Vol. 96: 69–82, 2011
doi: 10.3354/dao02382

DISEASES OF AQUATIC ORGANISMS
Dis Aquat Org

Published August 29

Seasonality and heterogeneity of live fish movements in Scottish fish farms

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ABSTRACT: Movement of live animals is a key contributor to disease spread. Farmed Atlantic salmon *Salmo salar*, rainbow trout *Onchorynchus mykiss* and brown/sea trout *Salmo trutta* are initially raised in freshwater (FW) farms; all the salmon and some of the trout are subsequently moved to seawater (SW) farms. Frequently, fish are moved between farms during their FW stage and sometimes during their SW stage. Seasonality and differences in contact patterns across production phases have been shown to influence the course of an epidemic in livestock; however, these parameters have not been included in previous network models studying disease transmission in salmonids. In Scotland, farmers are required to register fish movements onto and off their farms; these records were used in the present study to investigate seasonality and heterogeneity of movements for each production phase separately for farmed salmon, rainbow trout and brown/sea trout. Salmon FW–FW and FW–SW movements showed a higher degree of heterogeneity in number of contacts and different seasonal patterns compared with SW–SW movements. FW–FW movements peaked from May to July and FW–SW movements peaked from March to April and from October to November. Salmon SW–SW movements occurred more consistently over the year and showed fewer connections and number of repeated connections between farms. Therefore, the salmon SW–SW network might be treated as homogeneous regarding the number of connections between farms and without seasonality. However, seasonality and production phase should be included in simulation models concerning FW–FW and FW–SW movements specifically. The number of rainbow trout FW–FW and brown/sea trout FW–FW movements were different from random. However, movements from other production phases were too low to discern a seasonal pattern or differences in contact pattern.

KEY WORDS: Disease transmission · Epidemiology · Contact structure · Aquaculture

INTRODUCTION

Finfish culture in Scotland produces Atlantic salmon *Salmo salar*, rainbow trout *Oncorhyncus mykiss*, brown/sea trout *Salmo trutta* and other species such as arctic charr *Salvelinus alpinus* and halibut *Hippoglossus hippoglossus*. Brown trout and sea trout belong to the same species, and are not distinguished in this study. Hereafter, brown trout refers to both brown and sea trout.

Scottish production includes ca. 144,000 tonnes of salmon, 6800 tonnes of rainbow trout and 200 tonnes of brown trout per year (Marine Scotland Science 2010b). Salmon (and some brown trout) are anadromous and have a freshwater (FW) and a saltwater (SW) phase. In FW, salmon eggs are fertilized and hatched in a hatchery. Next, fry are transported to FW farms. After approximately 12 to 16 mo, the fish (smolts) are moved to marine waters, where they achieve their harvest size after approximately a further 18 mo. Occasionally, salmon are moved between farms during the marine phase. Furthermore, SW–FW movements are needed to provide FW farms with broodstock (i.e. mature fish kept for breeding).

Rainbow trout can also be anadromous and their life cycle is similar; however, most rainbow trout are reared in FW without a marine phase. Live rainbow trout movements mainly occur between hatcheries and on-growing farms where juvenile fish are kept till harvest or moved to fisheries for re-stocking. The movement structure of these cultured fish species is pyramidal, with more movements going from the top

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(hatcheries) to the bottom (smolt producers or on-growers), which can be compared with the movement structure of industries such as of pigs (Lindstrom et al. 2010) and poultry (Cox & Pavic 2010).

Live fish movements are a risk for pathogen transmission between farms (Murray et al. 2002, Murray & Peeler 2005). Pathogens can also be introduced by other pathways such as well-boat visits (Murray et al. 2002) and on a local level by water movement (Jonkers et al. 2010) or by wild fish movements (Uglem et al. 2009). Disease outbreaks can cause reduced appetite, reduced growth and increased mortality rates, depending on the disease (OIE 2009), reducing production and profitability (Murray & Peeler 2005). In addition, disease outbreaks can cause welfare problems (Turnbull & Kadri 2007), and pathogen accumulation in fish farms may lead to transmission of pathogens to wild fish populations (Wallace et al. 2008).

If fish are infected and transported there is a great risk that the receiving farm will become infected (Murray & Peeler 2005). Therefore, movements from source farms known to be infected with a notifiable disease are prohibited (Joint Government/Industry Working Group 2000). However, notifiable and other infections can go undetected (Murray & Peeler 2005, Graham et al. 2006, Lyngstad et al. 2008). Therefore, pathogens may spread through live fish movements before pathogens are detected (Jonkers et al. 2010). For example, the spread of infectious salmon anaemia virus (ISAV) between regions during the 1998–1999 outbreak in Scotland was largely due to live fish movements (Murray et al. 2002), and movements are also thought to have played an important role in other outbreaks such as those in Chile (Mardones et al. 2009). Live fish movements have been identified as a risk factor for pathogen transmission for diseases such as viral haemorrhagic septicaemia (VHS) (Thrush & Peeler 2006), sleeping disease (Branson 2003) or for the potential introduction of *Gyrodactylus salaris* in the UK (Peeler & Thrush 2004).

Some fish pathogens are only infectious in one environment (either FW or SW) or during a specific life stage. For example, *Gyrodactylus salaris* can survive only in FW, and ISAV causes clinical diseases only in SW (OIE 2009). Infectious pancreatic necrosis virus (IPNV) and bacterial kidney disease (BKD) affect salmonids in both FW and SW; initially, both these diseases emerged in FW and only later were the pathogens observed to cause disease in SW. IPNV causes clinical outbreaks in fry or during the first weeks after transfer to sea (Smail et al. 1992, Bruno 2004). BKD affects almost all age groups, especially when the water temperatures are rising, except in very young salmonids (Marine Scotland Science 2010a). Where diseases affect one species more than another, carrier species could play an important role in spreading a pathogen, as infections are likely to be hard to detect. For example, potential undetected sub-clinical spread of *G. salaris* with trout movements can lead to infection of salmon, where it causes serious disease (Peeler & Thrush 2004). This combination of environment and host will determine which species or life stage is most relevant for disease transmission.

Network models are often used to understand the transmission of pathogens between epidemiological units, e.g. animals or farms. They have been used for modelling foot and mouth disease (FMD) (Green et al. 2006, Kiss et al. 2006) and avian influenza (Dent et al. 2008), amongst other diseases. These models are valuable because they can identify farms that are important in the spread of pathogens and provide a valuable tool for designing and investigating the effectiveness of control strategies (Green et al. 2011).

Contact between farms often shows a large variation in the number, timing and direction of contacts (Thrush & Peeler 2006, Green et al. 2009, Munro & Gregory 2009). Heterogeneity, i.e. variation in the number of contacts, affects the transmission pattern in a network (Anderson & May 1992). It is often stated as a rule of thumb that 20% of the population can cause approximately 80% of the infections (Anderson & May 1992, Woolhouse et al. 1997, Volkova et al. 2010). Previous work has shown a high variation in the number of contacts between farms for live salmon movements (Munro & Gregory 2009) and that a targeted surveillance strategy in a small number of farms will substantially decrease the risk of an epidemic (Green et al. 2009). Reproduction rate (R_0, i.e. the number of secondary infections caused by one primary infection) and clustering are both likely to affect the final epidemic size. When $R_0 < 1$, there will be a small epidemic, whereas when $R_0 > 1$, this is likely to result in a large epidemic (Anderson & May 1992). A high degree of clustering will reduce the final epidemic size and R_0 (Keeling 1999, Kiss et al. 2005).

Sheep movement data in the UK (Kiss et al. 2006), Italian cattle movement data (Natale et al. 2009) and Swedish cattle data (Noremark et al. 2009) show clear seasonality. Seasonality is commonly not included in aquatic network studies. However, epidemics are more likely to start and to become widespread during a period of high movement activity (Kiss et al. 2006), which was illustrated during the FMD epidemic in the UK in 2001 (Gibbens et al. 2001). Moreover, studies in cattle (Bigras-Poulin et al. 2006, Natale et al. 2009) and pigs (Bigras-Poulin et al. 2007, Lindstrom et al. 2010) showed differences in the contact structure across different production phases, which are likely to affect the course of an epidemic. This suggests that there is value in studying aquaculture network structures in more detail.

The aim of the present study was to provide a detailed description of the number of live fish movements per farm and their timing for Atlantic salmon, rainbow trout and brown trout in Scottish aquaculture stratified by production phase. This can be used to improve and develop pathogen transmission models in Scottish aquaculture. It is of interest whether we can treat the movement network as static or whether we need to include seasonality or production phase. Because of the differences in husbandry conditions, there was a need to investigate whether there were differences in the timing of movements and contact structure between salmon, rainbow trout and brown trout movements. This could have implications for biosecurity strategies, including timing of official surveillance.

DATA ANALYSIS

In Scotland, fish farmers are required to record the live fish movements onto and off each farm (including movements that occur between farms of the same owner). The fish health inspectors at Marine Scotland, Aberdeen, hold these records. We used the movement records from 1 January 2002 to 31 December 2004 for salmon and from 1 January 2003 to 31 December 2004 for rainbow trout and brown trout. More recent data were not available in a database format. These records included both ova and fish. Confirmed records (i.e. movements recorded at both source and destination farm) were entered in a database. Movements onto or off unregistered sites (such as fisheries), or movements only recorded at either the source or destination farm, could not be validated and were excluded. For example, fisheries can be treated as sinks, as they only receive fish and do not move fish off the site; fisheries were therefore excluded from this study. Movements onto or from sites outside Scotland and movements to harvest stations were recorded separately. An overview of the different stages of data organisation from movements between registered farms is given in Fig. 1.

Movements were divided into 5 categories: freshwater to freshwater (FW–FW), freshwater to saltwater (FW–SW), saltwater to saltwater (SW–SW), saltwater to freshwater (SW–FW) and 'other'. 'Other' includes movements onto and off farms that have both FW and SW facilities (N = 10). These farms were mostly research facilities (N = 7), which transport relatively small numbers of fish; 3 farms were commercial hatcheries with both FW and SW capabilities. The classification of these movements was based on the facilities available on the farms.

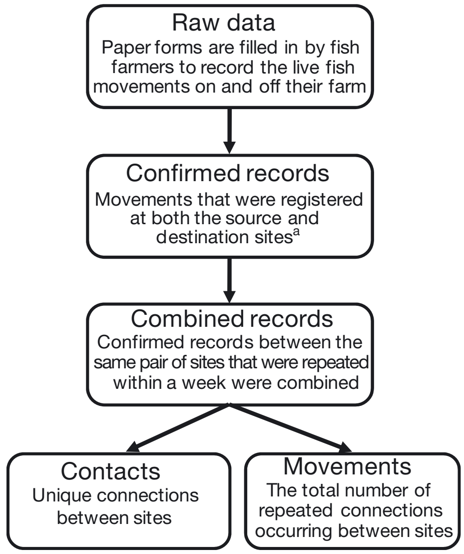

Fig. 1. An overview of the different data levels. [a]Movements onto and off Scottish farms from outside Scotland and harvest movements could not be validated and were entered into a different data set; these movements were not included in the on and off counts in the data described in this figure

A degree of consistency in the live fish movement network structure is shown in a previous study for the years 2002 to 2004 (Green et al. 2011); therefore, the Scottish live fish movement network is somewhat stable and it is likely some contacts will repeat across years. To investigate the concordance of contacts between the years 2003 and 2004, we calculated the mean arc persistence (MAP) by dividing the number of contacts present in both years (a) divided by the geometric mean of the numbers of contacts present in each year (x = 2003 and y = 2004):

$$\mathrm{MAP} = \frac{a}{\sqrt{xy}} \qquad (1)$$

This was performed for the different movement types of salmon and 'all' movements of rainbow trout and brown trout.

Salmon

During 2002 to 2004, 3730 salmon movement records were confirmed. However, approximately 36% of these movements were multiple movements between the same pairs of farms within the course of a week. The infection status of the source farm is relatively unlikely to have changed over such a short period; we therefore decided to combine the movement records that occurred within 1 wk between the same pair of farms and to record them as one movement (Fig. 1).

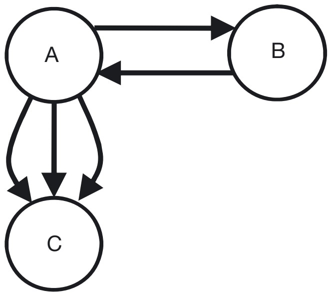

Fig. 2. Simplified graphical view of part of the network to explain the differences between movements and contacts. In this example, farm A has 4 movements off the farm divided over 2 contacts (Farm B and C) and has 1 movement (and contact) onto the farm. Farm B has 1 movement (and contact) onto and 1 movement (and contact) off the farm. Farm C has 3 movements onto the farm coming from 1 contact

Moreover, in some cases the receiving farm recorded multiple movements whereas the source farms recorded the same movements as one movement (or vice versa). To be consistent, we combined the multiple movements in these cases and recorded them as one movement. The movement dates of these combined records were the starting date of these series of movements and numbers of fish were added together. This resulted in 2401 salmon movements. The proportion of movement records that were combined were similar across the different types of movement and varied from 32% in FW–SW movements to 39% in SW–FW movements.

We made a distinction between contacts and movements. Contacts in this study are unique connections between farms and lack temporal perspective, whereas movements are the total number of repeated connections occurring between farms, which may occur more than once (Fig. 1). In Fig. 2, a simplified network is shown. We made this distinction as live fish movements to different farms are presumed to have a different impact on pathogen transmission in the network than multiple movements between the same pair of farms.

During 2002 to 2004, 499 salmon farms were active (i.e. farms in a production growing cycle either having stock or fallowing), of which 186 were FW farms, 304 were SW farms and 9 farms had both FW and SW facilities. The majority of movements occurred between FW farms, whereas FW–SW movements contained more contacts (Table 1).

Rainbow trout

There were 432 confirmed rainbow trout movement records during the years 2003 and 2004. Combining the movement records that occurred within 1 wk resulted in 343 combined records. During the study period there were 55 active rainbow trout farms: 46 FW farms, 7 SW farms and 2 farms with both FW and SW facilities. The majority of rainbow trout movements occurred between FW farms; the remaining movements were classified as FW–SW and 'other' (Table 1).

Brown trout

Of the confirmed movement records, 36% occurred within 1 wk; after combining those movement records, 82 combined brown trout records remained. Recorded movements took place between 34 active brown trout farms, of which 28 were FW farms, 5 were SW farms and 1 had both facilities. Again, the majority of movements were between FW farms, followed by FW–SW, SW–SW, SW–FW and 'other' movements (Table 1).

Harvest movements and movements to and from Scotland

Salmon were often not processed at the marine farm where they achieved their harvest weight, but were transported to harvest stations for processing. The live fish movements towards these harvest stations are listed as harvest movements. Movements to harvest stations should not be epidemiologically relevant if fish are maintained in biosecure transport and blood is disposed of hygienically (Munro et al. 2003). However, if

Table 1. Number of movements and contacts between farms stratified by type of movement. FW: freshwater; SW: saltwater; other: movements/contacts are onto or off a farm with both facilities

Type	Movements	Contacts
Salmon (total)	2401	1208
FW–FW	1181	400
FW–SW	810	595
SW–SW	237	154
SW–FW	54	22
Other	119	37
Rainbow trout (total)	343	69
FW–FW	310	59
FW–SW	30	9
Other	3	1
Brown trout (total)	82	31
FW–FW	60	22
FW–SW	12	5
SW–SW	6	1
SW–FW	2	2
Other	2	1

Table 2. Number of Scottish salmon import and export movements per year

	2002	2003	2004	Total
Imports	77	59	56	192
Exports	17	18	26	61

harvest sites become contaminated, they can be a very serious focus for disease spread (Murray et al. 2002).

In addition to the movements mentioned above, there were 1980 salmon harvest movements recorded during the period 1 January 2002 to 31 December 2004. Movements to the same harvest station that reoccurred within 1 wk were combined and reported as 1 movement, which resulted in 829 combined harvest records. The number of movements to harvest stations is likely to be larger than that obtained in our data set as many harvest movements may not have been recorded as live fish movements. We have no records of dead fish moved to processing plants.

Records of Scottish imports and exports of live fish were treated similarly as the harvest records, which reduced the number of movement records from 331 to 253. There were 192 movements onto Scottish farms from outside Scotland and 61 Scottish exports in 2002–2004 (see Table 2). These international movements are in addition to the national and harvest movements.

Seasonality

To test whether the number of movements per month was significantly different from random, we performed a chi-square test for all types of movements that had an expected number of movements (total number of movements/time period) of ≥5 per month (which were salmon: all movements, FW–FW, FW–SW and SW–SW; rainbow trout: all movements and FW–FW). For the less common movements, we combined the movements belonging to the same season (salmon: other, brown trout: all movements and FW–FW). The expected numbers of salmon SW–FW, rainbow trout FW–SW and other, and brown trout FW–SW, SW–SW, SW–FW and other were <5, even after combining the months belonging to the same season; therefore, there was no chi-square test performed on these movements.

In addition, we investigated by least-squares regression whether there was a significant sinusoidal seasonal trend with a period of 1 yr (for all types of movements with an expected number of movements ≥5 per month). In the regression model, we fitted the number of movements (y) as follows:

$$y = a + b\cos\frac{2\pi m}{t} + c\sin\frac{2\pi m}{t} + d\cos\frac{4\pi m}{t} + e\sin\frac{4\pi m}{t} + \varepsilon \quad (2)$$

where ε is the error term, a is the mean, and b, c, d and e together determine the magnitude and phase for yearly (b, c) and twice-yearly (d, e) seasonal patterns. The variable m represents the time step, which relates to $t = 12$ mo. If the residuals did not follow a normal distribution, data were square-root- (salmon: all movements and SW–SW) or $\log_{10}$-transformed (salmon FW–SW) to normalise the residuals. We performed the analysis in Minitab 16.

RESULTS

Timing of movements

The highest total number of salmon movements per month was in April (372 movements; Fig. 3A). The number of movements per month was significantly different from random (chi-square, $p < 0.001$, df = 35) and showed a significant seasonal trend ($F_{4,31} = 12.96$, $p < 0.001$, $r^2 = 62.6\%$).

Timings of salmon movements differed among the type of movements (Fig. 3A). The number of salmon FW–FW movements increased during May (n = 146), June (n = 152) and July (n = 142). SW farms were supplied with smolts mainly in March and April (n = 149 and 275) and October and November (n = 84 and 81). Salmon SW–SW movements were more constant throughout the year; however, they showed seasonal variation between years. Salmon SW–FW movements occurred mainly during September (n = 12) and October (n = 17). The number of movements per month from FW–FW, FW–SW, SW–SW (chi-square, $p < 0.001$, df = 35) and other (chi-square, $p < 0.001$, df = 11) were significantly different from random. FW–FW ($F_{4,31}$ = 17.80, $p < 0.001$, $r^2 = 69.7\%$) and FW–SW movements ($F_{4,31} = 20.96$, $p < 0.001$, $r^2 = 73.0\%$) showed a significant seasonal trend. Salmon SW–SW movements did not show a significant seasonal trend ($F_{4,31} = 0.37$, $p = 0.827$, $r^2 = 4.6\%$).

Timing of rainbow trout movements were more constant throughout the year compared with salmon movements; however, fewer rainbow trout movements occurred during the winter period (December, n = 6; January, n = 13; February, n = 17; Fig. 3B). The number of movements per month for the total number of rainbow trout movements and rainbow trout FW–FW movements were significantly different from random (chi-square $p < 0.001$, df = 23) and showed a seasonal trend for both total number of rainbow trout movements ($F_{4,19} = 8.72$, $p < 0.001$, $r^2 = 64.7\%$) and

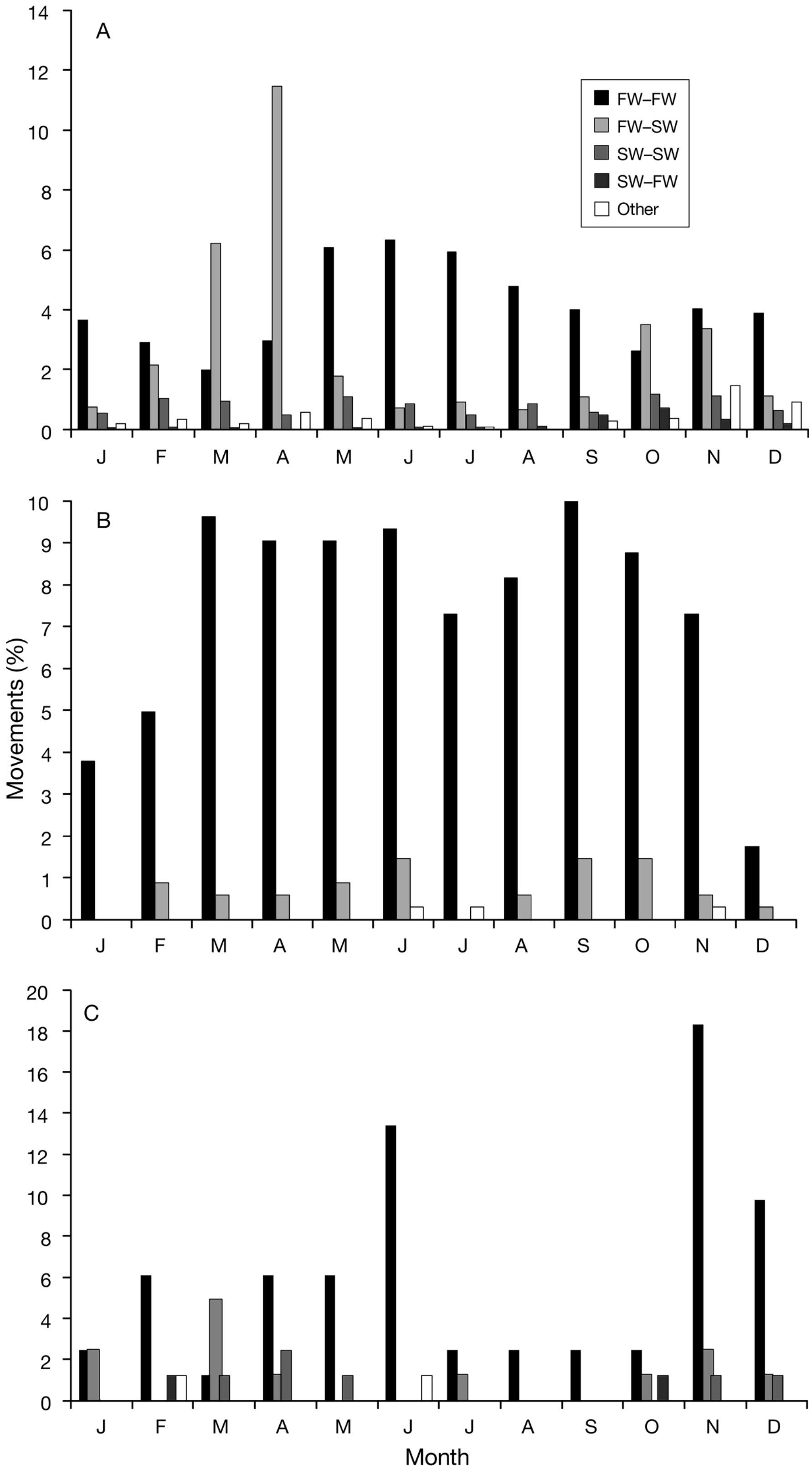

Fig. 3. Seasonal patterns of live fish movements of Scottish aquaculture, stratified by production phase (FW: freshwater; SW: saltwater). 'Other' movements are movements onto or off farms with both FW and SW facilities. (A) Data for 2002–2004 for salmon (n = 2401). (B) Data for 2003–2004 for rainbow trout (n = 434). (C) Data for 2003–2004 for brown trout (n = 82). Numbers of movements per month are represented as the percentage of the total number of movements of the specified species

rainbow trout FW–FW movements ($F_{4,19}$ = 7.81, p = 0.001, r^2 = 62.2%). The residuals of both rainbow trout models showed a temporal trend. Rainbow trout FW–SW movements peaked at different times compared with salmon movements, namely during June and September–October. However, the numbers of movements were too low to discern any seasonal patterns.

Brown trout FW–FW movements mainly occurred in June (n = 11), November (n = 15) and December (n = 8) during the period studied (Fig. 3C). The numbers of movements per season were significant different from random (chi-square, p < 0.001, df = 7) for both all movements and FW–FW movements.

Variation in contact structure

During 2002–2004, 299 salmon farms had movements off the farms. As was anticipated from the industry structure, there were more farms that had movements onto their farms (n = 471); however, the number of movements and contacts per farm was lower (Table 3). Many movements were repeated between the same pairs of farms. The number of unique contacts per farm was therefore lower compared with the total number of movements per farm (Fig. 4A); there was a larger variation in the number of movements per farm than in the number of contacts per farm (Table 3).

The variation in number of movements and contacts differed across the salmon production phases (Table 3). Salmon FW–FW movements had the largest range of total number of movements onto (min = 1, max = 38) and off (min = 1, max = 52) per farm, whereas FW–SW movements had the highest number of contacts going onto (min = 1, max 11) and off (min = 1, max = 24) their farms. Approximately 40% of the salmon SW farms received smolts from 3 or more different suppliers (Fig. 5).

We did not stratify the rainbow trout and brown trout movements to study the contact structure across production phases because by far the majority of movements were between FW farms. Forty-four rainbow trout farms had movements onto their farms and 28 farms had movements off their farms during 2003–2004. The maximum number of movements and contacts onto farms was higher than the number of contacts and movements off farms (Table 3).

There were fewer brown trout farms than rainbow trout or salmon farms. During 2003 to 2004, 28 farms had brown trout movements onto their farm and 21 farms had movements off their farm. The number of movements and contacts per farm were lower for movements onto farms than for movements off farms.

Table 3. Descriptive statistics for movements and contacts per farm for salmon (2002–2004 data, stratified by production phase), rainbow trout and brown trout (2003–2004 data)

Type	Movements		Contacts	
Statistic	On	Off	On	Off
Salmon (all)				
Median	4	4	2	2
Mean	5.1	8.0	2.6	4.0
Variance to mean ratio	13.3	4.9	1.1	5.0
Maximum	38	65	11	24
Salmon (FW–FW)				
Median	5	7	2	2
Mean	7.3	10.8	2.5	3.7
Variance to mean ratio	5.8	11.9	1.0	3.7
Maximum	38	52	8	20
Salmon (FW–SW)				
Median	3	4	2	3
Mean	3.4	6.3	2.5	4.6
Variance to mean ratio	2.0	6.6	1.0	3.4
Maximum	16	44	11	24
Salmon (SW–SW)				
Median	1	2	1	1
Mean	2.1	2.1	1.4	1.3
Variance to mean ratio	2.6	1.0	0.5	0.3
Maximum	22	10	6	4
Salmon (SW–FW)				
Median	3	3	1	1
Mean	3.4	4.2	1.4	1.7
Variance to mean ratio	1.4	3.3	0.3	1.1
Maximum	8	15	3	6
Salmon (other)				
Median	4.5	1	1	1
Mean	6.0	5.4	1.9	1.7
Variance to mean ratio	2.9	14.8	0.8	1.4
Maximum	13	36	5	6
Rainbow trout (all)				
Median	4	4.5	1	1
Mean	7.8	12.3	1.6	2.5
Variance to mean ratio	11.6	23.3	0.5	2.7
Maximum	45	62	4	12
Brown trout (all)				
Median	1	2	1	1
Mean	2.9	3.9	1.1	1.5
Variance to mean ratio	3.0	3.5	0.1	0.3
Maximum	11	13	2	3

There was a moderate concordance in the contacts between years 2003 and 2004 for salmon FW–FW contacts (MAP = 0.51) and other contacts (MAP = 0.55), as well as for all rainbow trout contacts (MAP = 0.50) and all brown trout contacts (MAP = 0.56). The MAP for the remaining salmon contacts was low; 0.05 for FW–SW, 0.18 for SW–SW and 0.20 for SW–FW.

Harvest movements

The majority of the harvest movements (540) were recorded in 2004, compared with 94 in 2002 and 195 in

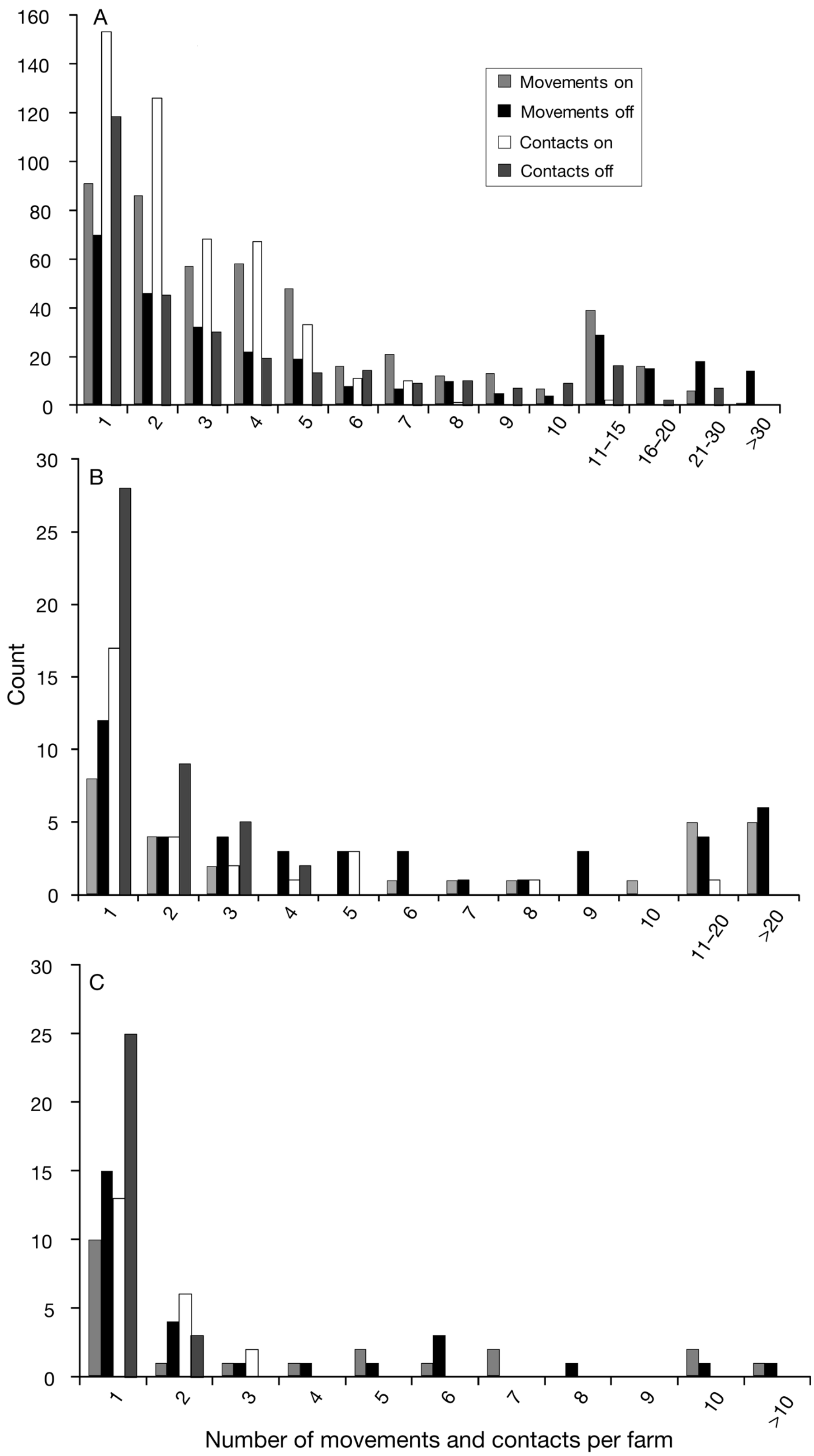

Fig. 4. Number of movements and contacts per farm for (A) salmon (n = 2401), (B) rainbow trout (n = 434) and (C) brown trout (n = 82). The majority of the farms had multiple movements from one contact; therefore, a distinction was made between the total number of movements per farms and the number of contacts per farm. Farms often had multiple movements going onto or off their farm; therefore, there are more farms with a lower number of contacts than number of movements

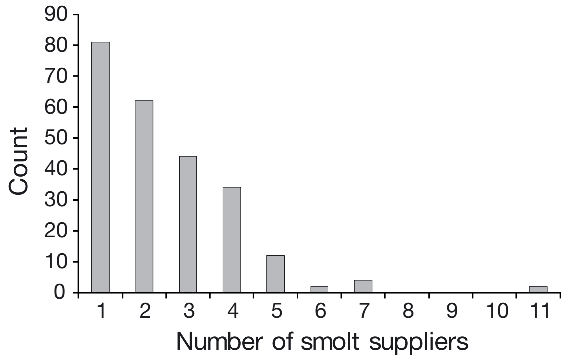

Fig. 5. Distribution of the number of smolt suppliers per farm for salmon farms

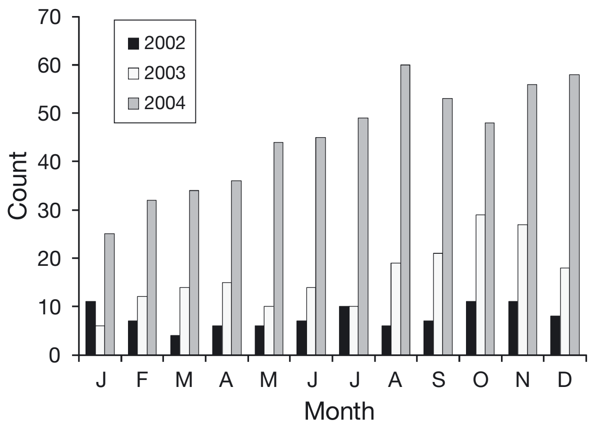

Fig. 6. Number of salmon harvest movements per year

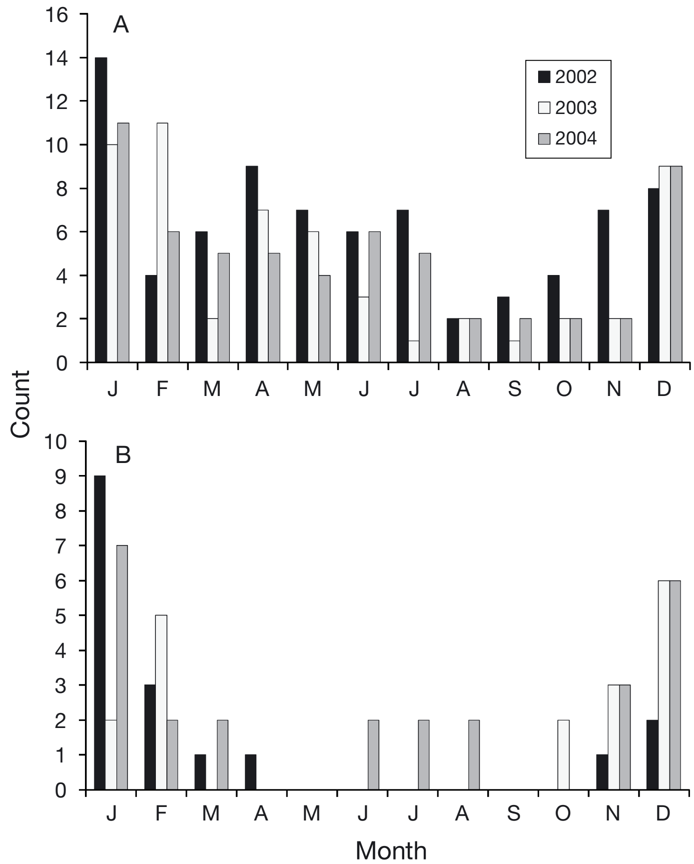

Fig. 7. Salmon movements in/out of Scotland. (A) Imports; (B) exports

2003 (Fig. 6). In 2003 and 2004, the number of harvest movements increased during August and December, which made these months an extra risk of a source of infection for farms in close proximity to harvest stations.

Movements to and from Scotland

There are strict biosecurity measures for live fish imported from other countries, with the exception of movements to or from Wales and England; however, there is still a risk of introduction of pathogens. This might have occurred with IPNV in Ireland (Ruane et al. 2009).

There were 192 movements going onto Scottish farms (Fig. 7A) originating from outside of Scotland. Imports of live fish occurred from Ireland, the Isle of Man and England, whereas imports of ova occurred from Iceland, Australia, Denmark (trout ova only), Norway (salmon ova only) and the USA. There were also 61 movements to farms outside Scotland (Fig. 7B). Destinations for live fish were England and Ireland, whereas ova were exported to EU member states and Chile. Eight farms had movements going on or off the farms outside Scotland. In January and December, there was a peak of both the export and import of live salmon. The lowest numbers of imports were during August to November. Epidemic models that simulate the introduction of exotic diseases introduced by international movements should take into account the seasonality of these movements. However, the timing of these movements showed differences between the years studied (Fig. 7A).

DISCUSSION

To our knowledge, this is the first study describing seasonality and contact structure stratified by production phase of live fish movements.

Contact structure

These data show heterogeneity in the number of movements and contacts across different production phases; these differences could change the course of an epidemic considerably (Bigras-Poulin et al. 2006, Bigras-Poulin et al. 2007, Natale et al. 2009, Lindstrom et al. 2010). Salmon SW–SW, SW–FW and other movements had lower numbers of movements and contacts per farm compared with salmon FW–FW and FW–SW movements and contacts. An index case in a salmon hatchery or other salmon FW farm is likely to result in a larger epidemic (especially when farms with many off contacts are infected) than an epidemic that starts in a salmon SW farm because of differences in direction and number of contacts. Salmon FW farms are likely to be sources for infections, whereas salmon SW farms are more likely to be sinks. Because of the low numbers of FW–SW and SW–SW movements compared with FW–FW movements in rainbow trout and brown trout, differences in contact structure between the different types of movements were not distinguished.

The number of smolt suppliers supplying a farm has often been identified as a risk factor for disease outbreaks on salmon production farms, such as for IPN (Jarp et al. 1995, Murray 2006) and ISA (Vagsholm et al. 1994, Jarp & Karlsen 1997). In the present study, FW–SW movements showed a large range of contacts per farm. Although it might not always be possible to limit the number of smolt suppliers, a further reduction of the number of FW–SW contacts per farm is likely to decrease the risk of infections in SW farms.

The reduced risk of pathogen transmission between SW farms is mainly because of reduced movements of fish between SW farms, which has been improved since the Scottish ISA outbreak in 1998–1999. Scottish sea farms are now divided into management areas, and good code of practice prohibits fish farms from moving post-smolts between management areas (Joint Government/Industry Working Group 2000). The use of management areas combined with fallowing strategies has proven to be effective in reducing epidemic spread in a theoretical study (Werkman et al. 2011) and in the field during the recent ISA outbreak in 2009, where the outbreak affected only one management area (Murray et al. 2010).

Broodstock could theoretically be a source of vertical infection, as ova can become infected with, for example, BKD (Marine Scotland Science 2010a). Broodstock were only moved occasionally and these fish movements are under strict surveillance. Furthermore, the number of contacts for SW–FW was low during the period studied compared with FW–FW contacts. A decrease in the number of contacts reduces the change of infection. This, in combination with the strict biosecurity measures, protects broodstock from infection. If broodstock are infected, transmission to other freshwater farms is extensive. And, from these freshwater farms, transfer may occur to multiple seawater farms, which underlines the importance of strict surveillance of broodstock.

Large numbers of movements occurred between FW farms. The data presented here showed that the number of total movements and contacts in salmon SW–SW movements was considerably lower than salmon FW–FW and salmon FW–SW movements. This suggests that there is a need to investigate the possibilities of biosecurity measures for FW farms, similar to the management areas applied to SW farms. Some of these movements are essential to aquaculture; fish must be moved off hatcheries to on-growing sites and smolts must be moved to sea. Receiving farms minimise the costs of fish moved onto them, which may involve sourcing from different locations, and this is essential for their economic sustainability. Use of stocks from different sources increases genetic variability; this may increase the risk of pathogen introduction but reduce its impact, should this occur. However, pathogen transfer risk may be reduced by removing strategic nodes that link clusters of farms (Green et al. 2009), so a strategic review of movement, rather than blanket reduction, may be the most effective modification of the network.

Despite the lower number of total rainbow trout live fish movements compared with salmon, the numbers of movements per farm were comparable for rainbow trout and salmon. However, the numbers of contacts per farm were considerably lower for rainbow trout because movements between pairs of rainbow trout farms occurred more frequently compared with the salmon movements. The salmon movement network had more connections between farms and diseases could therefore spread easier between salmon farms than between rainbow trout farms, all other factors, such as the transmission rate of the pathogen, being equal. However, multiple movements between the same pair of farms increase the risk of the receiving farm becoming infected from the source farm, as multiple movements occur during the year. It should be kept in mind that only 2 yr of data were considered for rainbow trout data and 3 yr for salmon data.

In this study we did not include the effects of size of farms (i.e. production) on the number of movements or contacts. However, it is likely that larger farms would have more movements and contacts onto and off their farm, and, therefore, have a higher risk of becoming infected and transmitting pathogens to a large number of farms.

Seasonality

The timing of movements is important, as a peak in the number of live animal movements has been shown to increase the size of an epidemic considerably

(Gibbens et al. 2001). During peak periods of movements, fish farmers should be extra vigilant for clinical signs of diseases before moving live fish; this is important in order to prevent potential transmission of pathogens to other farms and, in some cases, large numbers of farms.

Salmon data showed a high degree of seasonality, particularly for FW–FW and FW–FS movements, as would be expected because of the seasonal nature of smolt transfers. During periods of high peak in activity there are increased numbers of movements between contacts, and epidemics are more likely to become widespread in a network containing more (direct) connections between farms (Kiss et al. 2006). Targeted biosecurity aimed at identifying pathogens before the increased activity will help to prevent or reduce pathogen spread to other farms. However, eradication strategies might have less of an effect when outbreaks are widespread before detection (Keeling 1999, Kiss et al. 2005, Thrush & Peeler 2006, Natale et al. 2009, Ward et al. 2009, Werkman et al. 2011). This was shown during the 2001 FMD outbreak, where 57 farms were infected with FMD before the disease was detected (Gibbens et al. 2001, Eales et al. 2002). This was also the case with ISA in Scotland, where the 1998–1999 outbreak spread nationwide before detection (Murray et al. 2002), whereas the 2008–2009 outbreak was limited to a relatively small area of southwest Shetland (Murray et al. 2010). Thrush & Peeler (2006) estimated that in case of introduction of *Gyrodactylus salaris*, 50% of the catchments in England could be infected before diagnosis of the parasite, in the worst-case scenario. However, this study did not include seasonality of movements. Subclinical infections can go unnoticed (Bruno 2004, Graham et al. 2006, Lyngstad et al. 2008, Murray et al. 2010). Performing clinical tests increases the change of detecting subclinical infections and movements can be stopped when a farm tests positive. Therefore, performing clinical tests during periods of a high peak in activity of movements can minimise the risk of spreading pathogens. The control of widespread diseases can be very difficult if the necessary resources and infrastructure are not available, such as the lack of trained personnel, which exacerbated the UK FMD outbreak in 2001 (Eales et al. 2002).

Because salmon FW–FW and FW–SW movements and rainbow trout movements are seasonal, control strategies performed before these high peak seasons will have a positive impact on disease control. This strategy prevents farms from having many movements off (during a relatively short period of time) with possibly infected fish. As SW–SW movements occur more constantly throughout the year, targeted control surveillance has less of an effect compared with targeted control for FW–FW and FW–SW movements.

Some diseases, such as BKD, are more likely to occur during the spring when water temperatures are rising (Marine Scotland Science 2010a). The spring is also a period with an increased number of FW–FW and FW–SW movements, which increases risk of this disease.

The inclusion of seasonality or timing of movements in simulation models will not only include peaks of live fish movement activity during specific periods of the year, but will also include the sequence of movements. For example, if movements occur from A to B and from B to C and A is the source of infection, C will only get infected if movement from A to B occurred first. Therefore, the sequence of movements is important for predicting the course of epidemics in more complex dynamic models when compared with static networks. Further studies are needed to quantify the effects of seasonality on the course of epidemics.

Harvest data

Close proximity (<5 km) to a harvest station has often been identified as a risk factor for disease transmission (Vagsholm et al. 1994, Jarp & Karlsen 1997, Munro et al. 2003). Harvest stations could be a source of infection to adjacent farms via pathogens and escaped live fish from the harvest station contacting fish in adjacent farms (Munro et al. 2003). Well boats transporting live fish to harvesting plants can also be responsible for pathogen transmission to farms en route to the harvest stations (Munro et al. 2003, McClure et al. 2005). During periods of increased movement activity towards harvest stations, disease risk is increased to farms adjacent to or en route to harvest stations.

Some farms transported salmon to more than one harvest station. To reduce the risk for farms in close vicinity of the harvest station, it would be better to transport live fish to one harvest station, because in case of infection only one harvest station will be affected, although this might not be possible in all cases for logistical and economic reasons. Companies will seek to sell their fish to the processor offering the best price, this is especially the case for small independent companies, whereas larger companies are more likely to own and operate company processing plants. The specific harvest stations could not be validated in all cases in this study, as in some records only the area was included and the name of the harvest station was missing.

During the studied period, as a result of the ISA outbreak of 1998–1999, improving practices led to fewer fish being slaughtered on site and hence more live fish movements to harvest stations. This could have led to the increased harvest movements in 2004. However, we believe this increase could also be partly due to improved record keeping, also as a result of the ISA outbreak, as some movements to slaughter may not have been recorded because these fish were not being moved to another farm.

Other routes of infection

Live fish movements are not the only route of pathogen transmission between fish farms. Pathogens can also spread at a local level, as wild fish can become infected and transfer pathogens when they are in the vicinity of infected farms and susceptible farms (Uglem et al. 2009). In addition, diseases such as ISA and pancreas disease are known to spread at a local level (<10 km; McClure et al. 2005, Lyngstad et al. 2008, Aldrin et al. 2010). Effects of local transmission are likely to be reduced when the distance between the susceptible farm and the source farm is increased (Aldrin et al. 2010). In the present study, spatial analysis was not conducted. However, movements occur to and from farms; therefore, the number of movements and contacts is likely to be positively correlated with the number of farms in an area. This can have a substantial effect on pathogen transmission and makes areas with a high production more vulnerable to disease outbreaks, both through local transmission and long-distance movements.

Long-distance transfer of live fish will almost certainly cause infection on the receiving farms when the transferred fish are infected (Murray & Peeler 2005). Furthermore, long-distance movements are easier to control than local transmission pathways such as movements of water and wild animals. Controlling and decreasing long-distance movements can therefore have a substantial impact in reducing the risk of epidemics in Scottish aquaculture (Werkman et al. 2011). Moreover, local transmission tends to have a lower R_0 than long-distance transmission. Because of clustering of infection on a local level, infected farms are competing for the same neighbours to infect (Keeling 1999, Kiss et al. 2005). However, economic reasons may mean that fish are sourced some distance from the receiving site. For example, in Shetland, the area of FW production is small relative to the area for SW production; in this case, salmon smolts may be sourced from Yorkshire and ova from Norway (Murray et al. 2010).

Data collection

It would be useful to collect movement data electronically. Movement records are currently documented on paper forms and held by fish health inspectors at Marine Scotland. Collecting the data electronically would improve the traceability of the movements and makes it easier to check whether data are recorded at both the source and destination farms. Furthermore, electronic data collection will increase the speed of identifying the movements on and off the index case or other infected farms. Collecting the movement data physically causes a delay in identifying the possible secondary infections. As a consequence, movement restrictions might have to be applied across the whole country in the case of an outbreak of an exotic disease such as *Gyrodactylus salaris*, at least until data are collected and analysed. This is especially relevant when the disease is subclinical, and when the source (e.g. wild reservoir or international movement) cannot be identified, which means that the duration of infection and degree of spread is unknown.

CONCLUSIONS

In this study we have shown variation in the timing of movements and number of movements and contacts across different species and production phases (for salmon). Therefore, it is important to include seasonality, heterogeneity of the number of contacts and production phase in simulation models. Salmon movements between SW farms show less heterogeneity in the timing of movements and contacts. Therefore, simulation models considering these networks only may be treated without seasonality of live fish movements.

Disease outbreaks affecting mainly FW farms can spread easily throughout the network because of the high number of contacts per farm. If the number of these movements can be reduced, then disease risk from pathogens with a FW phase might be reduced substantially, as has occurred for SW farms. Simulation models should consider disease-specific parameters and include network properties affecting the relevant subpopulation.

Acknowledgements. Data access was provided by Marine Scotland Science. M.W. and D.M.G. are sponsored by Marine Scotland.

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Editorial responsibility: Julie Bebak, Auburn, Alabama, USA

Submitted: April 13, 2011; Accepted: June 6, 2011
Proofs received from author(s): July 28, 2011