International Journal for Parasitology 49 (2019) 277–286

Contents lists available at ScienceDirect

International Journal for Parasitology

journal homepage: www.elsevier.com/locate/ijpara

Identifying ‘firebreaks’ to fragment dispersal networks of a marine parasite

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ARTICLE INFO

Article history:
Received 12 July 2018
Received in revised form 2 November 2018
Accepted 3 November 2018
Available online 17 January 2019

Keywords:
Atlantic salmon
Lepeophtheirus salmonis
Aquaculture
Epidemiology
Graph theory
Network analysis
Node removal

ABSTRACT

Marine ecosystems are beset by disease outbreaks, and efficient strategies to control dispersal of pathogens are scarce. We tested whether introducing no-farming areas or ‘firebreaks’ could disconnect dispersal networks of a parasitic disease affecting the world’s largest marine fish farming industry (~1000 farms). Larval salmon lice (*Lepeophtheirus salmonis*) are released from and transported among salmon farms by ocean currents, creating inter-farm networks of louse dispersal. We used a state-of-the-art bio-physical model to predict louse movement along the Norwegian coastline and network analysis to identify firebreaks to dispersal. At least one firebreak that fragmented the network into two large unconnected groups of farms was identified for all seasons. During spring, when wild salmon migrate out into the ocean, and louse levels per fish at farms must be minimised, two effective firebreaks were created by removing 13 and 21 farms (1.3% and 2.2% of all farms in the system) at ~61°N and 67°N, respectively. We have demonstrated that dispersal models coupled with network analysis can identify no-farming zones that fragment dispersal networks. Reduced dispersal pathways should lower infection pressure at farms, slow the evolution of resistance to parasite control measures, and alleviate infection pressure on wild salmon populations.

1. Introduction

In terrestrial agricultural systems, approaches to halt diseases that spread rapidly over long distances include quarantine, vaccination, mass culling and restrictions on animal movement (Ferguson et al., 2001; McCallum et al., 2004; Tildesley et al., 2006). These approaches aim to disconnect or disrupt the infection pathways and rely on an understanding of epidemiological factors that govern the speed and direction of disease spread. Equivalent disease control strategies are less common in marine production systems, which are under rapid expansion globally (Duarte et al., 2007). Marine farming systems have introduced billions of farmed animals into coastal waters, providing persistent, high density populations of susceptible hosts, and offer ideal conditions for the emergence of disease epidemics (McCallum et al., 2004).

Marine production systems are qualitatively different from terrestrial systems in multiple ways: (i) they are more open and connected; (ii) enclosures in the ocean have direct contact with the environment, and (iii) the rates of spread of marine epidemics (and marine organisms in general) can be higher than those observed in terrestrial systems (McCallum et al., 2003, 2004). The latter is partly due to the lack of hard barriers to dispersal in the ocean (Treml et al., 2015), and in some cases, the long-term survival of the free-living stages of certain parasites (McCallum et al., 2003).

Combined, these processes make disease transmission in the ocean harder to predict and control, and traditional models and management tools might not be fully applicable (Murray, 2009). Disease management could benefit from modelling approaches that can uncover drivers of disease epidemiology and identify ‘barriers’ to dispersal in the ocean (Groner et al., 2014, 2016). Enforcing barriers that separate production regions via implementing no-farming zones or ‘firebreaks’ may work as effectively as restrictions on animal movement, reactive ring vaccination or broad-scale culling of livestock in terrestrial agriculture (Ferguson et al., 2001; Tildesley et al., 2006).

In the world’s most farmed marine fish, Atlantic salmon, infestation with ectoparasitic sea lice (*Lepeophtheirus salmonis* and *Caligus* spp.) is the most problematic disease (FAO, 2016). These

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https://doi.org/10.1016/j.ijpara.2018.11.005
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external parasites are directly transmitted between hosts as infective planktonic larvae, causing substantial economic losses to the industry and threatening wild fish populations (Costello, 2009a, b). Louse eggs hatch into non-feeding planktonic larvae that mature in the water column (Costello, 2006), and drift with ocean currents away from their release source until they find a suitable host to attach to. This results in connectivity, or dispersal potential of individuals (lice), between salmon farms over large distances (Samsing et al., 2017). Unlike immunizing protocols, topical delousing treatments, commonly used in salmon aquaculture in the treatment of lice, do not confer long-lasting protection. Accordingly, louse re-infestation from neighbouring farms can occur soon after these costly treatments are applied. In contrast, treatment synchronization between neighboring farms (within an ~10 km radius) has been associated with lower levels of adult lice per fish (Arriagada et al., 2017). This example illustrates how modelling louse dispersal and quantifying connectivity can be crucial steps for management and control of louse epidemics (Arriagada et al., 2017).

Transmission dynamics in the ocean are variable and complex due to the influence of oceanographic mixing and fluctuations in water chemistry (Salama and Rabe, 2013; Groner et al., 2016). To address this complexity, Salama and Rabe (2013) proposed a step-wise framework of different models which, working together, should enable the study of louse environmental transmission. This framework starts with a hydrodynamic numerical model that provides the inputs (water currents, temperature, salinity) for a dispersal or particle tracking model. Coupled together, these biological-physical dispersal models can account for the influence of water circulation patterns, abiotic environmental influences and larval biology (development, behaviour and mortality) on dispersal trajectories and outcomes (Albretsen et al., 2011; Johnsen et al., 2014). Results from these dispersal models allow further investigation of connectivity patterns using network analysis (Adams et al., 2012, 2015; Salama and Rabe, 2013). Ultimately, these network models of louse dispersal can be applied to develop effective management strategies based on spatially explicit louse connectivity. These strategies include the detection of key sites that hold the network together and can be targeted through the establishment of firebreaks to louse dispersal.

Algorithms derived from network analysis in different disciplines (e.g., social sciences, mathematics, physics), have become a powerful tool in the study of landscape connectivity (Urban and Keitt, 2001; Urban et al., 2009). To construct a network for modelling landscape connectivity, we must clearly define nodes, or vertices, and links, or edges (Galpern et al., 2011). In our system, nodes represent salmon farms and links represent louse dispersal probabilities. This simple yet powerful model of salmon louse movement allows the identification of key nodes disproportionately responsible for maintaining network cohesion or enabling rapid flow throughout the network. Similar models have been used in conservation for the establishment of protected areas (Kool et al., 2013; Melià et al., 2016). In contrast, the ‘removal’ or ‘immunization’ of influential nodes and the creation of ‘firebreaks’ to dispersal can fragment networks into smaller sub-networks or components, and can be a practical approach to protecting a system against epidemic processes (Hébert-Dufresne et al., 2013). Components are groups of connected nodes and represent structural subunits of the network (Rayfield et al., 2011; Kobayashi and Masuda, 2016). An organism inhabiting any node within a component can move or disperse to any other node within the same component, but not between components (Hébert-Dufresne et al., 2013).

There are numerous definitions of influential nodes in network theory. The total number of outgoing or incoming connections from/to a node does not necessarily dictate the global influence of a given node (Alstott et al., 2009; Mourier et al., 2017), but often informs local dynamics. A node’s position in the network or its role in connecting distant sections of the network can be more important (Verma et al., 2014). In the salmon-louse system, where salmon farms are connected through the dispersal of louse larvae, removing or relocating farms can be a challenging task in reality. Therefore, if ‘removal’ strategies are to be implemented, the industry must identify the least amount of farms that need to be removed or relocated to achieve the largest effect on louse movement. In this paper, we use a biophysical dispersal model and tools from network analysis to predict population connectivity of salmon lice between all salmon farm locations in Norway. Predicted dispersal pathways were used to build inter-farm networks of louse dispersal with the aim of identifying potential areas of no-production or firebreaks to fragment the louse dispersal network along the Norwegian coastline.

2. Materials and methods

An existing spatially explicit biophysical model (Asplin et al., 2014; Johnsen et al., 2014) was used to simulate dispersal of salmon lice (*Lepeophtheirus salmonis*) released from salmon aquaculture sites along the Norwegian coastline for a full year. The louse dispersal model consisted of a hydrodynamic model and an advanced particle tracking component. The emergent dispersal pathways from this model were used to build networks of louse dispersal.

2.1. Study area

The study domain covered the entire Norwegian coastline (55.9–75.3°N, 1.5–38.1°E), a topographically complex system characterized by fjords, islands, narrows and bay (Asplin et al., 2014; Johnsen et al., 2014).

All marine salmon aquaculture sites, hereafter referred to as farms, were assumed to be available habitat for the settlement of infective salmon louse larvae (copepodids). The locations of the 967 salmon farms in our model domain were obtained from the Norwegian Directorate of Fisheries (2017 http://www.fiskeridir.no/fiskeridir/akvakultur/registre), using all approved farm locations at August 2017. We excluded from our model other salmon louse sources such as wild fish populations. Salmon farms are the main source of lice in Norway (Heuch et al., 2005) as evidenced by the high ratio of farmed to wild salmon (~728:1 in 2015), based on the number of fish held in farms and the number of salmon estimated to return to Norwegian rivers each year (Norwegian Directorate of Fisheries, 2016 https://www.fiskeridir.no/fiskeridir/Akvakultur/Statistikk-akvakultur; Thorstad and Forseth, 2016 https://brage.bibsys.no/xmlui/handle/11250/2394052).

2.2. Hydrodynamic model

The hydrodynamic model was an implementation of the Regional Ocean Model System (ROMS; http://myroms.org) called NorKyst800 (Albretsen et al., 2011). The model had a horizontal resolution of 800 × 800 m and 35 vertical levels. Realistic forcing from atmosphere, tides and rivers are included as described by Asplin et al. (2014) and Johnsen et al. (2014, 2016). Model results consisted of hourly values of three-dimensional currents, salinity and temperature, and were used as inputs in the particle tracking louse dispersal model. Given that most of the variability in salmon louse dispersal occurs between seasons (and not years) (Samsing et al., 2017), we decided to cover 1 year with a high temporal resolution (capturing weekly matrices of connectivity, see Section 2.4). The simulation covered a period of 52 weeks (7 days per week) from January 1, 2016 onwards. Further details on hydrodynamic model configuration (Asplin et al., 2011, 2014; Johnsen et al., 2014, 2016) and validation are presented in previous publications (Sandvik et al., 2016).

2.3. Particle tracking dispersal model

The salmon louse advection and growth component was based on the Lagrangian Advection and Diffusion Model (LADIM), described in Asplin et al. (2014) and Johnsen et al. (2014). Particles representing salmon lice during the three planktonic stages (two pre-competent or non-infective nauplius I and II, and a competent or infective copepodid) were released from each of the 967 farms in the model domain and advected based on the currents from the hydrodynamic model. To capture temporal variations in connectivity, we modelled louse dispersal for the entire year, recording weekly arrivals of louse particles at each destination farm.

The modelled particles represented lice as super individuals (one particle = 100 lice; Scheffer et al., 1995), and were constantly released from all farms during the simulation at a rate of five particles hour^{-1} (>43 thousand (k) particles per farm; >42 million (mil) total). Mortality was assumed to be constant and parameterized at 17% day^{-1} (Stien et al., 2005). All particles that entered the offshore grid boundary were assumed to be lost at sea and excluded from further analysis. Particles in the model were given vertical behaviour where they would swim up towards surface light, and downwards to avoid low salinity (<20) with an absolute swimming speed of 1 mm s^{-1} (Samsing et al., 2016a). In the absence of environmental stimuli, particles were transported horizontally by ocean currents and mixed by turbulent forces on a sub-grid scale. Development was temperature-dependent and parameterized as a function of degree-days, which is the product of water temperature and number of days. Louse particles became infective (or competent) copepodids at 40 degree-days (duration of pre-competency period) and had a total lifespan of 150 degree-days (maximum pelagic larval duration or competency period). Past this time, louse larvae were assumed to have died of starvation or senescence. This competency period translates into approximately 15 days at 10 degrees dispersing in the seascape.

Infective copepodid particles were assumed capable of settling at suitable sites (967 salmon farms in the model domain) during their competency period if they passed within a target area of 3×3 model grid cells (800×800 m grid cells) around a farm. This target area is unrealistically high compared with the actual size of a farm, but was chosen to sample enough incoming particles, enabling us to analyse variability between farms with a low number of connections. Sensitivity analyses to different model parameters (mortality rate, vertical swimming behaviour and size of the target area), presented elsewhere (Johnsen et al., 2014, 2016), show that spatiotemporal patterns in dispersal were robust to moderate changes in all parameter values (Ådlandsvik, 2015, https://www.regjeringen.no/no/dokumenter/forslag-til-produksjonsomrader-i-norsk-lakse–og-orretoppdrett/id2460242/). The outputs from the particle tracking model specified weekly counts of particles that arrived at a destination farm (after mortality) coming from upstream source farms and were used to build a matrix representing the probability of connectivity, as described Section 2.4.

2.4. Connectivity matrices and louse dispersal networks

For every week in the simulation period, we created a 967×967 source–destination matrix (row-column) S, whose elements Sij represent the sum of particles arriving at a destination farm j that come from a source farm i after accounting for mortality. Connectivity matrices were extracted weekly, but the simulation and release of louse particles was continuous. This source–destination matrix was rescaled by the size of the population of fish at each source farm (i.e., maximum allowable fish biomass) to obtain a flux matrix (Urban and Keitt, 2001), where values represent realistic values of louse movement between farms. In Norway, salmon farms are allowed a maximum biomass in tons of fish per farm which varies between sites (Norwegian Directorate of Fisheries, 2017), and is correlated with abundances of planktonic lice (Penston et al., 2008; Penston and Davies, 2009; Harte et al., 2017). Here, we used the maximum allowed biomass per farm to rescale our source–destination matrix S and calculate a realistic flow of lice. All the elements in the flux matrix were then divided by column-sums to obtain a migration matrix, M, representing the likelihood that lice found in a destination farm came from a source farm. Finally, the migration matrix was converted to an 'oceanographic dispersal distance' matrix ODD (Crandall et al., 2014) using $\log(M^{-1})$ to transform the values to be the same rank-order as geographic distance (high proportion of settlers then have a short distance) required for many network-based algorithms.

The connectivity matrices described previously represent the edges in our networks. We derived 52 respective networks of our salmon louse system, one for each week of the simulation period. To identify firebreaks, connectivity matrices were aggregated into four consecutive 13-week periods: winter (weeks 4–13), spring (weeks 14–26), summer (weeks 27–39) and autumn (weeks: 40–52). The first three weeks of the simulation were not included in our analysis because particles in the simulation released in week 1 take ~3 weeks in winter to become infected and reach a source farm. This time-frame was chosen because establishing temporal 'firebreaks' could be an effective management strategy. This is the case for fallowing, in which farms are 'removed' from production for a period of time after harvest, for a duration of approximately 12 weeks (Bron et al., 1993). In addition, spring is considered a critical period in the year as it encompasses the season when salmon smolts migrate out into the open ocean, and are vulnerable to louse infestations. Therefore, regulatory authorities in Norway dictate that louse levels at farms have to be kept to a minimum during that time (0.2 adult female lice per fish between weeks 16 and 21) (Norwegian Food Safety Authority, 2012).

A critical step in the construction of a network is the selection of an appropriate edge threshold. The selection of an appropriate edge threshold is somewhat arbitrary, but the value should exclude 'weaker' connections, to allow the study of network properties with an appropriate network resolution. A low threshold may produce a fully connected, impractical network with no clear structure, where community-sorting algorithms will identify only one large community (Kininmonth et al., 2010). In contrast, if the threshold is such that few edges remain in the network, communities become isolated nodes and the network is also uninformative. Here, we used edge threshold values of 0.001 and 0.005 on the weights of our migration matrix M (bounded between 0 and 1) before transforming M to ODD matrix. Sensitivity analyses were performed for smaller and larger edge threshold values (0, 0.0001, 0.01, 0.1), and we settled for 0.001 and 0.005 because those produced networks with a relevant level of connectivity before farm removal, removing weak, less probable connections (average median weight for no edge threshold = 0.00018; average median edge distance = 85.6 ± 25.4 km), but keeping most demographically relevant links in the network (e.g. Treml and Halpin, 2012). These networks had approximately four components in each season, a realistic median edge distance similar to other studies (~30 km) (Kristoffersen et al., 2014; Rees et al., 2015; Shephard et al., 2016), but where most farms (~98%) were still connected in the largest connected component (LCC), rendering this metric efficient at assessing global (dis)-connectivity (see Section 2.6).

2.5. Identification of areas of no production or 'firebreaks' to louse dispersal

Community structure, or clustering, is one of the most relevant features of real-world networks (Fortunato, 2010). Network communities should have a high level of within-group connectivity (more internal edges), relative to between-group connectivity, termed modularity (Newman, 2006). However, communities often overlap such that nodes simultaneously belong to multiple groups (see Fig. 1 in Palla et al., 2005). High membership nodes or structural hubs (Hébert-Dufresne et al., 2013) are nodes in the network that belong to multiple overlapping communities simultaneously. These nodes are considered structural hubs as they act as bridges between communities and their removal may create barriers to dispersal or movement through the network. We used the link community algorithm developed by Ahn et al. (2010), and implemented in the 'linkcomm' package in R (Kalinka and Tomancak, 2011), to extract communities and detect nodes with high membership. This algorithm groups links, and so the nodes they join, rather than the nodes themselves, thereby allowing each node to belong to multiple overlapping communities.

For every season in the simulation, we selected the farms with the highest membership scores, the structural hubs, and removed them together with their direct downstream neighbours (first order out-neighbours). These clusters of neighbouring farms were considered potential firebreaks (=structural hub + first order out-neighbours). Effective firebreaks, however, were those that met two set conditions: (i) the firebreak was smaller than 25 farms (2.5% of total farms) to maintain realistic feasibility (i.e., implementation costs) and (ii) its removal created significant breaks in the network, a condition which was assessed with the metrics described in Section 2.6.

2.6. Connectivity metrics

To quantify network (dis)-connectivity we calculated the size of the LCC and a fragmentation (Fr) metric. The decrease in size of the LCC is an effective way to quantify partitioning of a graph and has been used in node removal scenarios across different disciplines (Alstott et al., 2009; Rayfield et al., 2011; Verma et al., 2014; Kobayashi and Masuda, 2016; Mourier et al., 2017). Two farms are part of the same component if they are connected by at least one path or series of edges or links between them. A drop in size of the LCC of more than 10% of its original size was considered here a significant disconnection of the network into smaller components.

The total number of components could be another obvious metric to quantify (dis-) connectivity. However, this value does not consider the sizes or numbers of farms in the different components. The removal of one node could break the network into smaller components, but one of the new components could be just a single isolated node while the majority still remains part of the LCC. Therefore, we also calculated the Fr metric developed by Borgatti (2003), which considers number and sizes of the new components:

$$\mathrm{Fr} = 1 - \frac{\sum_k S_k (S_k - 1)}{n(n-1)} \tag{1}$$

where S_k was the number of farms in component k and n was the total number of farms in the network. This metric ranges between 0 and 1, with 1 indicating the largest fragmentation.

3. Results

3.1. Spatio-temporal variability in salmon louse dispersal

Temporal and spatial variations in louse connectivity were observed over the study period and across farms in the model domain. Winter had the greatest connectivity in terms of total numbers of connections (network size), whereas summer had the lowest, with 40% less connections. This lower connectivity was distinguished by a smaller network size, and a higher number of components prior to firebreak removal (Table 1). Connections in summer were also shorter in geographic distance than connections in other seasons, but were on average stronger, as indicated by a higher mean edge weight in M. The number of out-going connections from each farm (a node's out-degree) also varied spatially across the 13 recently established production zones for salmon aquaculture in Norway (Ministry of Trade Industry and Fisheries, 2017; https://lovdata.no/dokument/SF/forskrift/2017-01-16-61?q=produksjonsomr%C3%A5deforskriften) (Supplementary Fig. S1). Weeks 1–3 were excluded from further analysis because particles released at the start of the simulation require time to become infective, particularly in cold winter weeks (January 1), and arrive at destination farms to build informative connectivity networks.

3.2. Identification of firebreaks to fragment the louse dispersal network

Removing the five farms with the highest membership score and their direct out-neighbours identified at least one effective firebreak smaller or equal to 25 farms (2.6% of total farms) for all periods in the simulation (Table 2). Removal of these effective firebreaks decreased the number of farms left in the LCC by more than 25% (mean decrease in LCC of 25%; Table 2) and increased network Fr by more than 0.2 (mean Fr = 0.46 after removal; Table 2). In spring and summer, an edge threshold of 0.005 substantially fragmented the network prior to removal of farms (Fr = 0.49 and 0.55, Table 1). Therefore, in spring and summer we tested firebreaks (structural hubs + out-neighbours) identified with an edge threshold of 0.005 (higher resolution network), but on a larger (more connected) network constructed with an edge threshold of 0.001. For spring (critical for salmon smolt out-migration), this identified two effective firebreaks (Fig. 1) that divided the network into three large unconnected components (Fig. 2). However, in summer this strategy only found firebreaks larger than 39 farms.

For winter and spring, we identified northern firebreaks at ~67°N around Vestfjorden (Table 2), east of the Lofoten Islands (Figs. 1 and 2). In spring, the size of this firebreak was 21 farms (2.2% of total farms) for a larger network (edge threshold th = 0.001) and only 10 farms (<1% of total farms) in a network built with a higher edge threshold (th = 0.005; Table 2). During winter, a firebreak in the same area was only 11 farms (1.1%). For spring and autumn, we identified the same southern firebreak at ~61°N near the northern border of zone 4 (Norhordaland to Stadt; Fig. 1). This was a smaller firebreak of only 13 farms in spring (th = 0.001) and only 16 farms in autumn (th = 0.005). For summer, our algorithm found a different firebreak, located in zone 6 at ~63°N (area of Sør-Trøndelag) constituted by 25 farms (th = 0.001).

4. Discussion

We believe this is the first national scale study analysing disease dispersal for the most problematic parasite in marine aquaculture, and the first to detect firebreaks capable of altering dispersal connectivity for a marine disease. Compared with terrestrial agriculture, marine aquaculture is an industry characterised by rapid and recent domestication (Duarte et al., 2007). The study of disease transmission in marine systems, however, still lacks the equivalent level of understanding and modelling tools developed for the control of diseases in terrestrial agricultural systems (Groner et al., 2016). Here, we propose an innovative method that

Table 1

Salmon lice (*Lepeophtheirus salmonis*) network metrics for each consecutive period (P) in the simulation from 1 January, 2016. Edge thresholds of 0.001 and 0.005 were applied to the weights of the migration matrix M (bounded between 0 and 1) to construct the networks. Edge threshold are presented in italics as column headers for each season.

Structural level	Definition	Epidemiological significance	Winter: weeks 4–13		Spring: weeks 14–26		Summer: weeks 27–39		Autumn: weeks 40–52	
Graph-level metrics	*Measure connectivity for the entire network*		*0.001*	*0.005*	*0.001*	*0.005*	*0.001*	*0.005*	*0.001*	*0.005*
Graph size	Total n° of links in the network	Reflects overall network connectivity	36,723	20,790	33,058	19,309	24,232	14,496	30,991	17,695
N° of components	Total n° of unconnected sub-graphs in the network	Highly connected networks have fewer components. They increase as the network fragments.	3	4	3	8	4	13	5	7
Median edge weight (migration matrix)	Median link weight obtained from the migration matrix, M	Proportion of lice (0–1) that arrive to each destination farm from each source farm	0.0066	0.0174	0.0071	0.0184	0.0079	0.0220	0.0067	0.0179
Median edge length (km)	Lines measured along the surface of the earth	Geographic length of links in the network	40.7	27.4	33.1	23.5	26.6	19.2	34.8	23.7
Component-level metrics	*Measure connectivity for groups of connected salmon farms*									
Number of farms in largest connected component (LCC (% of total farms in the network))	Total n° of nodes in the largest connected sub-graph or component	A bigger LCC reflects higher overall network connectivity	952 (98.5%)	950 (98.2%)	956 (98.9%)	619 (64%)	956 (98.9%)	567 (58.6%)	950 (98.2%)	943 (97.5%)
Fragmentation (Fr)	N° of components in relation to n° of nodes in the network (bounded between 0 and 1)	Maximum fragmentation occurs when every farm in the network is disconnected or isolated. Epidemic processes are generally contained within components	0.03	0.03	0.02	0.49	0.02	0.55	0.04	0.05

Table 2

Location and size of firebreaks smaller or equal to 25 farms (2.7% of total farms) for all periods (P) in the simulation year. Structural hubs are the nodes with the highest membership score in the network (Ahn et al., 2010).

Location of structural hub			Membership of structural hub (n° communities)	Size of firebreak (n° of outgoing neighbour farms from structural hub)	Size of firebreak (%)	Size LCC after firebreak removal (n° farms)	Decrease in LCC[a] (n° farms)	Decrease in LCC[a] (%)	Increase in number of components	Fragmentation (Fr) after removal
Longitude	Latitude	Zone								
P1 th = 0.005										
15.2	68.3	9	11	24	2.48	701	−249	−26.2	+3	0.40
15.1	68.3	9	11	24	2.48	700	−250	−26.3	+3	0.40
P2 th = 0.001										
18.5	69.9	11	12	25	2.59	850	−106	−11.1	+1	0.18
17.9	69.5	10	10	24	2.48	838	−118	−12.3	+2	0.20
P2 th = 0.001 (for edges); 0.005 (for identifying structural hubs)[b]										
5.0	61.5	4	13	13	1.34	633	−323	−33.8	+1	0.45
14.7	67.4	9	12	21	2.17	672	−284	−29.7	+2	0.42
P2 th = 0.005										
5.0	61.5	4	13	13	1.34	619	0	0.00	+2	0.48
14.7	67.4	9	12	10	1.03	353	−266	−42.9	+1	0.69
P3 th = 0.001										
6.2	62.6	5	12	25	2.59	576	−380	−39.75	+2	0.49
P3 th = 0.005										
8.2	63.3	6	6	24	2.48	452	−115	−20.28	+2	0.65
8.4	63.4	6	6	23	2.38	450	−117	−20.63	+2	0.65
P4 th = 0.005										
5.0	61.5	4	10	16	1.65	620	−323	−34.25	+3	0.47

[a] *LCC* = largest connected component, *Fr* = fragmentation, *th* = edge threshold applied to migration matrix.

[b] With a higher edge threshold (th = 0.005) networks in P2 and P3 had a high fragmentation before removal, and therefore we tested the effect of removing structural hubs identified with a higher resolution (th = 0.005), but on a more connected network (th = 0.001). In period 3, this only identified effective firebreaks larger than 39 farms (data not presented here).

identifies firebreaks to the dispersal of a marine parasite by removing key nodes in a network model.

Our method identified at least one effective firebreak smaller than 25 salmon farms (2.6% of total farms in the region) for all seasons. Furthermore, for a critical period of the year (spring), where louse levels must be minimised to protect out-migrating wild salmon smolts, we identified two firebreaks (at ~61°N and 67°N) that fragmented the entire network into three largely unconnected groups or components. Firebreaks in spring were created by removing 13 and 21 farms (~1.3% and 2.1% of all farms in Norway), and their removal left no connections between components in a highly connected network constructed with a low edge threshold value (0.001). Overall, our study illustrates how louse dispersal models coupled to network analysis can aid future spatial planning

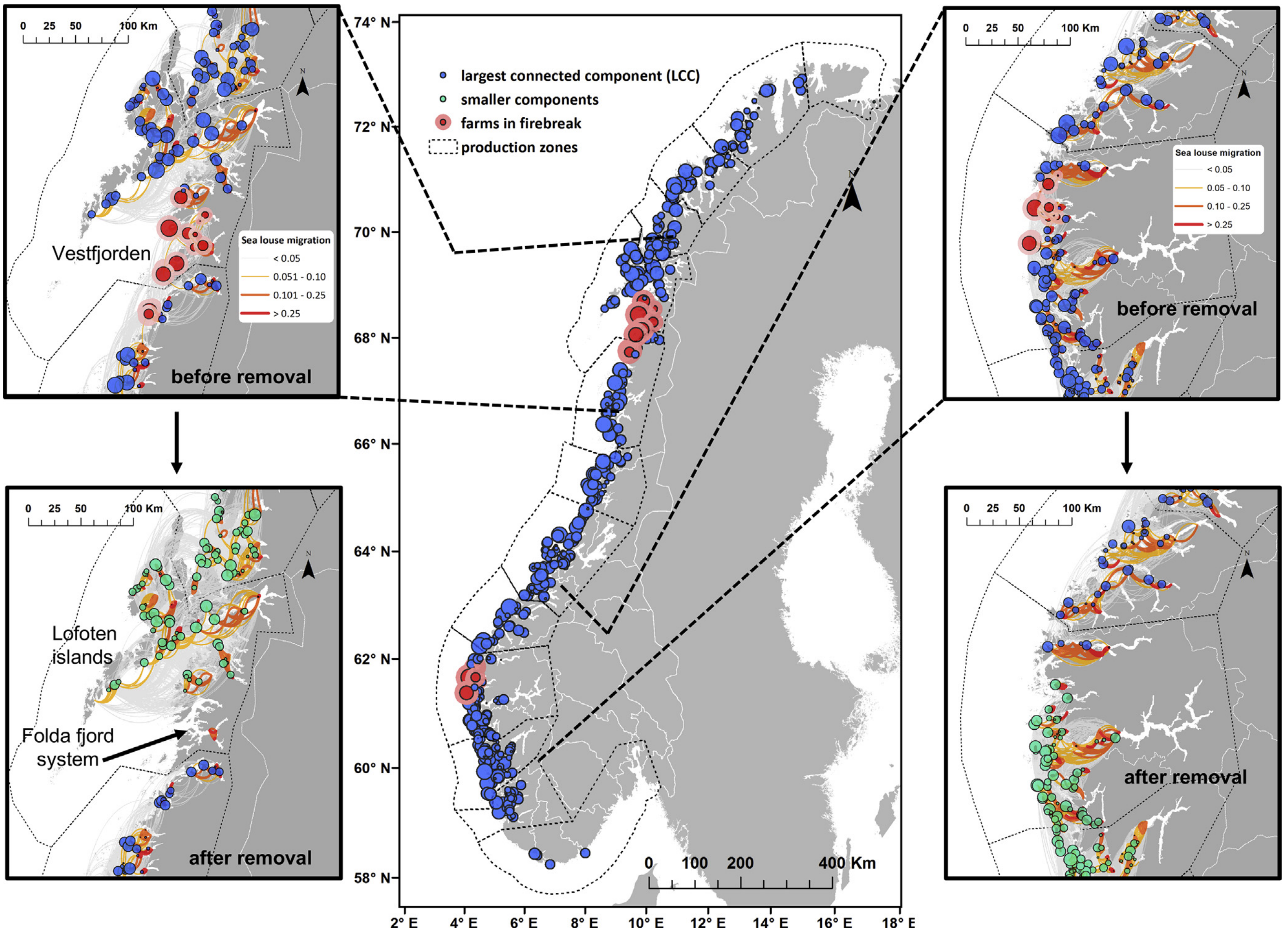

Fig. 1. Main firebreaks identified for the salmon louse (*Lepeophtheirus salmonis*) dispersal network during spring (period 2, weeks 14–26). Firebreaks are constituted by structural hubs (farms that belong to multiple overlapping communities) and their direct out-neighbours. The size of the northern firebreak (inset; Vestfjorden, before removal) was 10 farms with a higher edge threshold (th = 0.005) on the migration matrix (M), and 21 farms with a lower edge threshold (th = 0.001). The southern firebreak (far right panel, before removal) was only 13 farms in period 2 (th = 0.001 and 0.005), and was also effective at splitting the largest connected component in period 4 (weeks 40–52) with only 16 farms (th = 0.005). Circles represent all farms in the model domain belonging to different components and their sizes are scaled according to betweenness. Lines represent links or edges with values from the migration matrix (M) showing connections equal to or greater than 0.001 (edge threshold). Dotted polygons represent the 13 production areas (numbered from south to north) for salmon aquaculture in Norway (Ministry of Trade Industry and Fisheries, 2017). White borders represent county boundaries in Norway.

of the salmon industry and identify farm locations critical to the connectivity of the entire system.

Until recently, studying the dispersal of marine pathogens was hindered by a lack of appropriate modelling tools (Adams et al., 2012; Groner et al., 2016). But today, after more than a decade of research, we have in our toolbox a state-of-the-art dispersal model (Asplin et al., 2004, 2011, 2014; Johnsen et al., 2014) capable of accurately predicting transmission of salmon lice and realistic infection pressure at different locations (Samsing et al., 2016a; Sandvik et al., 2016). This work has enabled the development and implementation of model-based management strategies based on realistic patterns of louse dispersal. The recent establishment of the 13 salmon production areas in Norway is a direct outcome of this approach (Ministry of Trade Industry and Fisheries, 2017; https://lovdata.no/dokument/SF/forskrift/2017-01-16-61?q=produksjonsomr%C3%A5deforskriften). Here, we used results from the dispersal model and applied network analysis to simulate different connectivity scenarios for louse dispersal at a nation-wide scale. Our study shows that network metrics can be used to identify potentially cost-effective management strategies in a highly complex marine aquaculture system, which may ultimately restrict the uncontrolled spread of lice epidemics and set barriers to disease propagation.

Graph theory has long been concerned with the identification of influential nodes and the robustness (or vulnerability) of different networks to node removal scenarios (Hébert-Dufresne et al., 2013; Verma et al., 2014). The purpose of identifying key nodes varies across different real-world networks and different disciplines. In conservation biology, finding and protecting nodes that hold the network together is a vital process in the design of protected areas (Kininmonth et al., 2011; Melià et al., 2016). In this context, network analysis can identify strategies to maximize connectivity by allowing the dispersal of individuals between habitat patches (e.g., coral reefs) and thus the flow of genes among populations (Matz et al., 2018). Breaks and isolation, on the other hand, may lead to population bottlenecks and loss of genetic diversity. Accordingly, network models can also be used to explore processes/methods to limit or decrease harmful connectivity (Hock et al., 2014). To protect a network against epidemic processes, network models can be used to identify influential nodes and develop efficient 'immunization algorithms' (Hébert-Dufresne et al., 2013; Kobayashi and Masuda, 2016). At the onset of a disease outbreak,

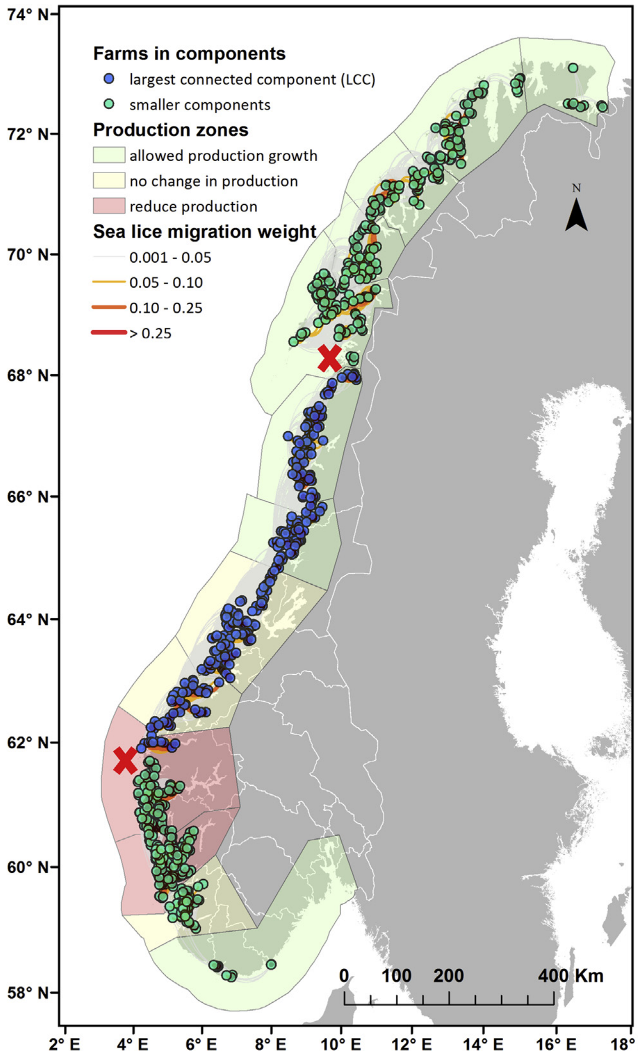

Fig. 2. Fragmentation of the salmon lice (*Lepeophtheirus salmonis*) after the removal of farms in the northern and southern firebreaks during spring (period 2, weeks 14–26). Firebreaks are constituted by structural hubs (farms that belong to multiple overlapping communities) and their direct out-neighbours: 10 or 21 farms constitute the northern firebreak (depending on edge threshold, 0.005 and 0.001, respectively) and 13 farms the southern firebreak independent of edge threshold. Removal of these firebreaks (crosses) fragments the network into three large components, leaving no connections between them for the entire 13 week period. Circles represent all the farms left in the model domain belonging to different components. Lines represent links or edges with values from the migration matrix (M) showing all connections equal or greater than 0.001 (edge threshold). Polygons represent the 13 production areas (numbered from south to north) for salmon aquaculture in Norway, and those are shaded according to the status given to each one by the latest 'traffic light system' regulation (Ministry of Trade Industry and Fisheries, 2017; https://lovdata.no/dokument/SF/forskrift/2017-01-16-61?q=produksjonsomr%C3%A5deforskriften). In the production zones, dark shaded/red zones mean farmers must reduce production, pale shading/yellow means no change in production level and medium shading/green offers production growth. Reduction of biomass in dark shaded/red zones will first be implemented in 2019.

for example, mass immunization campaigns generally have a limited budget, and therefore must be optimized to identify the least number of nodes to immunize or 'remove' to achieve the largest fragmentation of the network.

One way of doing this is by modelling the sequential removal of nodes from a network. With this method, connectivity metrics, such as betweenness, are re-calculated at each step until the desired level of (dis)-connectivity is reached (Hébert-Dufresne et al., 2013). A node's betweenness is the proportion of shortest paths between all node pairs in the network that pass through a given node (Newman, 2006). Mapping betweenness scores on a dispersal graph highlights the 'most used' routes or important dispersal pathways, highlighting key stepping-stones in a dispersal network (Treml et al., 2008). However, this stepping-stone analysis does not have the ability to effectively identify those nodes which form important bridges between different parts of the network.

An alternative approach to sequential removal of nodes from a network is what we propose here: establishing firebreaks by removing structural hubs. Local information on a given node and its surrounding neighbours is sufficient to estimate a node's membership and its role as a structural hub. Moreover, local measures of connectivity, as opposed to global ones, are less sensitive to incomplete or incorrect information about the entire network (Hébert-Dufresne et al., 2013). At a local structural level, removal or relocation of farms will only affect the membership of farms directly in the neighbourhood of the adjustment. In contrast, similar alterations can impact betweenness scores of distant nodes anywhere else in the network due to cascading effects (Hébert-Dufresne et al., 2013). This means that the sequential removal strategy, which re-calculates metrics at each step, can be highly vulnerable to variations in the order in which farms are removed from the network, rendering this strategy harder to implement. Conversely, the simultaneous removal of a block of nodes around a structural hub and the consequent establishment of a firebreak is, in practical terms, easier to implement.

The establishment of firebreaks is highly relevant in the field of epidemiology. The process of removing keys nodes and consequent partitioning of the network into smaller components can limit or restrict an epidemic outbreak. If a disease outbreak starts within a group of connected nodes, the transmission of the disease within this group will not lead to new outbreaks. However, when the agent crosses over to another group of densely connected nodes through a structural hub bridging groups, the epidemic process propagates and the outbreak is harder to control. This is the principle behind the establishment of host-free areas or firebreaks to control disease dispersal. When nodes are isolated within separate components it means that there are no connections left between them. In our study, where lice were released from every farm at a constant rate and connectivity was captured every week, a firebreak capable of restricting all connections between components for a 13-week period represents a robust barrier to disease propagation.

Firebreaks could reduce louse infection pressure on downstream farms. Louse dispersal models show that the majority of infective louse particles are transported out of the fjords (Figs. 1 and 2) and northwards along the coast (Samsing et al., 2017). Consequently, southern firebreaks reduce infection pressure on areas located further north. The southernmost firebreak, located in the northern border of zone 4 at ~61° (Nordhordland to Stadt), can shield the rest of the country, or at least neighbouring zones 5 and 6, from the influx of parasites coming from the two most densely farmed areas in the country: zones 3 and 4. Based on their persistently high levels of lice per fish and the density of farms in the area, these problematic zones have recently been given a 'red light' under a new regulation implemented in Norway (Ministry of Trade Industry and Fisheries, 2017). This new regulation, the so-called 'traffic light system', is based on the predicted impact that aquaculture can have on wild salmon populations within each zone based on the number of farms per area, historic levels of lice on farmed fish and the predicted exposure of wild fish populations. Under this new legislation, areas given a 'red light' must decrease production by 2019 to reduce their impact on wild fish. Areas 5 and 6 were given a 'yellow light', which means no change in production level, but no growth either. Accordingly, a firebreak located between zones 4 and 5 could significantly reduce infection pressure on yellow zones 5 and 6.

A second firebreak, effective in spring, was located south from Vestfjorden and around the Folda fjord system. This firebreak was constructed with the structural hubs detected by the algorithm (Ahn et al., 2010) on a higher resolution graph constructed with less connections (edge threshold = 0.005), but tested on the more connected version of the network (edge threshold = 0.001). We did this to test how robust structural hubs were to variations in edge threshold, and to examine how efficient firebreaks were at fragmenting more connected versions of the network. This demonstrated that when graphs are structurally informative, structural hubs are fairly robust to edge threshold level. Further, it reveals that the firebreak will efficiently partition the network and restrict louse connectivity. If introduced, it could reduce infection pressure on farms around the Lofoten Islands and disconnect all farms in northern Norway from farms further south.

Firebreaks could be practically achieved in multiple ways: (i) farm removal, (ii) farm relocation to 'safer', less connected locations, (iii) requiring farms within a firebreak to produce fish using methods that completely uncouple them from the wider environment, such as closed-containment farming systems (e.g., Nilsen et al., 2017), or (iv) via mandatory establishment of coordinated fallowing periods of ~13 weeks between production cycles to create temporal firebreaks to louse dispersal (Werkman et al., 2011). In addition, our methodology could help optimize future farm siting, allowing industry growth without significantly increasing connectivity. For example, within the new production zones proposed by Norwegian authorities for salmon aquaculture (Ministry of Trade Industry and Fisheries, 2017) a network approach could map 'hot spots' for connectivity, and rank geographic sites according to their contribution to overall connectivity.

The permanent removal or relocation of farms in the firebreak could slow down the evolution of drug resistance in sea lice by hindering the spread of genes that may have emerged at specific locations. Wild salmon can carry sea lice with genes that code for drug resistance and they may be responsible for distant dispersal of point mutations that originated at a specific site (Besnier et al., 2014). However, in Norway, wild Atlantic salmon (*Salmo salar*), which migrate into the open ocean, and may therefore be responsible for long-distance dispersal of genes that code for drug resistance, have a very limited population size compared with farmed Atlantic salmon (see Section 2). This means that the great majority of lice originate at farms, and reducing connectivity of farm-originated louse populations could have a significant impact on controlling the evolution of sea lice against chemotherapeutants.

Our method could also be used to define the redistribution of maximum allowable biomasses to reduce connectivity. Edges in our graph were weighted, and the weight was calculated from the number of particles going from a source farm and arriving at a destination farm, re-scaled by the maximum allowable biomass of fish at each source. This is a practical approach for quantifying variations in connectivity based on a node's size (Galpern et al., 2011). Changing the weight of these connections modifies connectivity patterns. For example, reducing the maximum allowable biomass of fish at key structural hubs could virtually 'remove' influential farms from the network and increase fragmentation. Moreover, our analysis could also test the redistribution of biomass to other less connected sites, maintaining production levels in a given area.

A complementary approach that could be modelled using our method would be the redistribution of louse quotas. The current regulation states that all farms have to treat fish when they reach a treatment threshold of 0.5 female lice fish^{-1} (0.2 female lice^{-1} fish during spring migration of salmon smolts from weeks 16 to 21). The number of female lice fish^{-1} multiplied by the total number of fish at each site determines the louse output from a given farm. The main issue with low louse quotas, which are the same for all farms irrespective of size and position, is that farmers must treat their fish multiple times during a production cycle to satisfy these strict regulations. This, in turn, accelerates the evolution of treatment resistance and begins a vicious cycle: lice become resistant and more treatments are required to meet the regulations (Aaen et al., 2015). A strategic redistribution of lice quotas could let certain locations to have more or less allowable lice per fish based on their contribution to overall connectivity.

Our firebreak modelling framework could also be applied at a smaller regional scale to define fallowing areas or no-production areas within production zones. This could be done for sea lice, but also for other marine pathogens. For salmonid alphavirus (SAV), a virus of increasing concern along the southwest coast of Norway, and the pathogenic agent that causes pancreas disease (PD), our model could help control outbreaks by strategically defining no-production areas or by identifying farms that need to be removed to control an outbreak. Compared with other viruses, SAV can remain viable in the water column for extended periods of time (up to 60 days) (Graham et al., 2007), and therefore hydrodynamic dispersal models are necessary to understand and control the transmission pathways of this virus.

Our findings on louse dispersal and connectivity are based on models. As such, they encode multiple assumptions. We assume, for example, that arrival of louse particles at a destination farm equals louse settlement. However, environmental drivers such as water temperature will influence settlement rates of louse copepodids. At lower temperatures, models show that lice can be transported very long distances (up to 400 km) (Samsing et al., 2017), but successful settlement rates are hindered by temperatures lower or equal to 5 °C (Samsing et al., 2016b) due to the depletion of energy reserves in these non-feeding larvae (Tucker et al., 2000a). If successful settlement rates were included in our connectivity models, winter simulation periods and northern locations would have lower connectivity than predicted in our model. As such, our northern firebreaks could be smaller and still deliver the same effect. In addition, we used an effective connection threshold of 0.001 and 0.005 on our M matrix (bounded between 0 and 1), which produced networks with a realistic connection length (~30 km) (Kristoffersen et al., 2014; Rees et al., 2015; Shephard et al., 2016), similar to that determined by other studies. Most weak connections, removed by applying a threshold on the M matrix, are long distance connections with a low probability of occurrence (low edge weight). From a technical point of view, with no edge threshold, the network retains a great proportion of unrealistically long and weak connections (median edge length >40 km, median edge weight <0.007, Table 1), with many of those on the scale of hundreds of km. This highly connected network is not very informative since its underlying structure is masked by many long, weak connections, and the clustering algorithms may fail to detect sensible sized firebreaks. From a biological point of view, we are confident in our choice of threshold. A lower threshold, or no threshold at all, would create a network where approximately 30 or 40% of connections are too long (>100 km), and even though such dispersal events may occur, they would likely have little impact on louse epidemics due to low settlement rates of older copepodids (Tucker et al., 2000b). Finally, there might be inter-annual variations in currents and connectivity not captured by our simulation, but most variations in connectivity are driven by season (and not year) (Samsing et al., 2017), and therefore we are confident that our 1 year high resolution model captures the network structure of salmon louse dispersal.

We demonstrate that establishing firebreaks around structural hubs can disconnect the salmon louse's dispersal network at a national scale. The demographic and/or evolutionary outcomes of this process, however, require further investigation. In the short term, reducing louse connectivity could decrease louse infection pressure on both farmed and wild salmon. In the longer term, disconnection of the louse dispersal network could constrain the spread of genes that code for drug resistance and slow the evolution of this process. Complete disconnection of populations is, however, unlikely, as salmon lice are thought to constitute a single panmictic population in the North Atlantic (Besnier et al., 2014). Nonetheless, disconnecting the louse network, as much as practically possible, will still benefit all players in the system.

Ultimately, the establishment of firebreaks based on realistic connectivity can effectively control transmission of other waterborne pathogens in marine ecosystems (e.g., Hock et al., 2014). To implement this, different biological parameters can be coded into the particle tracking model and the structural elements of the network (nodes and links) can be adjusted to reflect different seascape features and disease processes. Accordingly, our model-based approach could be used to inform the sustainable management of different marine pathogens and set the baseline for a new paradigm for controlling diseases in the ocean.

Acknowledgements

Funding was provided by the Research Council of Norway through the Havbruk program to project # 244439 “Regional lice assessment - towards a model based management system” to FO and TD, an Australian Research Council Future Fellowship to TD, and an Australian Postgraduate Training Research Scholarship (IPRS) to FS.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2018.11.005.

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