Using biological-physical modelling for informing sea lice dispersal in Loch Linnhe, Scotland
Salama, Nabeil; Dale, Andrew; Ivanov, Vladimir; Cook, Paul; Pert, Campbell; Collins, Catherine; Rabe, Berit

Published in:
Journal of Fish Diseases
Publication date:
2017
Publisher rights:
© 2017 John Wiley & Sons Ltd
Funded by Scottish Government. Grant Numbers: FC11111, AQ00040, FW0050
The re-use license for this item is:
CC BY-NC
The Document Version you have downloaded here is:
Peer reviewed version

The final published version is available direct from the publisher website at:
10.1111/jfd.12693

Link to author version on UHI Research Database

Citation for published version (APA):

General rights
Copyright and moral rights for the publications made accessible in the UHI Research Database are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights:
1) Users may download and print one copy of any publication from the UHI Research Database for the purpose of private study or research.
2) You may not further distribute the material or use it for any profit-making activity or commercial gain
3) You may freely distribute the URL identifying the publication in the UHI Research Database

Take down policy
If you believe that this document breaches copyright please contact us at RO@uhi.ac.uk providing details; we will remove access to the work immediately and investigate your claim.

Download date: 01. Oct. 2019
Using biological-physical modelling for informing sea lice dispersal in Loch Linnhe, Scotland

Salama, N.K.G.1*, Dale, A.2, Ivanov, V.V.3, Cook, P.F.1, Pert, C.C.1, Collins, C.M.1 Rabe, B.1

1 Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen, UK
2 The Scottish Association for Marine Science, Scottish Marine Institute, Oban, UK
3 Arctic and Antarctic Research, Institute, St. Petersburg, Russia

Corresponding author: *nabeil,salama@gov.scot

Running title: Sea lice modelling in Loch Linnhe

This is the peer reviewed version of the following article:


which has been published in final form at https://doi.org/10.1111/jfd.12693. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.
ABSTRACT

Sea lice are a constraint on the sustainable growth of Scottish marine salmonid aquaculture. As part of an integrated pest management approach farms coordinate procedures within spatial units. We present observations of copepodids being at relatively greater density than nauplii in upper waters which informs the development of surface layer sea lice transmission modelling of Loch Linnhe, Scotland, for informing farm parasite management. A hydrodynamic model is coupled with a biological particle tracking model, with characteristics of plankton sea lice. Simulations are undertaken for May and October 2011 – 2013, forced by local wind data collected for those periods. Particles are continually released from positions representing farm locations, weighted by relative farm counts, over a two week period and tracked for a further five days. A comparison is made between modelled relative concentrations against physical and biological surveys to provide confidence in model outputs. Connectivity between farm locations is determined in order to propose potential coordination areas. Generally, connectivity depends on flow patterns in the loch and decreases with increased farm separation. The connectivity indices are used to estimate the origins of the sea lice population composition at each site, which may influence medicinal regimens to avoid loss of efficacy.

Keywords: sea lice, dispersal modelling, salmon aquaculture, biological-physical model, disease management
1. **Introduction**

The sea or salmon louse (*Lepeophtheirus salmonis* Krøyer) is a ubiquitous, endemic ectoparasite of salmonids, such as Atlantic salmon (*Salmo salar* L.) in the North Atlantic Ocean (Boxaspen 2006). As such it can become a pest in farmed populations, and can have detrimental effects on farmed (Soares *et al.* 2012) and wild salmonids (Volsett *et al.* 2016) including mortality if untreated. Therefore efforts are made by governments and industry to manage lice burdens. This can be a costly process (Liu & Bjelland 2014) as sea lice management has been estimated to cost €0.25 kg\(^{-1}\) harvested salmon (Costello 2009) with much of this cost attributed to medicinal treatments. Although this number is likely to be outdated (Shinn *et al.* 2015) possibly due to changes in drug resistance (Aaen *et al.* 2015), improvements in practices (Code of Good Practice management group 2015), increases in treatment frequency (Murray 2016a), or increases in lice burdens (Murray 2016b). Applying this estimate would correspond to some €45M across the Scottish industry, which produced 179kt in 2014 (Munro *et al.* 2014). Recent quarterly reports from the major salmon farming companies (e.g. Marine Harvest 2014) state yearly increases in costs associated with lice treatment. Shinn *et al.* (2015) suggest that sea lice control on farmed Atlantic salmon is a major contributor to the estimated cost of parasite control in UK aquaculture totalling up to 16.5% of production value. Much of the economic losses are a result of increases in medicine use (Murray 2016a) as a consequence of reduction in efficacy; therefore alternate or additional methods of sea lice control are required leading towards an integrated pest management (IPM) approach (Kogan 1998).

Kogan (1998) provides a description (although structured around sustainable plant production) of levels of IPM ranging from single species control strategies, multiple pest interactions and control, to multi-pest in multi-host systems. Although progress is being made
in salmon aquaculture towards the higher levels of IPM, such as the recent re-introduction of cleaner fish (e.g. Leclercq et al. 2014), host behaviour modification (e.g. Frenzl et al. 2014), and the use of bivalve filtration (Bartsch et al. 2013), addressing Level I IPM requirements of coordinated management of a pest species at a host population level requires further development. Although cleaner fish use can contribute to IPM for sea lice, it can also contribute to the risk of transmission of other disease agents (Hall et al. 2013; Murray 2016c) requiring a multi-species, multi-pest approach to IPM as outlined by Kogan (1998) as Level III. One widely accepted approach to managing fish disease agents at the host population level is through coordinated practices (such as stocking, fallowing, and medicinal treatments) in discrete spatial units. These units can be determined based on physical structures, such as for example embayments, resulting in Single Bay Management (see Jackson et al. 2011). Units can also be based on approximate physical properties, such as disease management areas (DMA) developed from simple model approximation of principles associated with tidal excursions for the control of infectious salmon anaemia (ISA) in Scotland (Scottish Executive 2000), or more subjective structures accounting for business operations and a range of disease challenges, such as Barrios in Chile (Kristofferson et al. 2014). The benefit of having such structures in Scotland has been highlighted through the successful eradication of the notifiable disease ISA (Murray et al. 2010) and has led to the current statutory requirement outlined in the Aquaculture & Fisheries (Scotland) Act 2013 for farms to provide a management statement or agreement describing practices to be undertaken within their management area. As such an understanding of consistent environmental characteristics over time is valuable for establishing farm interactions and thus determined spatial units for establishing documented workable management agreements.
Determining the characteristics of management structures for individual systems is not currently implemented due to the limited number of site specific studies (see Salama & Rabe 2013). General approximations may be possible with regards to transport distances of sea lice (Salama et al. 2016), relative risk of transmission (Aldrin et al. 2013), and probability of farm connectivity (e.g. Adams et al. 2012) at different distances between farms. Such generalisations may also be useful in defining approximation descriptions of risk to wild salmonids (Serra-Llinares et al. 2014); however they will not provide a description of site specific characteristics. This can only be made on the basis of a system-by-system study, most likely through the use of coupled biological-physical models (Salama & Rabe 2013).

One of the limitations in developing such approaches is the need for bespoke physical models which can be costly and time consuming to establish. These physical models need to include bathymetry, wind forcing, and freshwater input, all important characteristics of each system, to model the circulation realistically. However, increasingly it may be possible to use existing models developed for non-aquaculture purposes such as renewable energy, flood predictions, or effluent discharge. Here we describe a hydrodynamic model of Loch Linnhe (Ivanov et al. 2011) coupled to a biological particle-tracking model (Amundrud & Murray 2009) to model sea lice transport from aquaculture facilities in one of Scotland’s largest fjordic systems.

Previous descriptions of sea lice transport in Loch Linnhe (Salama et al. 2013) used consented biomass as a proxy for sea lice inputs from different farms. Here we use information, voluntarily provided by operators, to augment the previous work and improve it. A description is provided of the field methods and data for assessing both the physical and biological outputs of the model. This will assess whether such models can reproduce sea lice distribution. We will also provide additional data informing on the model parameter describing distribution depth of sea lice in the water column. Lastly we will use the dispersal
model outputs to describe the potential mean connectivity over six simulation periods in order to establish consistent interactions over time which may be of use for determining defined management areas. The connectivity values are also used to describe the origins of on-farm population composition, between farms in Loch Linnhe and illustrate how this knowledge could be applied to inform management strategies and possible spatial structures where coordination can occur for improved IPM.

2. Materials and Methods

Some of the materials and methods have previously been described in Salama et al. (2013) and Salama and Rabe (2013) but some details of the data and the respective analysis have been modified and an overview will be given here.

2.1 Study area

This project focussed on Loch Linnhe (Figure 1), a sea loch on the west coast of Scotland. The loch is about 60 km long, up to 8 km wide, 200 m deep, and is surrounded by mountains. These mountains channel the wind up and down the loch axis in a NE-SW direction. Multiple side lochs, connected to the main loch via shallow sills, provide freshwater sources for the main loch. High rainfall on the west coast of Scotland leads to a large amount of freshwater that enters the system through these side lochs or rivers, for example outflow from rivers Lochy and Nevis in the Upper loch can reach 1480 m$^3$ s$^{-1}$ with a long-term mean of 66 m$^3$ s$^{-1}$. Due to this large freshwater input and a connection to the open sea a salinity gradient develops leading to an estuarine circulation with, in a simplistic view, the fresh surface layer flowing out of the loch and salty deeper layers flowing into the loch with large variability in time and space depending on the system (Hansen and Rattray 1965; Farmer and Freeland 1983; Stigebrandt 2012). Wind plays a significant role in the horizontal and vertical
redistribution of properties in fjords. In broad fjords, those whose width exceeds the internal 
Rossby radius (Cushman-Roisin et al. 1994), strong and persistent winds trigger upwelling-
downwelling circulation. The physics of these events is generally in line with classical theory 
of coastal upwelling (Csanady 1982), although the upwelling and downwelling zones lie 
close to one another and interact, complicated by irregularities of seabed topography and 
coastline. Examples of the response of Loch Linnhe to persistent wind forcing were obtained 
during surveys in 1991 (e.g. Taylor 1997, Figure 6.16). For the present study only the main 
loch (divided into Upper and Lower loch) and no side lochs are considered.

Loch Linnhe is divided into two farm management areas (FMAs), one in the north-east and 
one in the south-west. The loch includes ten finfish farms with two side lochs with additional 
farms. Figure 1 shows a map of the region including geographical features, side loch 
locations, and farm management boundaries.

2.2 Biological-physical model

Coupled biological-physical models consist of a hydrodynamic circulation model, which then 
is the basis for a particle-tracking model. Section 2.2.1 describes the hydrodynamic model 
that was used in this study in detail and section 2.2.2 explains the particle-tracking model.

Throughout this paper, except in sections 2.2.1 and 2.2.2, we refer to the coupled biological-
physical model as “the model” unless otherwise stated.

2.2.1 Hydrodynamic model
For this study, the hydrodynamic context was simulated using POLCOMS, a three-dimensional, baroclinic and hydrostatic model, described in detail in the literature (Holt and James 2001). The computational grid had a regular spacing of 100 m in the horizontal and an $s$-grid configuration in the vertical, in which 25 levels of 0.25 -22 m were scaled vertically to match the topography while maintaining high near-surface resolution in deep water. This $s$-grid approach was intended to provide good representation of the behaviour of relatively fresh surface layers and their interaction with meteorological forcing. Sub-gridscale turbulence and mixing were represented by a Mellor-Yamada-Galperin 2.5 scheme in the vertical (Mellor and Yamada 1974; Galperin et al. 1988) and a Smagorinsky approach in the horizontal (Smagorinsky 1963). Model boundaries to the Firth of Lorn and Sound of Mull were open, whereas those to adjoining lochs were walled but subject to fresh water inflow (see below). Tidal wetting and drying of the coastline were not represented, with depths of less than 1 m considered to be land and a minimum depth of 2.5 m imposed on water points. Small, poorly resolved islands were replaced with shallow water. The Corran Narrows, linking Upper and Lower Loch Linnhe, was not adequately resolved at the model resolution so was artificially widened to 300 m.

The model was initially spun up for four annual cycles subject to climatological boundary values of temperature and salinity (UK Hydrographic Office) as well as tidal elevation and velocity ($M_2$ and $S_2$ constituents derived from a coastal station at Oban and a nearby admiralty tidal diamond). Climatological meteorological forcing, based on 6-hourly NCEP re-analysis data (Kalnay et al. 1996) averaged over the period 1949-1990, was applied from year 2 onwards and freshwater inflow from year 3 onwards. In the absence of directly gauged river inflow, freshwater was introduced as distributed sources representing contributions from the side-lochs Loch Eil, Leven, Creran, Etive and A’Choire (Figure 1).
Daily inflow values were based on annual totals for each source loch (Edwards and Sharples 1986) with an imposed seasonality following the annual cycle of precipitation at Dunstaffnage. The temperature of the inflowing freshwater was taken equal to the temperature of the closest grid point in the domain. The final year of the four-year spin-up was taken to represent a climatological annual cycle for Loch Linnhe. The spin up was carried out for the year 1991 when a detailed one-year survey of Loch Linnhe was performed, and therefore the observational data could be used for model validation.

2.2.1 Hydrodynamic simulations of target periods

Model states from within the climatological cycle were used as initial conditions for detailed simulations of six periods of interest:

- 2011: May 9 – May 22 and Oct 21 – Nov 9
- 2012: April 27 – May 16 and Oct 1 – Oct 19
- 2013: April 29 - May 18 and Sept 30 – Oct 19

In each case, the detailed simulations began one week prior to the start of the target period to allow adjustment to immediately preceding conditions. Meteorological forcing was at two-hourly resolution using observed data from weather stations deployed locally during the modelled period (Figure 1). Pressure, temperature, and humidity were taken from the weather station at Dunstaffnage, and assumed to be constant across the model domain. Wind was gridded by means of linear interpolation from meteorological stations to the coarse model grid (0.05° in longitude and 0.1° in latitude) allowing some spatial variation and steering by topography (magenta vectors in Figure 1) although the wind interaction with
Atmospheric temperatures in 2013 were anomalous when compared to long-term average conditions. In particular, spring was anomalously cool and summer was anomalously warm. These anomalies were reflected in observed water temperatures within the loch. A simple temperature offset was uniformly applied to all depths to the climatological starting state, and boundary conditions, of the 2013 simulations in order to improve the temperature fit with minimum dynamical interference (the temperature offset was applied uniformly across the model domain). May 2013 temperatures were reduced by 1.2°C and October 2013 temperatures were increased by 1.7°C.

2.2.2. Particle tracking model and farm connectivity structure

The hydrodynamic model provided surface currents for coupling with a particle tracking algorithm used for the smaller Scottish system of Loch Torridon (Murray & Amundrud 2007, Amundrud & Murray 2009). The surface currents were taken from the top level, which varies in extent but due to the model configuration retains high resolution at all grid points. The modelled surface currents transport lice between grid locations. At each time point, the location of each louse particle and its age were recorded. The time periods of May and October were chosen as they are the periods of the spring smolt emigration (Butler 2002) and the peak period in sea lice counts on farmed fish (Murray 2016c) respectively. Advection by surface currents is integrated with diffusion, horizontal dispersion and a stochasticity parameter in a fourth order Runge-Kutta solver of the Lagrangian motion equation (Salama et
Within the model domain, should a particle be moved into a grid box designated as land, then it will remain at its last sea location until the current direction changes, i.e. shorelines are sticky boundaries. At the open sea boundaries particles are lost out of the system. Farms do not influence the behaviour of the particle.

The model is initiated by releasing particles over a 14d period at a fixed rate of 5 per 0.5h from 12 positions in the model domain (Figure 1). The release locations represent ten active fish farms within the system, and two at the boundaries of Loch Creran and Loch Leven representing lice exiting sites in these side lochs. Although salmonid farms are located in Loch Etive, no particles were released at this boundary because salinity there is substantially below that at which sea lice remain viable (Holt 1991, Austin & Inall 2002, Bricknell et al. 2006). Furthermore, for the corresponding modelling period no lice treatments were reported in Loch Etive to SEPA or the fish health inspectorate implying no discernible levels of lice were present for the corresponding modelling periods of May and October 2011 – 2013.

After releasing particles for 14d all particles are tracked for a further 5d to enable all nauplii particles to mature to the infective copepodid stage lice. As particles move they mature at a fixed rate of 10% h\(^{-1}\), a simplification of the 50 degree days for nauplii lice to moult through to copepodid stage (Asplin et al. 2014; Johnsen et al. 2014). Although sea lice have a nauplii I and II stage (Hamre et al. 2013), there is no distinction between non-infective nauplii stages as these are merely passive dispersing stages. At the time of the study, as with previous studies constant mortality was applied (Salama et al. 2013; Adams et al. 2012, Amundrud & Murray 2009), similarly the model is approximated for ease of application by avoiding the inclusion of the influence of salinity or temperature on development or mortality. Lice die at a constant rate of 1% h\(^{-1}\) for both nauplii and copepodid stage lice which is an approximation...
of the observations of Stien et al. (2005) of nauplii mortality rate of 0.17 day\(^{-1}\) and copepodid lice of 0.22 day\(^{-1}\).

The recording of lice presence in each grid per time step enabled the production of an aggregated relative distribution map for each simulation. Each farm within the system stocks varying numbers of fish and will have differing lice burdens, therefore the constant lice input value (as previously used) was altered to reflect relative site contributions. The producers in the system agreed to voluntarily produce a metric which reflected their relative lice burdens, that is to say no actual lice count was provided, merely a transformed relative score. This value was normalised against the highest reported score. This enabled weighted contributions from the different sites, to the aggregated relative concentration score of lice of each stage, over each 19d simulation, which made up the relative distribution map. The concentration score of a grid square is not predictive of expected lice numbers, as the actual inputs are unknown, but rather they are relative aggregates. For example a grid square with a score of 10 may have experienced 10 particles for 1 time step, 5 particles for 2 time steps or 1 particle for 10 time steps etc. Simulations in MATLAB R2007b (Mathworks Inc) allowed access to the value at each grid location for use in model assessment against field data (section 3.2).

To construct an assessment of farm interconnectivity we apply the same methodology as Adams et al. (2012). At each farm site, \(j\) (plus the surrounding 500m to allow for variability), the proportion of surviving copepodid particles, \(P\), compared to the total number of those released from the originating site, \(N_i\), accounting for mortality rate, \(\lambda\), and transport time, \(t\), between sites, \(i\) and \(j\) of the \(n^{th}\) particle, i.e. \(t_{ijn}\) originating from itself \((i=j)\) or another release locations, \(i\), are recorded such that:
This enabled the construction of a connectivity matrix for each of the simulations and also a mean aggregate matrix. The aggregate matrix is the sum of all the individual simulation matrices divided by the number of simulations. Model simulation outputs vary due to hydrodynamic conditions and relative lice input into the system, therefore an attempt is made to assess the variability between simulation outputs using a generalised linear model to demonstrate the necessity for undertaking multiple simulations to establish consistent environmental characteristics for establishing statutory required documented spatial management structures as opposed to relying on an individuals which may only represent rare events.

The connectivity observations can be manipulated to estimate the contribution from each of the sites to establish the likely origin (assuming all lice have equal settlement ability) in determining site population composition. Should a site X have a connective probability from site X at 0.04, and site Y at 0.001 and Z at 0.009 assuming all sites have equal contributions, this would result in 80% of the exposure population at site X being derived from site X itself, 2% from Y and 18% from Z. For all sites in Loch Linhne the connectivity values are used to estimate the proportional population origins for each site.

2.3. Field data

2.3.1 Physical data

The physical data can be divided into two categories: wind data to force the hydrodynamic model for the six different scenarios, and oceanographic data to validate the hydrodynamic model and investigate the circulation and environmental conditions within the loch.
To obtain wind data multiple weather stations were installed around the loch to capture the
variable wind within the loch system. Exact locations are marked on the map (Figure 1) with
not all stations functioning at all times due to instrument failures. Two-hourly wind data was
gridded on a coarse grid using linear interpolation to force the hydrodynamic model during
the different scenarios, as described in section 2.2.1.

Oceanographic data consisted of water level, Conductivity-Temperature-Depth (CTD), and
current data. A water level recorder was deployed at the northern end of the Upper loch at
Fort William; this data was mostly used to validate the hydrodynamic model. CTD casts at
multiple locations throughout the loch (close to plankton sampling sites) collected vertical
profiles of temperature and salinity and were used to adjust the hydrographic conditions for
model runs in the loch for the anomalous conditions in 2013. Currents were measured with
an Aanderaa 600kHz Recording Doppler Current Profiler 600 on the northern shore of the
outer loch at 56.68 degrees N and 5.32 degrees W. The instrument set-up included a ping
count of 300, a ping interval of 2000 ms in burst mode with a 600 s recording interval, 2 m
cell sizes, and 80% cell overlap. This physical data was used to evaluate the circulation of the
loch, explained in more detail in Rabe and Hindson (2016).

2.3.2. Biological data

2.3.2.1 Sentinel cages

A series of plankton trawl and sentinel cage deployments were undertaken throughout the
loch system (Figure 1). The sentinel cage methodology is described in Pert et al. (2014) and
therefore only summarised here.
Atlantic salmon smolts (mean length 202.21 mm and weight 92.48 g) were kindly supplied by Marine Harvest from freshwater sites from within the Loch Linnhe management area throughout the trial. Fish were held for four weeks at Drimsallie Mill Hatchery, Glenfinnan, in a 4 m circular fiberglass tank with a tank volume of 6000 L and a flow rate of ~108 L min⁻¹. Fish were maintained on 2 mm commercial pellets (Skretting smolt diet) and fed 1.2% bodyweight per day prior to transfer to sentinel cages. Sentinel cages were cylindrical (1.5 m in diameter x 2 m height). Each cage was supported by four rings made of polyethylene pipe covered with 13 mm knotless mesh netting.

Nine sentinel cages, each containing 50 Atlantic salmon, were deployed in the surface 3 m for 2 x 1 week periods during April/May and September/October between 2011 and 2013. Fish were euthanised by overdose of MS222, placed in individual bags and returned to the laboratory where lice numbers, developmental stage, location on fish, as well as fish weight and length recorded. A subsample of lice was tested by molecular means (McBeath et al. 2006) to confirm identification.

2.3.2.2 Plankton Sampling

The plankton sampling methodology followed Penston et al. (2008) and involved the deployment of a 1.5 m long bongo net which consists of two aluminium drums with a mouth diameter of 0.5 m. Attached to it is a 1.5 m long 150 µm conical plankton net terminating in a 150 µm cod end, deployed from the vessel Sir John Murray. The bongo net was towed horizontally at a depth of 1 m at a speed of 2 knots for 5 min. Attached within the mouth of each bongo net was a flowmeter to measure the volume of water sampled through each net. Flowmeters were designed and manufactured in-house at Marine Scotland and designed to be...
water activated so only started recording when they were immersed preventing any false
readings from winds. After 5 min the net was recovered and suspended so the net could be
washed down with filtered (1.2 µm) seawater before the cod ends were removed and the
contents transferred into a sample bottle and fixed in a 4% Buffered Formal Saline solution.
Samples were prepared for light microscopy by filtering them through a 500 µm sieve
(Endecotts, London, UK) which removed coarse material before further filtration and sample
concentration through a 68 µm mesh. The second mesh (68 µm) retains the desired fraction
of the sample containing planktonic stages of L. salmonis larvae.

Samples were then examined under a dissecting microscope (Olympus SZ-CTV Southend-
on-Sea, UK) with any lice found transferred into 70% ethanol in specimen tubes for
preservation. Sea lice were identified to species level using descriptions in Johnson &
Albright (1991) and Schram (1993) with additional confirmation carried out using real time
Polymerase Chain Reaction (PCR) (McBeath et al. 2006).

2.3.2.3 Depth distribution of sea lice in the water column
From the outset, a requirement of the model was to apply previously developed particle-
tracking principles without modification to highlight the utility of not having to produce
bespoke models for systems of interest. The previous work by Amundrud & Murray (2009)
used modelled surface currents and did not include vertical migration of lice which was used
for more recent work (Johnsen et al. 2014). We assessed whether such simplification of
using only surface layers was reflective of where lice can be predominantly found within the
water column (Heuch 1995).
To determine this, a series of plankton trawls were undertaken in Grutting Voe, West Shetland in September 2009 (Figure 1 insert, 60° 12’.068 N 1° 31’.563 W) which, anecdotally, was considered to have high sea lice abundance at the time of study. This location was chosen to minimise low lice abundance in the environment especially at the nauplii stages (Penston et al. 2008). We recognize that hydrographic conditions might present a different environment compared to Loch Linnhe but even though this is not a perfect representation of conditions in Loch Linnhe (which has a fresher surface layer in general) this site represented a good practice ground for sea lice sampling during day and night. Each trawl sampled 75m³ using 40cm diameter bongo nets with 150 µm mesh at 2m, 5m, and 20m during night and day. Four trawls, in duplicate, (n = 8 samples in total) were conducted over a 25 h period, and temperature and salinity was recorded during sampling. Net contents were washed into screw top bottles with fixative (70% ethanol), and fixed samples returned to the laboratory. Plankton samples were screened using a stereo microscope magnification of 100x (Zeiss SV11, Zeiss, Hertfordshire, UK). Animals putatively identified as L. salmonis were attributed to two life stages, nauplius or copepodid, but no attempt was made to differentiate the naupliar stages. Individual sea lice were rinsed in water and transferred into individual vials for real time PCR analysis (McBeath et al., 2006).

2.4 Comparing field data to model outputs

2.4.1. Assessment of modelled sea lice concentrations against biological observations

In order to provide reassurance of the model outputs an assessment of an aspect of the model was undertaken using field sampling of sentinel caged fish and plankton trawls. It became apparent that there was substantial variation between simulations; therefore an aggregated comparison of all field observations against all simulation outputs was
undertaken. For each study period measures of the settled number, intensity, abundance, and prevalence of lice on caged fish were ranked allowing a spearman’s rank correlation to be undertaken in R2.15 (R core team) against ranked simulated densities of copepodid stage lice for corresponding cage locations. Similarly rank correlations were considered for plankton sampled copepodid staged lice and simulated copepodid densities. Simulated concentration results represent the summation of simulated copepodid densities in the corresponding location over the 19 d period and, similarly to the connectivity assessment, simulated densities found within 500m radius of such position.

2.4.2 Validation of hydrodynamic model with physical data

An initial check had been made that the model represents well the large-scale tidal fluxes within the loch, involving a comparison between modelled elevation and water level recorder observations at the same point in the model domain. A Taylor diagram (Taylor, 2001) provides a graphical framework to evaluate different statistical components (Figure 2a): the correlation coefficient, centred root-mean-square difference (RMSD), and the ratio of the variances (standard deviation) between modelled and observed time series. Data from the north-eastern end of Loch Linnhe in Fort William was used. Ideally models have a high correlation coefficient and a low RMS error. If modelled elevation agrees well with observed elevation, then its marker is located close to the observed marker on the x-axis of the Taylor diagram.

The location of each number in Figure 2a quantifies how closely the POLCOMS modelled surface elevation for the different validation periods (represented by the different numbers) matches the observed surface elevation. The correlation coefficient (blue lines) for all periods is between 0.89 and 0.98 except for October 2013, which was based on predicted tides due to
instrument failure (correlation coefficient of 0.76). With a correlation coefficient close to one, it means that an almost perfect linear relationship between the model and the observation exists, which was the case for five out of the six periods. The RMSD, green contours around the observations (denoted by letters), are best for October 2012 with 0.23 m and between 0.23 m and 0.43 m for all other periods (except for October 2013 with 0.66 m). These low RMSD of less than half a meter give us confidence in the modelled elevations. The standard deviation of the modelled elevation, represented by the black contours, is proportional to the radial distance from the origin. The values range between 0.94 m and 1.08 m compared to standard deviations of the observations between 0.88 and 1.02 m. The closeness of the standard deviation of the model to the observation gives an indication of the robustness of the pattern variations. Standard deviations are close for all periods, giving us confidence in the pattern variations.

We ran a tidal harmonic analysis (not shown) on the modelled and observed surface elevations to evaluate how well the model represents the actual tides. For M2 the percentage variance predicted/variance original is 99.9% for all four periods in 2012 and 2013 and drops to 81% and 77.5% for May and October 2011, respectively. The amplitude difference between model and observation stays within 8% for M2 for all time periods. Phase differences are largest for 2011 (May and October) and May 2012. These poorer statistics can be largely attributed to the response of the modelled water level to the atmospheric forcing.

Current observations at 10 m have been compared with the model outputs at the nearest grid point and Figure 2b shows one example for the 19-day October 2012 period. The currents have been rotated by 45 degrees to represent the along (positive up-loch) and across (positive
to the SE) loch components. The along-loch component matches reasonably well (correlation coefficient of 0.66), although we can observe some anomalous periods which could maybe relate to wind events. The across-loch component matches less well but overall the mean speed and direction are comparable though with both observations and model mean speeds of 0.06 ± 0.04 and directions of 147 ± 107 for the observations and 113 ± 100 for the model in October 2012 at 10 m depth. This supports that the dispersion of sea lice is being reasonable. Due to the complex dynamics in the system (internal waves, fronts, mixing processes, surface layer dynamics) that any hydrostatic model at this scale will struggle with, all the variability will not be perfectly represented. Overall the hydrodynamic model performed well for all six validation periods with October 2013 being slightly worse, possibly related to comparison with tide predicted elevations compared to observed elevations. Therefore the underlying hydrodynamic circulation model is fit for purpose and a valid model to be coupled to the particle-tracking model to investigate sea lice dispersal.

2.4.3 Case study to evaluate the effect of wind forcing on surface water properties and lateral differences

A more demanding requirement for the model is that it represents well the density structure of the loch, and in particular the surface currents resulting from freshwater outflow and wind forcing. To simulate the basic features of the wind response we carried out a case study, in which the model was forced by persistent unidirectional wind. The wind direction, relative to the axis of the loch, determines the location of upwelling and downwelling zones, with wind
directed along the axis being most efficient at producing vertical motion as it drives Ekman
transport normal to the coastline. The model response to 48 hours of westerly wind at 15 ms\(^{-1}\)
(indicated by the wind rose) is shown in Figure 3a. Pronounced upwelling zones form along
the north-western coastline of the loch. Cold water from a depth of ~30-40 m rises to the
surface, creating narrow fronts with a typical spatial scale of the order of the internal Rossby
radius of deformation, and the least dense surface waters are driven towards the south-eastern
coastline.

In a contrasting case, during October 2012, winds were from the north-north-east at speeds of
3 m s\(^{-1}\) (see wind rose, figure 3). Another way to visualize the lateral difference in outflow is
through the modelled sea surface salinity. The least dense, lower salinity water of around 33
(compared to salinities of 35 at the open boundary) can now be observed to flow along the
north-western coast. Freshwater is released from the Upper loch through the Corran Narrows
and from Kingairloch and spreads south-westward. This fresher surface water stays along the
north-western coast within the spatial scale of the internal Rossby radius of deformation.
Figure 3b shows particle tracks when releasing particles from Kingairloch (arrow). Particles
congregate inside and just outside this side loch before flowing out of the main loch along the
north-western coast. The particles that flow out of the loch stay close to the coast and within
the internal Rossby of deformation radius as the loch is wide enough to be influenced by the
Earth’s rotation. No northward or eastward transport exists due to the wind influence on the
surface layer which leads to the general outflow of the surface layer to the southwest. A
change to westerly or south-westerly wind would drive upwelling at the north-western coast.
In reverting to conditions resembling Figure 3a, particles would become more widely
distributed across the loch.
2.5 Comparing variation between model runs

Each of the model outputs produces a 365 x 488 gridded matrix containing values representing the simulated relative lice densities. These data were transformed in R 2.15 (R core team) to produce a column within a data frame, with a corresponding grid location identifier, X and Y grid coordinates, Euclidean distance from (0,0), simulation run identifier, year, and month. Grid squares representing land were excluded. This enabled an assessment of the similarities in the model outputs across simulation runs using a simple generalised linear mixed model (GLMM) accounting for simulation run as a categorical random effect, and Euclidean distance from grid location (0,0) as a fixed effect determining the relative lice concentration at such location. Attempts at model constructions including two fixed terms being X and Y coordinate value, or categorical label for each individual grid square, and also substituting run for month and year, resulted in little discernible difference in the final model suitability. By producing a GLMM it is possible to ascertain the variation in simulation outputs attributable to simulation run. The “lme” function contained within the “nlme” package (Pinheiro et al. 2015) was used to estimate parameters for the above model.

3. Results

3.1 Depth distribution of sea lice in the water column

Lice were found to be present in all but two of the 48 samples with the majority of nauplii (57.0%) and copepodid (72.0%) stage lice being sampled within the upper 2m (Table 1). Lice abundance appears to be greater in the surface layers at night (65.6%) than in the day (34.4%), although the total number of copepodid stage lice in the surface layer was constant. Hydrographic conditions in Grutting Voe at the time consisted of a well-mixed water column
with salinities around 35.1 and temperatures between 12 and 12.2 C. Given the lack of stratification at the time of sampling, other environmental variables would have affected the vertical position of the lice.

3.2 Model assessment

Comparing the ranks of the aggregated simulated and environmentally sampled lice data at corresponding geographical locations (Figure 1) it is seen that there is a correspondence between lice observations and simulated concentration (Figures 4, 5), suggesting that the model is able to reflect a feature of the Loch Linnhe system. Simulated concentration rank correlated with cage count rank (ρ(52)=0.51***), prevalence rank (ρ(52)=0.51***), abundance (ρ(52)=0.48***), and intensity (ρ(52)=0.45***), and also plankton rank copepodid concentration (ρ(526)=0.19***).

3.3 Lice relative distributions

The weighted mean simulated relative distribution of lice, on aggregating the scenario outputs for May and October 2011 – 2013, are shown in Figure 6 for relative nauplii and copepodid distributions. The lice input weighting is based on information provided by producers. It must be noted that a zero reporting may indicate either not stocked or that no lice were observed. In each simulation period not all sites had a non-zero count, which also contributes to the observed variation between simulations. There are clearly similarities between nauplii distributions and those in corresponding copepodid distributions; this merely reflects that present nauplii that survive to become infectious stage lice occur in the corresponding areas. It appears that on average lice are almost ubiquitous in distribution with
nauplii lice observed in all but 1319 of the grid squares, whilst copepodid lice are simulated
to be located in all but 1437 of the 182,358 sea grid squares. The majority of the lice free
squares are located in the north of the system towards the river Lochy close to Fort William
and in Ardmucknish Bay close to Dunstaffnage. Each individual simulation condition
produces variable distributions with the GLMM demonstrating that the residual effect
promotes some 84% variability between simulation runs, that is to say there is substantial
differences between each of the simulation outputs (Table 2) and as such, demonstrates the
need for multiple scenarios instead of relying on individual model runs.

3.4 Connectivity

Figure 7 shows a representation of the probability of connectivity observed between sites
aggregated across all simulations. Sites are reported anonymously to remain consistent with
reporting aggregated and not individual site details as is the case with the annual production
survey (Munro & Wallace 2016) and industry wide sea lice status (e.g. Murray 2016b). Due
to the variability between simulations, the connectivity varies with each run therefore the
aggregate provides a consistent overview under all observable conditions.

No site within Loch Linnhe is isolated from forming an association with other sites. All sites
which were reported to have observed lice (excludes site I) self-exposed with copepodid
stage lice. Site (H) forms the most connections, exposing itself and six other farms, whilst site
L receives lice from itself and five other sites. It appears that the range of connectivity is of
the order 1×10^{-5} - 1×10^{-2}. There is variability between sites of receiving and emitting
connections (Figure 7) to other farms. The majority of sites have greater outwards connectivity of sea lice to neighbours, compared to inwards connectivity from all other sites.

The aggregated mean connectivity between farm sites follows a general trend (Figure 8) for increased farm separation reducing the probability of connection between sites. However it must be noted that there exists sites which are geographically close together but connectivity is zero or connectivity is reduced compared to sites with greater separation. Additionally the majority of connectivity occurs between sites within 10 km.

Figure 9 demonstrates that there are two distinct regions within the system determined by connectivity: Upper Loch Linnhe and Lower Loch Linnhe separated by the Corran Narrows. However this accounts for no direction between sites or connectivity probability, i.e. this is simply a binary representation of relationships. Taking into account probability of connectivity, such that relationships can be formed based on interactions, as an example Figure 9 demonstrates the connectivity with thresholds at a level of greater or less than $1 \times 10^{-4}$, it could be the case that three distinct regions exist; north of the Corran Narrows, north-west of Lismore Island, and south-east of Lismore Island. However there are sites which would act as connectors between the two regions.

Some sites are net exporters of lice (Table 3) for example site D exports lice to all other sites at a rate of over eight times more than it receives from all sites, whilst others are net importers of lice with ratio below 1 (Table 3). Another metric observed is the relative contribution to lice exposure from self-exposure compared to external exposure, for example sites A and B experience seven times more lice from self-exposure compared to incoming
lice from all other sites, whereas only ~1 in 20 lice experienced at site H originated from site H.

3.5 Informing population composition on farms

The relationships between each site determined through the connectivity estimates can be used to estimate the origin composition of the lice population at each production site (Figure 10). The single largest contribution to each site's population is from lice originating from that site, however there are sites where combined immigration from other sites contribute more to the population than the site itself for example site H, whilst other sites, such as site A and site B, are dominated by internal origin sources of lice.

Discussion

Models can only be useful if they represent aspects of reality and features of the outputs have a potential application (Salama & Rabe 2013; Foreman et al. 2015). However, models are not required to be completely parsimonious with reality as they would cease to have purpose due to the complexity, which may also lead to over-complex models which need to be highly specific and would be cumbersome (Murray 2008; 2009). Here we present the use of a biological-physical model (Salama et al. 2013) which couples a hydrodynamic model with a previously described particle tracking model. The latter includes features of sea lice biology to ensure that the model is based on, and also reflects, aspects of reality. The structure of the
particle tracking model was informed through field work, which identified where the majority of infective lice reside within the water column. The hydrodynamic model runs were driven by meteorological observations, and scenarios were chosen at times of the year, which are of biological importance to the sea lice issue. Hydrographic observations were used to validate the hydrodynamic model to gain reassurance in the model before coupling it with the particle tracking model. Hydrographic data and simplified model runs also led to a better understanding of the circulation and lateral variations in surface conditions within the system. To assess whether the model reflects an aspect of reality, field work was conducted during corresponding time points to enable a comparison of model simulated lice relative densities and observed lice concentration in the environment. Finally, we present a potential application of the dispersal model in determining the connectivity between farms within the system and suggest possible management structures based on probability of connectivity between sites.

An aspect of this work was to utilise existing model structures in order to demonstrate that it is not necessary to have bespoke biological-physical models for every system of interest. We therefore applied a previously described biological particle-tracking model (Amundrud & Murray 2009) with a hydrodynamic model of Loch Linnhe run by SAMS (Ivanov et al. 2011). Should a non-specific design be possible then it may enable the application of other coupled hydrodynamic particle-tracking models such as those developed for e.g. effluent discharge or oil spill modelling. Amundrud & Murray (2009) focused the dispersal of lice in the surface layer as does the work of Adams et al. (2012; 2015) in Loch Fyne, although more recent modelling work (Johnson et al. 2014) include vertical migration. It appears from observations presented here from a site in Scottish waters in Shetland that as a generalisation for modelling purposes the majority of the infective stage lice (which are the stages of
importance in terms of sea lice parasitism) are found within the surface layers. Even though the waters in the Shetland Voe presented a different environment to Loch Linnhe, it could still be used as a testing ground for plankton sampling and give an indication of vertical distribution. However, it must be noted that only a small proportion of nauplii were sampled from the upper 2m. It appears that proportionally more copepodid lice are found at greater depths at night than in the day which is consistent with lice being phototaxic (Flamarique et al. 2000). Because of the variability in nauplii depth distribution, future modelling work should account for differences in vertical current speed and direction which could result in varying overall modelled infectivity profiles of a system, compared to simply observing the surface currents.

Larval sea lice are difficult to find in nature (Boxaspen 1997). The densities reported by Penston et al. (2008) are of the same order of magnitude reported here. They conducted trawls at 0m and 5m, and found a similar pattern of copepodid lice located higher up the water column, whereas nauplii were distributed at deeper layers. This is consistent with the findings in the Faroe Islands where nauplii were less abundant in the upper layers compared to copepodid stages (á Norði et al. 2015) Copepodid lice were at higher abundance in the surface layer (0m) than at 5m. á Norði et al. (2015) postulate that this difference in stage distribution may be a result of nauplii residing in relatively deeper, warmer waters to shorten development time and reduce predation mortality. For the purpose of simulating the general dispersal characteristics of the majority of infective sea lice, the upper layers of the water column could be a sufficient first approximation, however improvements to model accuracy would require the inclusion of diel vertical migration (DVM). This needs to be accompanied by corresponding improvements/confidence in the model representation of currents and mixing in the upper water column. e.g. related to fresh surface layers and stratification.
Hydrodynamic models would be required to accurately represent pulsed freshwater releases and the intermittent presence of a surface fresh layer of varying thickness. It must also be appreciated that the interaction between dispersing infective sea lice and farmed fish occurs in the upper water column in the region where cages are located (Samsing *et al.* 2016), however should DVM influence the patterns of dispersal as reported in Johnson *et al.* (2014), then it will remain an important feature for future model improvements, however the data presented here on vertical distribution and those observed in the Faroe Islands (*á Norði  et al.* 2015), it is likely to be the case that dispersal in the upper most layers are likely to be dominant. As planktonic lice are phototactic (Genna *et al.* 2005), and that the majority reside towards the surface, this reduces the effect of dilution through vertical movements which results in patchy concentration fields observed with aggregations towards the shore and in likely frontal regions.

The sea lice distributions in Loch Linnhe are spatially and temporarily heterogeneous (Figure 6) as is the case in other salmon producing systems (e.g. Asplin *et al.* 2014; Johnson *et al.* 2016). Comparisons demonstrate that there are sizeable differences between the simulation runs for the distribution outputs for both nauplii and copepodid; this is a demonstration of not only temporal differences in relative lice numbers observed on farms within the system, but more likely a result of the complexity of hydrodynamic conditions experienced during the study periods. Although the majority of wind forcing roughly follows the south-west - north-east orientation of the sea loch (with variability during each scenario), this is not reflective of the predominant dispersal structures within the loch as the circulation is not only driven by the winds. Freshwater input at the top of the loch leads to a density-driven circulation, an estuarine circulation, which means that the surface layer is flowing out of the loch. Tides lead to mixing, and overall, Loch Linnhe shows complex circulation patterns. For the six
simulation periods there is considerable variability in relative particle concentration, at the
same locations, between different runs. As such it cannot be claimed that a certain grid
location of the system will consistently have relatively higher or lower sea lice. However it
appears that there is a tendency towards particles being transported down the north-west coast
of the loch leading to relatively higher densities within each simulation period along this
cost. This is caused by the influence of the Earth’s rotation as the width of the Lower loch is
larger than the internal Rossby radius of deformation. The flow down the north-west coast is
modified though by typical winds from the south-west which distribute surface waters much
more widely across the loch. Sites located on the north-west coast of Lower Loch Linnhe
(where the outflow can be enhanced) may experience substantial lice exposure, compared to
other areas of the Lower loch. However, the fresh outflow along this coast also means
salinities that could be too low for sea lice to survive in. The enhanced outflow leads to better
flushing of potential sites but also larger lice exposure if conditions are suitable for sea lice.
As operators have a good appreciation of the local conditions, it may be a reason for the lack
of sites along this coast as not only lice flow would be elevated. Strong flows may make
conditions inhospitable for cages. The only site (Kingairloch) operating on the west portion
of the loch is located within a side loch which would be relatively sheltered, although from
simulations this side loch consistently appears to experience elevated lice concentration. The
GLMM was designed to compare parity between simulation runs and not determine the
expected relative lice concentration within the system. The variability between simulation
concentration outputs may also be an artefact of the number of degrees of freedom due to the
grid resolution (182,358 squares) representing sea locations. However, the variability
between simulations demonstrates that multiple scenarios are required to gauge the
characteristics of a system, and underlines the need for multiple scenarios to establish
patterns for informing spatial management structures.
Hydrographic conditions within the sea loch are variable depending on location, season, year, etc. Lateral sea surface temperature and salinity variability depend on wind forcing and freshwater outflow. Sea lice dispersal in the surface layer relies on realistic, variable wind forcing which in turn will lead to realistic sea surface temperature and salinity variations across the sea loch driven by the temperature and salinity structure, winds and tides. In this study only the surface currents have been used for the biological model, not temperature and salinity. An additional limitation of this study is the use of the variable depth surface layer currents as opposed to using mean currents from the top 2 m for example. Small variations in depth can lead to different circulation patterns according to estuarine circulation theory. An analysis with vertically moving particles could therefore result in different outcomes, but that analysis is beyond the scope of this study. Winds, tides, rotational effects, and freshwater inflow all influence the estuarine circulation, which has been resolved for the purpose of sea lice dispersal.

Variability between hydrodynamic simulation outputs is frequently observed, and in order to obtain generalities of the system of interest, “average” characteristics are determined either through an averaging of the sea lice dispersal outputs (e.g. Adams et al. 2012; 2015) or averaging of forcing characteristics (e.g. Gallego et al. 2013; Lundqvist et al. 2009). Here, we average the simulation outputs to obtain relative lice distributions and connectivity. Although, understanding variability may be important for individual sites practices, coordinated sea lice management is undertaken in farm management areas agreed by all producers as part of farm management agreements which are required by statute. Having the behaviour over a longer term provides a sea lice “climate” within the system to allow for spatial IPM, as well as possibly identifying new site locations to avoid sea lice exposure.
Sea lice field sampling report that there is spatial heterogeneity within the distribution of sampled plankton and settled stage lice. This enables the possibility of comparing the relative observed lice in the field over all corresponding time points with the outputs from the simulations, to assess whether a feature of the distribution of lice in Loch Linnhe can be replicated by the model. Although there are considerable zero counts for plankton stage lice, there is a significant level of correspondence between the ranked observed plankton lice in the field and the simulated gradation in relative concentration for the corresponding field location. Similarly, there is a correspondence between graded measures of parasitism on sentinel caged fish and corresponding rank relative concentration for lice simulated by the model. There are some discrepancies between the simulated and observed measures of lice and this could be attributed to the model being a highly simplified reflection of reality. The model does not account for DVM, variable mortality and maturation influenced by environmental conditions such as temperature (Stien et al. 2005) and salinity (Bricknell et al. 2006) which determines the density of plankton sea lice (Harte et al. in 2017), lice predation, or unaccounted lice originating from sources outside the system, or non-farm sources within the system. The latter could represent between a third and a quarter of the lice in the system during spring of the first year of production. Future work should consider the need for further biological realism. Furthermore, the assessment of the model’s reflection of reality might be improved through the inclusion of lice counts and locations from wild and farmed fish. By having such information, it may be possible to predict a count of lice expected at locations within the system which could be compared to field observations. Relating field observations to model simulations has been difficult in other systems; Adams et al. (2012) found few lice in the plankton to validate models; attempts at the use of sentinel cages in Hardangerfjord are only recently to be reported (Sandvik et al. 2016); and wild fish surveys in the Broughton
Archipelago simply reported lice on wild fish in areas where lice were predicted to be with no information on correlation in observed and predicted levels, or data from areas where no lice found or not predicted to be found (Stucchi et al. 2011).

Although farm related results are presented anonymously here, the details of this study has been discussed with operators in the system to provide supplementary information alongside their own knowledge of the system for their consideration as part of their IPM plans.

The observed connectivity (Figures 7, 8) between sites within Loch Linnhe is of a similar order to that reported by Adams et al. (2012) ranging between $10^{-5} - 10^{-2}$. Although no onsite population modelling is undertaken here, such connectivity probabilities are sufficient to influence on farm sea lice population dynamics for sites in Loch Fyne (Adams et al. 2015). As with Loch Fyne, sites were found to self-expose, however unlike Loch Fyne, 5 of the 11 sites reporting lice in Loch Linnhe have greater self-exposure compared to lice originating from external sources. Additionally, Loch Linnhe farms form fewer connections overall than sites located in Loch Fyne. This demonstrates the importance of having location specific models for understanding the connectivity and thus management structures for individual systems. Loch Fyne is a relatively narrow system which appears to funnel lice between sites, whilst Loch Linnhe is much wider and lice are dispersed within clusters of farms.

Simulations demonstrate that there are two completely distinct regions which could be considered as two separate units for managing sea lice (Figure 9). However should rare events be excluded it may be possible to consider Loch Linnhe as three sea lice management units (Figure 9). It is important to keep in mind that this result is based on only six different scenarios and Loch Linnhe is a highly variable system. Currently the Loch Linnhe system is divided into two FMAs, which account for coordinated practices such as disease control and
producer operations. The units obtained here may enable operators to undertake sea lice management in smaller units with fewer sites which may aid timely co-ordination of intervention, which is demonstrated to support more effective lice control (Murray & Salama 2016).

Simulating farm relationships also highlights sites which may play a more influential role in lice transmission within the system and thus could be targeted before less influential sites within the cluster. Site H is the most connected site; Site G has the highest relative exposure, whilst site J has the greatest mean exposure per connection. Table 3 highlights that some sites are net exporters of lice whilst others are importers, it could be the case that these net exporting sites are influential sites for coordinated control. Further work is needed to ascertain, which is the most influential site within the network in terms of lice production. Producing metrics of site exposure may influence the order in which sites manage lice; furthermore such information may provide use for the fish health inspectorate’s (FHI) risk based surveillance.

We find a general trend towards decreasing connectivity with increased separation between farms (Figure 8). This is a similar pattern to a decrease in the proportion of transported lice with increased distance (Salama et al. 2016), as was the case in decreasing connectivity in Loch Fyne (Adams et al. 2012), however it must be noted that in both systems there are geographically close sites which have lower or no connection compared with connections to sites more separated. This highlights that generalities may be drawn, but for system specific conditions and relationships, individual systems require modelling. It must be noted that
transport does not equate to parasitism, which is a function of settlement due to environmental conditions and survival of parasites.

By gaining information relating to the population structure based on origin (farm) of lice on each individual farm (Figure 10) it can inform producers on how to manage lice more effectively. For example, should a neighbouring site contribute a high proportion of lice to a receiving site, and a treatment event on the former result in a suboptimal response, then the receiving site should consider whether it would be beneficial to use an alternate treatment method. Conversely, if a treatment is demonstrated to be effective on a neighbouring site, then perhaps the application of the same treatment could be considered.

Previous work in Loch Torridon (Amundrud & Murray 2009) highlighted that the dispersal of lice was highly influenced by wind direction. In Loch Linnhe (Rabe and Hindson 2016) and Loch Fyne, (Adams et al. 2012), which are both substantially larger systems, more complex drivers influence lice transport. In Loch Linnhe the Earth’s rotation plays a role due to the sea loch’s width. Large freshwater inflow leads to an estuarine circulation while tides lead to mixing. Winds influence the surface layer but are highly variable in the system (Rabe and Hindson 2016). More detailed studies will be necessary in the future to investigate pulsed fresh water releases and their evolution under varying conditions in the loch. Models need to show a high skill in representing the observed behaviour of surface waters in Loch Linnhe as these are crucial for sea lice dispersal.

Should it be desirable to have improved estimation of sea lice dispersal in Loch Linnhe and other systems, then it would be necessary to move away from a fixed grid to a variable grid system such as those used for Loch Fyne (Adams et al. 2012), Hardangerfjord (Asplin et al.)
2014), and Broughton Archipelago (Foreman et al. 2015). The Scottish Shelf Model (Wolf et al. 2016, Price et al. 2016) includes a high-resolution Loch Linnhe case study with a variable grid, which resolves geographical features like the Corran Narrows and bays in more detail. This model will be available for future use and further analysis. However, one of the purposes of this study was to establish the use of existing models without the need for special development of alternate models, as such pre-existing hydrodynamic models coupled with biological representative particle tracking models may be useful in establishing site interconnectivity for informing spatial management. DVM may have a substantial influence on sea lice dispersal (Johnson et al. 2014), and as demonstrated here, sea lice can be found at different depths. Addressing this aspect may lead to added assurance in model simulations. In terms of the current Loch Linnhe model, this may be possible to include as we used the resolved surface currents only, although currents at different depths layers are available. The model also outputs salinity and temperature variations with depth and time; it may be beneficial to consider variable biological realism by linking the conditions at each location to lice lifecycle parameters.

4. Conclusion

Here we described the use of a hydrodynamic model coupled with a previously described particle tracking algorithm that reflects an approximate features of sea lice biology. We provide some evidence based on field observations that the majority of infective sea lice are located in the upper layers of the water column which is consistent with previous findings (Heuch 1995, Samsing et al. 2016) both during day and night time indicating that surface layer currents may be sufficiently representative to describe the dispersal of sea lice in the environment as was the case in Loch Torridon and Loch Fyne. Currents (especially the along-loch component) were represented reasonably well in the hydrodynamic model and are forced
by winds, freshwater input, tides and influenced by the rotation of the Earth. The outputs highlight that there is a high level of spatial and temporal heterogeneity and that there is high variability between simulations. By using sentinel cages and plankton trawls to survey the environmental lice abundance it is shown that there is a correspondence between model simulation outputs and environmental observations. This gives some reassurance to the model which has previously been difficult to assess in other similar model studies. By calculating connectivity between sites it may be possible to form clusters of farms which could form sea lice management units depending on the acceptable likelihood of connectivity. Based on the observations of this study, three units could potentially be proposed for Loch Linnhe. The actual strength and frequency of connectivity can be used to inform order in which sites are managed, or influence the surveillance scoring for monitoring purposes. There is a general trend for decreasing connectivity with increased separation. However there are some anomalous sites which are nearby and have weaker (or no) connections compared to further separated farms, indicating site specific detail can only come about through site specific modelling. Although it is possible to refine the biological and physical features of the model, it requires considerable effort and expertise, whereas it appears that using a simplified procedure may be sufficient to ascertain general characteristics using previously described and available model components.
This work was funded by the Scottish Government under projects FC11111, AQ00040, FW0050. Thanks goes to Marine Scotland Science colleagues and ships’ crews for their contributions to this multidisciplinary project including John Dunn, John Fraser, Stuart Wallace, Jenny Hindson, Paul MacDonald and Alexander Murray; Marine Harvest Scotland for their assistance with instrument deployment, supplying fish and information on relative lice loads on farms; Scottish Sea Farms; the Scottish Environmental Protection Agency for providing ship time, crew, and instrumentation; The Crown Estate; Argyll Fisheries Trust; Lochaber Fisheries Trust; the Underwater Centre; Castle Duart; Kingairloch Estate; Aggregate Industries, and Mr K. Malcolm for their efforts providing aid in obtaining data. Thanks to the reviewers for their helpful comments.
6. References


Asplin L., Johnsen I.A., Sandvik A.D., Albreten J., Sundfjord V., Aure J., Boxaspen K.K.,
225.


Filtration of sea louse, Lepeophtheirus salmonis, copepodids by the blue mussel, Mytilus
edulis, and the Atlantic sea scallop, Placopecten magellanicus, under different flow, light and


Bricknell IR, Dalesman SJ, O’Shea B., Pert CC. Luntz AJM (2006) Effect of
environmental salinity on sea lice Lepeophtheirus salmonis settlement success. *Diseases of
Aquatic Organisms*. **71**, 201 – 212.


and Skern-Mauritzen, R., 2013. The salmon louse Lepeophtheirus salmonis (Copepoda:
Caligidae) life cycle has only two chalimus stages. PloS one, 8: p.e73539.

dynamics of larval sea lice density at East and West coast locations in Scotland. Diseases of

(Lepeophtheirus salmonis) in steep salinity gradients. Journal of the Marine Biological
Association of the UK 75, 927–939.

Committee, Peterborough.

European continental shelf - 1, Model description and density structure, Journal of
Geophysical Research-Oceans, 106, 14015-14034.

Marine Research 23, 104–122.

Geographical. Research Abstracts 13, 4461


Kalnay E., Kanamitsu M., Kistler R., Collins W., Deaven D., Gandin L., Iredell M., Saha S.,
American meteorological Society, 77, 437-471.

developments, Annual Reviews in Entomology 43, 243 – 270

Kristoffersen A.B., Rees E.E., Stryhn H., Ibarra R., Campisto J.L., Revie C.W., St-Hilaire S.
(2013) Understanding sources of sea lice for salmon farms in Chile. Preventive Veterinary
Medicine 111, 165-175.

(Labrus bergylta) against Lepeophtheirus salmonis infecting Atlantic salmon (Salmo salar)
post smolts. Pest management science 70, 1274-1282.

Preventative Veterinary Medicine 117,469- 477

stutchburyi restoration sites using hydrodynamic models of larval dispersal. New Zealand
Journal of Marine and Freshwater Research 43, 735-748.

Government, Aberdeen.
Marine Harvest (2014) Fourth Quarter Marine Harvest Group available at: 


Murray, A.G. (2009) Using simple models to review the application and implications of different approaches used to simulate transmission of pathogens among aquatic animals. Preventative Veterinary Medicine 88, 167-177.


Samsing F., Oppedal F., Dalvin S., Johnsen I., Vågseth T, Dempster T (2016) Salmon lice (Lepeophtheirus salmonis) development times, body size, and reproductive outputs follow universal models of temperature dependence. Canadian Journal of Fisheries and Aquatic Sciences. 10.1139/cjfas-2016-0050


Skiftesvik A.B., Blom G., Agnalt A.L., Durif C.M.F., Browman H.I., Bjelland R.M.,
Harkestad L.S., Farestveit E., Paulsen O.I., Fauske M., Havelin T., Johnsen K., Mortensen S.
(2014) Wrasse (Labridae) as cleaner fish in salmonid aquaculture - The Hardangerfjord as a

Smagorinsky J. (1963) General circulation experiments with the primitive equations: I. the


Vollset K.W, Krontveit R.I, Jansen P.A, Finstad B, Barlaup B.T, Skilbrei O.T, Krkošek M,
Figure 1: The study area showing locations of geographical features, particle release points (star), plankton (red circle), sentinel cage (black triangle), and hydrographic sampling (white square, white circle) sites, and approximate FMA boundaries (black lines). The purple arrows represent an example of instantaneous winds to evaluate the spatial structure of the wind forcing for the model. Insert map of Scotland shows the Loch Linnhe domain (dotted box), and Grutting Voe, West Shetland sampling region (solid box).
Figure 2: a) Taylor diagram evaluating model elevation against measured water elevation at Fort William. Standard deviation (black) and RMSD (green) are presented in meters. The correlation coefficient is presented in blue. Modelled elevation are denoted by: 1 - May 2011, 2 - October 2011, 3 - May 2012, 4 - October 2012, 5 - May 2013, 6 - October 2013, and observed elevations by A – F for the associated time periods (in October 2013 we did not have observations due to instrument failure and have
therefore used predicted tides). b) Currents from observations and the corresponding position in the hydrodynamic model during the 19-day October 2012 period at 10 m depth. Along-loch component (top) is positive up the loch and across-loch (bottom) is positive to the SE.

Figure 3: a) Simulated surface temperature following 48 hours of persistent westerly winds at 15 ms\(^{-1}\). b) Particle tracks from particles released in Kingairloch (red arrow) during 10 days in October 2013. c) Simulated surface salinity snapshot in October 2012 during comparable wind conditions as b) showing fresh outflow along the northern coast.
Figure 4: Rank correlations between simulated relative lice density and corresponding observations of a) counts b) prevalence c) abundance and d) intensity at locations corresponding to positions within the model domain.
Figure 5: Rank correlations between simulated relative plankton lice density and corresponding observations from plankton trawls made at locations corresponding to positions within the model domain.

Figure 6: Mean simulated relative nauplii and copepodid lice densities.
Figure 7: The relative aggregated mean simulated connectivity probability between source and receiving sites. The larger the dot, the greater the relative connectivity between sites.
Figure 8: Increasing Euclidean farm separation tends to reduce the probability of connection between sites. Dashed line represents confidence interval of the mean.
Figure 9: A representation of the connectivity between farm sites in Loch Linnhe with probability of connectivity above (black) and below (grey) $1 \times 10^{-4}$. Note that the edges are not directional or weighted to connectivity scale.
Figure 10: Origin composition of lice population informed through connectivity values. The legend insert indicates source of lice.
Table 1: Mean density (sea lice m⁻³) and 95% confidence interval of sea lice sampled from 8 samples at each of the depths, collected during day and night.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Day</th>
<th>Night</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nauplii</td>
<td>Copepodid</td>
</tr>
<tr>
<td>2</td>
<td>0.0714[0.0524,0.0905]</td>
<td>0.1285[0.0964,0.1783]</td>
</tr>
<tr>
<td>10</td>
<td>0.0071[0.0019,0.0124]</td>
<td>0.0071[0.0019,0.0124]</td>
</tr>
<tr>
<td>20</td>
<td>0.0268[0.0105,0.0430]</td>
<td>0.0222[0.0107,0.0338]</td>
</tr>
</tbody>
</table>

Table 2: Parameter estimates for assessing the variability between simulation run outputs.

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.4157</td>
<td>0.3425</td>
<td>0.7443</td>
<td>2.0870</td>
</tr>
<tr>
<td>Distance from Coordinate (0,0)</td>
<td>-0.0139</td>
<td>0.0003</td>
<td>0.0147</td>
<td>0.0132</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Random effect</th>
<th>Variance</th>
<th>Std. Dev.</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Residual</td>
<td>4.2942</td>
<td>2.0722</td>
<td>2.0655</td>
<td>2.0790</td>
</tr>
<tr>
<td>Simulation run</td>
<td>0.7034</td>
<td>0.8387</td>
<td>0.7506</td>
<td>0.9378</td>
</tr>
</tbody>
</table>

Table 3: The relative (averaged over all six simulations) inbound connectivity and external connectivity for each release site and the ratio of Internal: External transfer.

<table>
<thead>
<tr>
<th>Site</th>
<th>Export Ratio</th>
<th>Internal:External ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1.16637</td>
<td>6.833832</td>
</tr>
<tr>
<td>B</td>
<td>0.85736</td>
<td>7.680862</td>
</tr>
<tr>
<td>C</td>
<td>0.89863</td>
<td>1.516393</td>
</tr>
<tr>
<td>D</td>
<td>8.06682</td>
<td>2.171759</td>
</tr>
<tr>
<td>E</td>
<td>1.81613</td>
<td>0.598733</td>
</tr>
<tr>
<td>F</td>
<td>6.56134</td>
<td>0.3777</td>
</tr>
<tr>
<td>G</td>
<td>1.43655</td>
<td>0.263828</td>
</tr>
<tr>
<td>H</td>
<td>4.72514</td>
<td>0.057271</td>
</tr>
<tr>
<td>I</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>J</td>
<td>2.14018</td>
<td>1.904604</td>
</tr>
<tr>
<td>K</td>
<td></td>
<td>4.187822</td>
</tr>
<tr>
<td>L</td>
<td>5.28606</td>
<td>0.967493</td>
</tr>
</tbody>
</table>