The effectiveness of fallowing strategies in disease control in salmon aquaculture assessed with an SIS model.

Werkman, M.[(a)], Green, D.M.[(a)], Murray, A.G.[(b)], Turnbull, J.F.[(a)]

[(a)] Institute of Aquaculture, University of Stirling, Stirling, FK9 4LA, UK

[(b)] Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen, AB11 9DB, UK

Author for correspondence: email: marleen.werkman@stir.ac.uk

Abstract

Salmon production is an important industry in Scotland, with an estimated retail value >£1 billion. However, this salmon industry can be threatened by the invasion and spread of diseases. To reduce this risk, the industry is divided into management areas that are physically separated from each other. Pathogens can spread between farms by local processes such as water movement or by long-distance processes such as live fish movements. Here, network modelling was used to investigate the importance of transmission routes at these two scales. We used different disease transmission rates (β), where infected farms had the probability of 0.10, 0.25 or 0.50 per month to infect each contacted farm. Interacting farms were modelled in such a way that neighbours within a management area could infect each other, resulting in two contacts per farm per month. In addition, non-local transmission occurred at random. Salmon are input to marine sites where they are raised to harvest size, the site is then fallowed; in the model the effects of different fallowing strategies (synchronised, partial synchronised and unsynchronised fallowing at the management area level) on the emergence of diseases were investigated. Synchronised fallowing was highly effective at eradicating epidemics when transmission rate is low ($\beta = 0.10$) even when long distance contacts were fairly common (up to 1.5 farm^{-1} month^{-1}). However for higher transmission rates, long distance contacts have to be kept at much lower levels (0.15 contacts month^{-1} where $\beta = 0.25$) when synchronised fallowing was applied. If fallowing was partially synchronised or unsynchronised then low rates of long-distance contact are required (0.75 or 0.15 farm^{-1} month^{-1}) even if $\beta = 0.10$. These results demonstrate the potential benefits of having epidemiologically isolated management areas and applying synchronised fallowing.

Keywords: Fallowing, disease transmission, Atlantic salmon, SIS-model, epidemiology.

1. Introduction

Scottish production of Atlantic salmon was around 130,000 tonnes per year in the years 2005-2009 (Marine Scotland Science, MSS, 2009b). In 2006 the worldwide retail value of Scottish Atlantic salmon production was estimated to be >£1 billion (Scottish Salmon Producers' Organisation, SSPO, 2009). Scottish salmon production created 849 full-time jobs and 100 part-time jobs in 2008 (MSS, 2009b) in remote areas with few alternative employment opportunities. For these reasons, salmon production is important for the Scottish economy. Diseases such as infectious pancreatic necrosis (IPN) and pancreas disease (PD) can cause anorexia and high mortalities (Bruno 2004a; McLoughlin and Graham, 2007; World organisation for animal health, OIE, 2009), infectious salmon anaemia (ISA) is subject to controls under EU legislation (Murray et al., 2010), and all pose an economic threat to the industry (Murray and Peeler, 2005). For example, the cost of the ISA outbreak in 1998/1999 was estimated to be >£20 million (Hastings et al., 1999).

Preventing aquatic diseases is not only important from an economic perspective. Diseases also have an impact on (farmed) fish welfare (Huntingford et al., 2006), which can affect markets given growing awareness of fish welfare among consumers (Ashley, 2007). In addition, it is possible for pathogens of farmed fish to be transmitted to wild fish populations (Wallace et al., 2008).

Pathogen transmission between farms can occur on a local level, as hydrodynamic transmission can be responsible for pathogens spreading between farms for short distances (McClure et al., 2005; Gustafson et al., 2007; Amundrud and Murray, 2009; Viljugrein et al., 2009). Close proximity to an infected farm has been indentified as a risk factor for transmission of, for example, ISA (McClure et al., 2005; Gustafson et al., 2007; Lyngstad et al., 2008; Aldrin et al., 2010) and PD (Kristoffersen et al., 2009; Aldrin et al., 2010). Local transmission also occurs through wild fish movement between farms (Uglem et al., 2009). Wild fish may be infected in the vicinity of infected farms (Wallace et al., 2008) and transmit those pathogens from farm to farm (Uglem et al., 2009).

Anthropogenic activities, such as sharing equipment between sites, visits from well boats, or movement of live fish can increase the risk of transmission of pathogens between farms (Murray et al., 2002; Munro et al., 2003; Munro and Gregory, 2009). Live fish movements can be over long-distance, for more than 100 km (Murray et al., 2002) or even international (Ruane et al., 2009), which can cause more dispersed disease patterns.

The effects of hydrodynamic movements were shown in the recent (2008/2009) outbreak of ISA in the Shetland area of Scotland, infecting six farms in a geographically confined area (Murray et al., 2010). This may be contrasted with an outbreak in 1998/1999, which spread between areas through the use of well boats for transporting live fish or for harvest (Murray et al., 2002). Data from the ISA outbreak in Chile (2007/2008), showed clusters of outbreaks appearing around the index case, suggesting hydrodynamic transmission has caused the local spread of the virus. However, at the early stage of the ISA epidemic in Chile, anthropogenic activities were found to be important, which caused a highly dispersed pattern (Mardones et al., 2009).

To reduce the risk of local disease transmission in Scotland, management areas were established in 2000 based on the maximum spring-tide current speeds (Joint Government/Industry Working Group, JGIWG, 2000). All active farms were divided between 46 management areas (but the numbers change as farms are opened, closed or relocated), with a minimum distance of 13 km between management areas, except for Shetland where it is 7.6 km due to lower tidal currents (JGIWG, 2000). Wild fish movements are also typically at the same scale (Uglem et al., 2009). Separation between management areas is intended to form adequate ‘fire breaks’ to reduce the risk of pathogen transmission between management areas (JGIWG, 2000). Concentration of production in separate areas may help in the control of pathogens (Green, 2010). Management areas are used for the control of epidemics. For example under current control schemes a new ISA outbreak would result in all the fish on the affected farm being slaughtered and other farms in the same management area would be placed under strict surveillance. Suspected ISA-infected farms would be controlled and fish movements from suspected farms would be restricted (JGIWG, 2000) to prevent spread of pathogens between management areas.

An important strategy used to reduce the risk of disease emergence is fallowing, whereby sites are emptied and not restocked for a period of time. The hypothesis is that pathogens will die out due to the absence of hosts (Wheatley et al., 1995; Bruno, 2004b). There is strong evidence that fallowing a whole site can reduce the risk or at least the severity of infections (JGIWG, 2000). The effectiveness of fallowing is linked to the persistence of the pathogen in the water with a reduced biomass of hosts and the length of the fallowing period (JGIWG, 2000). However, as diseases can spread from adjacent farms it is important that farmers in a management area make agreements regarding synchronised fallowing. In general, coordinated management of farms at the management area level is recognised as an effective method of managing diseases and parasites. For example coordinated treatments are applied to control sea lice infestation (Code of Good Pratice, CoGP, Working Group,(CoGP Working Group, 2010). By 2008, 18 management area agreements had been signed and many include coordinated fallowing (Tripartite Working Group, 2010).

The presence of external hosts such as wild fish is also relevant as they can become infected (Wallace et al., 2008) and possibly cause re-infection (Rae, 2002; Plarre et al., 2005; Costello, 2009). Fallowing period length is normally at least four weeks, but can be up to a complete year (MSS, 2009b). Fallowing takes place for at least six months when a farm was confirmed with ISA (JGIWG, 2000). A history of infection on a site is not a significant risk factor for recurrence of IPNV (seawater) in Scotland, where farms are commonly fallowed after every cycle (Murray, 2006a). This indicates fallowing is effective for these cases. Individual farms may fallow at different times or fallowing of farms in a management area can be synchronised.

The objective of this study was to identify the importance of local and long-distance contact for the transmission of pathogens, which we simplified as a network of contacts at these two levels as has been modelled by Watts and Strogatz (1998). In addition, we examined the effectiveness of different fallowing strategies on controlling disease transmission. This study focuses on transmittable diseases in sea water, such as IPN and PD. However, to estimate and validate parameters, data from the last Scottish ISA outbreak were used. This model is flexible and can be used to assess factors that may lead to emergence of new diseases as well. The model does not explicitly include vertical or freshwater transmission and does not allow for change in practices when the pathogen is detected and so best describes marine non-notifiable diseases. This is a theoretical study (and sensitivity analysis), though grounded in real data in the form of the amount and sizes of management areas, which were based on the management area maps compiled by the Fisheries Research Services (FRS), Aberdeen (now Marine Scotland Science, 2009a).

2. Materials and Methods

2.1 Contact structure

A stochastic SIS model (susceptible – infectious – susceptible) was constructed to investigate the effect of local (within a management area) and long-distance contacts (directed movements both between and within management areas) and different fallowing strategies on the spread of diseases between farms. This model was restricted to Scottish marine farms. There were $n = 263$ marine farms dispersed among 53 management areas, each containing 1 to 30 farms (MSS, 2009a), as shown in figure 1. An undirected adjacency matrix A (i.e. wherever there is contact from node i to node j, there is contact in the opposite direction) was constructed of size $n \times n$: an element A_{ij} contains either 1 (potentially infectious contact exists from farm i to j) or 0 (no contact). Matrix A was based on the management area maps compiled by MSS (MSS, 2009a). The basic structure of each modelled management area was a ring model where each farm can infect two neighbour farms (figure 2A) except for small management areas where $n = 1$ or $n = 2$. This resulted in 243 edges (undirected contacts) by hydrographical connections.

In this model the transmission rate (β) was defined as the monthly probability of an infected farm infecting a susceptible farm when there was contact between an infected and a susceptible farm. We modelled β for 0.10, 0.25 and 0.50 per month. A minimum rate to cause an epidemic for β is 0.028, because otherwise the basic reproductive rate $R_0 < 1$ even in ideal conditions for transmission of the pathogen, assuming an eighteen-month production cycle and transmission in two directions ($0.028 \times d \times 2 = 1.008$). Maximum transmission rate can be high: for example ISA spread from an index case to five other sites in eight months by local spread (Murray et al., 2010), which is equivalent to β=0.3 per month, assuming each farm is connected with two others as described earlier.

In this model, susceptible farms became infected through potentially infectious contact from a connected infected farm, subject to transmission rate β; there was no change in status when an infected farm was subject to further infectious contact. The length of production cycles as modelled was eighteen months ($d = 18$) and proceeded through five production cycles (time, $0 < t \leq 90$) with a time step size of one month. Farm infectious status (0 for susceptible sites, 1 for infected) at time t was stored in a vector I of size n farms. At time $t = 1$ one farm was selected at random as the index case. ISA outbreaks, for example, are normally traced back to one index case (Stagg et al., 2001; Mardones et al., 2009; Murray et al., 2010).

2.2 Infection between management areas

Long-distance contacts were included in a second adjacency matrix (L). These contacts were directed: contact from node i to node j does not imply contact from j to i (figure 2B). Long-distance contacts were fixed and chosen randomly at the beginning of each simulation. The timing of these contact events was random, but occurred on average once in every cycle (five times per simulation). This means that $L_{ij} = 1$ does not imply a constant connection. The pairwise probability of directed contact between all farms (v) varied between 0.0025 and 1.00. For $v = 0.0025$, there were $\frac{1}{d}0.0025 \times (n(n-1)) = 9.6$ directed long-distance contacts for the whole industry per month and $9.6/n =$ 0.036 directed contacts per farm per month. In addition, when $v = 1.00$ every possible connection between farms existed, which resulted in 14.6 contacts farm^{-1} month^{-1}. Epidemiological investigations into a recent ISA outbreak on the Shetland Islands (Scotland) showed eighteen farms had a total of seven live fish movements to or from sites in other management areas in 2008 (Murray et al., 2010), this equalling 0.03 contacts farm^{-1} month^{-1}. Other long-distance contacts could have occurred via movements of well boats, however these are less likely to spread infection, even if the boat is contaminated, although the risk is not negligible (Murray et al., 2002; Murray et al., 2010).

For the stochastic model vector B of size n was derived containing the number of inward contacts from infected farms.

$$B_i = \sum_j I_{j,t}\left(A_{ji} + L_{ji}\right)$$

Risk depends on the number of contacts and associated probability of transmitting infection, however the probability of infection can never exceed 1.0. Therefore, we define p_i as the probability of receiving pathogens either through long-distance movement or hydrodynamic connections at time t. Variable $Q_i = 1$ represents stochastically the receipt of pathogens through contact.

$$p_i = 1 - (1 - \beta)^{B_i}$$

$$Q_i \sim \text{Bernouilli}\left(p_i\right)$$

The new infectious status of each farm was stored in the vector $I_{i,t+1}$ of size n.

$$I_{i,t+1} = I_{i,t} + (1 - I_{i,t})Q_{i,t}$$

2.3 Adding contacts within a management area

In this model all farms in a management area could infect two neighbouring farms within the same management area (see section 2.1). After examining the location of the farms this assumption did not appear realistic in every case, because multiple farms were within close proximity (MSS, 2009a) and as a result could potentially spread pathogens to more than two other farms. Therefore, we investigated how the proportion of additional local contacts (within a management area) affected the spread of disease and its persistence. For this an undirected contact matrix was compiled, which represented the contacts within a management area (figure 2C). A pairwise probability of connection between all farms in the same local area (g) was considered. These connections were added to contact matrix A. Parameter g was modelled for values between 0 and 1.00; if $g=1$ all local connections between nodes existed resulting in a total of 1089 additional undirected local connections.

2.4 Imperfect management area separation

The previous model (section 2.1) assumed that management areas were perfectly separated, meaning there was no contact between adjacent management areas, except through long-distance movements (see section 2.2). However, diseases can spread between adjacent management areas when the separation distance is not great enough and the pathogen is sufficiently persistent in the environment (Aldrin et al., 2010). For this reason we examined how effective management area boundaries need to be in order to prevent disease transmission by hydrodynamic contact to adjacent management areas. Here, management area boundaries imply sufficient separation by seaway distance to prevent spread of pathogens.

In this ring model, all farms had two neighbouring farms as in the other models, except those farms on the boundary of a management area. These farms could transmit diseases by hydrodynamic contact to the adjacent management area (figure 2D). However, such between-management-area contacts were subject to a multiplier h ($0 \le h \le 1$). Models were simulated for $h=0$, 0.25, 0.50 and 1.0, where $h=0$ means the boundaries are 100% impermeable, while $h=1.0$ means the boundaries have no effect on transmission rate. We preferred this approach as it keeps the number of neighbouring farms similar to the model as described in section 2.1. Management area sizes were once again based on the management areas maps that were compiled by MSS (MSS, 2009a), however the proximities of the management areas were chosen arbitrarily.

We investigated the effects of both extra local contacts (section 2.3) and imperfect management area boundaries for transmission rates $\beta = 0.10$ and 0.25, along with long-distance movements proportions $v = 0.0025$ and 0.01 (see section 2.2).

2.5 Fallowing

Farms were assumed to have an eighteen-month production cycle between input of smolts and restocking the farm. Other species such as rainbow trout do have a shorter production cycle, and so diseases would have less time to spread before harvest. If fish of different species with different production times are farmed in the same management area then coordinated fallowing will be more problematic. However, salmon occupy by far the majority of sea cages in Scotland: there were 256 marine salmon salmon farms in 2008 (MSS, 2009b). As a simplification we assumed that all farms had the same production cycle. After harvesting, the farms were fallowed and left without fish for a short period. The fallowing period was one month (one time step). It was assumed that after fallowing, farms were free from infection, as all fish used for restocking were free of disease. Consequently farms were susceptible once more at the following time-step of the simulation. Time since last fallowing at time t is represented for farm i by $m_{i,t}$.

$$m_{i,t+1} = m_{i,t} + 1$$

At $m_{i,t} = 18$ farms became clear of infection so that $I_{i,t+1} = 0$ and $m_{i,t+1} = 1$.

In this model, fallowing occurs after infection and therefore may occur in the same time step. The maximum median prevalence could therefore never be 1.00, as prevalence was counted after fallowing, which means there was a 5.56% chance $(1/d)$ that the index case was fallowed at $t = 1$. In this case the index case could not infect other farms.

The effects of three fallowing strategies were investigated. Timing of fallowing could be different between sites. However, length of production cycle and fallowing period was similar for all sites and all three fallowing strategies: synchronised fallowing (SYN, all farms in one management area were fallowed simultaneously), unsynchronised fallowing (UNS, the start of fallowing period occurred randomly inside management areas) and partial synchronised fallowing (PAR). In this last management strategy, areas with eight or fewer farms were subject to synchronised harvesting and management areas of nine or more farms were subject to unsynchronised harvesting. We used this cut-off point as approximately 50% of the farms were divided over small (or large) management areas. This results in an intermediate strategy between synchronised fallowing and unsynchronised fallowing. Because larger areas may contain multiple companies, agreement to synchronise fallowing is more difficult, for example the 2008/2009 ISA outbreak occurred in a large management area that had never been synchronously fallowed (Murray et al., 2010). Using the Scottish marine farms as a base, there were eight large management areas and 45 small management areas, containing in total 126 and 137 farms, respectively (figure 1). Furthermore, we investigated the differences in epidemic size between initiating an epidemic in a small or large management area for the most realistic scenarios ($\beta = 0.10$ and $\beta = 0.25$ and for $v = 0.0025$ to 0.01).

An overview of the parameters used and their description is given in table 1. The model was run 1000 times for each parameter set and the median prevalence over time, percentage of runs where the epidemic was eradicated prior to t=90 and the 90th percentile of the median prevalence at t=90 was recorded. Analyses were performed in R (R Development Core Team, 2005) and Excel (Microsoft excel, 2008).

3. Results

In this section, we use the term equilibrium, by which we mean the point in the graph where the line visually levelled off, as variation is always present in a stochastic model. Increasing the transmission rate β increased the median prevalence over time (figure 3A and 3B). Similar, increasing the proportion of long-distance movements v increased the median prevalence. However, β and v were not related to each other. Increasing β increased the probability of infection when there was a contact, while increasing v simply increased the number of long-distance contacts between farms.

3.1 Median prevalence and eradication of epidemics

Fallowing strategies had a clear effect in reducing the median prevalence and the probability to eradicate an epidemic when the proportion of directed long-distance movements (v) was between 0 and 0.10 (=1.5 movements per farm per month) especially for $\beta = 0.10$. For $v = 0.10$ and $\beta = 0.10$, the equilibrium was 0.65 (PAR) and 0.68 (UNS), while the epidemic died out prior to $t = 90$ for SYN. For $v \geq 0.25$ (≥ 3.6 movements farm^{-1} month^{-1}) equilibria were established at 0.75 or higher for all three fallowing strategies ($\beta = 0.10$). In general, equilibria were established earlier and median prevalence was higher for $\beta = 0.50$ compared with $\beta = 0.25$ (figure 3A and 3B). For $v \geq 0.25$, median equilibria were 0.90 or higher for all the fallowing strategies for both $\beta = 0.25$ or 0.50, but there were no important differences found between fallowing strategies.

We investigated if an epidemic would die out prior to $t = 90$ (five production cycles), to examine in which situations an epidemic is likely to be controlled. SYN increased the probability to eradicate an epidemic prior to $t = 90$ compared with PAR and UNS, when $v \leq 0.10$ for $\beta = 0.10$ and $v \leq 0.05$ (0.073 movements farm^{-1} month^{-1}) for $\beta = 0.25$ (figure 4A). For $\beta = 0.10$ the proportion of eradicated epidemics was ≥ 0.90 for PAR and $v \leq 0.01$. However, for the same scenarios but with $v = 0.05$ the proportion of eradicated epidemics dropped to 0.59. Similar reductions in the proportions of eradicated epidemics were seen for the other fallowing strategies for $\beta = 0.10$ and $\beta = 0.25$, except for SYN and $\beta = 0.10$, where the reduction of the proportion of eradicated epidemics was seen between $v = 0.05$ and $v = 0.10$ (figure 4A). Probabilities of eradicated epidemics prior to $t = 90$ were lower for $\beta = 0.50$ compared with $\beta \leq 0.25$. For $\beta = 0.50$, 100% (SYN), 54.9% (PAR) and 17.7% (UNS), of epidemics died out prior to $t = 90$ when there were no long-distance movements added. For $v = 0.01$, 44.6% (SYN), 27.2% (PAR) and 14.8% (UNS) of the epidemics died out prior to $t = 90$ ($\beta = 0.50$); for $v \geq 0.05$ less than 14% of the epidemics died out. When $v \geq 0.50$, fallowing strategies had no substantial effect on the proportions of eradicated epidemics, therefore there were too many movements.

There were no differences in epidemic size between initiating an epidemic in a small or large management area at $t = 90$ for all SYN scenarios ($v = 0.0025$ to $v = 0.01$) and for PAR and UNS when $\beta = 0.10$. For $\beta = 0.25$ and when PAR was applied, median prevalence was 0 when the index case was in a small management area ($v = 0.0025$ to $v = 0.01$) and varied from 0.11 ($v = 0.0025$) to 0.50 ($v = 0.01$) when the index case was in large management areas. When UNS was applied, median prevalence was also higher when epidemics were initiated in large management areas (varied from 0.15 to 0.73, for respectively $v = 0.0025$ and $v = 0.01$) compared to small management areas (varied from 0.02 to 0.68, for respectively $v = 0.0025$ and $v = 0.01$), however this difference was relatively smaller when v increased. The chance to eradicate an epidemic was larger when the index case was in small management areas compared to large management areas. The largest difference was noticed when PAR was applied; the chance to eradicate an epidemic for $\beta = 0.25$ dropped from 93.4% to 19.9% ($v = 0.0025$); 84.1% to 18.2% ($v = 0.005$); 70.8% to 16.0% ($v = 0.01$) for respectively initiating an epidemic in small and large management areas. For PAR and $\beta = 0.10$, the chance to eradicate a pathogen was between 16% and 18% lower when the index case was in large management areas compared to small management areas. For UNS and $\beta = 0.10$ and $\beta = 0.25$ the chance to eradicate an epidemic was between 5% and 17% lower when the index case was in large management areas.

3.2 Worst-case scenario

Worst-case scenarios as defined as 90th percentile (figure 4B) were in general lower for $\beta = 0.10$, compared with $\beta = 0.25$. As seen with median prevalence and epidemic persistence to $t = 90$, SYN has a beneficial effect, especially for $v \leq 0.05$ and $\beta = 0.10$. For $v = 0.05$, 90th percentiles were 0 (SYN), 0.21 (PAR) and 0.55 (UNS) for $\beta = 0.10$, there was no difference seen for this scenario for $\beta = 0.25$. However, fallowing had a substantial effect for $\beta = 0.25$ and $v = 0.01$. For this scenario, 90th percentiles were 0 (SYN), 0.46 (PAR) and 0.77 (UNS). The required parameters for a 90th percentile below 0.1 for UNS were $v < 0.01$ and $\beta = 0.10$, and when no long-distance movements were added for $\beta = 0.25$. There were no substantial differences noticed in the worst-case scenario between initiating an epidemic in small or large management areas, except when PAR was applied and for $\beta = 0.25$. However, this difference decreased when v increased. Worst-case scenarios increased from 0 to 0.25 ($v = 0.0025$); 0.20 to 0.42 ($v = 0.005$) and from 0.51 to 0.58 ($v = 0.01$) for respectively initiating an epidemic in small and large management areas.

3.3 Adding contacts at local level

Adding contacts at a local level decreased the chance of eradicating an epidemic prior to $t = 90$ for $\beta = 0.10$ when PAR and UNS was applied (figure 5A). Adding 54 undirected local contacts on the whole network ($g = 0.05$, equivalent to 0.2 extra local out contacts per farm) reduced the chance of eradicating an epidemic compared with the original model where every farm has two local contacts (except for small management areas, see section 2.1). For example, for $\beta = 0.10$, using PAR and UNS decreased the chance of eradicating an epidemic prior to $t = 90$ by 0.15 to 0.20 ($g = 0.05$, figure 5A), for this scenario, compared with the original network with two contacts per farm ($g = 0$). However, when applying SYN, additional contacts at a local level had no substantial effect. Conversely, with $\beta = 0.25$ and $v = 0.01$ the proportion of eradicated epidemics was reduced from 0.98 (no extra local contacts) to 0.89 when local connections were added ($g = 0.05$) and SYN was applied. No reduction was observed for this scenario and $v = 0.0025$ (figure 5B). Using PAR or UNS showed no substantial reduction in the probability to eradicate an epidemic for $\beta = 0.25$ and $g = 0.05$.

3.3 Imperfect management area boundaries

Weakening the management area boundaries with constant h had no substantial effect on eradicating epidemics for $\beta = 0.10$ and for the three different fallowing strategies (figure 5C).

However, for $\beta = 0.25$, the proportion of eradicated epidemics at $t = 90$ decreased from 0.54 ($h = 0.25$) to 0.36 ($h = 0.50$), for PAR and $v = 0.0025$ (figure 5D). For SYN and $\beta = 0.25$ the proportions of epidemics that were eradicated prior to $t = 90$ was 0.91 when $h = 0.50$ and decreased to 0.69 when $h = 1.00$. Similar, for UNS harvesting the ability to control an epidemic became smaller when the management area boundaries were weakened, although less dramatically (figure 5D).

4. Discussion

The significance of long-distance movements in disease transmission has been shown before in for example, foot and mouth disease (Green et al., 2006) and for ISA in Atlantic salmon (Murray et al., 2002). Movement of live fish between sites would almost certainly transmit pathogens if the source site was infected, but movement of fish infected with a notifiable disease such as ISA is prohibited (JGIWG, 2000). However, subclinical infections might go undetected (Murray and Peeler, 2005). IPNV is often subclinical (Bruno, 2004a) and there is evidence that even ISAV may persist for months on sites sub-clinically (Murray et al., 2010) which makes it harder to detect pathogens. In such circumstances long-distance movements can spread pathogens without knowing (Murray and Peeler 2005). Contact by vessels might be a low risk, but there may be many of such contacts. Long-distance contacts are likely to be rare relative to local spread and therefore lower values of v will be more realistic. For example, ISA tends to occur in clusters, indicating higher rates of local spread compared with pathogen transmission over long-distances (Mardones et al., 2009). In this study we found that the amount of long-distance movements should not exceed 0.073 per farm per month assuming synchronised fallowing is not commonly used in all Scottish marine farms. Higher probabilities of long-distance movements (v) decreased the chance to eradicate an epidemic substantially with high transmission rates $\beta \geq 0.25$. This emphasises the value of epidemiologically isolated management areas. Even pathogens with slow rates of local spread being managed by synchronised fallowing were unlikely to be eradicated if long-distance transmission events were more common than 3.6 movements per farm per month.

The higher median prevalence and decreased chance of eradicating an epidemic when an epidemic is initiated in large management areas compared to small management areas when unsynchronised fallowing is applied is because pathogens can spread more easily between farms and persist longer at a local level. Local spread will be more important if long-distance movements occur less often then two movements per farm per month. Because large management areas have simply more farms, there is a higher prevalence when the index case is in large management areas. The difference between median prevalence and the chance to eradicate an epidemic is larger between an index case in small and large management areas when partial synchronised fallowing is applied. This is because synchronised fallowing is only applied in small management areas and large management areas apply unsynchronised fallowing.

Local contacts should be fewer than 2.2 local contacts per farm, for the Scottish marine sites. However, it is likely that the results are different when the number of farms within a management area differs, since reducing the same number of contacts in small management areas and large management areas results in a too small reduction of contacts in large management areas. In this study we assumed that neighbouring farms within the same management area were assumed to have an equal risk of infection. We did not take into account the seaway distance, currents or wind direction. The direction of spread is complicated as described in Amundrud and Murray (2009).

The importance of local contacts is also seen in the ISA epidemic in Chile where long-distance movements and local transmission were both found contributory in the transmission of the virus (Mardones et al., 2009). In addition, it is likely that if pathogens are persistent in the environment or wild hosts that they would re-infect farms (Rae, 2002; Plarre et al., 2005), which makes it harder to eradicate pathogens. Synchronised fallowing can increase the probability to eradicate an epidemic as synchronised fallowing quickly removes local spread.

Moreover management areas must have epidemiologically appropriate boundaries. If separation does not prevent at least 75% of spread then eradication becomes substantially less likely for pathogens with high rates of spread ($\beta \geq 0.25$) as described in section 3.4.

In the model, the first production cycle after a disease outbreak is critical for control. If the pathogen is not eradicated during this time period, it is likely that a large number of farms will have been infected (figure 3). In this case, the disease is likely to become established as an endemic disease and eradication is unlikely or at least expensive. The Scottish ISA outbreaks of 1998/1999 which became widespread before detection (Murray et al., 2002), and 2008/2009 which was localised due to early detection, illustrate this point (Murray et al., 2010). During the British FMD outbreak in 2001, there was a delay in detecting the index case which resulted in a major epidemic (Gibbens et al., 2001). For this reason it is necessary to control emerging diseases at an early stage.

Pathogens may transmit vertically through ova, as well as horizontally. For vertical transmission to be important after introduction the risk of transmission has to be significant relative to horizontal transmission. In Norway the spread of ISA did not appear to be related to vertical transmission (Lyngstad et al., 2008). In Scotland parent fish are screened for key pathogens and ova are disinfected (Bruno et al., 2004a). This model can be applied to diseases where vertical transmission is a relatively small risk compared to horizontal transmission, although vertical transmission, even at low risk, might be a source of infection to the index case. Not including vertical transmission is a limitation of this model; however this model is on site level rather than fish level. Therefore, not including vertical transmission is appropriate in this case.

Moreover, farms owned by the same company do have an increased risk of infection when a farm in that company is infected as shown with the ISA outbreak in Chile (Mardones et al., 2009). The random transmission in this model was a simplification and did not include the network structure.

Clearing farms has been proven to reduce the risk of re-infection of *Salmonella* infections in poultry (Namata et al., 2009) and in pigs (Beloeil et al., 2004; Lo Fo Wong et al., 2004), where all-in/all-out systems are commonly used. There are few studies of the effectiveness of fallowing strategies in aquaculture. Wheatley et al. (1995) demonstrated a reduced mortality rate in cycles where farmers applied fallowing strategies. Furthermore, it is believed that fallowing helps to control the sea louse *Lepeophtheirus salmonis* (Bron et al., 1993; Rae, 2002), however, is seems that fallowing is less effective in the control of the other sea louse species *Caligus elongatus* (Bron et al., 1993; Revie et al., 2002). From the experience of ISA outbreaks in the past, the time between diagnosis and clearing and fallowing the farms seems to be highly influential on subsequent spread (Mardones et al., 2009). So far, Scotland is the only country where an ISA outbreak has been eradicated. During the ISA outbreak in Scotland (1998/1999), farms were cleared within one month after confirmed diagnosis of ISA (Stagg et al., 2001). However, time between confirmed diagnosis and depopulating the affected farms has been estimated to be four to five months in the ISA outbreak in Chile (Mardones et al., 2009). In this study the fallowing time was one month, which is realistic when pathogens are not diagnosed (MSS, 2009b), as may occur when there are no clinical signs.

The use of this simple SIS model was valuable for showing the effectiveness of different fallowing strategies and the importance of reducing long-distance movements. However, the real-life situation is more complex in both pattern of contact between farms and disease characteristics. Long-distance movements occured at random in this study, while reality is more complex and shows a high variance in the number of contacts between farms (Thrush and Peeler, 2006; Munro and Gregory, 2009; Green et al., 2009). Heterogeneity, i.e. variance in the number of contacts, is likely to affect the transmission pattern of disease significantly. It has been suggested that 80% of the infections are in general caused by 20% of the population (Anderson and May, 1992). The assumption of homogenous spread has been used to model the spread of IPNV through the salmon farming industries of both Scotland (Murray 2006b) and Ireland (Ruane et al. 2009). In this study, we assumed that long-distance movements were homogenous as unpublished data showed that variance in the number of contacts is substantially smaller between sea water contacts compared to contacts between fresh water sites.

Live fish movements do not occur at random, but are dependent on the size of the fish and the season. Timing of movements will be important for disease transmission. For example BKD outbreaks are more likely to occur during spring (MSS, 2010) and IPN outbreaks occur mainly after transfer to sea (May-August) (Bruno, 2004a). Therefore movements during spring may be more risky for BKD transmission compared with other periods of the year.

Different model types could be more appropriate for diseases with different characteristics, different modelling objectives, or different management systems. In this study we choose an SIS model, however, an SEIS (susceptible-exposed-infectious-susceptible) can take into account the variations of latent periods, which may vary largely between different diseases. In our SIS model a farm becomes infectious after one month. However, in the real-life situation this varies. For example, IPN outbreaks occur mainly after transfer to sea (Bruno, 2004a). During this vulnerable stage, transmission rates of IPN could be higher, and it is likely that this effects the time for a farm to become infectious. Furthermore, our model assumes that all farms were similar, excepting their membership of a particular management area, whereas Scottish farms have different stocking sizes (from <50 to >1000 tonnes, MSS, 2009b) and stocking densities. Stocking density can be important, as an outbreak of a viral disease is sensitive to a minimum effective concentration, which is influenced by stocking densities in farms (Hammell and Dohoo, 2005; Thrush and Peeler, 2006).

5. Conclusion

This simple model demonstrates the importance of long-distance movements in the spread of pathogens. In this model, even applying synchronised fallowing in combination with a low transmission rate could not prevent an epidemic when there were high numbers of long-distance movements between farms. However, when long-distance contacts are rare compared to local contacts, synchronised fallowing greatly improves the chance of controlling outbreaks. Therefore, it is important both to reduce the number of long-distance movements and to implement good biosecurity measurements to reduce disease spread and to synchronise fallowing to enhance eradication.

Acknowledgements

Marleen Werkman and Darren Green's contribution to this work was funded through Marine Scotland.

Tables

Table 1. Description of the model parameters used in this stochastic SIS-model to describe the spread of pathogens between Scottish marine fish farms.

Parameter symbol	Description
β	Transmission rate per month.
v	The pairwise probability of directed contact between all farms, both between and within management areas.
g	A pairwise probability of connections between all farms in the same management area.
h	Permeability of management area boundaries ($0 \le h \le 1$). Boundaries are 100% impermeable when $h = 0$ and ineffective for $h = 1$.

Figures

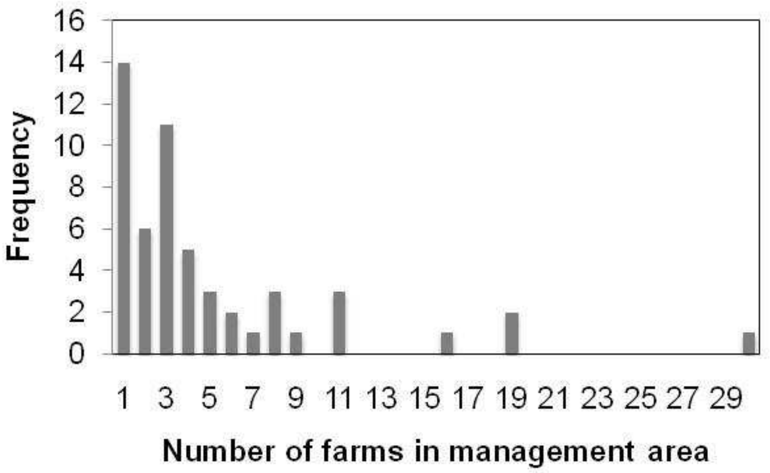


Figure 1: Frequency of number of farms per management area. Management areas with eight or fewer farms were classified as small management areas, while management areas containing nine or more farms were classified as large management areas.

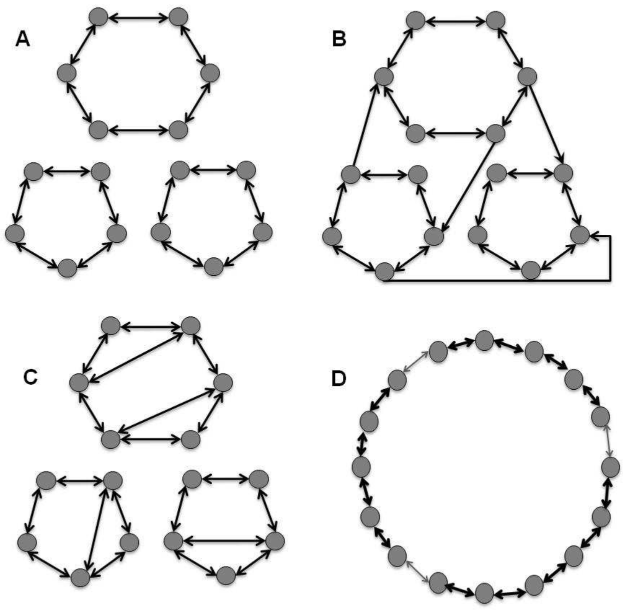
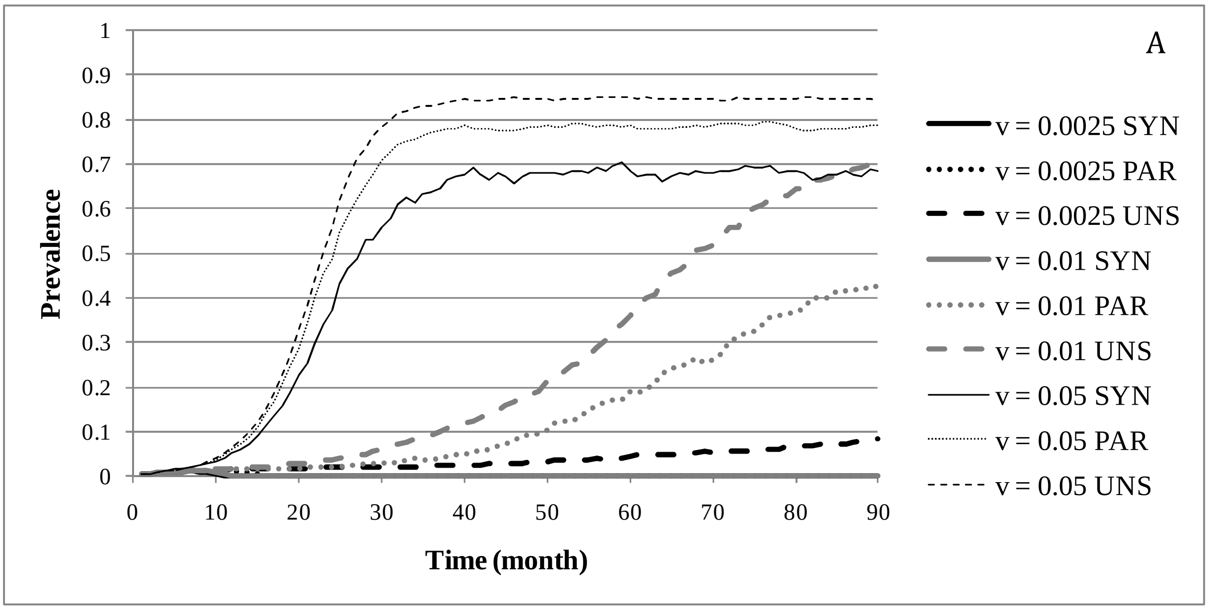


Figure 2: Graphic representation of the models used in this study: basic structure (A), adding long-distance movements (directed) to basic structure (B), adding local contacts (undirected) to basic structure (C), imperfectly sealed management areas. The grey arrows represent the weakened boundaries between management areas (D).



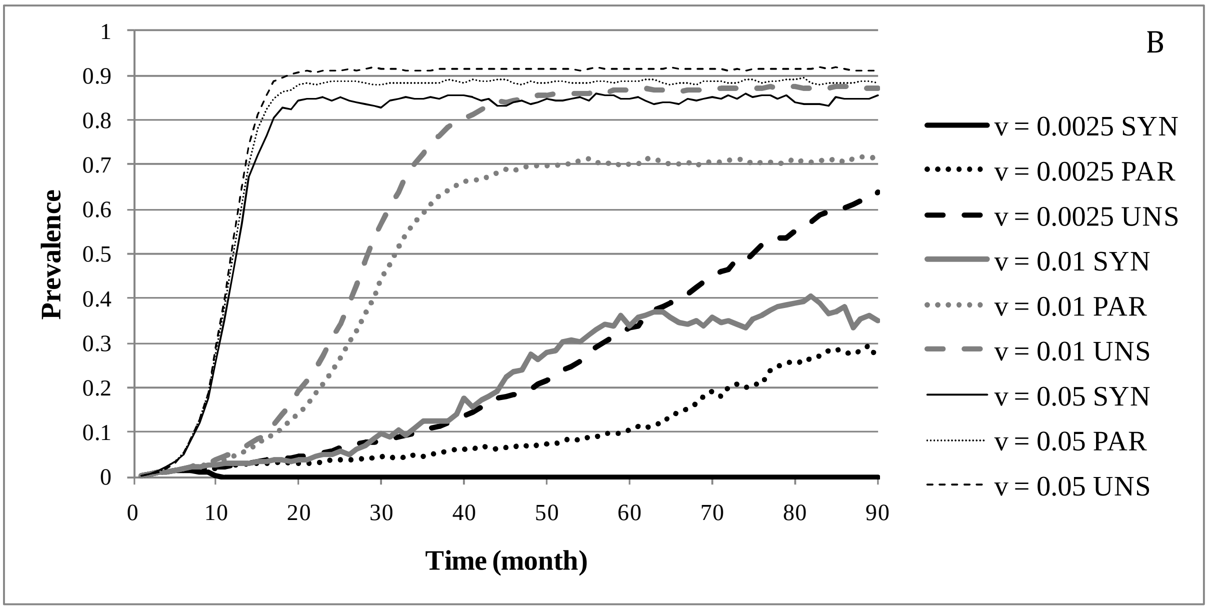


Figure 3: Median prevalence over time for three different fallowing strategies: synchronised (SYN), partial synchronised (PAR) and unsynchronised (UNS) and for transmission rates, $\beta = 0.25$ (A) and $\beta = 0.50$ (B). Median prevalences are shown for the probability of long-distance contact, $v = 0.0025$ to $v = 0.05$.

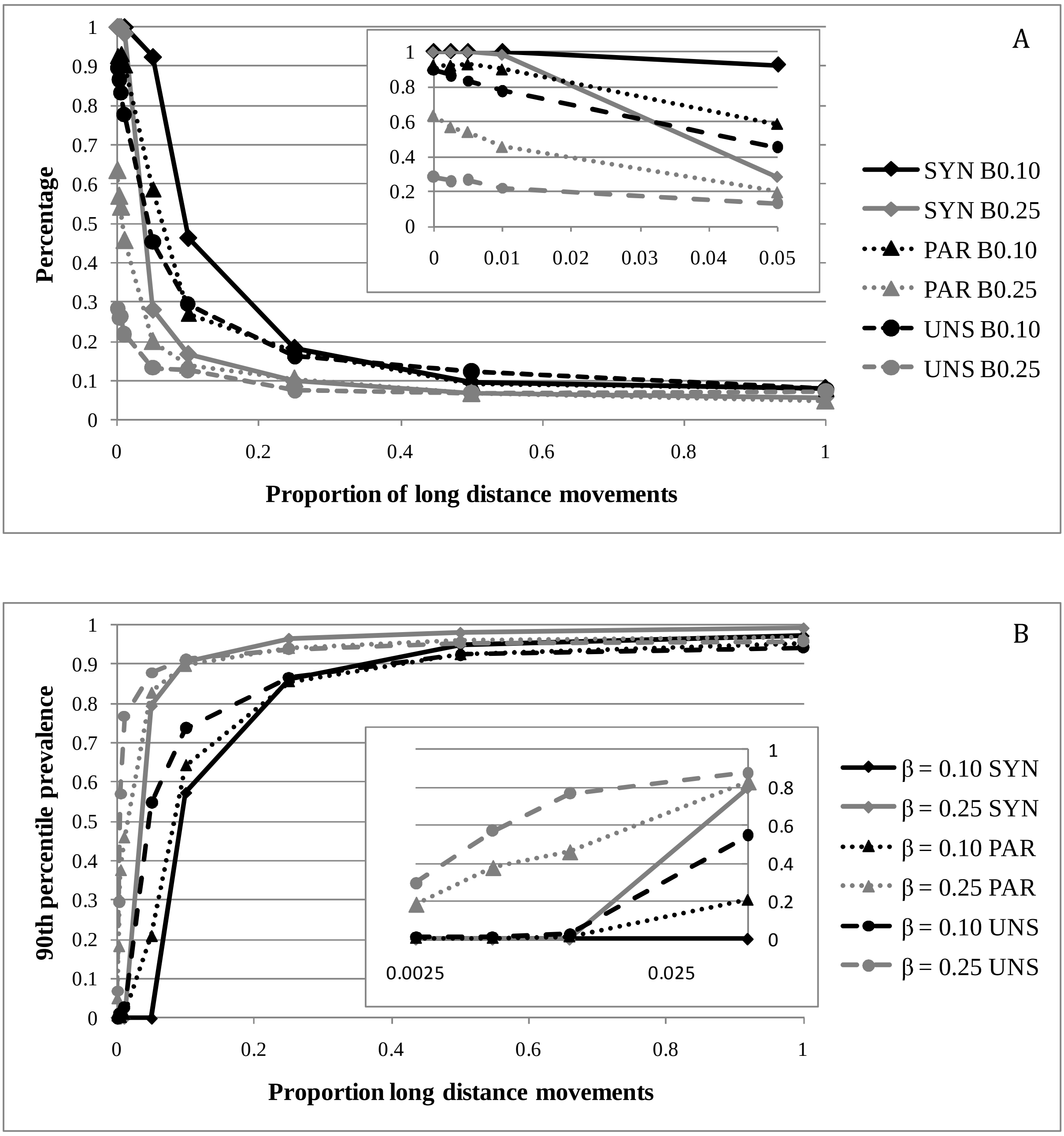
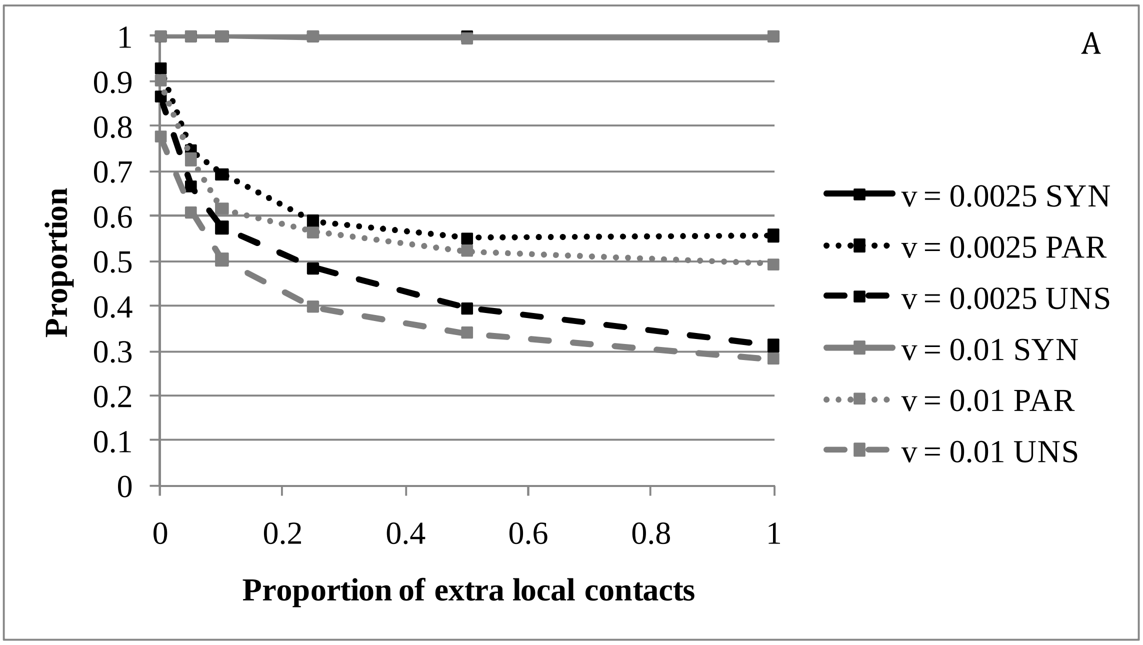
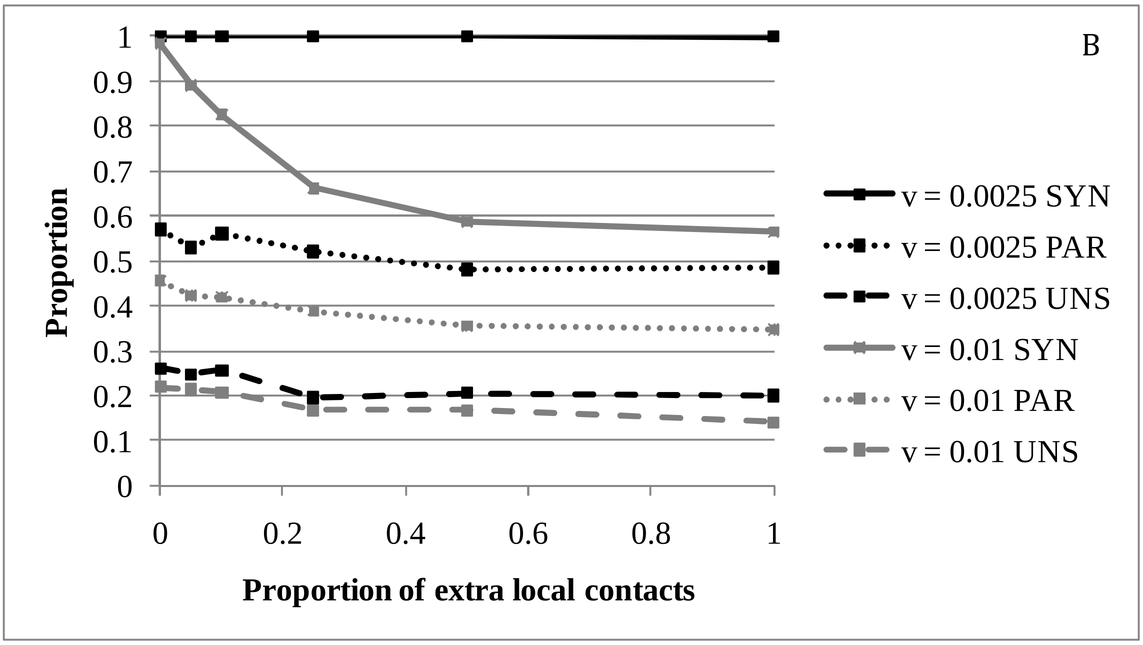
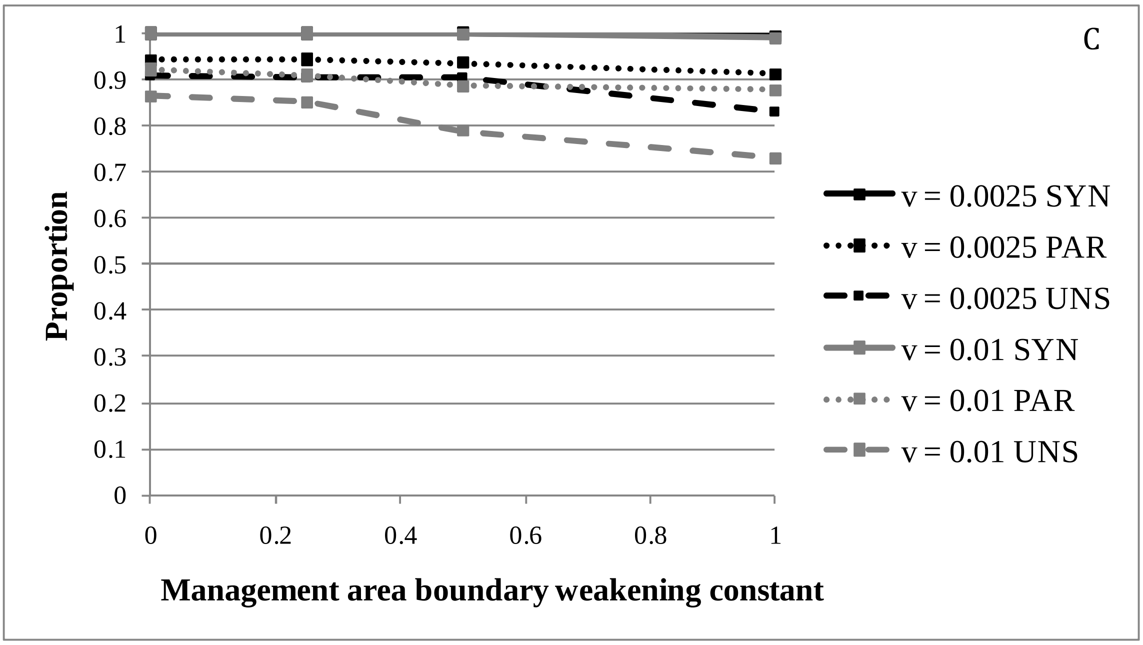


Figure 4: Proportion of runs where the epidemic died out prior to $t = 90$ (A) and worst-case scenarios presented by the 90th percentile at $t = 90$ (B). Both are represented for different proportions of long-distance movements v and different fallowing strategies synchronised (SYN), partial synchronised (PAR) and unsynchronised (UNS) and two different transmission rates $\beta = 0.10$ and $\beta = 0.25$.


A
Proportion
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
1
Proportion of extra local contacts
v = 0.0025 SYN
v = 0.0025 PAR
v = 0.0025 UNS
v = 0.01 SYN
v = 0.01 PAR
v = 0.01 UNS


B
Proportion
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
1
Proportion of extra local contacts
v = 0.0025 SYN
v = 0.0025 PAR
v = 0.0025 UNS
v = 0.01 SYN
v = 0.01 PAR
v = 0.01 UNS



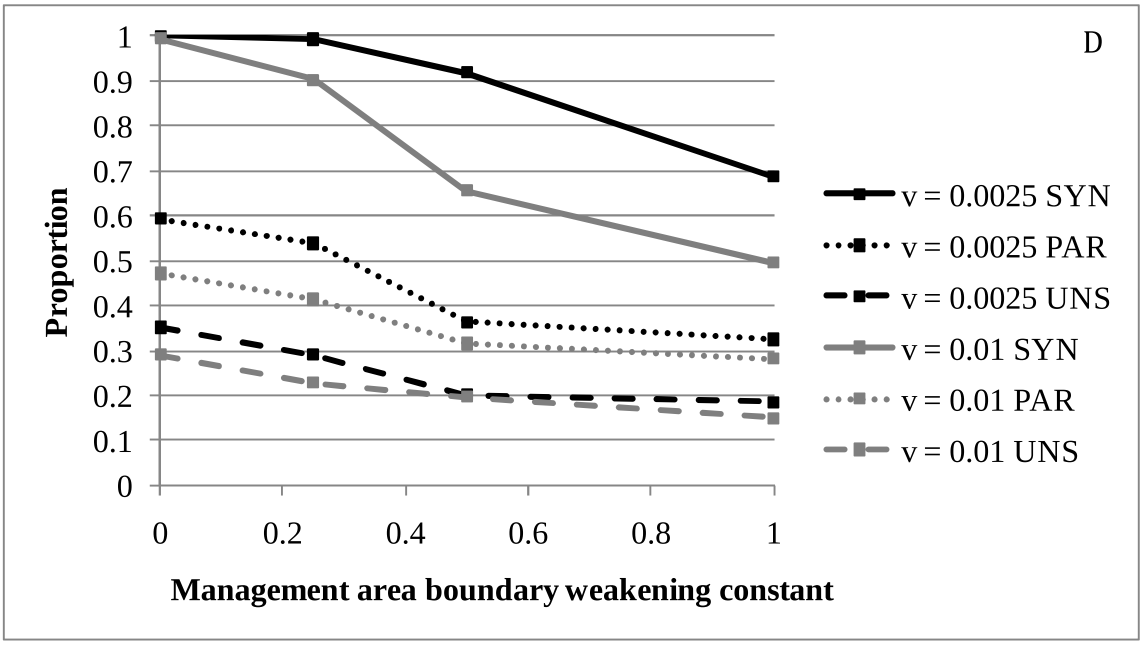


Figure 5: Percentage of runs where the epidemic died out prior to $t = 90$ in order to investigate the effects on epidemics when adding extra local contacts (in addition to the two neighbours). For the proportions of long-distance movements, $v = 0.0025$ and $v = 0.01$ and different fallowing strategies synchronised (SYN), partial synchronised (PAR) and unsynchronised (UNS) and for $\beta = 0.10$ (A) and $\beta = 0.25$ (B). The effects of weakening the management area boundaries on the amount of epidemics that die out prior to $t = 90$ for $\beta = 0.10$ (C) and $\beta = 0.25$ (D).

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