longer timescales the highly dominating Faroese tidal forcing will reflect the mean  
398 dispersion pattern, enabling valuable insight on the background connection between farms in Faroe  
399 Islands.

400 In summary, the basis is developed to create a robust biophysical model which can help find an  
401 optimal treatment and management plan for the Faroese aquaculture industry.

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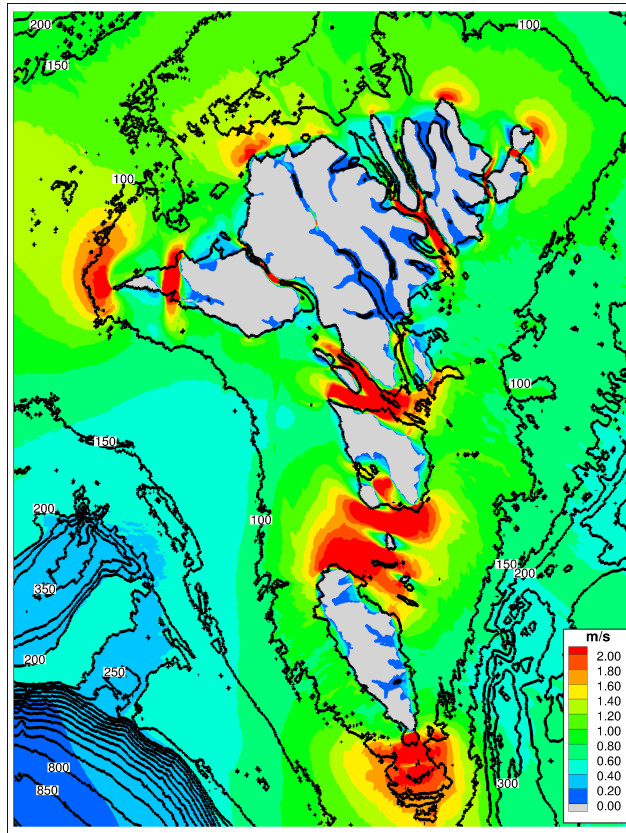


Figure 1: Maximum tidal current velocity provided as the sum of semi-major axis of the 6 dominating constituents (Simonsen & Niclasen, 2011). Thin contour lines provides the water depth. White arrow head shows the location of the large narrow strait.

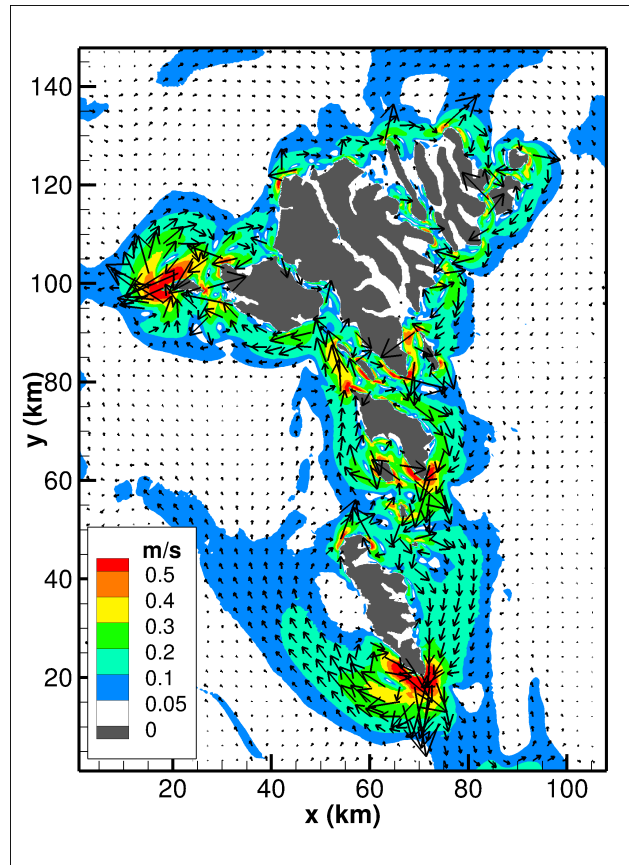


Figure 2: Residual tidal current velocity around the Faroe Islands. The vectors indicate the direction, and the color indicate the speed (Simonsen & Niclasen, 2011). Thin contours lines provides the depth.



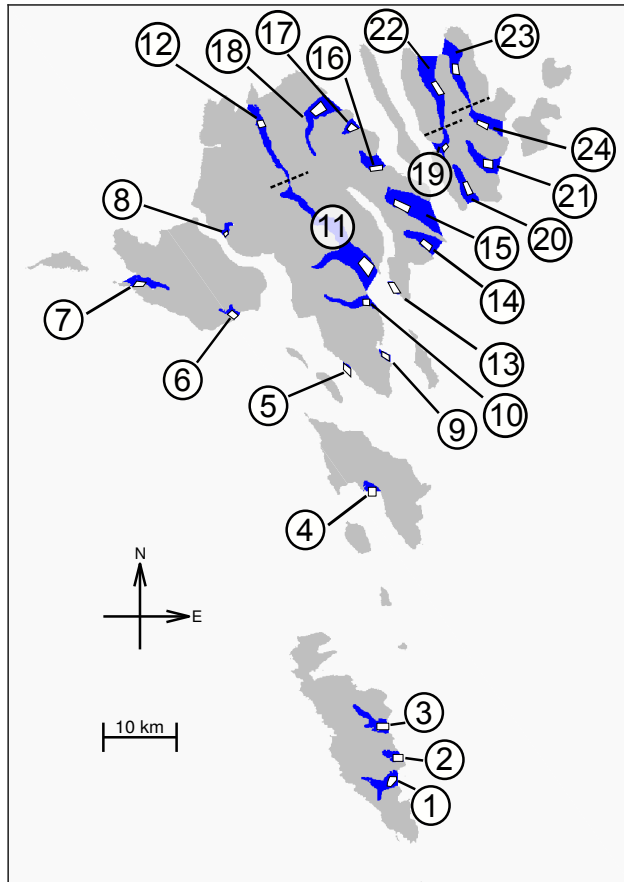


Figure 3: Farm area (blue) and lice release site (white square). Dashed lines distinguishes two farm areas from each other. There is water connection between farm areas 11 and 12, but not between 19 and 22 and 23 and 24.

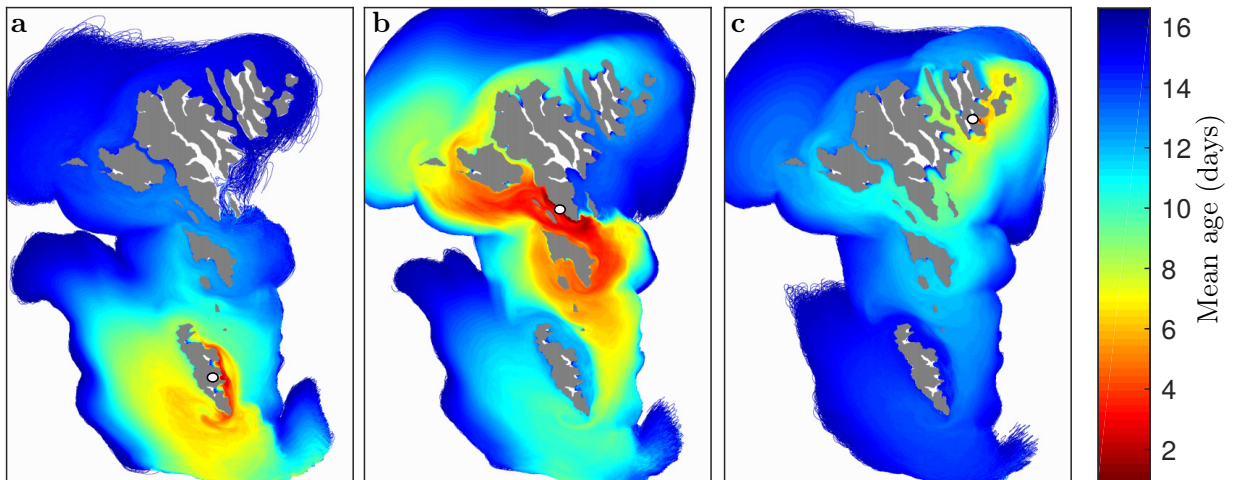


Figure 4: Mean age of particles in every grid cell over the 2000 hour simulation period. 900 particles are released every hour from farm 2, 5 and 21 (white dot) shown in (a), (b) and (c), respectively. Colorbar indicates mean age in days.

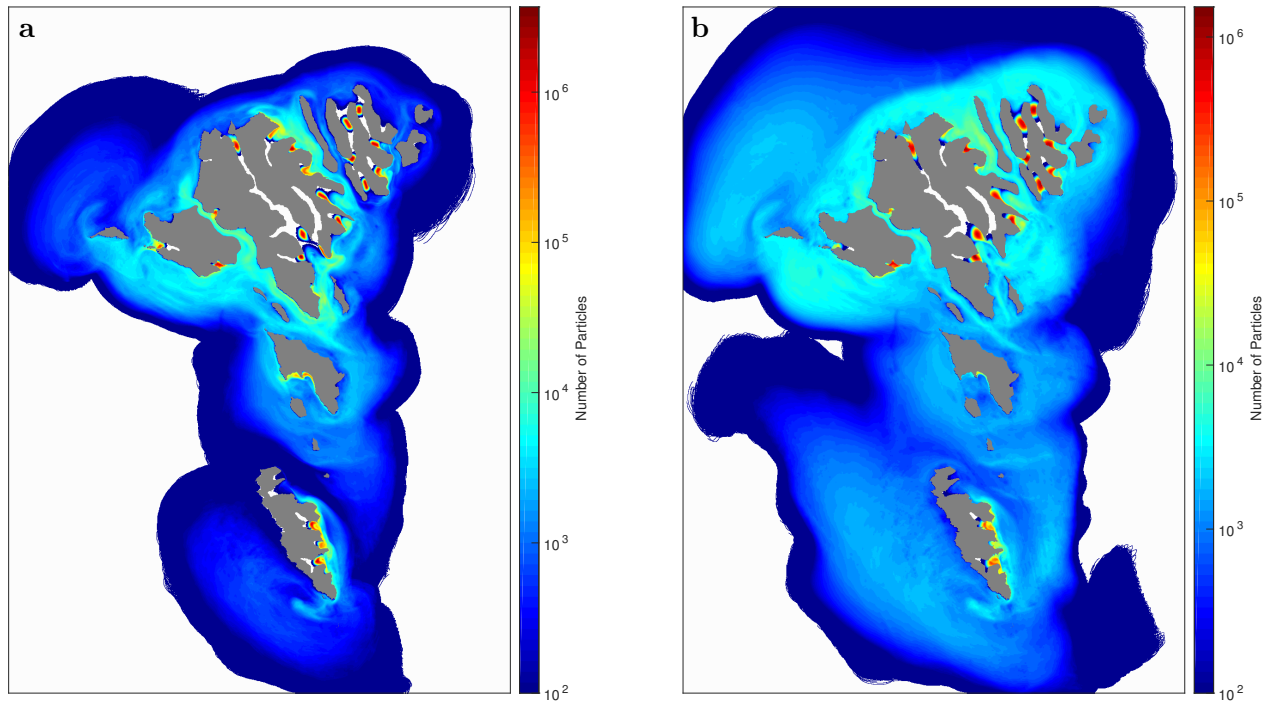


Figure 5: Relative density distribution attained by particles released from all 24 farm sites, by recording the number of particles in each 100x100m grid cell every time step including mortality over the whole 2000 hour simulation. (a) and (b) shows the number of nauplii and copepodid particles, respectively. Colorbar indicates number of particles on a logarithmic scale.

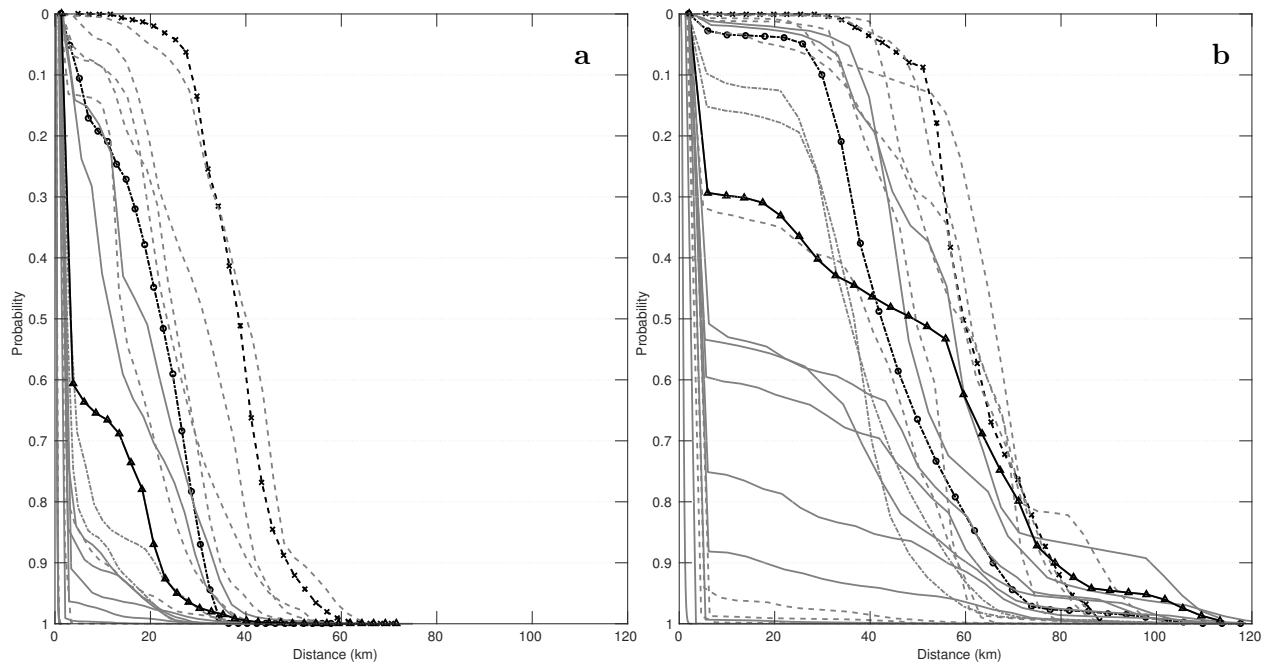


Figure 6: The cumulative frequency of the maximum Euclidean distance attained by particles released from all 24 sites. (a) and (b) shows the cumulative frequency of the maximum distance, not including the mortality, attained by napulii and copepodid, respectively. Dash-dotted lines are farms 1-3, dashed line are farms 4-13 and solid lines are farms 14-24. As examples, three farms are highlighted: farm2 (dash-dotted line with circle), farm 5 (dashed line with cross), and farm 21 solid line with triangle).

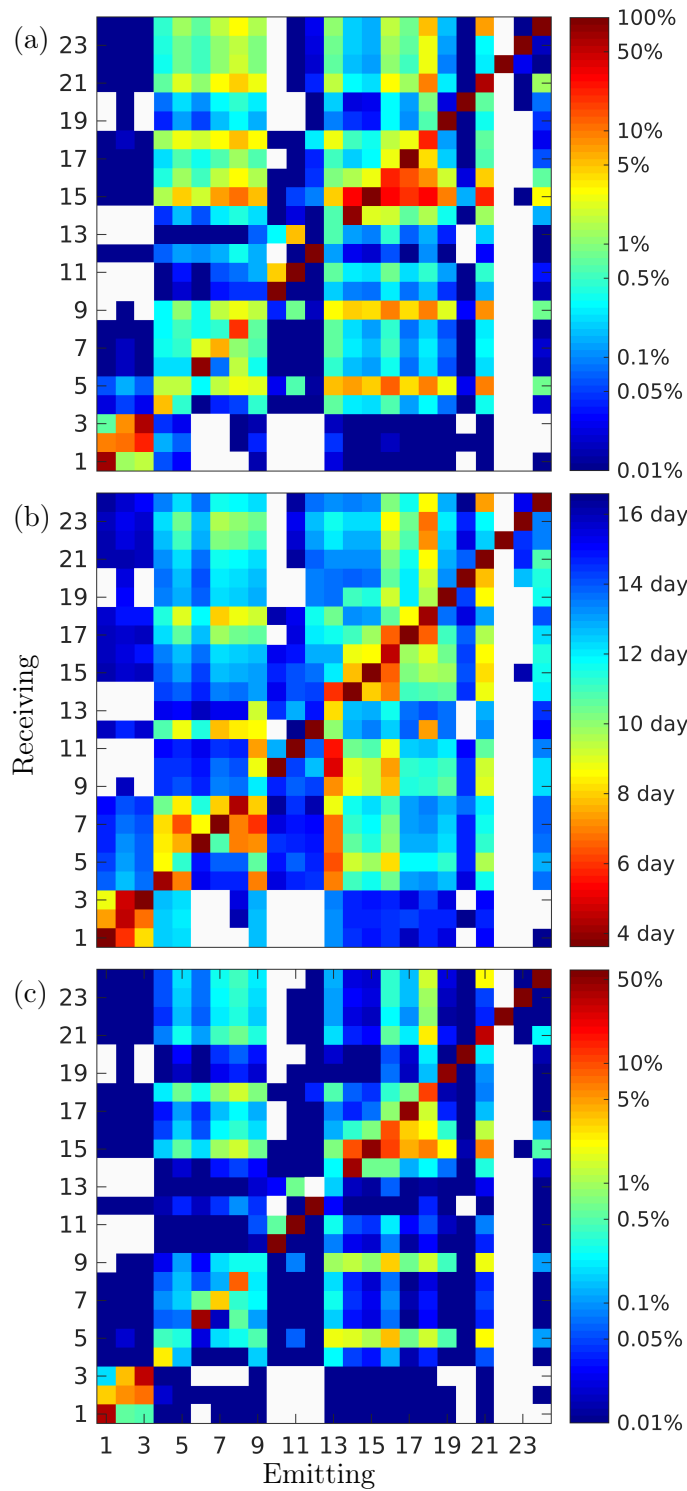


Figure 7: Connectivity matrix's with emitting farms on x-axis and receiving farms on the y-axis. **(a)** Percentage of unique infectious larvae released from one farm site entering any other farm site or its initial release site. **(b)** Mean age of the connections. **(c)** Connectivity including mortality. Colorbar indicates the percentage in **(a)** and **(c)**, scale is logarithmic. Colorbar in **b** indicates the mean age in days. White color indicates that there is no signal.

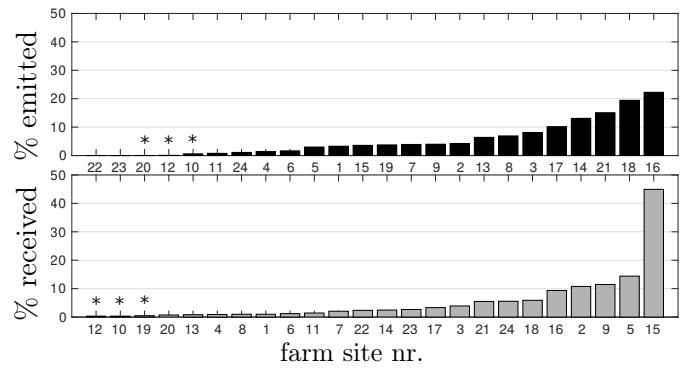


Figure 8: Barplot of % of salmon lice which farms emit (upper panel) and receive (lower panel) to and from other farms accounting for mortality and excluding self-infection. "\*" indicates the three highly isolated farms. Percentage is normalized with total amount of particles released from one farm.