Network analysis reveals strong seasonality in the dispersal of a marine parasite and identifies areas for coordinated management

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ABSTRACT

Context. Sea lice are the most significant parasitic problem affecting wild and farmed salmon. Larval lice released from infected fish in salmon farms and their transport by water masses results in inter-farm networks of lice dispersal. Understanding this parasite connectivity is key to its control and effective management.

Objectives. Quantify the spatial and seasonal patterns in sea lice (*Lepeophtheirus salmonis*) dispersal in an area with intensive salmon farming. Identify emergent clusters in the network, where associated salmon farms could be used for coordinated management and spatial planning of the industry.

Methods. We used a biophysical model to simulate lice dispersal from 537 salmon farms along the Norwegian coastline for two seasons (spring and winter) from 2009 to 2014. We used network analysis to characterize dispersal pathways and quantify the spatial and temporal patterns in connectivity.

Results. Lice dispersal patterns and network metrics varied greatly between seasons, but differences were consistent amongst years. Winter networks presented more connections, and links were on average two times longer (average winter median = 36.5 ± 7.6 km, mean $\pm$ SE; average spring median = 17.8 ± 1.7 km). We identified 12 emergent farm clusters, which were similar across seasons and with the production areas for salmon aquaculture proposed by the Norwegian government.

Conclusions. Seasonal variations in lice development times, oceanographic processes and the topological arrangement of salmon farms affect lice dispersal patterns. We have identified a biologically meaningful and politically tractable alliance structure for sea lice management consisting of closely-associated clusters of farms.

Key words: connectivity; spatial epidemiology; spatial planning; sea lice; *Lepeophtheirus salmonis;* cluster analysis; community detection; disease management.

INTRODUCTION

Large-scale epidemics are affecting ecologically and economically important marine species (Harvell et al. 2004; McCallum et al. 2004). The origins of most of these marine diseases are still poorly understood (McCallum et al. 2004), however over the last 50 years the expansion of industrial aquaculture has facilitated the proliferation of numerous marine pathogens (Harvell et al. 1999; Murray and Peeler 2005). In cold temperate coastal ecosystems, salmon farms are now common artificial elements (Dempster et al. 2009), producing globally over 2.3 million tons of fish per year (FAO 2016). Farming of salmon in open net pens has a range of ecological impacts, including the amplification of parasites (Costello 2009b). Sea lice (*Lepeophteirus salmonis* and *Caligus* spp.) are today the most significant parasitic problem affecting both Pacific and Atlantic salmonid species (Burka et al. 2012). These external parasites are directly transmitted between hosts by infective planktonic larvae, causing substantial economic losses to the industry (Costello 2009a) and threatening wild fish populations (Krkošek et al. 2011; 2013). To control sea lice on farmed fish, treatment with antiparasitic chemicals have been the preferred method (Helgesen et al. 2017), although mechanical treatments with fresh or warm water have become increasingly common in recent years (Norwegian Food Safety Authority 2016). Repeated pharmacological treatments combined with a limited number of delousing chemicals available in the market have accelerated the evolution of drug resistance in sea lice (Denholm et al. 2002; Aaen et al. 2015). A preventive-based approach to control sea lice is therefore paramount, and is a conservation and management priority.

Epidemiological theory has shown that to control disease transmission, either pathogen removal must be increased or the rate of new recruits must be reduced (Anderson and May 1979). Under this principle, effective lice control measures should aim at 'disconnecting' lice populations by strategically positioning habitat patches (i.e., salmon farms) at epidemiologically significant distances from each other or by effectively treating infected farms (Werkman et al. 2011; Murray and Gubbins 2016). Traditionally, treating infected farms consisted of using chemical approaches to kill sea lice, either delivered via medicated feeds or immersion in chemical baths (Aaen et al. 2015). As mentioned previously, drug resistance is a widespread problem with this approach, which often does not confer

long lasting protection. Consequently, after treating with these costly chemicals, if treatment is not coordinated within the surrounding seascape, immediate reinfection from neighbouring farms significantly reduces the effectiveness (Arriagada et al. 2017). A simple and cost-effective solution to improve treatment efficacy is to coordinate management among neighbours by synchronizing treatments (Bron et al. 1993; Green 2010; Murray and Gubbins 2016). Characterizing and quantifying sea lice movement among farms and identifying strongly connected neighbours may be a novel approach for understanding lice transmission dynamics and finding an optimal strategy for lice control.

Networks describing lice movement can be interrogated using graph theoretic approaches to identity highly connected neighbours and answer these 'disconnecting' questions. In the last decade, the use of graph (or network) theory has become a popular tool in the study of landscape connectivity and is often used to explore and quantify spatial and temporal patterns in real-world networks. Here we define connectivity as the dispersal potential of individuals (lice) between habitat patches (salmon farms). Structurally, our networks consist of a single set of salmon farms, represented by 537 nodes, and a series of functional connections (seasonal and annual lice dispersal pathways), represented by the links in our network.

No previous study has quantified lice dispersal across this large geographic seascape or quantified dynamics across seasons. Previous studies have analysed lice connectivity in spring only (Johnsen et al. 2014; Sandvik et al. 2016), in a single year (e.g., single year temporal domain, Adams et al. 2016), and for much smaller areas (e.g., one fjord, Johnsen et al. 2016). It is certainly vital to assess lice connectivity in spring since this is the period when wild juvenile Atlantic salmon (*Salmo salar*) migrate from rivers into the open ocean and sea trouts (*Salmo trutta*) are found feeding close to salmon farms (Sivertsgård et al. 2007; Thorstad et al. 2007; Middlemas et al. 2009). Moreover, in spring and summer higher water temperatures are associated with higher lice abundances on farmed fish due to higher infection success rates and shorter generations times (Samsing et al. 2016b). For farm management purposes, quantifying winter lice connectivity is also critical. Salmon farms generally experience a lice infestation peak during winter when temperatures are typically low (Heuch et al. 2003; Lees et al. 2008). In addition, sea lice grow larger and produce more eggs in colder waters (Samsing et al. 2016b),

and thus over-wintering females can release more larvae than summer brooders (Costello 2006). These previous studies use high-resolution models in space (e.g., 200×200 m grid cells, Johnsen et al. 2016) or time (e.g., weekly dispersal matrices, Adams et al. 2016), and can be better at resolving complex topographical features or fine-scale temporal variations. These fine-grain models can improve dispersal predictability and the understanding of local processes driving connectivity and are complementary to broad-scale studies.

Seasonal fluctuations in water temperature and currents could generate large variations in lice development times and connectivity patterns. Moreover, the planktonic larval lice respond to environmental cues such as light intensity and salinity gradients by migrating vertically in the water column (Heuch et al. 1995; Flamarique et al. 2000; Bricknell et al. 2006). These changes in their vertical position will likely modify the strength and direction of their horizontal transport due to the stratified nature of the ocean. To capture this complexity, we used models that combine detailed oceanographic parameters with the realistic biology of sea lice (Salama and Rabe 2013; Groner et al. 2016). Here, we use a coupled biological-physical model of lice dispersal that allows for temperature-development and vertical movement of simulated lice particles in response to oceanographic data to predict lice dispersal among salmon farms along the Norwegian coastline. The predicted lice dispersal patterns were used to build inter-farm networks to (1) quantify seasonal and annual variations in dispersal, (2) characterize and quantify dispersal distances between farms and (3) identify highly connected clusters of salmon farms. This innovative approach can be used to inform management policies and spatial planning of the salmon industry (e.g. future placement or translocation of salmon farms) to minimize lice transmission to both farmed and wild salmon populations.

METHODS

We used an existing spatially explicit biophysical model (Asplin et al. 2014; Johnsen et al. 2014) to simulate the dispersal of farm-originated *L. salmonis* larvae along the Norwegian coastline for two seasons (spring and winter) in every year from 2009 to 2014. The lice dispersal model consisted of a hydrodynamic model and a particle-tracking module. The emergent dispersal pathways from this

coupled model were used to build networks of lice dispersal. Although the focus of this study was the inter-farm connectivity of sea lice, our methodology is widely applicable to the characterization and management of epidemics across marine and terrestrial systems.

Study Area

Our study area encompasses the western fjords of Norway, a topographically complex area of fjords, islands, narrows and bays along the southwest coast of this country (Fig. 1; N 57-67°, E 3-13°). The variable topography and physical environment create a complex circulation system where large differences in currents, temperature and salinity occur over relatively small distances. Freshwater runoff from rivers, heat transfer between sea and atmosphere, wind, tides and internal waves control the movement of water masses close to the surface, where most sea lice reside.

   All marine salmon aquaculture sites, hereafter referred to as salmon farms, were assumed to be available habitat for the settlement of competent salmon lice larvae. The location of the 537 salmon farms in the model domain were obtained from the Norwegian Directorate of Fisheries (2015), using all approved farm locations on December 2015. We have excluded from our model other sea lice sources such as wild fish populations or farms outside our model domain. The ratio of farmed to wild salmon in Norway is high, based on the number of fish held in sea cages and the number of salmon estimated to return to Norwegian rivers (2015: ~728:1, Norwegian Directorate of Fisheries 2016; Thorstad and Forseth 2016), and therefore salmon farms are the main source of infective lice in our system. Our study includes 90% of the farms in Norway and there are no farms south of our model domain and few further north.

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. The grid cell resolution chosen for our study represents an appropriate compromise between the processing power required by the hydrodynamic model and the

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size of our study area, where we are interested in resolving processes of 3 to 100 km. 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 3-dimensional currents, salinity and temperature and were used as inputs in the particle-tracking dispersal module, covering the simulation period from year 2009 to year 2014. Further details on hydrodynamic model configuration and validation are given elsewhere (Asplin et al. 2014, Johnsen et al. 2014, 2016, Sandvik et al. 2016).

Particle-tracking dispersal module

The sea lice advection and growth module was based on the Lagrangian Advection and Diffusion Model (LADIM), described in detail in Asplin et al. (2014) and Johnsen et al. (2014). Particles representing sea lice *L. salmonis* across three planktonic stages (two pre-competent or non-infective nauplius I and II, and a competent or infective copepodid) were released at each of the 537 salmons farms and transported based on the currents from the hydrodynamic model and lice behaviour. To capture temporal variations in connectivity, we modelled lice dispersal for two seasons (spring: April to July and winter: November to February), from years 2009 to 2014. We released particles hourly over 120 days in spring and 122 days in winter from every farm (~ 3000 particles per season per farm) to capture the changing hydrodynamic conditions.

Particles in the module were given vertical behaviour where they swim up towards surface light and downwards to avoid low salinity water. In the absence of stimuli, particles did not swim actively and were transported 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 (Table 1). Infective lice copepodid particles were assumed capable of settling at suitable sites (all salmon farms in the model domain) for the duration of their lifespan if they passed within a target area of 3×3 model grid cells (800×800 m) around a farm. Most farms (99%) were separated by more than 3 grids cells. Sensitivity analyses to different parameters of our dispersal model (e.g., larval mortality rates, settings for vertical swimming, grid cell size and size of the target area) were completed elsewhere (Johnsen et al. 2014; Ådlandsvik 2015; Johnsen et al. 2016). Johnsen et

al. (2014), a sensitivity study, was used to improve the lice behaviour function of our particle-tracking module, now more realistically represented in our model. In addition, Johnsen et al. (2016) found that the vertical swimming velocity influenced both the horizontal distribution and horizontal dispersion. Here, we chose the vertical swimming velocity that gave the best fit to empirical data (verification study by Samsing et al. (2016a)). Finally, Adlanvik (2015) tested sensitivity to different target area sizes (1×1, 3×3 and 5×5 grid cells), and found that it had minor impact on connection strengths and network clusters. The outputs from the particle-tracking model specified total counts of particles from a source farm that arrived at a destination farm, and were used in the connectivity modelling.

Table 1 approximately here

Connectivity modelling

For each season and year we created the 537×537 source-destination (row-column) matrix S, whose elements represent the number or total counts of lice particles starting from a source farm *i* and arriving at a destination farm *j*. The local retention of lice within source farms and the dispersal probability matrix, P, were calculated by dividing S_{ij} by the total number of particles released in the simulation (i.e., 1,600,000 particles per season across all farms). A realistic migration matrix was then calculated by multiplying P by the size of each source farm (i.e., fish biomass). In Norway salmon farms are allowed a maximum biomass in tons of fish per site, varying between sites (Norwegian Directorate of Fisheries, 2015), 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 proportionally rescale our dispersal probability P and estimate the flow of lice (i.e., flux; Urban and Keitt 2001). This flow matrix was then divided by column-sums to obtain the migration matrix, M, which represents the proportion of settlers to each destination farm that came from each source farm, was used to build the edges in our networks. The diagonal of M represents *self-recruitment or self-infection* at each 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 have a short distance), and used throughout our network analysis, unless specifically noted.

Network analysis

Nodes in our networks were the 537 salmon farms in the model domain. The total number of nodes (graph's *order)* remained constant throughout the years. Edges consisted of a 'from*'* node or source farm, a 'to' node or destination farm, and a weight describing the strength of the connection. The connectivity matrices described in the previous section constructed the edges of our graph and were used to calculate network metrics. The total number of connections (graph's *size*) reflects overall network connectivity (Treml et al. 2008). Another way of quantifying network-wide connectivity is to calculate *betweenness* for every node. Betweenness is the proportion of *shortest paths* between all node pairs that pass through any given node (Newman 2005). A *path* is a route or series of edges connecting any two nodes in a graph (Urban and Keitt, 2001). Mapping betweenness scores on a dispersal graph may highlight key stepping-stones in the network. We also identified *cut-nodes*, which are critical for the connectivity of the entire network and their removal breaks the graph into two or more components. A node's *degree* measures the number of edges linking a node with it neighbours, and includes incoming (*in-degree*) and outgoing (*out-degree*) connections. High-degree nodes may act as population sources or sinks (Minor and Urban, 2008), and may be potential sites for targeted management. All definitions and biological significance of these network metrics are summarized in Table 2. All network metrics were estimated using the 'igraph' package in R (Csardi and Nepusz 2006). Seasonal and annual differences in network metrics were compared using Welch's t-tests, with significant P-value set at 0.05.

Management targeted at individual sites may impact local network connectivity. However, coordinated actions applied on a suite of farms that are clustered may have stronger impacts on network-wide connectivity (Werkman et al. 2011; Murray and Gubbins 2016). To effectively implement coordinated management actions, farms must be grouped according to their associations (i.e., annual or seasonal lice dispersal) with neighbouring farms. Here, we used a network-based leading

eigenvector community detection algorithm to identify the emergent clusters in our salmon farm networks (Newman 2006a, b). This algorithm identifies ideal clusters by maximizing network modularity (Newman and Girvan 2003), or the density of within-cluster connections while minimizing between-cluster connections, using the leading eigenvector of the modularity matrix. This method is unconstrained by the need to find groups of any particular size (Newman 2006a).

The clusters for each season and year were combined to form a consensus matrix based on the consistency between individual partitions using resampling statistics (Simpson et al. 2010). For the consensus clustering we used the R package 'clue' and the function 'cl_consensus' (Hornik 2015, 2016). We calculated similarities between spring clusters, winter clusters, spring consensus clusters, winter consensus clusters and total consensus clusters (alliance structure) using the Adjusted Rand Index (ARI, Hubert and Arabie 1985) and the Variation of Information (VI) metric, which quantifies the amount of information lost or gained between two clustering structures (Melia 2007; Treml and Halpin 2012). Clustering with ARI values closer to one are more similar, and conversely VI values closer to 0 are more similar. We also calculated the similarity between our consensus clusters and the new Production Areas (PAs) for salmon aquaculture that will operate in Norway from October 2017 (Ministry of Trade Industry and Fisheries 2017). This regulation establishes PAs for commercial licenses of salmon aquaculture sites, and regulates production capacities within each area. PAs were established based in part on biophysical models of sea lice dispersal using spring simulations for the entire coastline (Ådlandsvik 2015). PAs were defined based on minimizing transport of lice between them using a spectral clustering algorithm (Ng et al. 2001).

RESULTS

In this study, we quantified lice dispersal for both spring and winter, and recorded total sum of lice particles transported between farms and across seasons, capturing broad-scale patterns of connectivity.

Seasonal variations in dispersal and network metrics

Representing connectivity matrices as geo-referenced graph models (Fig. 1) allow us to examine geographical patterns in dispersal at different scales. From Figures 1 and 2 it is apparent that winter networks have more connections and longer dispersal links than spring networks. We found that lice connectivity, quantified across a variety of network metrics, varied greatly between seasons (Table 2). Graph size was approximately two times higher in winter networks compared to spring (Table 2). Consistent with this higher connectedness, winter networks had higher mean out-degree (Fig. 1) and higher median betweenness (2.1 and 1.9 times higher, respectively; Fig. S1), and a lower number of isolates and cut-nodes (3.6 and 2.9 times lower, respectively). We identified ten cut-nodes common to at least one spring and one winter simulation (Fig. 3). Seasons did not differ in their median connectivity probability (from P matrices; $t_4 = 2.3$, $P = 0.09$), but the median migration weights (from M matrices) were 2.4 times higher in spring simulations (0.04 ± 0.01; mean $\pm$ SD).

Figure 1 approximately here

Dispersal connection distances

The distribution of dispersal distances was highly skewed, but consistent within seasons (Fig. 2). Most dispersal connections were longer in winter (average median = 36.5 ± 7.6 km) than spring (average median = 17.8 ± 1.7 km; Table 2, Fig. 3). The most common dispersal distances (highest peaks in the dispersal kernels, Fig. 3) were on average 10.8 ± 0.6 km in spring and 18.9 ± 3.5 km in winter simulations. Mean local retention was 1.41 times higher in winter (0.003 ± 0.0003, $t_5 = -5.1$, $P < 0.04$; Fig. S2), and mean self-recruitment was 0.64 times lower (0.29 ± 0.02, $t_{6.5} = 6.5$, $P < 0.001$).

Figure 2 approximately here

Figure 3 approximately here

Clusters of salmon farms

The highest modularity score was calculated using the M matrix, without applying a minimum threshold (Kininmonth et al. 2010). The mean number of clusters (*k*) was $k = 20.2$ (± 3.8) in spring

simulations, 9.8 (± 3.9) in winter simulations, and 15.4 (± 6.5) averaged across all seasons and years.

For the consensus clustering we set the maximum number of clusters to $k = 15$ with 10,000 iterations, obtaining $k = 15$ spring consensus clusters (Fig. 1A) and $k = 9$ winter consensus clusters (Fig. 1B).

Aggregating across all seasons and all years, we found an optimal farm clustering strategy with k = 12 total consensus clusters, where lice dispersal was minimized between clusters (alliance structure: Fig. 3). The similarity matrix comparing clusters for all seasons and years is shown in Fig. 4 and Suppl. Table S1. Similarities based on both indexes (ARI and VI) varied ~ 30%. Spring clusters had a higher mean similarity between the different years (ARI = 0.78 ± 0.22; VI = 0.32 ± 0.05), than winter clusters (ARI = 0.53 ± 0.06; VI = 0.49 ± 0.07). However, our total consensus clustering structure (alliance structure) had a high mean similarity (ARI = 0.66 ± 0.12; VI = 0.35 ± 0.11) with all partitions, and high similarity (ARI = 0.81; VI = 0.22; Suppl. Table S2) with the new production areas (PAs) proposed by the Norwegian government (Ministry of Trade Industry and Fisheries 2017).

Figure 4 approximately here

Table 2 approximately here

DISCUSSION

Our network analysis shows strong seasonality in sea lice dispersal patterns and connectivity. Winter networks were highly connected, and had longer edges than spring simulations (Table 2). These longer connections are the result of longer maturation times (pre-competency period) and increased pelagic larval duration (PLD) due to colder water temperatures, and increased current speeds along the coast going northwards in winter (Skagseth et al. 2011). Similarly, our winter networks displayed all the proxies of higher connectedness compared to spring networks: larger size, longer links, larger clusters and a decreased number of cut-nodes and isolates. These networks, however, had lower connection strengths (i.e., migration weights). In other words, winter networks have more connections, but on average these connections are weaker than in the spring. Furthermore, winter networks had lower self-recruitment compared to spring. For the epidemiology of this parasite, this implies that peak concentrations of highly infective lice are likely to be located away from its source (due in large part to

the 40 degree-day pre-competency period, Table 1), unlike other marine pathogens that are immediately

infections, such as viruses, whose peak concentration is always at their source (Murray and Gubbins,

2016).

Local retention and edge length also varied geographically. In both seasons, higher local retention

and shorter connections were common in the south, whereas lower local retention and longer edges

were observed further north (Fig. 1, Fig. S2). This difference is associated to the position of farms along

the coastline: in the north they are closer to the coast in shorter and open fjords, and in the south they

are placed mostly in the inner parts of longer and deeper fjords (e.g., Hardangerfjord). Altogether,

seasonal differences in larval duration and hydrodynamics as well as the topological arrangement of

salmon farms in coastal areas are key factors affecting lice connectivity patterns.

Given the interactions between biological and oceanographic processes that govern lice dispersal,

we expect strength to vary with distance from the source population. The null expectation is an

isolation-by-distance model where connectivity strength declines with increasing distance (Hogan et al.

2012). Statistical models of lice epidemiology show spatio-temporal correlations between lice

abundances on farmed and wild salmon up to ~ 30 km apart (Kristoffersen et al. 2014; Rees et al. 2015;

Shephard et al. 2016). Our median dispersal connection was ~ 18 km in spring and ~ 37 km in winter,

and thus up to 50% of connections in both seasons occur at similar spatio-temporal scales to previous

studies. Within these local scales, however, currents of the upper water masses of fjord-coastal areas

vary significantly in time and space (Asplin et al. 2014) and lice connectivity varies accordingly

(Amundrud and Murray 2009; Stucchi et al. 2011; Shephard et al. 2016). As a result, within these local

scales (~ 30 km) geographic distances may not be a good predictor of connectivity strength (Groner et

al. 2016). In our study this is shown by the low correlation between geographic-based distance and

oceanographic dispersal distances (ODD; Fig. S3), highlighting the crucial role of biophysical

modelling for quantifying lice connectivity in marine systems.

Despite seasonal variability, our network analysis also reveals broad geographic consistency in

connectivity patterns with relatively high similarities between total consensus clusters and all other

scenarios (Fig. 4; Suppl. Table S1). Given the existing structure of the salmon industry, our results suggest that having a single alliance structure to facilitate the coordinated management of lice is achievable. Our total consensus clusters also had a high similarity (ARI = 0.81) with the production areas (PAs) recently proposed by the Norwegian government. This new regulation divides all farms along the coastline into 13 PAs with the purpose of regulating production capacities within each area based on environmental indicators, such as lice infection pressure on wild salmon populations. The PAs proposed by the government were established based on two years of spring simulation data, and the use of a spectral partitioning algorithm. Our network analysis was based on six years of simulation data, including both spring and winter seasons, and a clustering method that optimizes modularity using the leading-eigenvector algorithm (Newman, 2006). Spectral partitioning is constrained by the requirement of having to specify a priori the number of partitions, and unless we know this in advance, blind application of the method may not always find the an appropriate division of the network (Newman, 2006). Conversely, our modularity optimization method did not set the number of partitions for every season in every year in advance, but when all these partitions were combined in the consensus clustering to find the single alliance structure the maximum number of partitions was set to 15. After the PAs proposed by the Norwegian government start operating in October of 2017, the authorities will reassess every two years if the production capacity within each area can be adjusted (reduced, maintained or increased) based on its environmental indicators. Given the consistency with our results, the network analysis presented in this study could be a useful tool for future planning and reassessment of these PAs.

The establishment of PAs is the first step towards a coordinated management system of salmon aquaculture in Norway. However, the new regulation does not yet enforce it (Ministry of Trade Industry and Fisheries 2017). Coordinated management includes synchronizing treatments or fallowing, whereby farms are emptied and not restocked for a period of time to let the pathogens die out due to the absence of available fish hosts. Recent findings suggest that coordinated management can be one of the most efficient strategies to manage marine diseases (Green 2010) including sea lice (Werkman et al. 2011; Murray and Gubbins 2016; Arriagada et al. 2017). For coordinated management to work effectively

farmers within an area must adhere to the same production cycle and subsequently fallow the whole area for three months before restocking the sites (Ritchie and Boxaspen 2011). This level of coordination, however, is logistically challenging unless strictly enforced and regulated by local and regional authorities.

In addition to coordinated management, effective disease control involves having epidemiologically appropriate boundaries that physically separate management areas. A sensible estimate for calculating the distances of these boundaries could be the maximum peak of our dispersal kernels (Fig. 3), which show that most connections were ~ 11 km in spring and ~ 19 km in winter. Gillibrand and Willis (2007) observed similar results showing that infective sea lice copepodids peaked 7 to 12 km from their source. Furthermore, Scotland has management area boundaries based on the maximum spring-tide current speeds, which creates boundaries with minimum distance of 13 km (Werkman et al. 2011). These boundaries are intended to form adequate 'firebreaks' to reduce transmission risk of different pathogens affecting salmon aquaculture. A similar firebreak distance (~13 km) could be a sensible 'rule-of-thumb' distance to reduce transmission of sea lice in our study area. However, the specific placement of boundaries should be established case-by-case and could consider the geographic and seasonal variations in connectivity as presented in this study.

Future directions

The methodology presented here could be used to assess the impacts of management interventions on local and regional patterns of lice connectivity. We could test, for example, the influence of different node-removal scenarios and identify the optimal layout of the salmon industry for minimizing connectivity. We could also determine the optimal size and location of firebreaks to reduce lice connectivity between management areas, and therefore reduce the exchange of genetic information. A recent study concluded that the mutation that confers resistance towards a common pesticide used in the control of lice developed at a single location and rapidly spread across the Atlantic (Besnier et al. 2014). Effective firebreaks or management targeted on farms that act as key stepping-stones connecting

distant locations could reduce future gene flow and potentially slow down the evolution of drug resistance. The speed of this process could also be quantified using network analysis.

Our models do not consider all the processes involved in larval connectivity. Realized connectivity is the result of the complex interactions of four main contributing processes: initiation of emigration, transport, settlement and recruitment or post-settlement survival (Treml et al. 2015). Our model incorporates the first two of these four stages: we 'initiate' emigration from farms and model larval transport by water currents, but we do not incorporate settlement and recruitment. Non-dispersal processes may result in population connectivity not being identical to larval dispersal. Sea lice settlement may vary with salinity levels (Genna et al. 2005; Bricknell et al. 2006), current velocities (Samsing et al. 2015), water temperatures (Samsing et al. 2016b) and fish behaviour (Bui et al. *unpublished data*). Infection success is considerably lower at colder temperatures (Samsing et al. 2016b) and incorporating temperature-dependent settlement rates could significantly change our predicted connectivity patterns. Similarly, low salinity levels at the destination site could also drastically reduce lice settlement (Tucker et al. 2000). An integration of all these contributing processes needs to be incorporated in future modelling of sea lice connectivity.

Conclusions

Understanding how marine pathogens are spread in the ocean is essential for effective disease management. Transmission dynamics in the ocean are variable and complex, and this is further complicated by aquaculture incorporating billions of new hosts into marine environments. Understanding the drivers of sea lice connectivity can enable the design of management strategies to reduce lice transmission and eventually reduce gene flow, slowing down the evolution of drug resistance. Our network analysis reveals high seasonality in the spread of this marine parasite, but these differences are consistent throughout time. This suggests that a unified preventive strategy based on coordinated management is feasible and could mitigate the impacts of this parasite, improving the sustainability of the salmon industry.

ACKOWLEDGEMENTS

Table 1. Biological parameterization of simulated lice (*Lepeophtheirus salmonis*) particles in the particle-tracking dispersal module.

Parameter	Value	Units
Larval pre-competency period (nauplius I and II)	40	degree-days
Pelagic larval duration (PLD, infective copepodids)	150	degree-days
Absolute swimming speed	1	mm s-1
Larval mortality	17	% day-1

Table 2. Salmon lice connectivity and network metrics for the southwest coast of Norway (N 57-67°, E 3-13°) averaged for spring (April – July) and winter (November – February) from years 2009 to 2014. References: (1) Urban and Keitt, 2001, (2) Treml et al. 2008, (3) Minor and Urban, 2007, (4) Swearer et al 1999, (5) Newman, 2006, (6) Kininmonth et al. 2010.

Connectivity metric	Definition	Ecological significance	Spring		Winter		Welch's t-Test		
			Mean	SD	Mean	SD	t	df	*P*
Graph size	N° of links or edges	Reflects overall network connectivity	5105.8	588.1	10694.8	2444.2	-5.0	4.4	0.006
N° of isolates	Unconnected nodes	Highly connected networks have less isolates	5.0	1.8	1.0	1.7	3.8	8.7	0.005

Median betweenness	Proportion of shortest paths between all node pairs	Reflects overall network connectivity. Farms with high betweennnes may represent key stepping-stones in the network, and potential sites for targeted management.	82.2	42.3	158.2	43.3	-2.9	8.6	0.018
N° of cut nodes	A node whose removal breaks the graph into components	Potential sites for targeted management.	11.5	3.2	4.2	2.2	4.5	8.7	0.002
Median migration weight (M matrix)	M matrix is obtained by rescaling P matrix by maximum allowed biomass per farm and dividing by column sums	Proportion of lice (0-1) that arrive to each destination farm from each source farm (bounded between 0 and 1), taking into account fish biomass.	0.042	0.006	0.017	0.004	8.7	8.6	<0.001
Median edge length (km)	Lines measured along the surface of the earth, and estimated from our dispersal kernel	Geographic length of the links in the network	17.8	1.7	36.5	7.6	-5.4	4.3	0.004
Mean node out-degree	Number of outgoing connections from a farm	Reflects infection pressure on other farms	9.5	1.1	19.9	4.6	-5.0	4.4	0.006
Mean local retention (P matrix)	Diagonal of P matrix	Probability that lice released from a farm are transported back its	0.0018	0.0001	0.0026	0.0003	-5.1	5.0	0.004

source

Mean self-recruitment (M matrix)	Diagonal of M matrix	Proportion of lice (0-1) settling on a farm that originate from that farm	0.29	0.02	0.19	0.03	6.5	6.5	<0.001
Mean number of clusters	Groups of highly connected farms detected using a leading eigenvector community detection algorithm	Clusters of farms could represent alliances for coordinated management actions	20.2	3.8	9.8	3.9	4.5	8.5	0.002

Figure Captions

Figure 1. Sea lice (*Lepeophtheirus salmonis*) dispersal networks. Circles represent farms belonging to

different clusters (represented by the different colours) and their size is scaled according to their out-

degree (number of out-going connection and reflects infection pressure on other farms). Lines represent links or edges with values from the migration matrix (M) showing connections equal or greater than 0.05. The direction of edges in the map is represented in a clockwise manner. Lice connectivity varied greatly between seasons, but seasonal differences were consistent between years. A) Edges for summer 2013 and summer consensus clusters (number of clusters, $k = 15$). B) Edges for winter 2012 and winter consensus clusters ($k = 9$). Winter networks have more connections and longer edges than spring networks. White borders represent county boundaries in Norway.

Figure 2. Dispersal kernel plots for all spring (2009 – 2014, red lines) and winter (2009 – 2013, blue lines) networks. The tags at the bottom of the plot indicate the precise link or edge length values for all spring (red tags) and winter (blue tags) networks. The averaged peaks of the dispersal kernels were 10.8 ± 0.6 km in spring and 18.9 ± 3.5 km in winter.

Figure 3. Total consensus clusters ($k = 12$) and cut-nodes common to at least one spring and one winter network. Dotted lines represent the boundaries of production areas (PAs) for salmon aquaculture proposed by the Norwegian government that will operate from October 2017 (Ministry of Trade, Industry and Fisheries, 2017). This regulation establishes production areas for commercial licenses of salmon aquaculture sites, and will regulate production capacities within each area.

Figure 4. Similarity matrix based on Adjusted Rand Index values (ARI: 0 – 1) comparing clusters for all seasons and years and consensus clusters. ARI values closer to one are more similar. The figure shows that spring clusters in different years had a higher similarity between each other than winter clusters, but our total consensus clustering (alliance structure) had a high mean similarity (ARI = 0.66 ± 0.12) with all partitions.

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Supplementary Table S1. Similarities between the cluster partitions obtained for spring and winter from 2009 to 2014, spring consensus clustering, winter consensus clustering and total consensus clustering using Adjusted Rand Index (below the diagonal) and Variation of Information (above the diagonal). Adjusted Rand Index values closer to one are more similar, whereas Variation of Information values closer to 0 are more similar.

	spring 2009	spring 2010	spring 2011	spring 2012	spring 2013	spring 2014	winter 2009	winter 2010	winter 2011	winter 2012	winter 2013	spring consensus	winter consensus	total consensus
spring 2009		0.30	0.42	0.31	0.65	0.26	0.37	0.70	0.61	0.22	0.23	0.61	0.54	0.44

spring 2010	0.78		0.00	0.36	0.54	0.58	0.31	0.24	0.67	0.32	0.27	0.66	0.58	0.34
spring 2011	0.72	0.80		0.56	0.71	0.33	0.59	0.63	0.50	0.50	0.52	0.49	0.37	0.32
spring 2012	0.61	0.63	0.68		0.63	0.27	0.70	0.37	0.74	0.57	0.56	0.71	0.45	0.57
spring 2013	0.72	0.66	0.64	0.85		0.41	0.58	0.33	0.69	0.39	0.37	0.62	0.40	0.68
spring 2014	0.73	0.78	0.78	0.73	0.76		0.76	0.37	0.23	0.63	0.62	0.23	0.37	0.28
winter 2009	0.55	0.50	0.46	0.53	0.54	0.50		0.29	0.61	0.60	0.57	0.59	0.53	0.53
winter 2010	0.36	0.32	0.32	0.39	0.42	0.34	0.52		0.34	0.28	0.22	0.29	0.60	0.63
winter 2011	0.48	0.47	0.51	0.68	0.68	0.55	0.50	0.58		0.49	0.48	0.47	0.24	0.44
winter 2012	0.31	0.27	0.26	0.33	0.35	0.30	0.49	0.62	0.45		0.17	0.52	0.47	0.51
winter 2013	0.45	0.39	0.37	0.43	0.48	0.42	0.59	0.55	0.49	0.46		0.49	0.48	0.54
spring consensus	0.79	0.82	0.81	0.74	0.79	0.83	0.50	0.38	0.58	0.30	0.43		0.56	0.23
winter consensus	0.43	0.38	0.37	0.49	0.52	0.42	0.65	0.82	0.64	0.71	0.64	0.44		0.37
total consensus	0.69	0.63	0.63	0.82	0.86	0.71	0.63	0.51	0.68	0.42	0.57	0.75	0.62	

Supplementary Table S2. Similarities between spring consensus clustering, winter consensus clustering, total consensus clustering and production areas (PAs) for salmon aquaculture (Ministry of Trade, Industry and Fisheries, 2017) using Adjusted Rand Index (below the diagonal) and Variation of Information (above the diagonal). Adjusted Rand Index values closer to one are more similar, whereas Variation of Information values closer to 0 are more similar.

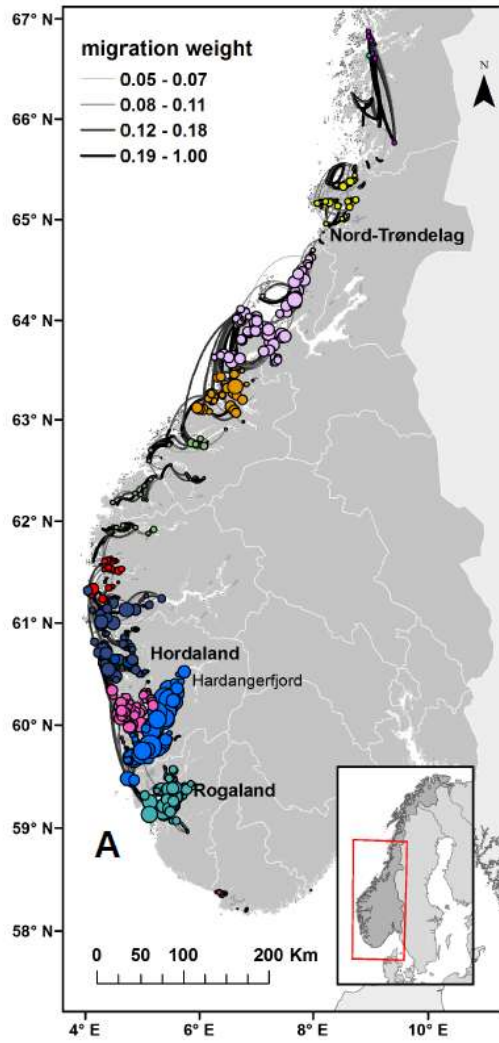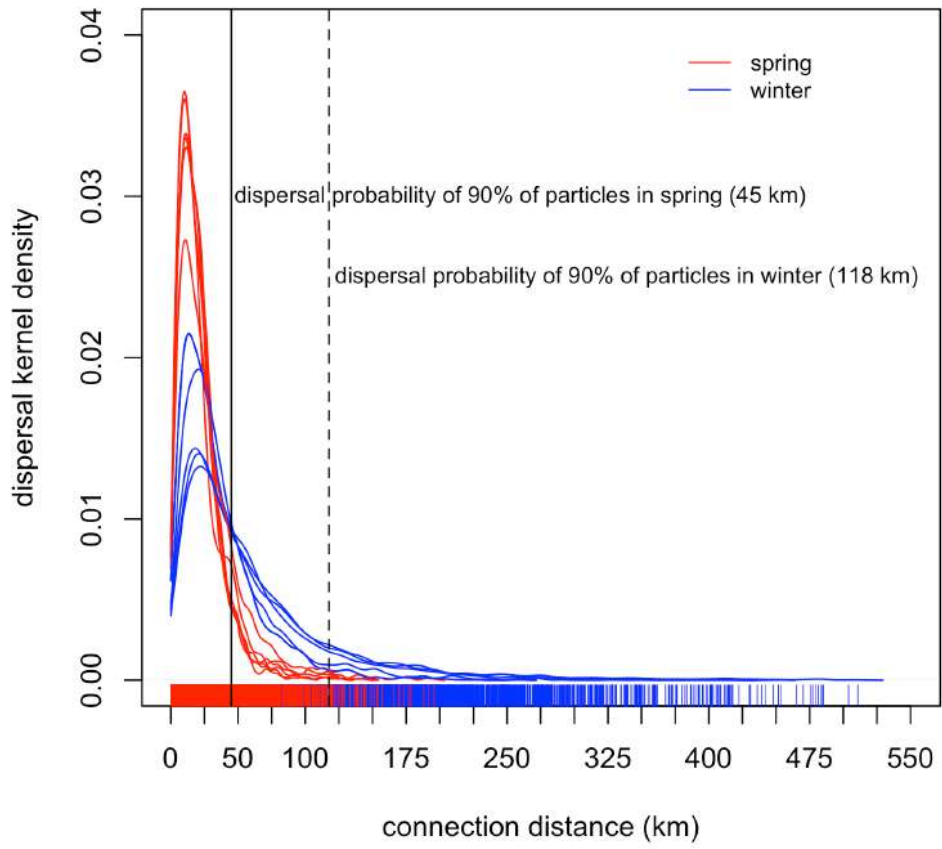|	spring consensus	winter consensus	total consensus	production zones
spring consensus		0.54	0.22	0.37
winter consensus	0.44		0.32	0.41
total consensus	0.75	0.62		0.22
production zones	0.63	0.56	0.81	

Figure S1. Salmon lice (*Lepeophtheirus salmonis*) connectivity networks between salmon farms along the Norwegian coastline. Circles represent farms and their size is scaled according to their betweenness scores. Betweenness is the proportion of shortest paths between all node pairs that pass through any given node (Newman 2005). Mapping betweenness scores on a dispersal graph highlights key stepping-stones in the network. A) Connections for summer 2013 and B) winter 2012.
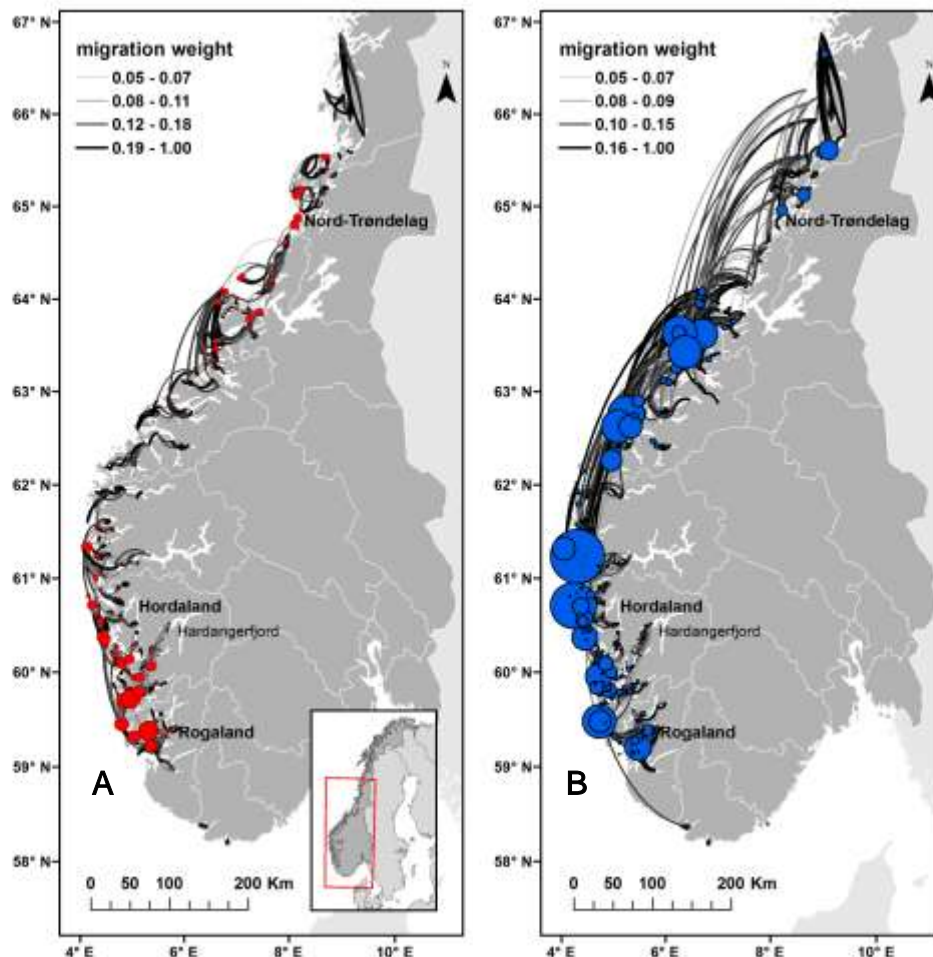
Figure S2. Salmon lice (*Lepeophtheirus salmonis*) connectivity networks between salmon farms along the Norwegian coastline. Circles represent farms and their size is scaled according to local retention. A) Connections for summer 2013 and B) winter 2012.
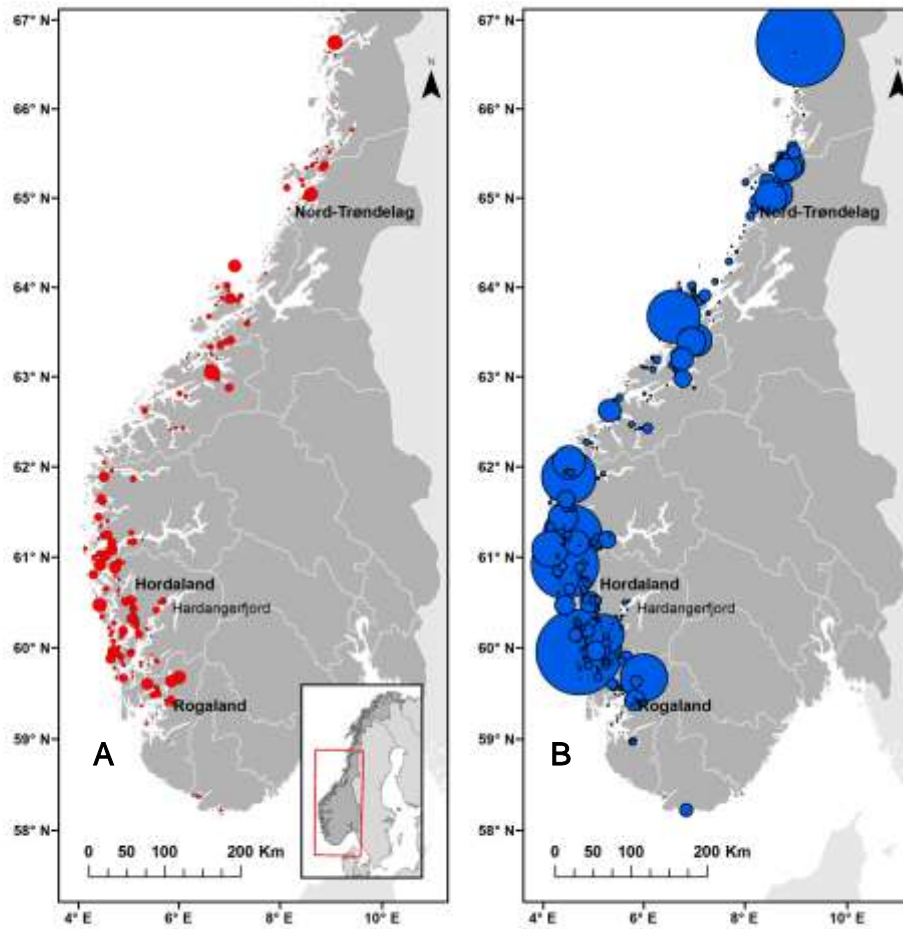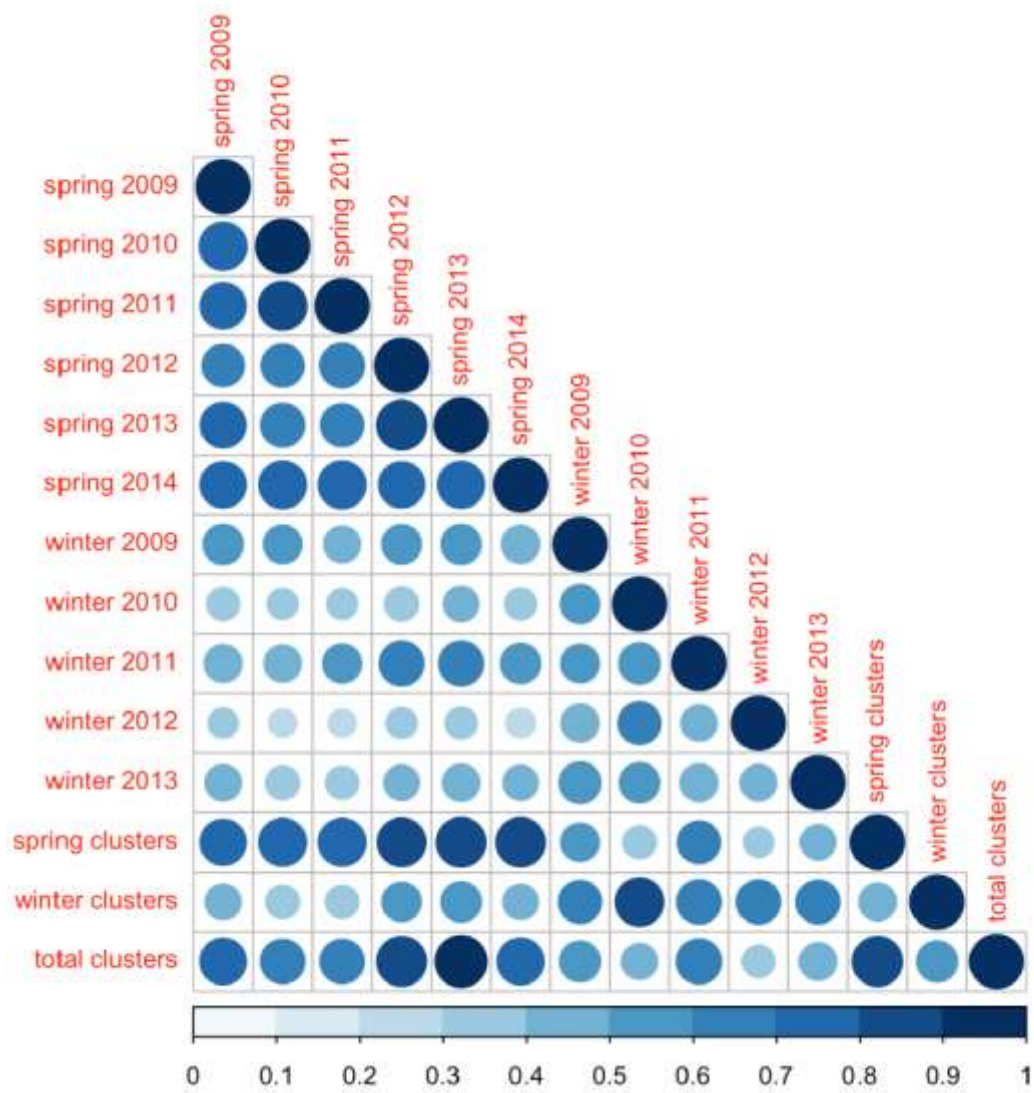
Figure S3. Correlation between geographic distance in km (log-transformed geodesic distance) and oceanographic derived distance (ODD) for A) summer 2013 (correlation coefficient from Mantel Tests $r_M = 0.31$) and B) winter 2012 ($r_M = 0.31$). To calculate ODD we convert the migration matrix, M, using $\log(M^{-1})$ to transform the values to be the same rank-order as geographic distance (high proportion of settlers have a short distance).
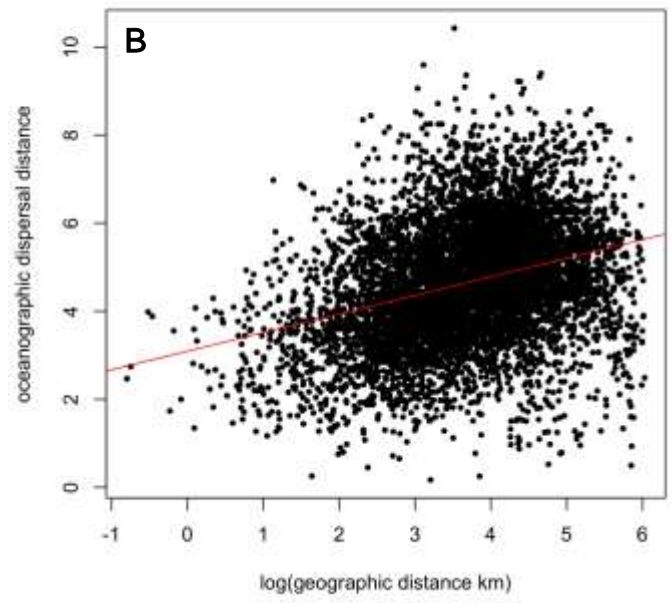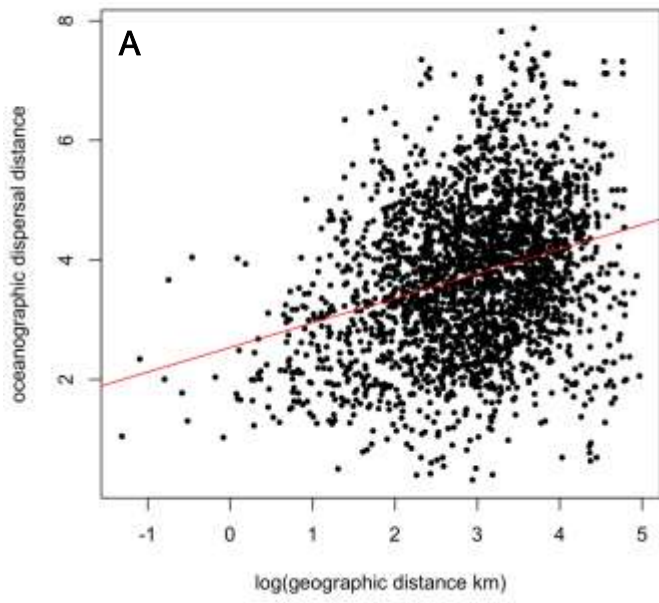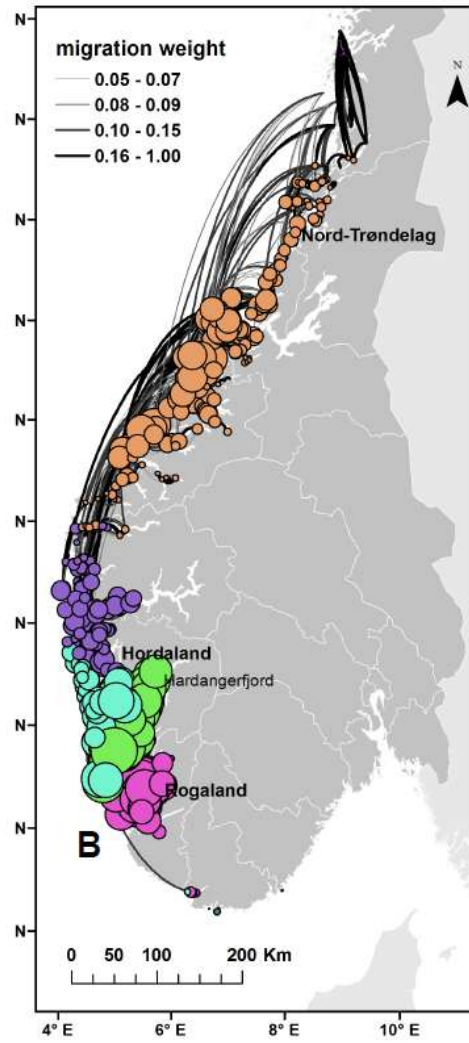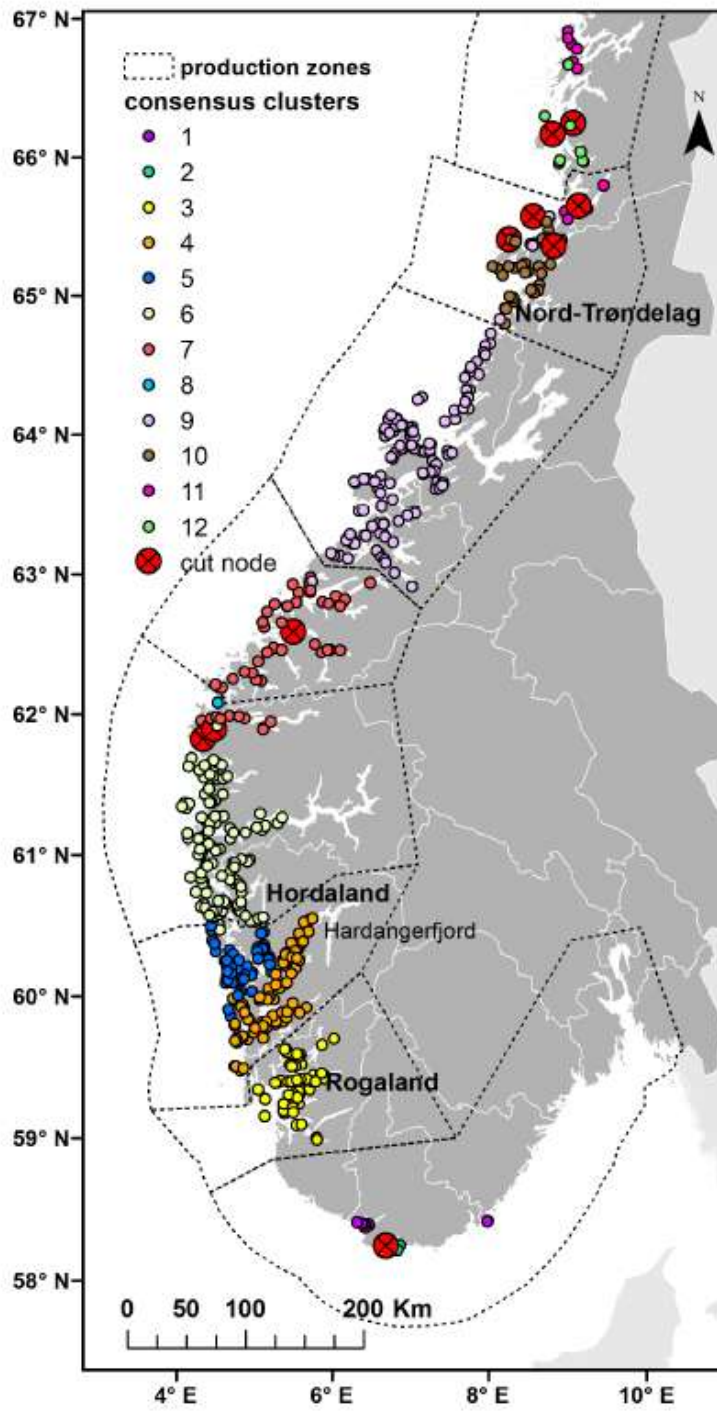
Author/s:
Samsing, F; Johnsen, I; Dempster, T; Oppedal, F; Treml, EA

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