

# A simple model of the role of area management in the control of sea lice



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## ABSTRACT

Sea lice are parasites whose treatment is a major cost on farming salmon, and sea lice from salmon farms can significantly increase lice numbers on wild salmonids in their vicinity. Effective sea lice control is thus an important consideration for sustainable salmon aquaculture. Sea lice have free-living planktonic larvae that are transported by currents and for this reason co-ordination of farm activities within management area (MAs) is increasingly used to control lice. Here we develop a simple model of co-ordinated management and resultant frequency of treatment required to maintain control of lice numbers in order to assess the benefits of using MAs. The model consists of a circle of salmon farms nodes that exchange larva lice with their neighbours on both sides. The farms are grouped into MAs, whose sizes are based on those of Disease Management Areas currently operating in Scotland. Transmission across MA boundaries is reduced, but is not generally stopped completely. Using this model, co-ordinated management within MAs is shown to reduce the number of treatments required to keep lice burdens under control. Co-ordinated following is always effective at reducing treatment requirements, however the benefits of co-ordinated treatment depend on hydrodynamic mixing regimes and the efficacy of medicines used. Benefits of co-ordinated management apply even when MA boundaries are epidemiologically ineffective, but strong boundaries can greatly increase MA benefits. There are thus robust clear benefits of the use of MAs and so simple modelling supports their use as a general policy. However, specific benefits in a particular area depend on the specific local environment which requires the use of more sophisticated hydrodynamic and population modelling to evaluate.

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## 1. Introduction

Atlantic Salmon (*Salmo salar*) production has expanded to become a major economic activity in cool temperate coastal waters such as those of Scotland where production exceeds 179,000 t (Munro and Wallace, 2015) and is estimated to contribute some £1.4BN to the wider economy (Alexander et al., 2014). Because of the importance of finfish aquaculture, Scottish Government supports the industry led targets of sustainably increasing production to 210,000 t by 2020 (Scottish Government, 2015). Limitations caused by disease and environmental concerns have emerged to restrict production and these must be overcome for production to increase.

Sea lice, copepodic ectoparasites of fish, are one such disease agent which is limiting the sustainable expansion of salmonid

aquaculture. The most important species that affect salmon are *Lepeophtheirus salmonis* in the northern hemisphere and *Caligus rogercressyi* in Chile. Other *Caligus* species also infest farmed salmon, but are considered to cause less serious problems. Sea lice also infect wild salmonids and infection on these wild fish can be enhanced from farmed sources (Middlemas et al., 2012). Although salmon lice may cause relatively little direct mortality on farmed fish (Soares et al., 2011) they have been estimated to cost €305M globally to control (Costello, 2009). A large amount of this cost is through the use of antiparasite medicines, whose frequency of use has increased (Murray, 2016) as a consequence of reduction in efficacy (Aaen et al., 2015). Environmental residues can result from excessive use, and these could potentially be toxic (Mayor et al., 2008). Therefore efficient use of these medicines is required as required as a part of a greater integrated pest management strategy (Kogan, 1998).

Larval sea lice disperse through hydrodynamic transport (Amundrud and Murray, 2009) which can result in farms interacting over distances of kilometres (Salama et al., 2016) both with other farms (Adams et al., 2012) and with wild salmonids

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(Middlemas et al., 2012). For this reason, area management is often used to control lice on farmed salmon whereby groups of farms in a local area are managed according to a local plan or agreement. For example, farm management areas (MA) in Scotland (CoGP, 2014) which is required to be described as part of statutory requirements (Aquaculture and Fisheries Act (Scotland) 2013) and disease management areas used in control of notifiable disease (MSS, 2015). Similarly, local barrios are used in Chile (Kristoffersen et al., 2013) and area management in Canada (DFO, 2011).

There has been considerable effort applied to modelling of sea lice in studies relating to: dispersal (e.g. Amundrud and Murray, 2009; Adams et al., 2012; Salama and Rabe, 2013; Adams et al., 2015), aspects of population modelling (e.g. Revie et al., 2005; Gettinby et al., 2011; McEwan et al., 2015), and statistical modelling such as of factors influencing lice treatment rates (Revie et al., 2003; Murray and Hall, 2014). However, there is no specific modelling analysis of the benefits of using area management strategies for lice control beyond recent modelling of interacting pairs of farms (Peacock et al., in press). There has been no theoretical basis for assessing if area management is effective, and for identifying the role of key factors influencing the extent of any benefit.

Therefore, we take a modelling approach that has been used to assess area management of emerging infectious diseases in Scottish farmed salmon (Werkman et al., 2011) and adapt it to describe lice dynamics in order to inform area management of sea lice parasitism on farmed salmonids. The model is used to assess the effect of subdivision of the population of salmon farms into area based sub-populations and, within these areas, the benefits of synchronisation of fallowing and treatment regimes relative to asynchronous regimes. These effects are investigated for different hydrodynamic dispersal regimes and hence exchange between farms.

## 2. Methods

A simple model of interaction of lice infection on salmon farms is developed and coded in R version 2.15.0 (R core team, 2012). This simple model is used to identify the behaviours of a system that are not dependent on details of local conditions and local interactions (Murray, 2001) and hence identify robust system responses to management. Other effects of management strategies will indeed depend on details of interactions between farms, and more complex modelling is required to assess the specific optimal strategies for such effects (Salama and Rabe, 2013). However, the robust benefits identified from simple modelling are precisely those which can be used to derive and support standardised sea lice control policies that are likely to be effective in most areas.

### 2.1. Basic structure of the model

The basic structure of the model is formed of nodes arranged in a ring to represent farms distributed along a coast (Fig. 1); there are 251 nodes as this is the observed number of farms (MSS, 2015). The use of a ring follows the standard Watts-Strogatz model (Watts and Strogatz, 1998) used for simulating spread of pathogens between nodes without introducing arbitrary boundary conditions and is similar to a structure used by Werkman et al. (2011) to model infectious disease spread in aquaculture. The ring avoids the need to consider boundary conditions, since all nodes have neighbours on both sides and pathogens can spread in both directions. The simple ring structure model assumes farms interact most strongly with neighbouring farms in the ring, which generally (but not always) will be their geographically closest neighbours. The ring structure makes exchange 1 dimensional, we are neglecting the 2-D structure of the coastal environment to simplify the model.

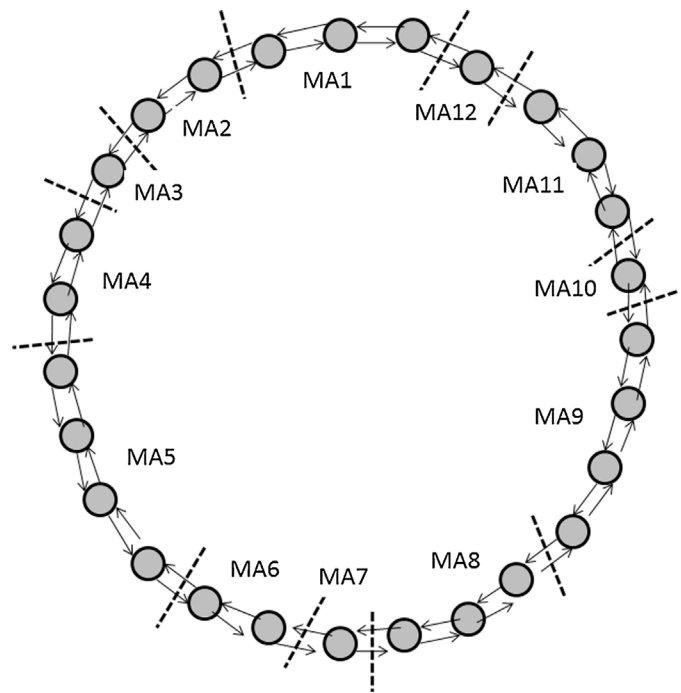
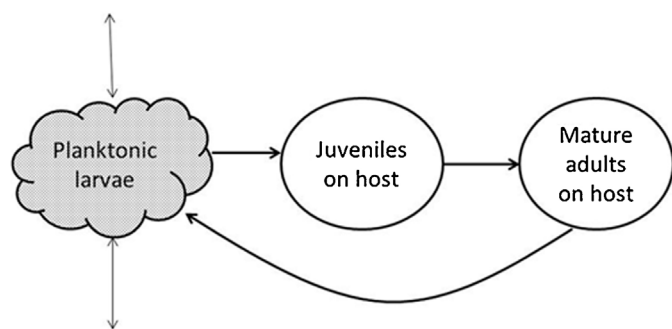


Fig. 1. Ring of farms that interact with neighbours and are divided into 12 MAs.

Strength of interactions between pairs of farms depends on both seaway distances between farms and local current strengths and on the adult lice population on the source farm. Essentially this is similar to the contact probability as a function of distance derived from more sophisticated statistical space time modelling (e.g. Aldrin et al., 2013), but we simplify this by assuming equal spacing of farms and excluding more distant contacts which contribute relatively little to infection pressure (Salama et al., 2016) for this simple model. These farms hold salmon on them, which can become infected with lice from environmental background sources, from re-infection from the farm itself, or with larval lice spread from neighbours.

The farms are grouped into management areas (MSS, 2015) with a reduced probability of infection transmission between neighbours if they are in different management areas because of physical separation between areas. In this paper we use disease management areas (MSS, 2015) as used for official disease control programmes, rather than industry farm management areas (CoGP, 2014). This is because the number of farms within DMAs can be obtained from the official maps of DMA, which is not the case for FMAs. The use of DMAs also makes this analysis consistent with earlier work (Werkman et al., 2011), although DMA boundaries are updated here to account for changes since the earlier analysis. As this is a simple model the DMAs are representative and used to illustrate the concept of area management, with real DMAs having interactions that are complex and variable, both internally and with neighbouring management areas.

Each simulated farm holds a population of salmon that are held on the site for an 18 month period after which the site is emptied for harvest, fallowed and repopulated; this approach was used by Werkman et al. (2011). Fallowing at the site level has been shown to be an effective means of reducing lice infestation (Bron et al., 2006) and is now ubiquitous on Scottish sites engaged in salmon production for harvest. When salmon initially are put onto a marine farm that has been fallowed they are free of lice since these parasites are exclusively marine, with rapid mortality in freshwater (Bricknell et al., 2006), and salmon are sourced from freshwater smolt production sites. Once on these farms the fish can become infested



**Fig. 2.** Lice population model: planktonic larvae disperse between farm locations and/or infect farmed salmon in month 1 which, in month 2, mature to sexually reproductive adults that produce more larvae and die at the end of this month.

with lice from background wild sources, or from interaction with neighbouring sites. Once lice are established on the farm then their larvae can re-infect that same farm.

Lice develop (Fig. 2) through planktonic phases (nauplii I, nauplii II and infectious copepodids), then non-reproductive juvenile phases (J) on the host fish of attached chalimus and mobile pre-adults, before finally becoming sexually mature adults (A). In the planktonic phases the lice are transported between farms, this is a relatively short period of a few days and is modelled as an infection pressure. In this simple model this infection pressure results in juvenile lice becoming established on the farmed fish, these mature to reproducing adults after a month, and then die after a further month. Louse survival time is variable depending on environment (Pike and Wadsworth, 1999) and a month is used here as an approximate average in this simple model. This model allows the lice life-cycle to be economically simulated. The model is a simplified form of the population model developed by Revie et al. (2005) but with the addition of explicit interaction with neighbouring farms.

At the start of a model run, the sites have an initial age assigned of 1–18 months so that they will occupy different stages of the production cycle production cycle during simulations and will not all fallow simultaneously across the entire model structure. This initial age is assigned at random, either for each farm individually or, for scenarios of area co-ordinated stocking, a single age is applied for all farms in a given MA. At this initial point of the simulation there are no lice on any of the farms and infection is seeded from the background infection pressure. For this reason the model is run for an initialisation period allowing lice numbers either to reach a dynamic stability with removal through treatment and fallowing equalling new infections, or there is a loss of control with lice numbers increasing indefinitely and unsustainably.

## 2.2. Modelling infection pressure

Infection pressure at farm F at time t,  $I_{F,t}$ , depends on background infection from wild reservoirs, c, re-infection by larvae produced from adult lice on the farm  $A_{F,t}$  (see 2.3. Modelling lice population), and infection produced from adult lice on neighbouring farms. Relative contribution depends on exchange between farms, which depends on local environment. Infection pressure from neighbouring farms is reduced by a factor q if these are in a different MA.

$$I_{F,t} = c + k(\alpha A_{F,t} + \beta(q_{-1}A_{F-1,t} + q_{+1}A_{F+1,t}) + \gamma(q_{-2}A_{F-2,t} + q_{+2}A_{F+2,t}))$$

Lice infection pressure depends on the lice population growth parameter k, which can range from zero to increase without limit. A single value of k is used in each scenario, but k is varied between

scenarios reflecting factors including the environment (salinity and temperature (Johnson and Albright, 1991; Bricknell et al., 2006) which determine lice survival) and the population of host fish which is an important factor in total lice production (Murray and Hall, 2014).

Hydrodynamics can also influence whether lice infect fish or are transported away from hosts and these affect relative contribution from  $\alpha$ ,  $\beta$ , and  $\gamma$ . Farm F interacts with neighbours that are 1 (at probability  $\beta$ ) or 2 (at probability  $\gamma$ ) steps away in either direction in the ring (with  $\alpha$  for self re-infection). This transmission model assumes that the strength of interaction drops with distance and that farms are typically separated by several kilometres so that, generally, exchange with farms more distant farms can be neglected in this simple model. For simplicity the model restricts interactions to the four most strongly connected neighbours, but this number could be increased to deal with more widespread interactions. Since the nodes are arranged in a ring the neighbours where  $F = 1, 2$  or 250 or 251 are adjusted; if  $F + x > 251$  then  $x = x - 251$  and if  $F - x < 0$  then  $x = -x + 251$ . This allows for the farms to interact as a circle where infection spreads across the end of the circle (251 is the number of farms used in the array, based on observed numbers (MSS 2015)). If neighbours are in different MAs the variable q adjusts infection pressure for reduced transmission across MA boundaries (see later) (Table 1).

Values for model parameters  $\alpha$ ,  $\beta$  and  $\gamma$  have been derived from analysis of dispersal patterns obtained from Loch Linnhe (Salama et al., 2013) and Loch Fyne (Adams et al., 2012). Parameters are calculated based on the numbers of lice  $h_z$  arriving at farm neighbour z. Subscript z ranges from 0 to 4, where  $n = 0$  represents self-infection of the farm and  $z = 1..4$  are the four other farms that receive, in declining order, most lice from this source farm 0; it is quite possible  $h_z$  may be zero for larger z and it is always zero for  $z > 4$  in this simple model. The infection loads  $h_z$  are used to calculate farm level values of the model parameters  $\alpha_f = h_0 / \sum h_z$   $z = 0..4$ ,  $\beta_f = (h_1 + h_2) / 2 \sum h_z$   $z = 0..4$  and  $\gamma_f = (h_3 + h_4) / 2 \sum h_z$   $z = 0..4$ . The farm-level values have been used to calculate parameter values for 3 scenarios using the lower quartile (D1) median (D2) and upper quartile (D3) for Loch Linnhe. Connectivity on average in Norway is between D1 and D2, with 66% of infection sourced within the farm (Aldrin et al., 2013), this is approximately equivalent to  $\alpha = 0.7$  (non-specific infection is treated differently in this model).

D1 Local  $\alpha = 0.75$ ,  $\beta = 0.125$ ,  $\gamma = 0$

D2 Moderate  $\alpha = 0.6$ ,  $\beta = 0.18$ ,  $\gamma = 0.02$

D3 Long-distance  $\alpha = 0.32$ ,  $\beta = 0.24$ ,  $\gamma = 0.1$

Connectivity from Loch Fyne showed very high levels of mixing between sites (Adams et al., 2012), often with the self-infection contributing a small proportion of total site infection. To simulate such conditions a 'well mixed' locality scenario D4 is used where all the farms in the neighbourhood contribute equally:

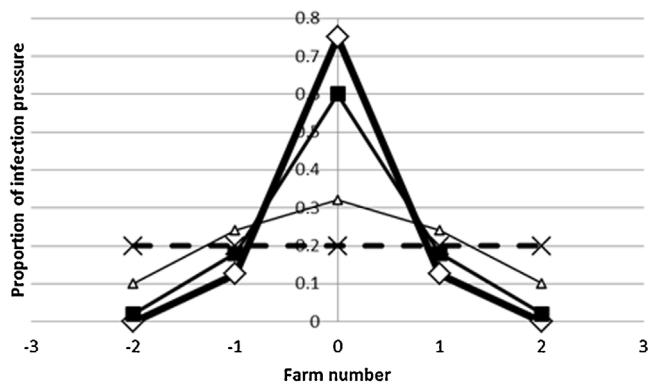
D4 Well-mixed  $\alpha = 0.2$ ,  $\beta = 0.2$ ,  $\gamma = 0.2$

The sum of  $\alpha + 2\beta + 2\gamma = 1$  for all scenarios, since these are the proportional contributions of these different sources to infection. These contributions are multiplied by k to give total infection pressure which incorporates mortality rate (which depends on temperature and salinity) and on dispersal patterns and farmed fish biomass which effect probability of contact with farmed fish by the larval lice while they are still viable. In the results presented in this paper scenarios D1 and D4 are used to illustrate the effects of mixing at either extreme (Fig. 3).

It is possible some lice may be transported over much longer distances when salmon are moved to slaughter houses and the lice

**Table 1**  
Model parameters, variables and scenarios identifiers; scenarios identifiers are noted as in units.

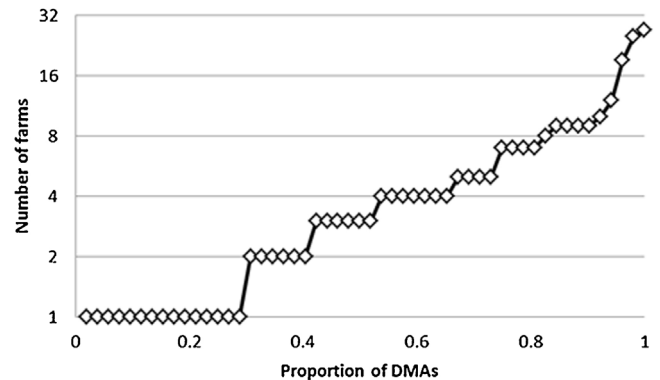
name	Description	Units	Value
L	Lice time step cohort, pretreatment	Lice fish <sup>-1</sup>	Variable
L'	Lice cohort after treatment	Lice fish <sup>-1</sup>	Variable
λ	Cohort number		1 – m
m	Oldest cohort, 2 months old		12
J	Juvenile lice per fish	Lice fish <sup>-1</sup>	Variable
A	Adult lice per fish	Lice fish <sup>-1</sup>	Variable
I	Infection pressure	Lice fish <sup>-1</sup> month <sup>-1</sup>	Variable
F	Location of farm in array		1–251
x	Distance in array of a farm from F		
G	Number of farms in MA		1–27
T	Time step	months	5/30 (5 day) default
R	Time from stocking to following	months	18
c	Background infection	Lice fish <sup>-1</sup> month <sup>-1</sup>	0.01
h <sub>z</sub>	Observed infection to neighbour z	Units cancel out	
z	Neighbour z = 0 is self-infection		0–4
α	Proportion re-infection of farm		(see D <sub>1</sub> ..D <sub>4</sub> )
β	Proportion infection from F-1 or F+1		(see D <sub>1</sub> ..D <sub>4</sub> )
γ	Proportion infection F-2 or F+2		(see D <sub>1</sub> ..D <sub>4</sub> )
k	Infection pressure multiplier	month <sup>-1</sup>	0–5, default 3
q <sub>x</sub>	Effect of boundaries F to F+x		0–1
n	Number of boundaries to source farm		0, 1 or 2
b <sub>e</sub>	Boundary efficiency		0–1, default 0.8
T <sub>e</sub>	Treatment efficiency		0–1, default 0.9
φ	Treatment threshold	Adult lice fish <sup>-1</sup>	2
A <sub>φ</sub>	Adult lice (farm or MA) to test φ	Adult lice fish <sup>-1</sup>	Variable
D1	Local mix scenario	Scenario	α = 0.75 β = 0.125 γ = 0
D2	Typical mix scenario	Scenario	α = 0.6 β = 0.18 γ = 0.02
D3	Long distance mixing	Scenario	α = 0.32 β = 0.24 γ = 0.1
D4	Well mixed (Fyne) scenario	Scenario	α = 0.2 β = 0.2 γ = 0.2
tf	Unsynchroised treatment, following	Scenario	Management Scenario
Tf	Synchronised treatment, unsynchronised following	Scenario	Management Scenario
tF	Unsynchroised treatment, synchronised following	Scenario	Management Scenario
TF	Treatment following, synchronised	Scenario	Management Scenario



**Fig. 3.** Proportion of infection pressure on farms distribution around source farm 0, scenarios local (D1, thick solid line), moderate (D2, medium line) long-distance (D3, thin line) and well mixed (D4, dashed line) scenarios.

survive to be discharged (Price et al., 2013). However the numbers moved are likely to be small relative to hydrodynamic transmission between neighbours, and from background sources, and so long-distance anthropogenic transmission (Werkman et al., 2011) is not included in this model.

Groups of farms are collected into management areas that are separated by boundaries across which transmission is weakened resulting in reduced interaction between farms in different MAs. These boundaries are unlikely to be 100% biosecure, since small numbers of lice can transmit over 100 km in some circumstances (Asplin et al., 2014). Therefore the boundaries have an efficacy  $b_e$  by which they reduce transmission, and so transmission across a boundary for an immediate neighbour is  $(1 - b_e)\beta$  or from a neighbour 2 steps away  $(1 - b_e)\gamma$ . Transmission from a neighbour two



**Fig. 4.** Distribution of DMA sizes as number of farms present in each of 15/4/15, from MSS (2015).

steps away would be  $(1 - b_e)^2\gamma$ , if there is an intervening MA containing only one farm. This is implemented as  $q_x$  where:

$$q_x = (1 - b_e)^n$$

Here  $n$  = the number of MA boundaries (0, 1 or 2) that must be crossed to get to farm  $F$  from farm  $x$ , where  $x = F+1, -1, +2$  or  $-2$  as determined by subscript.

Management Areas vary in size and larger areas may play an important role in establishing infection. There were 52 MAs holding 251 farms between them (as of 15/May/2015). The distribution of farms is aggregated with many more small areas with one or two farms and a few large areas (Fig. 4). The model allows for this pattern of variability in MAs using the distribution of MAs is taken from the observed Scottish distribution of disease management area (MSS, 2015) with two very large MAs with 27 and 25 farms to 15 MAs with only one farm each (Fig. 4). MA sizes are selected from the list,



without replacement, and farms are assigned to these MAs until all farms are assigned to an MA.

### 2.3. Modelling lice population

With each time step infection increases at a rate dependent on infection pressure in the neighbourhood  $I$ , minus the mortality of the existing lice. This mortality is the adult population resulting from infection that occurred 2 months earlier (unless the site was followed within the two months, in which case there will be no lice of terminal age). For simplicity we assume both maturation to adulthood, and from maturation to mortality take one month.

To avoid artificially synchronising all treatments within a month the model is solved using a 5 day time step, this means sub-dividing the lice population at farm  $F$  at time  $t$  into  $m$  sub-components  $L_{F,t,\lambda}$  where  $\lambda = 1-m$  and  $m$  equals the two months lice life-cycle time divided by the five day time step. In this case  $m = 12$ , of which  $\lambda = 1-6$  are juvenile  $J$  and  $\lambda = 7-12$  are adult  $A$  sub-components. The number of these sub-components are varied if the model time step is changed.

$$L_{F,t,1} = I_{F,t}$$

$$L_{F,t,\lambda} = L'_{F,t-1,\lambda-1}$$

$$J_{F,t} = \sum L_{F,t,\lambda} \lambda = 1..0.5 m$$

$$A_{F,t} = \sum L_{F,t,\lambda} \lambda = 0.5m + 1..m$$

In the model treatment is applied at the point adult lice numbers  $A_\phi$  reach a threshold level,  $\phi$ . The threshold test can be imposed on the site alone ( $A_\phi = A_{F,t}$ ), or for synchronised treatments when mean load at the MA level exceeds the threshold ( $A_\phi = \sum A_{F,t}/G$ ,  $F = y + 1..y + G$ ), where  $G$  is the number of farms in the management area, where  $y$  is the last farm in the previous MA. The default value of the treatment threshold used is  $\phi = 2$ , which, assuming equal sex ratios, is treatment threshold at one 1 adult female per fish a level which is in practice a point at which treatment is recommended (Murray 2016), real thresholds vary with season but seasonality is not included in the simple model. When treatment is applied lice all stages, both juvenile and adult, are reduced in numbers proportionate to the effectiveness of the treatment:

$$\text{If } A_\phi > \phi \text{ then } L'_{F,t,\lambda} = L_{F,t,\lambda} (1 - T_e)$$

$$\text{else } L'_{F,t,\lambda} = L_{F,t,\lambda}$$

A 100% effective treatment clears the farm of all lice, and a 0% treatment has no effect. Effective medicines such as deltamethrin will normally reduce populations by over 90% (Jimenez et al., 2012), but there may be considerable variation and a general decline in efficacy occurs if single medicines are relied on for too long as a result of evolution of resistance (Aaen et al., 2015). For example the efficacy of emamectin benzoate appears to have declined significantly in Scotland (Lees et al., 2008) and there has been a general increase in the frequency with which Scottish salmon farms are treated (Murray, 2016).

Treatments last for different times, bath treatments are largely effective only for the duration of the treatment itself, since the agents are dispersed quickly following treatment. Treatments with in-feed medicines, particularly emamectin benzoate (Slice) are retained within the tissue of the fish for a period and so remain effective at controlling lice for some days after treatment. In this simple model we use a 5 day time step and this means treatments are simulated as effective over 5 days with farms treated within a single time step effectively treated synchronously and so this gives an appropriate time step for the model.

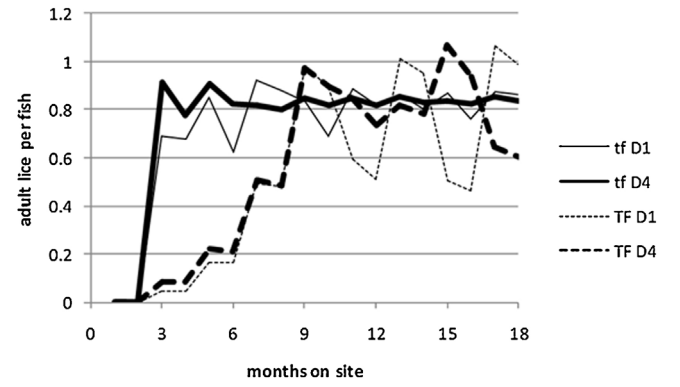


Fig. 5. Averaged adult lice loads with time on site under two management strategies (TF synchronous (dashed) or tf asynchronous (solid)) and two dispersal scenarios (D1 (thin), D4 (thick)),  $k = 3$ ,  $b = 0.8$ ,  $T_e = 0.9$ .

Treatment occurs at a maximum rate of once per month, i.e. following treatment there is a gap of at least 5 time steps (of 5 days) before another treatment event can occur. If treatment were allowed each time step and the time step were allowed to be decreased to an arbitrarily small value then numbers of treatments could increase without limit, if this occurred lice numbers could always be controlled for any treatments more than 0% efficient. However, a limit on treatment rate does exist for technical, environmental and economic reasons and we have selected once per month for the purpose of this simple simulation. Treatments at frequencies averaging every other month do occur at some sites in practice (Murray, 2016).

Eighteen months from the time at which it was stocked a farm will be harvested and fallowed. At this point the lice population is set to zero  $L_{F,\lambda} = 0$  for all  $\lambda$  (or  $A_F = J_F = 0$ ) and the site must be re-infected from neighbours or from background sources.

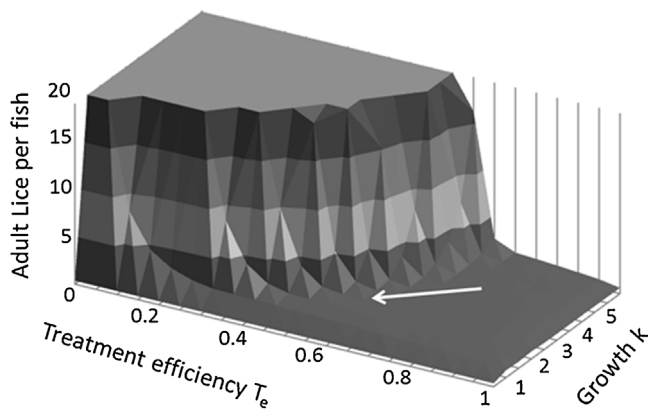
The model is run for 600 months. There is a 50 month run-in period during which results are not recorded to allow the model outputs to stabilise. The model uses a 5 day time step. This is considered a reasonable numerical approximation given that site treatments may take a few days for bath treatments and in-feed treatments will give farms protection from lice. Longer time steps lead to artificial synchronisation of treatment (e.g. a 1 month time step would mean all treatments occurring within a month would be simulated as synchronous) leading to under-estimation of the benefits of actively synchronising treatment. Conversely, too short a time step leads to an impractically narrow definition of synchronisation in practice and increases run time of the model.

Four management scenarios are investigated using the model: tf = asynchronous treatment and fallowing, TF = synchronised treatment but asynchronous fallowing, tf = asynchronous treatment but synchronised fallowing, and TF where fallowing and treatments are both synchronised across the MA.

## 3. Results and discussion

### 3.1. Time on site and accumulation of lice

When salmon are introduced to a site they are initially free of infection (month 1), infection is introduced but lice are still juvenile in month 2, so infestation with adult lice only shows up in month 3 of the salmon being on site. Numbers of lice then accumulate dependent on local infection pressure which itself depends on lice numbers on the farm and its neighbours and on the hydrodynamic environment (Fig. 5). If management is not synchronised, then farms surrounding a newly restocked farm are likely to have not recently fallowed and so lice numbers on them may be high. There-



**Fig. 6.** Lice per fish for treatment efficiency versus growth parameter  $k$  ( $D = 1$  TF, localised mixing and synchronised treatment). Plotting is capped at 20 adult lice per fish because of the rapid increase beyond this point. Arrow shows how if treatment efficiency dropped from 80 to 60% a previously sustainable  $k$  of 3.5 might have to be reduced below 2 to maintain sustainable loads.

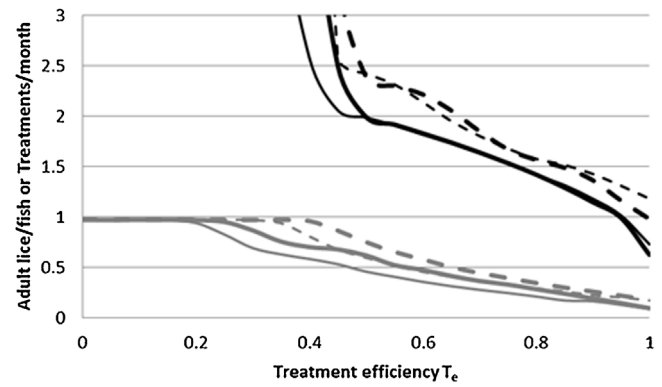
fore neighbourhood infection pressure is high and so lice numbers on the restocked farm increase rapidly to the point at which treatment intervention becomes necessary and lice numbers thereafter are only stabilised by repeated treatment. If management is synchronised then lice numbers increase only slowly because there is no large source of lice in the MA. However the increase in lice numbers accelerates as the population of lice on the farm and its neighbours increases, leading to an exponential increase, again this lice population is capped once treatment takes effect. These results are for a situation in which infection pressure is low enough that treatment can effectively control lice loads.

### 3.2. Basic system properties

Ability to control lice depends on population growth,  $k$ , and treatment efficiency,  $T_e$ . These parameters interact with a relatively rapid loss of control should treatment efficiency drop below a threshold, which depends on the growth rate parameter  $k$ . Should this threshold be crossed a rapid loss of control may result (Fig. 6). However, while  $T_e$  is high lice can be controlled even when  $k$  is high, efficient medicines may allow very high biomasses, with resultant high  $k$ . However, should efficiency be lost owing to the evolution of resistance then substantial reduction in  $k$  may be required to keep lice under control, and this may mean farmed biomasses could have to be cut substantially if treatment efficiency is lost.

A more detailed analysis of the effect on the system of changes in  $T_e$  is illustrated for 4 scenarios (TF D1, tf D4, TF D1 and tf D4) that illustrate the range of hydrodynamic mixing and management co-ordination on both lice count and treatment (Fig. 7). In all cases there is a loss of control with falling treatment efficiency and a relatively sudden increase to very high levels. The exact threshold depends on management and hydrodynamics, with synchronisation of management meaning that less effective medicines can still maintain control in a given environment and maintain the lice populations at lower levels with less frequent treatment. In the lead up to this collapse lice loads are increasing only slowly, but treatment rates increase at an accelerating rate.

As treatment efficiency drops toward the threshold lice numbers increase more slowly, but treatment rate increases more rapidly as lice are held near treatment threshold by frequent application of treatments. Therefore it may be that increasing treatment rate is a more important indicator of a system under pressure than is increasing lice count. Furthermore, increasing application of medicines also creates conditions in which selection of resistance is enhanced (Aaen et al., 2015).



**Fig. 7.** Lice per fish (black) and treatment rate per month (grey) for treatment efficacies of 0–1 and  $k = 3$ , under two management (synchronous (TF, solid line), asynchronous (tf, dash line)) and two dispersal scenarios (D1 (thick), D4 (thin)).

### 3.3. Area management

Management strategies do affect the level of treatment required for sustainable salmon farming, as can be seen from the previous results (Figs. 5 and 7). We therefore further analyse treatment strategies. These have three components, the effectiveness of the boundary itself, synchronisation of stocking and fallowing in areas and the synchronisation of treatment of farms within areas.

#### 3.3.1. Area boundaries

Lice can, under some circumstances, be transported over very large distances (sometimes 100 km, Asplin et al., 2014). It is therefore unlikely that any practical boundary will be 100% efficient, although it may approach this if separation distance is large and in some circumstances lice may be mostly retained within a relatively small area (Salama et al. in 2016). So the model is investigated for boundaries that vary from 0% to 100% efficient. A 0% efficient boundary means that transmission between a site and its neighbour in the next MA is as large as transmission to a neighbour within the same MA, effectively 0% occurs if MA boundaries are drawn arbitrarily and not related to epidemiological factors, e.g. political boundaries or cluster of farms owned by one company. The situation at 0% efficient boundaries and unsynchronised (tf) management is the equivalent of having no area management in place.

Even a completely permeable boundary provides substantial reduction in treatment required if management is synchronised within the MA (Fig. 8). Synchronisation may become more difficult as the number of parties operating in an area increases (Murray, 2014), therefore suboptimal boundaries that allow collaboration are likely to be better than perfect boundaries without collaborative management. However, if MAs are very small with minimal separation they would effectively operate as a large unsynchronised area.

As MA boundary efficiency increases from 0% the treatment required to control lice drops (Fig. 8), this drop is linear and relatively small if management in the MAs is not synchronised, but non-linear when management is synchronised. This reduction is moderate with asynchronous management, but is 50–70% for synchronous management for the case illustrated. Much of this reduction occurs at the highest end of the scale, owing to the non-linear nature of the relationship, however even moderately effective boundaries can substantially reduce treatment requirement and even synchronising management within a 0% effective boundary can substantially reduce the number of treatments required.

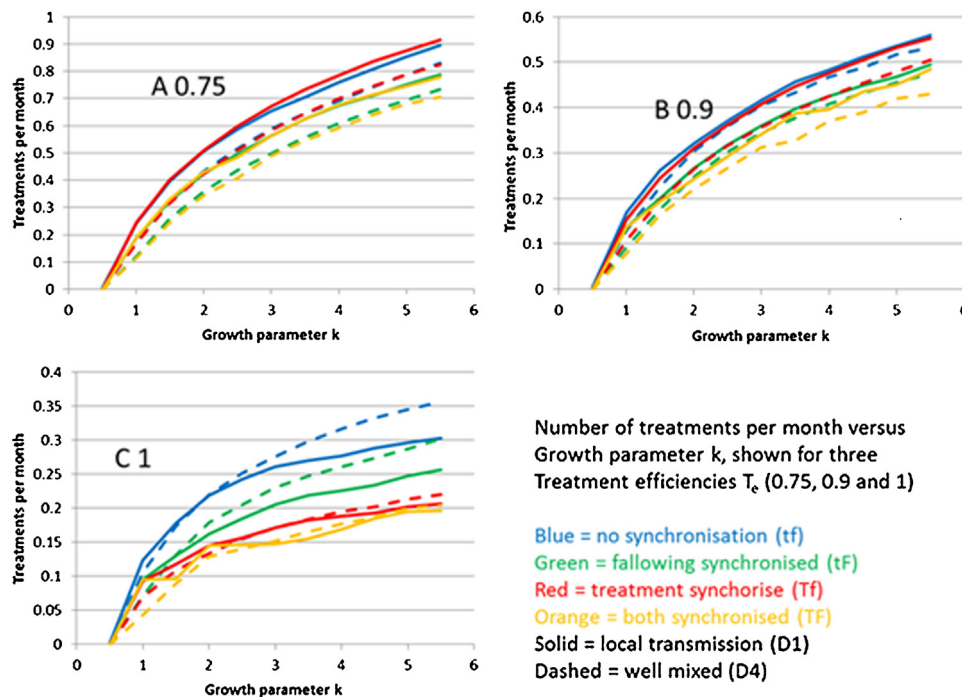


Fig. 9. Lice treatment rates with  $k$ , for three treatment efficiencies, four management synchronisation strategies and two mixing scenarios.

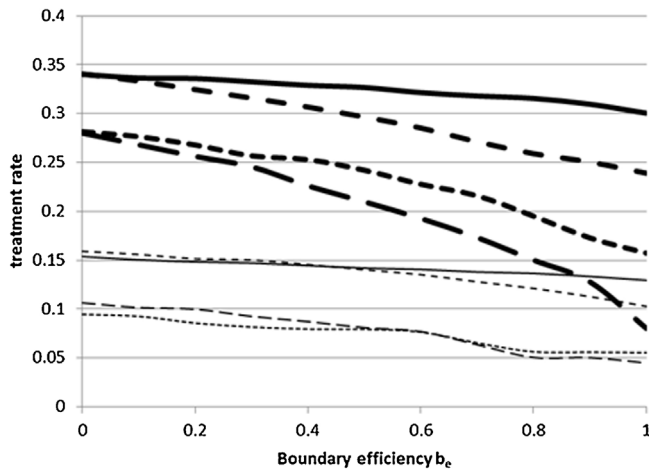


Fig. 8. Treatment rate for boundary efficacies of 0–1 and  $k=3$  at  $T_e=75\%$  (thick large text) and 100% (thin small text) under two management and two dispersal scenarios (tf D1, tf D4, TF D1 and TF D4).

### 3.3.2. Co-ordinated following and treatment

Management within areas occurs at two levels: management of stocking and following so that all farms in the area follow the same production cycle, and co-ordination of treatments so that all sites within an area are treated synchronously.

When treatment and following are both synchronised there are benefits in terms of a reduced average number of treatment events per production cycle (Fig. 9). There is a robust benefit to synchronised management apparent from this simple modelling. However, the contributions of synchronised following and synchronised treatments to this reduction in treatments is variable.

Benefits of co-ordinated following are clearly apparent as the treatment rate under co-ordinated following is always lower than comparable conditions ( $k$ ,  $D$ ) in the absence of coordinated following (Fig. 9). Co-ordination leads to reduced numbers of treatments per cycle and increases the maximum value of population growth

parameter  $k$  or reduces the minimum treatment efficiency at which lice can be controlled (Fig. 7). Co-ordinated following therefore presents a robust benefit to lice management whose existence does not depend on other components of the model.

The benefits of co-ordinated treatment are more dependent on other conditions with clear benefits only for the 100% effective treatment (Fig. 9a), in this case synchronised treatment without synchronised following is almost as effective as synchronisation of both. Synchronised following without synchronised treatment is also beneficial, but there is no great synergistic benefit. When treatment is 90% effective, there is only a reduction in number of treatments under the high dispersal scenario (Fig. 9b). Under the poor treatment (75% effective) there is no benefit of synchronising treatment, even under D4, indeed there is a slight increase in treatments under D1 because of unnecessary treatments of sites with lower lice loads. So the benefits of co-ordinated treatment do depend on local hydrodynamic conditions of the site and the efficacy of treatment.

### 3.4. Comparison with other models of sea lice populations

A range of models have been developed that describe interactions between farms using coupled hydrodynamic and particle models, for example these have been applied in Scotland (Adams et al., 2012; Salama et al., 2013) and Norway (Asplin et al., 2014). Another approach, that similarly looks at interaction between neighbours uses statistical analysis of lice counts with distance based kernel as a risk factor for interaction between neighbours for example in Chile (Kristoffersen et al., 2013) and Norway (Aldrin et al., 2013; Kristoffersen et al., 2014). Either approach allows for much more detailed understanding of the interactions between particular pairs of farms or farms generally in an area.

Similarly more detailed models of lice population dynamics allow detailed simulation of lice populations using delayed differential equations (Revie et al., 2005; Gettinby et al., 2011) or individual based models (McEwan et al., 2015). These give detailed descriptions of dynamics on farms, and are particularly useful for planning interventions.

These models are being combined to include transport processes that reflect local hydrodynamics and population models that detail the dynamics of sea lice populations (Gettinby et al., 2011; Adams et al., 2015; Peacock et al., in press). These detailed models are being used to inform effective controls for sea lice, and will increasingly be applied to inform specific management practices for specific farms as more widespread hydrodynamic model output of sufficient resolution becomes available and quality data on lice counts is rapidly made available to managers.

Local environments of differing favourability to lice settlement (Bricknell et al., 2006) and population growth (Johnson and Albright, 1991) further alter the effects of synchronising treatments (Peacock et al., in press). The point is that the simple model cannot identify clear benefits of synchronised treatment, and so more detailed knowledge of local conditions is required to assess or model the value of synchronisation of treatment (and optimal strategy to apply it).

However, the modelling presented in this paper uses a different approach and is for a different purpose. In this model we have simplified the description of processes as far as possible with the aim of identifying those benefits of area management that apply robustly and are not dependent on specific local conditions (Murray, 2001). This approach is useful for assessing the validity of applying area management as a general policy in sea lice control, rather than identifying in detail optimal management practices that would apply for a specific area.

#### 4. Conclusion

A very simple model of the interaction of sea lice populations on neighbouring farms has been developed. Treatment rate required to control lice depends largely on treatment efficacy and lice population growth rate, and exhibits a threshold at which treating for control becomes impossible. Treatment rates increase faster than lice counts as the system approaches this threshold and so may be a more sensitive measure of loss of control. Area management involving co-ordination of treatment and, in particular fallowing, reduces the treatment rate required to control lice and increases the threshold of tolerance to loss of efficiency or increased lice population growth rate. Benefits of area management occur even if area boundaries are ineffective at preventing larval exchange. This means epidemiologically imperfect areas that can synchronise practices (particularly fallowing) may be more useful than areas with highly epidemiologically effective boundaries but within which there is less effective collaboration. However, required numbers of treatments declines as boundary efficacy improves, with the highest rate of reduction as the boundaries tend towards 100% effective. Co-ordinating treatments can reduce the number of treatments that are needed to control lice, but to a lesser extent and less robustly than co-ordinated fallowing. This suggests co-ordination of treatment needs more local knowledge to be effectively applied. The identified benefits support a policy of encouraging area management and maintaining epidemiologically meaningful separation between management areas.

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