



Temporal variability in sea lice population connectivity and implications for regional management protocols

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ABSTRACT: In modern large-scale salmon aquaculture, sites are managed within spatial units. In Scottish waters, several different definitions are used: operator-defined 'Farm Management Areas' (FMAs), regulator-defined 'Disease Management Areas' (DMAs) and 'Fish Health Management Reporting areas' (FHMRA). FMAs balance many operational requirements, while the sole purpose of DMAs is to limit the spread of disease. FHMRA are based on historical wild fish monitoring areas. One objective of these units is to monitor and limit the spread of water-borne agents such as infectious salmon anaemia and parasites such as sea lice, which present a perennial economic and ecological challenge. However, unit boundaries are either based on simplified hydrodynamic assumptions, or do not incorporate such information. Their effectiveness for infection control is therefore unclear. We used the latest developments in hydrodynamic modelling to predict population connectivity of sea lice between all current operational salmon aquaculture sites in the complex west coast of Scotland region over 1 yr (June 2013 to June 2014). Aggregating site connectivity matrices by management units, we identified the extent to which units supplied lice to (or received lice from) other units, and their effectiveness for infection control. Total estimated connectivity varied over time by a factor of 2. A general northward movement of simulated larvae was observed. Even the smallest management units reduced external infection by around 75% versus individually managed sites. Larger management units reduced estimated connectivity further. Optimised units derived by applying thresholds to site matrices suggested that management within water bodies at the scale of 50 to 100 km would be most effective.

KEY WORDS: Sea lice dispersal · Biophysical model · Population connectivity · Salmon aquaculture · Management area

INTRODUCTION

Farming of Atlantic salmon *Salmo salar* L. has increased dramatically over the last 4 decades, with production operations focussed on those areas providing the most suitable conditions for operation, with water temperatures within a specific range and fjordic coastlines offering shelter from highly variable oceanographic conditions. The majority of salmon production is carried out on the west coasts of Scotland, Norway, Canada and Chile, and the east coast of the USA and Canada (Marine Harvest 2015).

As industry expands within a given area, thought must be given to how sites are distributed along the coastline, and also to the most effective and efficient manner in which to manage these sites. These decisions may be motivated by a range of competing interests, such as ease of access, cost effectiveness, number of operators working in a water body, disease management and statutory reporting requirements, amongst others.

A particular challenge for the salmon aquaculture industry in recent years has been the control of infectious agents such as parasitic sea lice (primarily

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Lepeophtheirus salmonis and *Caligus* sp.) and infectious salmon anaemia virus (ISAV). For example, in 1997, a serious epidemic of ISAV resulted in compulsory (uncompensated) slaughter at several salmon farms on the west coast of Scotland (Rodger et al. 1998). In 2007, Chilean salmon farming suffered catastrophic losses of around \approx 1.8 billion (Aldrin et al. 2011) through an ISAV epidemic (Valdes-Donoso et al. 2013) which spread rapidly between farms. Annually, it is estimated that sea lice management measures cost the industry over \approx 33 million in the UK alone, and over \approx 305 million globally (Costello 2009). In contrast to parasitic infections, efficacious chemical treatments for viruses are rarely available, and some, such as ISAV or IHNV (infectious hematopoietic necrosis virus), may be transmitted in the water column (Foreman et al. 2015, Olivares et al. 2015). Sea lice populations (Revie et al. 2005, Gettinby et al. 2011, Groner et al. 2014) and ISA (Aldrin et al. 2011) have been investigated using non-spatial dynamic models, in addition to direct analysis of farm lice abundances via spatiotemporal statistical approaches (Aldrin et al. 2013, Kristoffersen et al. 2013, 2014). Regionally specific sea lice dispersal modelling is now carried out by groups in most major salmon-producing areas, in an effort to understand how best to minimise the spread of parasites over networks of sites, understand the risks to wild fish and optimise management strategies (Stucchi et al. 2010, Jackson et al. 2012, Salama & Rabe 2013, Johnsen et al. 2016).

Control of infection risk between farms has included a range of approaches, primarily chemical treatments and farm fallow periods. However, such methods are only effective if management involves a spatial element, i.e. that sites likely to pose a threat to one another are managed together. This has formed part of the motivation for the configuration of management units. In Scottish salmon aquaculture, several different area definitions are currently in operation. 'Disease Management Areas' (DMAs) were defined by Marine Scotland primarily to limit the spread of ISA. Limits are based on fixed tidal excursion estimates, giving an effective radius around sites which determines whether neighbouring sites must be considered within the same area. 'Farm Management Areas' (FMAs) are an industry-defined unit, serving a number of operational purposes for coordinated management. No strict criterion determines their physical arrangement, although management of sea lice is among the goals of their implementation (Code of Good Practice Management Group 2011). For this purpose, chemical treatments, fallow periods and stock

rotations are generally synchronised within FMAs. Typically, FMAs are smaller than other management units, and many contain only 1 or a few sites. 'Fish Health Management Reporting Areas' (FHMRA) are based upon historic Scottish Government reports of rod-caught salmon, but are now used by the Scottish Salmon Producers Organisation (SSPO) for monitoring sea lice abundances, which are reported monthly aggregated across each area (Scottish Salmon Producers Organisation 2014). A final type of management unit is that defined by 'Area Management Agreements', made historically on a local basis between farmers and wild fish trusts. This process was overseen by the Tripartite Working Group, and was described in the original Code of Good Practice. Their extent and spatial arrangement was similar to current FHMRA, but many are not in current use.

How effective these management units are in the control of disease and parasite infection is not currently well understood. As noted, this is not the only (or even prime) concern in all configurations. However, for those units where this is an important goal of their implementation, configuration has been made based upon application of rudimentary hydrodynamic principles. DMAs, for example, use a fixed tidal excursion radius to define interaction with other farms, which is reduced by a factor of 2 for Shetland sites (FRS Marine Laboratory 2000). No equivalent condition is applied in the definition of FMAs.

One reason that area management in Scotland has not been underpinned by an accurate representation of prevailing oceanographic conditions has been the lack of sufficiently advanced hydrodynamic models. The coastlines occupied by the salmon farming industry tend to be complex, with many fjords, islands and narrow channels, which cannot be resolved by regional scale hydrodynamic models implementing a regular grid for computation. Recent advances have made irregular grid models (allowing increased detail in complex areas and reduced detail in open water areas) more readily available to oceanographers (Chen et al. 2013), with several implementations now available for Scottish waters (Adams et al. 2014, Aleynik et al. 2016, Scottish Government 2016). In conjunction with increases in computer processing power, this means that simulation of large domains over longer time periods while retaining small-scale detail has become more feasible.

By making use of these advances in hydrodynamic modelling, we sought to investigate potential connectivity between salmon aquaculture sites on the west coast of Scotland, based on the dispersal characteristics of sea lice. In doing so, we investigated the

Table 1. Summary details for active seawater salmon aquaculture sites and management units in Scotland. Nearest-neighbour distances for management units are based upon the location of estimated unit centroids. Totals relate to all active sites and management units in Scottish waters, not only those within the model domain

Management unit	Abbrev.	Number	Mean nearest neighbour (km)	N_{sites} (mean, [range])	Notes
Sites	Sites	257	3.77		Active sites only
Farm Management Area	FMA	86	12.0	3.3 [1,17]	Industry defined (Code of Good Practice Management Group 2011)
Disease Management Area	DMA	52	19.5	4.8 [1,19]	Marine Scotland defined; control of infectious salmon anaemia (FRS Marine Laboratory 2000)
Fish Health Management Reporting Area	FHMRA	30	30.7	8.4 [1,45]	Industry body defined; reporting purposes (Scottish Salmon Producers Organisation 2014)

properties of the different management units currently in operation with respect to salmon aquaculture in Scotland, using area-aggregated metrics to identify how the effectiveness of units changes with definition and size. We analysed dispersal model output spanning a full year in order to identify the level of temporal variation in site and area connectivity. Finally, we applied thresholds to site-based connectivity estimates, in an attempt to identify how area units might be optimised with respect to control of sea lice infection pressure (Ådlandsvik 2015). We found that inter-unit connectivity decreases as unit size increases. Total connectivity varies over time, and specific connections are somewhat ephemeral, but clear geographic regions experiencing relatively strong connectivity (both within and between management units) emerge in the Clyde Sea, Loch Linnhe/Firth of Lorn, Loch Alsh and environs and the Outer Hebrides. Our results indicate a net northward ‘flow’ of larval sea lice between sites and units. They demonstrate clear benefits of the existing management area configuration for sea lice control, but also suggest that such benefits could be enhanced by enlarging these units.

METHODS

Study domain and habitat configuration

Our study domain covers the majority of the west coast of Scotland, extending from the Mull of Galloway in the south to Cape Wrath in the north, and from the Scottish coast to the east coast of the Outer Hebrides archipelago and the Northern Irish coastline (indicated by the hydrodynamic model mesh in Fig. 1).

Habitat for sea lice was assumed to be available at all seawater salmon aquaculture sites within the hydrodynamic model domain. Site locations were identified from publically available data (Scottish Government 2014), applying filters for ‘seawater’, stocking ‘Atlantic salmon’ and ‘active’ classifications. Within the study domain, there were 195 seawater salmon sites in total, with 133 identified as active.

We assumed that there was no influence of other lice sources (either wild fish populations within the domain, or other aquaculture sites outside the domain). There are no sites stocking salmon to the south of the domain. There are several sites on the west coast of the Isle of Lewis and many sites in Orkney and Shetland (north east of the Scottish mainland), but these are not expected to interact strongly with other Scottish sites due to prevailing oceanographic conditions. Sites exist in Ireland close to the western edge of the domain, but these are outside the scope of the current study.

Management units

We considered subdivision by 3 different management unit types in operation in Scottish salmon aquaculture: FMAs, Marine Scotland DMAs and SSPO FHMRA. Shapefiles for these management units were created using ArcGIS based upon published maps (Code of Good Practice Management Group 2011, Scottish Government 2014, Scottish Salmon Producers Organisation 2014). Salmon aquaculture sites were allocated to management units using the ‘Spatial Join’ tool. Summary information on sites and management units is given in Table 1, with full listings given in Tables S1–S3 in Supplement 1 at www.int-res.com/articles/suppl/q008p585_supp.pdf.

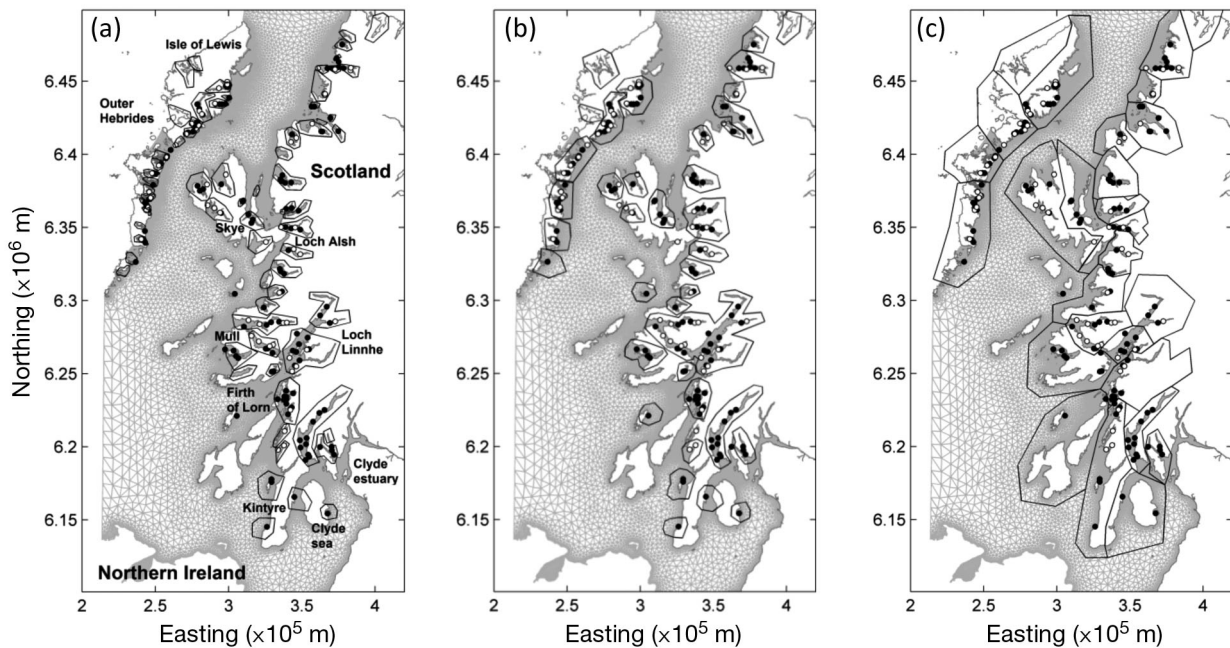


Fig. 1. Management units in operation for salmon aquaculture in Scotland, superimposed over the hydrodynamic model mesh. (a) Industry-defined Farm Management Areas (FMAs). (b) Marine Scotland Disease Management Areas (DMAs). (c) Scottish Salmon Producers Organisation Fish Health Management Reporting Areas (FHMRA). Small discs indicate active (black) and inactive (white) seawater salmon aquaculture site locations. Presented analyses are based upon networks of the active sites. Only sites within the hydrodynamic model domain are shown

Biophysical model

Modelling pelagic connectivity between aquaculture sites consists of 3 fundamental components: a hydrodynamic model, a particle tracking model and post-processing to compute connection probabilities. The domain for this study covers the west coast of Scotland (Aleynik et al. 2016), building upon previous work using smaller domains in the same locality (Adams et al. 2012, 2014, Aleynik et al. in press).

Hydrodynamic modelling

The underlying hydrodynamic model for this study was based upon the Finite Volume Coastal Ocean Model (FVCOM; Chen et al. 2013). This is a primitive-equation, free-surface, hydrostatic model. The system of differential equations of motion and continuity is solved numerically by flux calculations over predefined triangular mesh elements to obtain quantities such as surface elevation, temperature, salinity, velocity and turbulence parameters. Triangular elements allow variation in element size, meaning that complicated topography or bathymetry can be adequately resolved. This feature is particularly important in fjordic coastal environments such as the west

coast of Scotland, which contain features at many different spatial scales, and are impossible to represent accurately with reasonable computational cost in a regular grid model. Node spacing ranges between 4.6 km at the open boundary to around 100 m in constricted areas, such as narrow straits and the heads of fjords. Model bathymetry was based on gridded data (SeaZone 2007), refined in certain key areas using Admiralty charts and a number of multibeam surveys. The model used 79 244 triangular elements in the horizontal, with 11 layers in the vertical.

External forcing is provided by elevation timeseries constructed with 11 tidal constituents using a tidal inversion solution (Egbert et al. 2010) at the open (water) boundaries, with nodal correction and time origin adjusted to match exactly observed tidal phase, and temperature and salinity timeseries derived from a North-East Atlantic operational Regional Ocean Modeling System (ROMS) model (Dabrowski et al. 2014). Model open surface forcing is calculated with a regional Weather Research Forecast model, operational since 2015, nested within 0.25° Global Forecasting System model output (NCEP 2015) and downscaled to 2 km resolution. This was also used to estimate freshwater inputs by rainfall rate over catchment areas of 91 key rivers. More detailed information on hydrodynamic model configuration and validation are given

elsewhere (Aleynik et al. 2016). Hydrodynamic model simulations in hindcast mode used for this study covered 52 wk (1 yr) from 20 June 2013 onwards.

Particle tracking

The second key component underlying the analysis presented here is a biological particle tracking model including movement, maturation and mortality. The current formulation is very close to that described previously by Adams et al. (2012), based upon and sharing features with models developed for the purpose of modelling sea lice dispersal over the last decade (Murray & Gillibrand 2006, Stucchi et al. 2010, Salama & Rabe 2013). Movement of larvae incorporates advection due to local currents and a fixed random diffusion term, and assumes that lice remain in the surface layer of the modelled 3-dimensional current field. Velocities are interpolated from FVCOM's irregularly grid current output, and the model is integrated using a fourth-order Runge-Kutta scheme. Lice are non-infective nauplii for the first 3.63 d of their dispersal, after which they develop into infective copepodids, which are capable of settling at suitable sites for the remainder of their dispersal duration, if they pass within a 500 m radius. A constant rate of mortality ($\mu = 0.01 \text{ h}^{-1}$) is applied to each particle over its dispersal, providing a weighting for a successful dispersal event (modelled lice particles are effectively 'super-particles'); see below in 'Connectivity'.

Particle tracking runs were carried out beginning at 7 d intervals from 27 June 2013 to 19 June 2014 (52 'weekly' simulations). In each simulation, 1024 particles were released from each salmon aquaculture site within the model domain over a full day, limiting the impact of tide state. The start site, settlement (arrival) site and arrival time in hours of each particle (allowing mortality calculation) were recorded. If released particles did not reach any site successfully, 0 values were recorded for destination and dispersal duration.

Connectivity

Output from the particle tracking model detailing particle source site, destination site and dispersal duration allowed computation of dispersal counts and probabilities between each pair of sites. For each simulation (weekly release) the dispersal count from site i to site j was

$$N_{ij} = \sum_{k=1}^n I(\text{source} = i)I(\text{destination} = j) \quad (1)$$

where I are indicator functions (for example $I(\text{source} = i) = 1$ when the particle source site is site i , and 0 otherwise), and n is the total number of particles in the simulation. Dispersal probability between each pair of sites was computed as

$$C_{ij} = \frac{\sum_{k=1}^n I(\text{source} = i)I(\text{destination} = j)e^{-\mu t_k}}{\sum_{k=1}^n I(\text{source} = i)} \quad (2)$$

where the mortality rate μ is assumed constant and equal to 0.01 h^{-1} . t_k is the dispersal time for particle k (to move from site i to site j). N_{ij} and C_{ij} are arranged in 'connectivity matrices' \mathbf{N} and \mathbf{C} , each of dimension $n_{\text{sites}} \times n_{\text{sites}}$ (row = source site, column = destination site).

Network analysis

As noted above, connectivity matrices containing all possible pairwise connections were calculated for each weekly simulation. Connectivity matrices were considered both in their raw form and aggregated by each management categorisation (DMA, FMA and FHMRA).

Site connectivity

Site connectivity matrices were analysed to identify mean site 'betweenness' (number of shortest paths a site lies upon; Dijkstra 1959, Minor & Urban 2007), mean site influx (sum of incoming connections), mean site outflux (sum of outgoing connections) and mean site self-infection probability (Adams et al. 2012), over all weekly simulations.

Management unit connectivity

Using site-area allocations, site connectivity matrices were aggregated by each management unit (FMA, DMA and FHMRA), computing the mean (over sites) of connection probabilities between sites within one unit and sites in another unit. We computed mean and time-varying area connectivity matrices for each categorisation, calculating unit influx, outflux, self-infection probability and external infection (outflux minus self-infection probability). These metrics allowed comparison of the merits of the various categorisations.

Idealised management units

We removed connections from the mean site connectivity matrices, below a range of thresholds ($C_t = [0.0001, 0.001, 0.005, 0.01, 0.1]$). From the resulting connectivity matrices, we then identified clusters using the *igraph* package in R (*igraph.org*). Weakly and strongly connected clusters (respectively, requiring site–site connections in a single direction or both directions) in the matrices were identified at each threshold, and plotted on maps, allowing identification of idealised boundaries for management areas. This analysis was carried out for networks of both active and all sites.

RESULTS

All results are based upon active sites alone, unless specifically noted. The general behaviour of the hydrodynamic model and related particle tracking has been discussed previously elsewhere (Aleynik et al. 2016, in press) and will not be discussed here. Example particle tracking output figures from a single run are shown in Fig. S1 in the Supplement, but the main article will provide a more in-depth investigation of the estimated population connectivity for sea lice.

Site connectivity

Total connectivity over the study period fluctuated on a week by week basis, with a mean probability of between ~0.04 and 0.09 that modelled lice particles starting their journey at one site, and finishing their

journey at another. The first half of the period tended to exhibit higher total connectivity than the latter half (Fig. 2a,b). The proportions of non-zero connections in the network of sites is positively correlated with the total connectivity (Fig. 2c). Mean site influx, outflux and self-infection are shown in Fig. 3a–c. The Pearson correlation coefficient between influx and outflux (all values) was 0.46, and between site means, 0.68. A visual representation of this connectivity, including wind rose data, is provided as an animation in Supplement 2 at www.int-res.com/articles/suppl/q008p585_supp/.

Site betweenness was highest for sites around Kintyre, Loch Linnhe, the Sound of Mull, Loch Alsh and the mid Outer Hebrides (Fig. 3d). Pairwise site connection probability varied relatively uniformly between 10^{-6} and 10^{-1} (not shown).

Management unit connectivity

Plotting the logarithm of each mean connectivity matrix (sites, FMAs, DMAs, FHMRA), it was clear that there is likely to be some 'leakage' of larval lice between sites or management units in all cases (Fig. 4). In this figure, sites (or management units) are arranged approximately south to north, starting in the Clyde Estuary, moving northward along the main west coast region of Scotland, with the Outer Hebrides sites/units listed after all mainland ones (right-most column/topmost row refers to sites that did not fall within any management unit). Probabilities displayed are not comparable between site/unit panels within the figure, as they are relative to the minimum/maximum values for that management unit configuration.

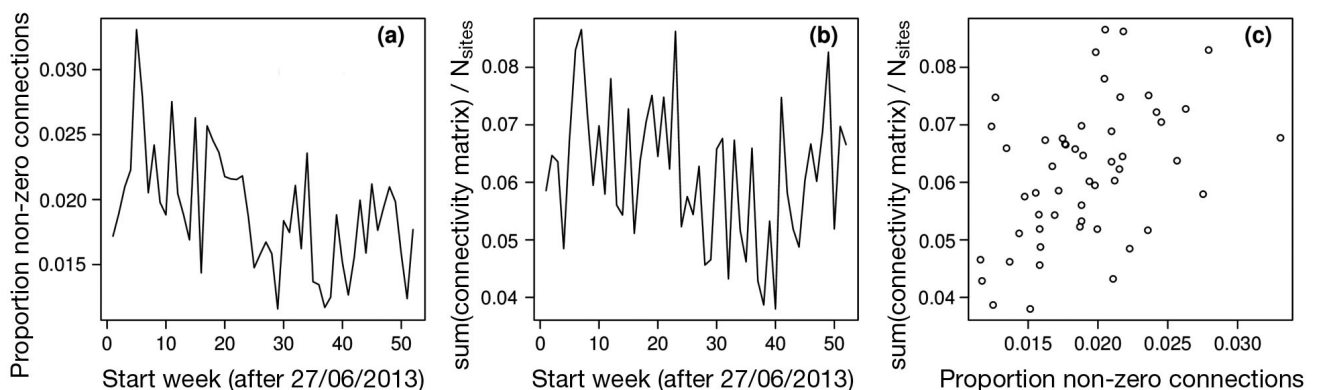


Fig. 2. Total connectivity over time. (a) Proportion of possible connections that were non-zero for each of the 52 weekly simulations. (b) Sum of the connectivity matrix, divided by the number of sites, for each weekly simulation. (c) Scatter plot of total connectivity against proportion of non-zero connections

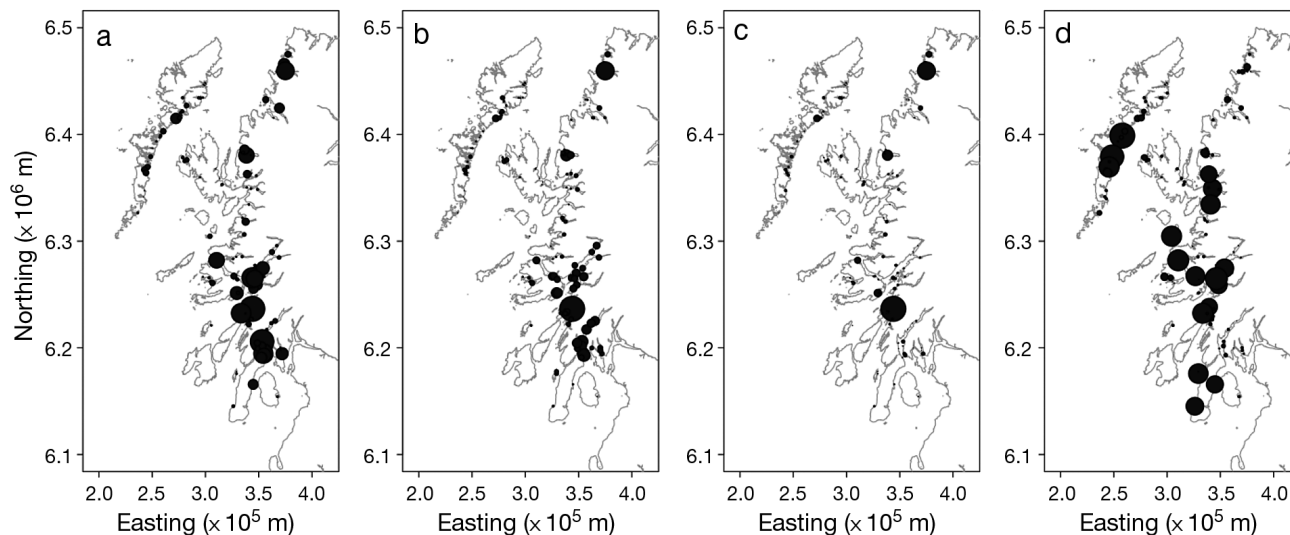


Fig. 3. Mean connectivity by site. (a) Relative mean influx for each site (sum of incoming connection probabilities). (b) Relative mean outflux (sum of outgoing connection probabilities). (c) Site self-infection probability. (d) Site betweenness (number of shortest paths a site lies on, as computed using Dijkstra's algorithm)

In terms of general dispersal patterns, several notable features were observed. Firstly, there were clusters of relatively well-connected areas. These occurred in (1) the Clyde Sea, (2) combined Loch Linnhe, Sound of Mull and Firth of Lorn area, (3) Skye and Loch Alsh area, (4) North-west mainland coast, and (5) Outer Hebrides. Secondly, a general northward spread of larvae between sites and areas was noted (there is a higher incidence of shaded cells in the upper left portion of each panel). Thirdly, in our model runs, most sites and areas on the main portion of the mainland west coast contributed some dispersing lice to Outer Hebrides sites and areas, but the reverse (dispersal from the Outer Hebrides to the mainland) was only true for sites and areas in the very northern reaches of the west coast. Finally, the great majority of 'off-diagonal' entries were relatively small. Redrawing the connectivity matrices omitting connection probabilities below a threshold of 10^{-3} , we saw a reduced number and size of visual groupings of sites and units (Clyde, Linnhe, Loch Long; Fig. S2 in the Supplement).

Considering how total connectivity varies over time, all management unit groupings had lower mean connectivity than did individual sites (Fig. 5a). In particular, the probability of external infection was much lower for all management area groupings than it was for individual sites (Fig. 5b). In the case of each of these 2 metrics, the larger the management unit, the lower the value of the metric (size: FMA < DMA < FHMRA; metric: FMA > DMA > FHMRA). There were some notable exceptions to this in the case of

DMA versus FHMRA in the external infection case. Probability of self-infection tended to be lower as management unit size increased, although there was not a dramatic difference (or indeed between sites and units; Fig. 5c).

Idealised management units

Removing connections below particular thresholds and identifying clusters within the resulting matrices may be quite instructive as to how management units might be idealised with respect to sea lice transmission management.

Weak clusters of sites are those connected by links of any direction; that is, any groups of sites that affect each other somehow. Note that there is not necessarily a possible transmission link from any one site within a cluster to any other in this case. Weak clusters with a range of thresholds are shown in Fig. 6. The threshold pairwise site connection in each case represents a 'tolerated' connectivity between sites that are not in the same cluster (which is therefore considered to be 0, and hence ignored). As the threshold tolerated connectivity between clusters was increased, the size of the cluster became smaller. If connectivity much lower than 10^{-3} between clusters was not tolerated, all sites fell within a single cluster/unit. As tolerated connectivity approached 10^{-1} , cluster size approached a single site. Between these extremes, clusters of sites emerge in the Clyde Sea, the main portion of the

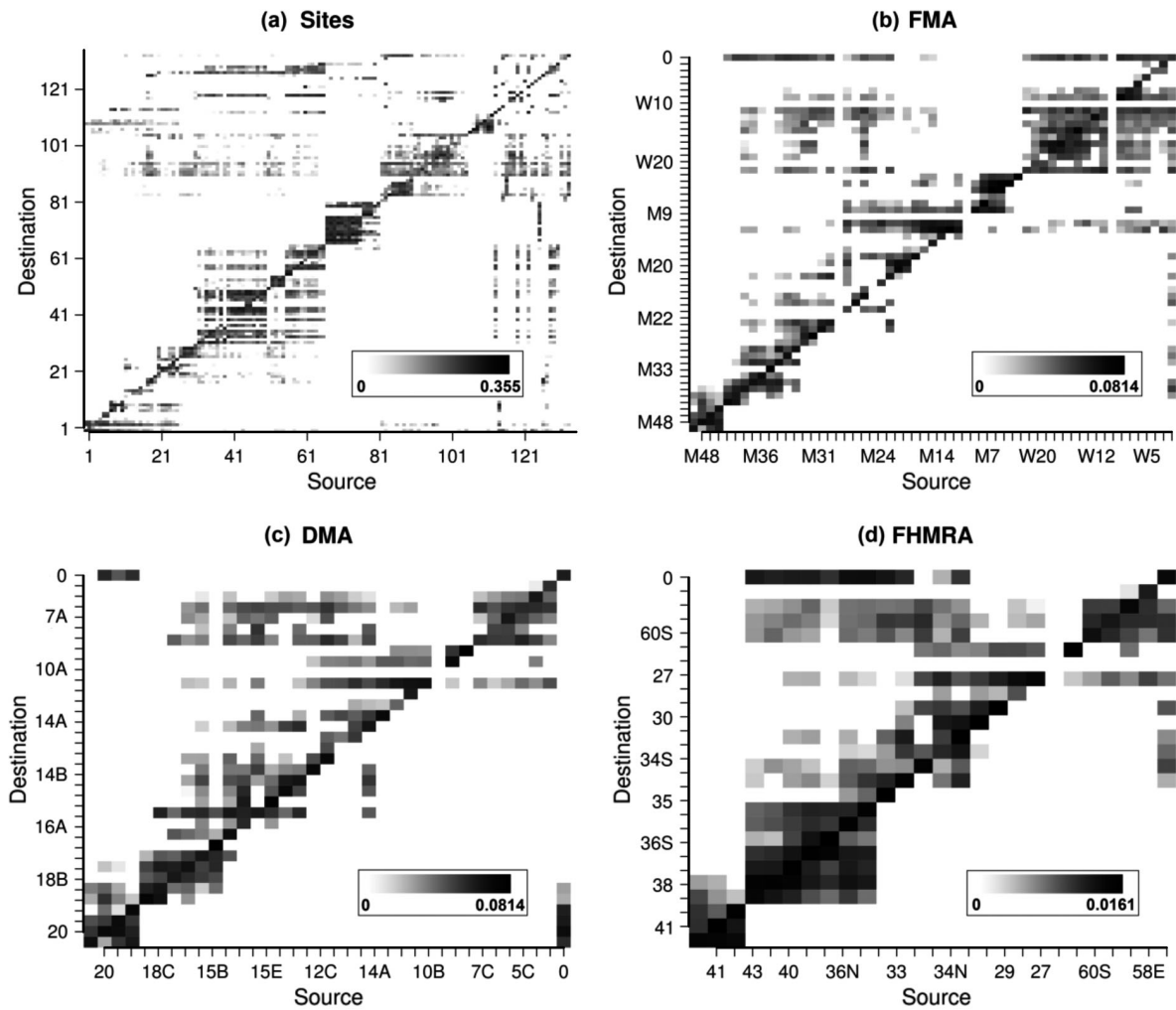


Fig. 4. Mean connectivity between (a) active sites, (b) Farm Management Areas (FMAs), (c) Disease Management Areas (DMAs) and (d) Fish Health Management Reporting Areas (FHMRA) on the west coast of Scotland (sites/management units arranged south to north). For codes and details on management areas see Tables S1–S3 in the Supplement at www.int-res.com/articles/q008p585_supp.pdf. Connectivity is shaded on a logarithmic scale between 0 and a different upper limit in each panel, indicated in the scale bars

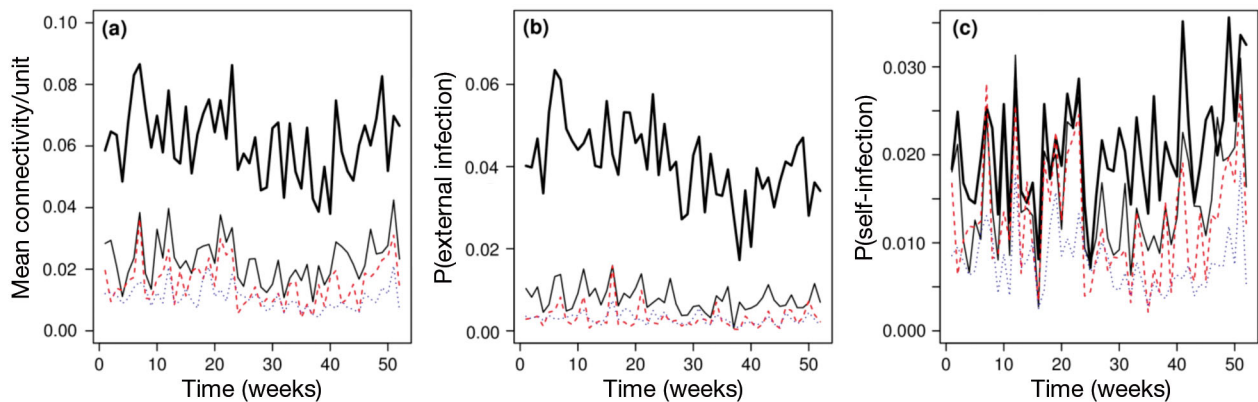


Fig. 5. Comparing sites and management units over time. Each graph shows sites (thick black line), Farm Management Areas (FMAs; thin black line), Disease Management Areas (DMAs; dashed red line) and Fish Health Management Reporting Areas (FHMRA; dotted blue line). (a) Mean connectivity per management unit over time (sum of connectivity matrix, divided by number of sites or units). (b) Mean probability of external infection over time (that is, between sites or units: mean connectivity minus self-infection). (c) Mean probability of self-infection of sites/units over time

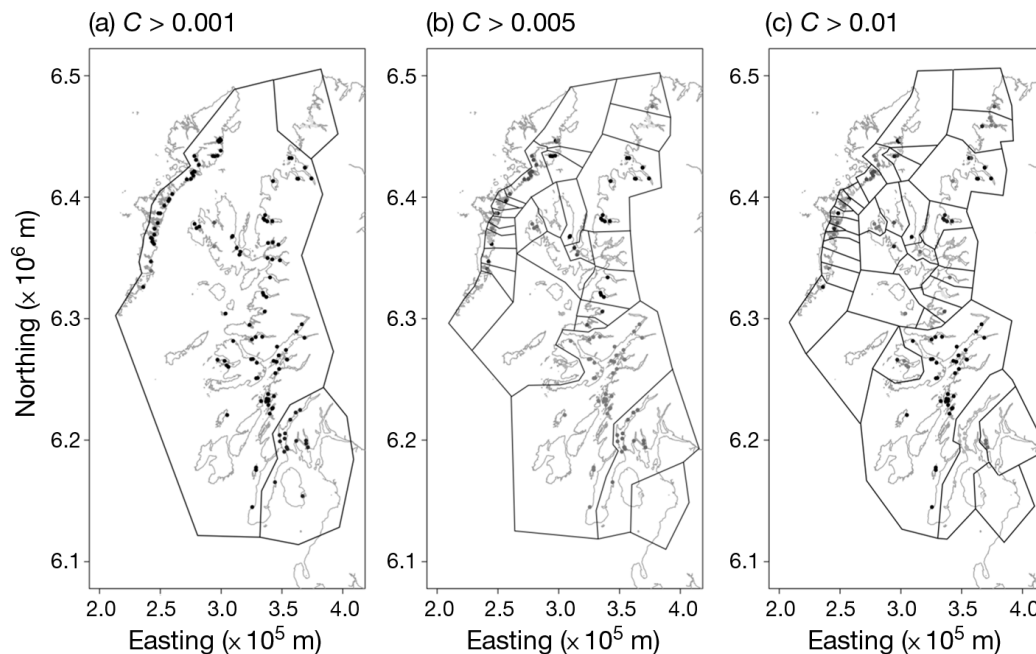


Fig. 6. 'Weak' active site clusters (sites linked by connections either to or from one another) created by including only mean connections greater than a range of thresholds. (a) $C_{ij} > 0.001$. (b) $C_{ij} > 0.005$. (c) $C_{ij} > 0.01$. In each panel, recommendations for unit boundaries based upon the chosen threshold are shown

mainland west coast and Hebrides (which may be clustered together depending on the threshold) and the far northwest mainland coast. Fig. 6a indicates several spurious sites on the coast of Skye and the southern tip of the Hebrides, which are close to the border of the model, and could be most safely treated as part of the main large cluster. Drawing an equivalent figure using all sites (including inactive sites) includes the Skye sites as part of the main cluster at the 10^{-3} threshold (Fig. S3 in the Supplement), and gives larger management units for each given threshold. Fig. 6 also delineates the major calculated clusters, in essence defining the optimal configuration of major connectivity-based management areas. The presented range of thresholds is that over which altering the threshold-tolerated connectivity between areas implies a shift from coordinated management at the national scale to the loch or bay scale.

Strong clusters of sites are those connected by bidirectional links. As such, it is possible for successive generations to be connected between any pair of sites in the same cluster. Clusters of strongly connected sites were much smaller for a given threshold (Fig. S4 in the Supplement). Here, clear clusters were only evident when the tolerated between-cluster connectivity was low: in the Clyde Sea, Loch Linnhe and the southern Outer Hebrides.

DISCUSSION

Until recently, investigations of regional-scale biological dispersal in complex coastal environments such as that of the west coast of Scotland have been hindered by the lack of suitable modelling approaches. Such models must be capable of accurately representing large-scale (50–250 km) hydrodynamic conditions while also incorporating small-scale (100 m) features affecting movement in specific localities. The advent of readily available open source finite volume models such as FVCOM (Chen et al. 2013) has made such applications a reality. Already, several validated implementations are available for Scottish waters, allowing researchers to investigate questions involving consideration over a wide range of spatial scales, and crucially, those that are of relevance to both individual biological organism processes and national-scale industry and management (Scottish Government 2016, Aleynik et al. in press). Within the spatial and temporal domain of our model, we made several important findings. Some of these are specific to our region of interest, while others are likely to be applicable much more generally. Even relatively small management units are likely to be beneficial for the control of disease and parasites, as indicated by the approximately 75% reduction in external infection between FMAs (the smallest,

industry-defined, management unit) in comparison with individual sites, throughout the year. It is also true that the probability of external infection is lower for the larger management units, indicating a likely reduction in sea lice abundances if coordinated management were to be carried out at larger scales.

Our model parasite larvae did not respect management unit boundaries entirely, regardless of unit extent. While a great majority of dispersing larvae caused 'self-infection' (that is, they returned to or remained within their source site or unit), some level of 'external infection' occurred at all scales of aggregation. This was generally observed within geographic areas in close proximity to one another, or occupying the same broad water body (e.g. the Clyde Sea). However, the model made 2 additional predictions which may be of interest to Scottish aquaculture stakeholders. The first is that the larval duration (up to 14 d) and expected mortality rate of sea lice is likely to allow regional-scale spread of the larvae, in particular from southern areas to those in the north. Secondly, dispersal across the Minch channel is likely to be possible for sea lice, in particular from the southern-mid west coast of the mainland to the Outer Hebrides, and from the Outer Hebrides to those sites on the most northern reaches of the mainland west coast. This may partly explain why certain northern areas have experienced high lice abundances over recent production cycles (Scottish Salmon Producers Organisation 2014). It also highlights that, depending on the threshold external infection (between-unit) probability that is tolerated, management for parasite control based on a more detailed understanding of the water bodies concerned may be more appropriate than the current arrangement. Our results suggested that unit boundaries mimicking geographic barriers at the scale of around 100 km may be the most effective. The suggested that boundaries are sensitive to precise site locations and the addition of further sites; should all presently available sites be used to stock fish, our results suggest that more conservative (larger) coordinated management areas would be required to have the same connectivity limiting effect (in particular between the Outer Hebrides sites; Fig. S3). Approval of further sites should take into account proximity to the suggested area boundaries.

It must be remembered that disease and parasite control is just one consideration in the determination of management units. The execution of coordinated management is likely to become increasingly problematic at larger spatial scales, and the presented results hint at the cost of placing strict thresholds on

parasite control. The specification of the ideal threshold for between-area connectivity is outside the scope of this article, and may be sensibly approached via more detailed spatiotemporal modelling of sea lice population dynamics (Revie et al. 2005, Adams et al. 2015) implementing the results obtained here, or otherwise determined by the regulator based upon analysis of sea lice life history and farm capacity characteristics.

Our results are based upon a single year temporal domain. As such, they do not incorporate the full range of conditions that it is possible to experience in the region, in particular storm events which may lead to unusually high or low dispersal probabilities between particular site/unit pairings over short time periods (Kinlan et al. 2005, Lo-Yat et al. 2011). While we consider temporal variation in connectivity, we do not consider how this variation affects population dynamics and whether this allows us to understand the true cause of the large variability between areas in terms of lice pressure (Scottish Salmon Producers Organisation 2014). Again, this requires spatiotemporal modelling incorporating additional factors such as seasonal and spatial variation in life history characteristics, and spatially varying wild-farm lice infection parameters (Adams et al. 2015, Lakey 2015).

Care must be taken in the interpretation of our connected cluster predictions for management purposes. Of particular importance, 'weakly connected' clusters do not necessarily indicate that it is possible for the successive generational offspring of lice to traverse the entire cluster. Furthermore, the 'strongly connected' cluster definition is too strict to allow us to state that lice will not spread to sites outside the identified clusters. Due to the presence of relatively robust (over time) unidirectional connections, the true situation lies somewhere in between. It must also be borne in mind that many of the sites (e.g. Outer Hebrides) are close to the model open boundaries or in tightly constricted sea lochs lacking validation data. Some of the 'recommended' areas in our study therefore conservatively include very close pairs of sites that were allocated to different clusters during analysis. Further work to validate predicted flow patterns in these areas would be beneficial.

While the hydrodynamic model has been calibrated using the best available information, our results also depend upon the various assumptions made in the modelling process. These include, for example, the radius within which model larvae are able to 'detect' sites and settle there. Secondly, the mortality rate of larvae in reality depends on the salinity and temperature of the water that they move

through (Bricknell et al. 2006). Our previous work has indicated that incorporating such a relationship leads to a slight reduction in connectivity on average, but with increased importance of particular sites (Aleynik et al. in press). Finally, vertical positioning of larvae affects their travel distance and resulting connectivity. Lice larvae are unlikely to make large vertical migrations (Heuch et al. 1995), but some recent work has noted an improvement in model predictive capability through the inclusion of such movements (Johnsen et al. 2016).

In summary, we applied state-of-the-art biophysical modelling approaches to understanding the likely implications of regional-scale sea lice dispersal for coordinated area management unit definition. Our results provide useful insights into the connectedness of water bodies in the region and the sites within them. As such, the study complements similar work which is underway in other major salmon-producing areas (for example Ådlandsvik 2015, Olivares et al. 2015), and may allow the industry and regulatory bodies to revisit the motivations for current management protocols, helping to control the abundance of parasitic sea lice in Scottish waters.

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