



REVIEW

# Disease management mitigates risk of pathogen transmission from maricultured salmonids

Simon R. M. Jones<sup>1,\*</sup>, David W. Bruno<sup>2</sup>, Lone Madsen<sup>3</sup>, Edmund J. Peeler<sup>4</sup>

<sup>1</sup>Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia V9T 6N7, Canada

<sup>2</sup>Marine Scotland Science, 375 Victoria Road, Aberdeen AB11 9DB, Scotland, UK

<sup>3</sup>Technical University of Denmark, National Veterinary Institute, Bülowsvej 27, 1870 Frederiksberg C, Denmark

<sup>4</sup>Cefas Weymouth Laboratory, Barrack Road, Weymouth, Dorset DT4 8UB, UK

**ABSTRACT:** Open marine net pens facilitate virus and sea lice transfer, occasionally leading to infections and outbreaks of disease in farmed salmon. A review of 3 salmon pathogens (infectious salmon anaemia virus [ISAV], salmon alphavirus [SAV] and the salmon louse *Lepeophtheirus salmonis*) shows that increased risk of exposure to neighbouring farms is inversely related to distance from and directly related to biomass at the source of infection. Epidemiological techniques integrating data from oceanography, diagnostics and pathogen shedding rates and viability contribute to improved understanding of pathogen transmission pathways among farms and permit the designation of areas of risk associated with sources of infection. Occupation of an area of risk may increase the likelihood of exposure, infection and disease among susceptible fish. Disease mitigation in mariculture occurs at 2 scales: area-based (coordinated stocking, harvesting and fallowing) and farm-based (vaccination, early pathogen detection, veterinary prescribed treatments and depopulation or early harvest in the event of viral disease). Collectively, implementation of mitigation measures results in virus disease outbreaks of shorter duration with lower mortality and therefore reduces the likelihood of pathogen transmission. In contrast, the mitigation of sea lice transmission is less likely to be effective in some areas due to the loss of parasite sensitivity to therapeutants and to dissemination of larval lice when parasites occur below management thresholds. For wild populations, risk of pathogen spillback is estimated from farm-based epidemiological data; however, validation, particularly for ISAV and SAV, is required using direct surveillance.

**KEY WORDS:** Aquaculture · Salmon · Pathogen · Disease · Interactions

## INTRODUCTION

In coastal waters of the North Atlantic Ocean, finfish are reared for mariculture in open net pens. Under these conditions, farmed fish populations are exposed to pathogens (viruses, bacteria or parasites) from sources in the marine environment (e.g. wild fish) (Johansen et al. 2011) which may lead to infections (Raynard et al. 2007, Garver et al. 2013b). Generally, the movement of pathogens among susceptible populations reflects a greater connectivity in aquatic ecosystems compared with terrestrial coun-

terparts (Uglem et al. 2009, Green 2010), which permits various pathways of transmission and may promote changes in pathogen characteristics (Nowak 2007, Pulkkinen et al. 2010, Kurath & Winton 2011). Occasionally, pathogens will move within and among mariculture sites, and when increases in pathogen abundance coincide with appropriate host and environmental contexts, outbreaks of disease are possible (McVicar 1997, Murray & Peeler 2005, Bergh 2007). Outbreaks of diseases have broadened awareness of pathogen dynamics and disease progression within and among mariculture sites and have provided

\*Corresponding author: simon.jones@dfo-mpo.gc.ca

much of the knowledge-base for the epidemiology of finfish diseases (Murray 2009, 2013, Salama & Rabe 2013). As a result, mariculture incorporates disease mitigation strategies (Table 1) that are practised at 2 spatial scales: area-based (coordinated stocking, harvesting and fallowing) and farm-based (vaccination, early pathogen detection, veterinary prescribed treatments and depopulation or early harvest in the event of viral disease).

Endemic disease and disease outbreaks in farmed fish may be associated with an increase in pathogen spillback to wild fish stocks (Kurath & Winton 2011). The potential threat of pathogen interactions between mariculture and wild fish has been considered for some time (Håstein & Lindstad 1991, McVicar 1997, Hedrick 1998) and more recently has been refined in reviews, models and risk assessments (Peeler et al. 2007, Johansen et al. 2011). However, in contrast to mariculture, the epidemiology of disease in wild finfish is poorly understood, and information on which to make judgments about pathogen spillback is sparse. There is evidence that the distribution of some pathogens in wild populations is correlated with the proximity to mariculture (Wallace et al. 2008); however, diseases are rarely observed in wild marine finfish (Hedrick 1998, Noakes et al. 2000, Bergh 2007, Riley et al. 2008, Johansen et al. 2011). Nevertheless, the potential importance of spillback from farmed to wild salmon has to be considered

given that in several regions for salmon mariculture the biomass of farmed salmon considerably outweighs the wild population. In Norway, ~400 million salmon are reared each year compared with ~400 000 returning adult salmon (Thorstad & Forseth 2010). These data, combined with the known risk of escapees and the close contact of wild and farmed salmon suggests that farmed salmon could act as an important reservoir of infection for wild salmon.

The goal of this paper is to assess the extent to which current epidemiological knowledge informs our understanding on the risks and consequences of pathogen transmission from farmed salmon populations. We consider these risks and consequences to be relevant both to wild and maricultured populations. As Atlantic salmon *Salmo salar* and rainbow trout *Oncorhynchus mykiss* constitute over 95% of the biomass of maricultured finfish in the northeast Atlantic Ocean (FAO 2012), the present paper focuses on 3 pathogens which cause diseases of considerable economic impact in salmon mariculture. For each of infectious salmon anaemia virus (ISAV), salmon alpha virus (SAV) and the salmon louse *Lepeophtheirus salmonis*, we review occurrence in wild populations and epidemiological considerations including mitigation practices in mariculture and evidence of spillback. For each disease, we then provide a qualitative risk assessment according to 3 pathways of effects (introduction, dissemination from farm, consequences) and estimate the differential collective impacts of disease mitigation strategies.

Table 1. Measures to mitigate pathogen introduction, dissemination and consequences in mariculture

<p><b>Infectious salmon anaemia virus</b></p> <ol style="list-style-type: none"> <li>1. All in–all out stocking and harvesting, fallowing</li> <li>2. Restriction of fish movements</li> <li>3. Coordination of sea lice control</li> <li>4. Vaccination</li> <li>5. Use of good quality smolts</li> <li>6. Reduction of farm stocking numbers</li> <li>7. Improved surveillance and diagnostic capacities</li> <li>8. Depopulation</li> </ol> <p><b>Salmon alpha virus</b></p> <ol style="list-style-type: none"> <li>1. Fallowing</li> <li>2. Vaccination</li> <li>3. Zones without farm between infected and uninfected areas (fire break)</li> <li>4. Improved surveillance and diagnostic capacities</li> </ol> <p><b>Sea lice</b></p> <ol style="list-style-type: none"> <li>1. Restrictions on locations of new farm developments</li> <li>2. Monitoring and treatment when lice levels exceed thresholds (which may vary with season)</li> <li>3. Fallowing</li> <li>4. Separation of year-classes</li> <li>5. Synchronous treatments</li> </ol>
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## MATERIALS AND METHODS

Pathways for pathogen interactions between wild and farmed populations are illustrated in Fig. 1. A risk analysis framework similar to that described earlier for aquatic animal health management (Peeler et al. 2007) is used to assess for each pathogen the effect of farm-based disease mitigation practices (Table 1) on the likelihood and uncertainty of each effects pathway and the consequences of pathogen spread. Definitions for descriptors of likelihood and uncertainty are given in Tables 2 & 3.

### Infectious salmon anaemia virus (ISAV)

#### Introduction

Infectious salmon anaemia (ISA) was first reported in farmed Atlantic salmon in Norway in 1984 (Thorud

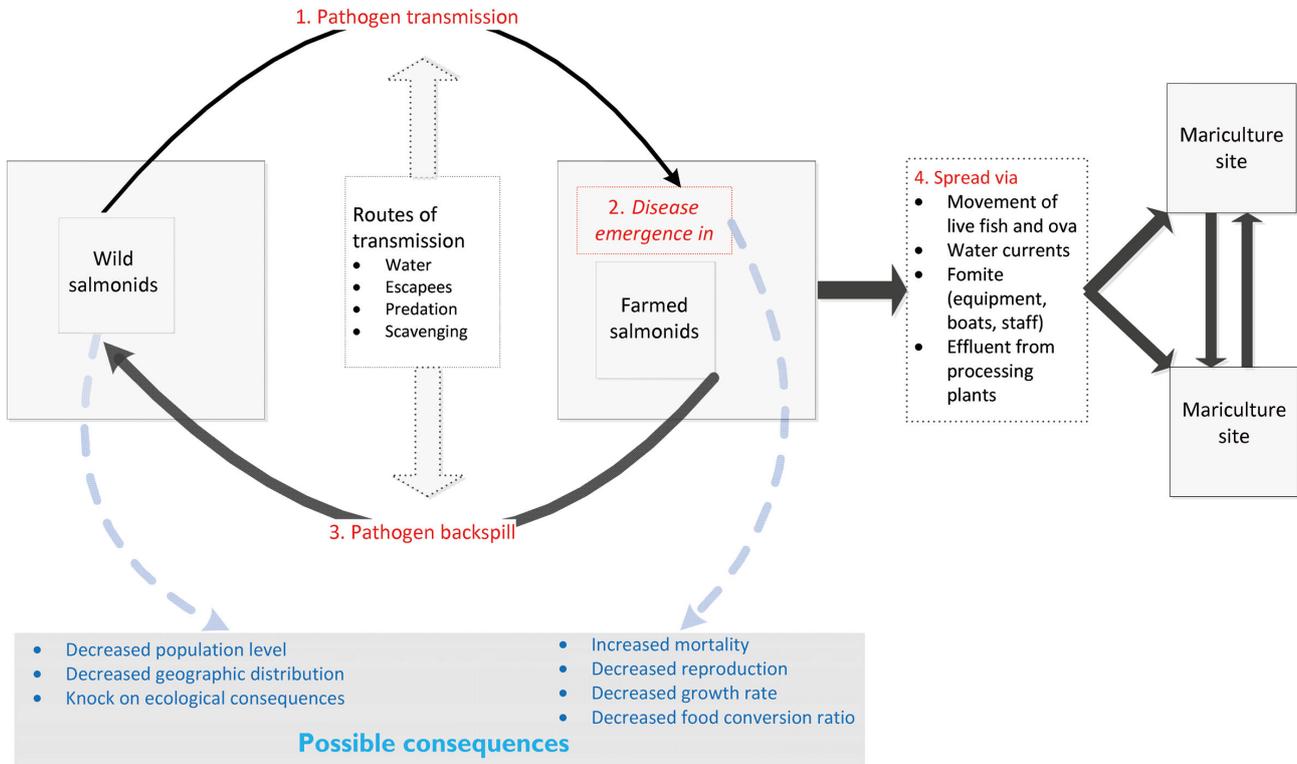


Fig. 1. Routes and consequences of pathogen interactions between farmed and wild salmonids (numbers indicate temporal sequence of processes driving emergences: 3. and 4. may occur simultaneously)

Table 2. Definitions of levels of uncertainty used in risk assessment (EFSA 2006)

Uncertainty	Definition
Low	<ul style="list-style-type: none"> <li>• Solid and complete data available; strong evidence in multiple references with most authors coming to the same conclusions, or</li> <li>• Considerable and consistent experience from field observations</li> </ul>
Medium	<ul style="list-style-type: none"> <li>• Incomplete, or only some data available; evidence provided in small number of references; authors' or experts' conclusions vary, or</li> <li>• Limited evidence from field observations, or</li> <li>• Solid and complete data available from other species which can be extrapolated to the species being considered</li> </ul>
High	<ul style="list-style-type: none"> <li>• Scarce or no data available; evidence provided in unpublished reports, or</li> <li>• Few observations and personal communications, and/or</li> <li>• Authors' or experts' conclusions vary considerably</li> </ul>

& Djupvik 1988) and since then in eastern Canada and the USA, Scotland, Chile and the Faroe Islands (Christiansen et al. 2011, Rimstad et al. 2011, Lyngstad et al. 2013). The disease is characterized by anaemia, haemorrhage and necrosis in several organs and is caused by ISAV. ISAV belongs to the genus *Isavirus* within the family Orthomyxoviridae. Different strains or genotypes of the virus occur. The low virulent variant (ISAV-HPR0) is found in apparently healthy wild and farmed fish, and Kibenge et

Table 3. Definitions of levels of estimated likelihood

Likelihood	Definition
Rare	Event may only occur in exceptional circumstances
Unlikely	Event could occur but is not expected
Moderate	Event might occur at some time
Likely	Event will probably occur in most instances
Almost certain	Event is expected to occur in most instances

al. (2012) list 3 hypotheses to explain the relationship between low virulent and virulent strains: ISAV-HPR0 in wild fish is ancestral to virulent ISAV variants (Rimstad et al. 2011), virulent ISAV mutates to a less virulent form, and HPR0 is the original consensus sequence of all HPR-deleted sequences during virus replication in a cell. However, HPR0 strains are also detected late during disease outbreaks and persist long after the disease has been eradicated (Christiansen et al. 2011, Kibenge et al. 2012). Fish are infectious well before clinical signs are observed (Totland et al. 1996) and shed viral particles within 3 d of initial infection via faeces, urine and skin mucus (Lyngstad et al. 2013).

The transmission of ISAV among Atlantic salmon is primarily horizontal in both freshwater and seawater (Totland et al. 1996, Jones & Groman 2001, Lyngstad et al. 2013), although vertical transmission has not been ruled out (Thorud & Djupvik 1988, Melville & Griffiths 1999, Marshall et al. 2014). ISAV occurs in gonadal tissue in spawning salmon (Nylund et al. 2003, 2007), and there is evidence that the virus was introduced to Chile in association with salmon ova (Vike et al. 2009).

#### Wild reservoirs and extent of surveillance

In addition to Atlantic salmon, the virus replicates in brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus* (Jones et al. 1999a, Kibenge et al. 2004). Atlantic herring *Clupea harengus* and American eel *Anguilla rostrata* may also be asymptomatic carriers (Totland et al. 1996, Devold et al. 2000, Kibenge et al. 2004). Pollock *Theragra chalcogramma* do not appear to be a reservoir for the virus despite wild populations having close contact with cultured Atlantic salmon (McClure et al. 2004). Pacific salmon (*Oncorhynchus keta*, *O. tshawytscha*, *O. kisutch* and *O. mykiss*) appear resistant to ISAV infections; however, the virus has been re-isolated from experimentally infected chum and coho salmon and from steelhead, suggesting these species are susceptible under certain circumstances (Rolland & Winton 2003). Relatively little research has been conducted on the prevalence and maintenance of ISAV infections in wild fish populations including those adjacent to affected Atlantic salmon mariculture sites. Serum antibodies to ISAV were measured in returning Atlantic salmon from the Connecticut and Penobscot Rivers in the eastern USA, suggesting the fish had previously been exposed to the virus (Cipriano 2009). The virus was isolated from sea trout in Scotland (Raynard et al. 2001), and there

was evidence of viral genomic RNA in Atlantic salmon parr and adults and in non-migratory and anadromous brown trout collected either close to farm operations or in rivers distant from farm operations, in the absence of clinical disease (Raynard et al. 2001). In Norway, brown trout collected from rivers were found to harbour the highest prevalence of the virus, while Atlantic salmon showed low prevalence of the virus (Plarre et al. 2005). No fish showed clinical signs of infection, and ISAV was not cultured from any of the samples tested but could be detected after a few weeks in disease-free salmon injected with tissue homogenates from RT-PCR-positive wild fish (Plarre et al. 2005). Therefore, Atlantic salmon, brown trout and sea trout are candidate reservoir species of ISAV HPR0 (EFSA 2012).

#### Epidemiological considerations in mariculture

Risk categorizations and themes for pathogen introduction into marine salmon farms have been evaluated by Oidtmann et al. (2013). Lyngstad et al. (2008, 2013) list the characteristics relevant to assessment of pathways of horizontal transmission for ISAV including live fish movements and egg movement, exposure via water, on-site processing, short distance mechanical transmission as well as distance independent mechanical transmission. The risk of ISAV dissemination from infected to adjacent farms is related to the salmon biomass and host density at the infected site (Ögüt et al. 2005, Hammell & Dohoo 2005, McClure et al. 2005, Salama & Murray 2011, 2013) and inversely related to seaway distances among the farms (Mardones et al. 2009, 2011, Aldrin et al. 2011, Murray 2013). The latter factor is linked to local hydrodynamic conditions, which influence the rate and direction of virus dispersal (Gustafson et al. 2007, Salama & Murray 2013), but generally, a short seaway distance to an ISA site is an important risk factor. ISAV might be spread by infected biological material including animal waste or discharge from slaughtering (Lyngstad et al. 2013), and this is directly related to the biomass of infected stock harvested (Munro et al. 2003). Mardones et al. (2014) found that multiple generations on a farm, mean smolt weight at stocking >120 g, farm area and increased number of shipments entering a farm were associated with reduced time to infection, whereas time-to-infection was longer for farms located farther away from an ongoing ISAV outbreak. Transport of infected fish in well boats or sharing of personnel and equipment among sites are important risk factors, particularly for transmission

over greater distances (Murray et al. 2002, Murray 2013). Outbreaks of ISA in Norway, Scotland, eastern Canada and the USA and Chile have led to the establishment of exclusion or management zones defined by clusters of sites sharing tidal excursions, embayments or other common waterways (Mardones et al. 2011, Murray 2013). Such disease management areas (DMAs) can be effective at preventing disease emergence, even with some transfer to neighbouring areas, if the number of long-distance contacts is kept to a minimum, and fallowing is synchronized (Werkman et al. 2011, Murray 2013).

#### Mitigating factors and spillback

The establishment of more stringent on-farm and among-farm biosecurity measures have reduced the risk of infection as indicated by the reduced longevity, reduced mortality and spatial limitations of more recent outbreaks (Murray et al. 2010, Mardones et al. 2014). Maintaining fish in good health may reduce their susceptibility to low virulent strains and thus lower the rate of new outbreaks (Lyngstad et al. 2011). Rapid removal of sick or dead stock is also effective in limiting virus transmission (Jarp & Karlsen 1997). Co-ordinated fallowing within management areas combined with risk-based surveillance lessens the likelihood that virulent ISAV will persist and re-establish (Murray et al. 2010). In Chile, disease control measures introduced in 2009 (summarized in Table 1) contributed to the recovery of the industry after the occurrence of ISA (Mardones et al. 2014). Ritchie et al. (2009) suggested that different ISAV strains will pose different risks following infection and showed that survivors of an earlier infection had greater resistance to subsequent infection. Similarly, mortality and virus levels in salmon previously exposed to a low virulence ISAV strain were lower following challenge with a high virulence strain compared with naïve controls (LeBlanc et al. 2012). Vaccination against ISA may be feasible (Jones et al. 1999b). While such management actions will mitigate the risk of virus transmission, there are no data on transmission of ISAV to wild fish. Occurrence of the HPR0 genotype in wild salmonids indicates that a reservoir of infection exists outside the farmed salmon population (EFSA 2012). Lyngstad et al. (2011) found the low virulent genotype to be frequently present in farmed Atlantic salmon in Norway and concluded that this strain transitioned into virulent genotypes causing solitary outbreaks or local epidemics. Although there is a theoretically higher risk for wild fish to acquire the infection the closer they are

to an infected site, failure to detect such patterns of infection likely reflects the limited effort to survey these populations (Lyngstad et al. 2013).

## Salmon alpha virus (SAV)

### Introduction

Pancreas disease (PD) was first reported from farmed Atlantic salmon in Scotland (Munro et al. 1984). A similar condition named 'sleeping disease' (SD) was subsequently described from freshwater-reared rainbow trout (Boucher & Baudin-Laurencin 1996). PD represents a chronic condition with associated mortality in farmed salmon and trout and consequently is of economic importance for farmed fish in Ireland, Norway and Scotland (Rodger & Mitchell 2007, Aunsmo et al. 2010, Jansen et al. 2014). Both diseases are caused by infection with SAV in the family Togaviridae (Weston et al. 1999), also known as salmon pancreas disease virus. Six SAV subtypes have been distinguished using phylogenetic analysis with partial E2- and nsP3-gene sequence data (Fringuelli et al. 2008), providing evidence that some subtypes are dominant in certain geographical regions. Following infection, virus RNA persists in tissues for extended periods (Andersen et al. 2007, Christie et al. 2007, Graham et al. 2010, Jansen et al. 2010), posing a possible risk to healthy fish. Salmonid alphaviruses are transmitted horizontally (Boucher et al. 1995) and have been detected in the salmon louse *Lepeophtheirus salmonis* by PCR (Pettersen et al. 2009), but in this case viral replication in lice and consequent transfer of the virus to a new host has not been demonstrated. This is in contrast to the 26 enveloped mammalian alphaviruses that cause disease in humans and domestic animals, and which require mosquitoes or other haematophagous arthropods to serve as vectors (Brown & Condreay 1986). The identification of potential vectors for SAV has been highlighted as an area for investigation, and knowledge in this area would improve management and understanding regarding risk and infection (McLoughlin & Graham 2007).

### Wild reservoirs and extent of surveillance

In Scottish waters, long rough dab *Hippoglossoides platessoides*, common dab *Limanda limanda* and plaice *Pleuronectes platessa* were identified as possible reservoirs of SAV based on the detection of low

levels of virus RNA in pooled tissues (Snow et al. 2010). Virus subtype V was subsequently isolated into cell culture from common dab (Bruno et al. 2014). Three of the 6 SAV subtypes were identified in dab in a locality remote from salmonid aquaculture, strongly implicating dab as a non-salmonid reservoir of the virus. Fringuelli et al. (2008) reported identical sequences at separate farm sites over several years, implying that this is a slowly evolving virus. This is supported by a virus evolution study by Karlsen et al. (2014), which concluded that all 6 subtypes of SPDV diverged prior to the 20<sup>th</sup> century and earlier than the first introduction of farmed rainbow trout into Europe. SAV positive tissues were detected by real-time RT-PCR and sequencing in common dab, plaice and megrim *Lepidorhombus whiffiagonis* from the Irish and Celtic Seas (McCleary et al. 2014). A very low prevalence of SAV subtype I was reported in common dab and plaice, except for 1 haul in Dublin Bay, Ireland where 25% of common dab were SAV positive.

#### Epidemiological considerations in mariculture

SAV II is the dominant subtype from Atlantic salmon reared in the Shetland Isles, Scotland, whereas salmon from the northeast of Scotland and the Western Isles show subtype V as dominant (Graham et al. 2012). Subtypes I, IV, V and VI have been isolated from Atlantic salmon in Scotland and Ireland (Weston et al. 2005, Fringuelli et al. 2008) and subtype II from rainbow trout in the UK and continental Europe. The subtype III is restricted to farmed Atlantic salmon in Norway. Recently, a subtype II has also been reported from Norwegian farmed salmon (Hjortaa et al. 2013, Jansen et al. 2014). There is also evidence that subtypes traditionally observed in one environment are now identified in new areas, for example, the finding of SAV II strains in saltwater reared Atlantic salmon (Graham et al. 2012) and SAV I strains occurring in freshwater salmonids (Lester et al. 2011). Statistical models regarding the most likely route of transmission of SAV among farmed fish suggest passive drift of virus in the water (Viljugrein et al. 2009, Stene et al. 2014). Horizontal transmission of the virus affects the probability of a disease outbreak in a single cohort (McLoughlin et al. 1996, Kristoffersen et al. 2009, Viljugrein et al. 2009). Evidence of vertical transmission of SAV III was not found in a study by Kongtorp et al. (2010). Madhun et al. (2014) detected SAV and piscine reovirus in recently escaped salmon in Norway, highlighting the potential contribution of escapees in virus transmission to other local salmon farms.

#### Mitigating factors and spillback

The available information indicates that SAV is transmitted among mariculture populations and that movement of the virus between marine reservoirs and mariculture populations is bidirectional. Fallowing of farm sites reduces or limits the build-up of infectious agents, a practice that is required in many countries. However, despite fallowing, SAV has re-emerged at some farms following restocking (McLoughlin et al. 2003), and persistence of the virus in sediments may serve as a source of infection. Experimental work has shown that SAV can survive for ~6 d at 10°C in sterile saltwater with organic loading (Graham et al. 2007). This suggests that the virus is sufficiently viable in the aquatic environment to be useful for modelling, as assumed by Viljugrein et al. (2009). Phylogenetic data of SAV subtype IV are consistent with a history of repeated transmission between dab and salmon. Common dab can move into brackish waters and then enter freshwater river systems in coastal areas (Elliott et al. 1990); hence, they could encounter subtypes other than those frequently attributed to marine salmon as reported by Lester et al. (2011). Graham et al. (2006) reported virus-neutralising serum antibodies in saithe *Pollachius virens*, a species commonly found in the vicinity of sea cages, but no disease was recorded. This indicates the possibility of inter-species transmission of SAV between wild and farmed fish. The precise role of common dab as a natural host with potential to transmit infection to farmed fish is not known, particularly if the virus is self-sustaining in aquaculture through farming practices (Kristoffersen et al. 2009, Bruno et al. 2014). Interestingly, Karlsen et al. (2014) suggest that SAV subtypes diverged prior to fish farming and therefore must have been associated with a marine reservoir. Mitigation to contain SAV in endemic regions also includes vaccination (Bang Jensen et al. 2012, Karlsen et al. 2012).

SAV occurs at low levels in wild non-salmonid fish and there is no evidence that infections are associated with disease. Overall the conditions that promote epidemics and disease occurrence in aquaculture may not occur for wild fish, thus limiting the occurrence of clinical disease and its effects on wild fish.

#### Sea lice

##### Introduction

Sea lice are parasitic copepods which are ubiquitous and inevitable pests of maricultured salmon, with an

estimated annual global cost to industry of €300 million (Costello 2009). In the northern hemisphere, the salmon louse *L. salmonis* is the largest and most aggressive species affecting salmon and therefore the target of management and treatment. Sea lice life cycles include a free-living phase, consisting of first and second stage nauplii and infective copepodids, and a parasitic phase consisting of 2 chalimus stages, 1 or 2 preadult stages and adults (Hamre et al. 2013). The free-living stages are non-feeding and dispersive and their longevity is defined by endogenous lipid and ambient temperature (Cook et al. 2010). The extent of dispersion during early larval development is largely determined by currents in the ambient seawater (Tully & Nolan 2002). Host-seeking and attachment by the copepodid is facilitated by anatomical, physiological and behavioural traits (see Mordue & Birkett 2009). In the absence of treatment, high host densities combined with appropriate environmental conditions support rapid growth in the size of the parasite population with associated scale loss, skin ulceration and haemorrhage (Brandal & Egidius 1977, Wootten et al. 1982, Johnson et al. 2004).

#### Wild reservoirs and extent of surveillance

Infestations with *L. salmonis* have been reported from anadromous salmonids for over 300 yr (Torrissen et al. 2013), and an historical perspective on scientific surveillance efforts in the North Atlantic and Pacific Oceans is provided by Pike & Wadsworth (1999). Recent research supports the view that the parasite is prevalent and abundant on salmonids throughout the northern hemisphere with some variation among host species. In Ireland, over 93% of 928 returning adult Atlantic collected off the Irish coast between 2004 and 2011 were infested with an average of nearly 12 *L. salmonis* per fish (Jackson et al. 2013b). In Scotland, all 94 adult salmon caught over 2 yr were infested with mean intensities of 26.1 to 28.7 *L. salmonis* per fish (Todd et al. 2000). In the northeast Pacific Ocean, more than 98% of returning adult salmon had mixed infestations with *L. salmonis* and *Caligus clemensi* and the mean intensity of adult female *L. salmonis* ranged among species from 1.6 to 8.5 (Beamish et al. 2005). In addition to the high prevalence, a common feature of infections on returning Pacific salmon is that most parasites are motile (preadults or adult stages). An autumn rise in sea lice abundance in mariculture has been associated with the seasonal return of infested adult Pacific salmon during their spawning migrations (Beamish et al. 2007, Saksida et al. 2007, Marty et al. 2010).

#### Epidemiological considerations in mariculture

Outbreaks with *L. salmonis* occurred on farmed salmon in Norway in the 1960s, in Scotland in the 1970s and in eastern Canada in the 1990s (Jones 2009). Thus, a need for management and treatment options for *L. salmonis* arose prior to a clear understanding of the epidemiology of the parasite. Early investigations explored the importance of parameters useful for farm-based parasite management, including level and type of treatment, cage volume, temperature effects on development, salinity, current speed, tidal flushing time, history of sea lice infections and fallowing (Bron et al. 1993, Revie et al. 2002, 2003, 2005, Heuch et al. 2003, 2009, McKenzie et al. 2004, Stien et al. 2005, Saksida et al. 2007, Lees et al. 2008). Host biomass or density is an important mariculture variable in some Norwegian fjords in which a large number of farms occupies a relatively small volume of water (Bjørn et al. 2011, Jansen et al. 2012). Mathematical models expanded on the earlier observations and estimated the dispersal of sea lice larvae according to the speed and direction of water flow in coastal ecosystems (Murray & Gillibrand 2006, Gillibrand & Kate 2007, Stucchi et al. 2011, Salama et al. 2013, Asplin et al. 2014). Aldrin et al. (2013) used Norwegian data to model the expected abundance of lice at a farm as a function of 1 mo-lagged abundance at the same farm, at neighbouring farms or at other non-identified sources. The model assumed lice populations followed a zero-inflated negative binomial distribution and found that the same farm accounted for two-thirds of the expected abundance, neighbouring farms accounted for slightly less than one-third and other sources, ~6% of the observed abundance (Aldrin et al. 2013). Analysis of data from Chilean farmed salmon infected with another parasitic copepod, *Caligus rogercresseyi*, found a significant relationship with infections on neighbouring farms during the preceding 2 wk (Kristoffersen et al. 2013). Direct measures of salmon louse infestation pressure using sentinel fish and surveillance of wild populations (Bjørn et al. 2011, Middlemas et al. 2013, Serra-Llinares et al. 2014) may be useful in validating the models. Together these studies are consistent with the 'neighbour' concept described in Aldrin et al. (2013) and indicate that elevated risk of salmon louse infestation can extend 30 km from a farm, as shown earlier (Krkošek et al. 2005, Jansen et al. 2012, Middlemas et al. 2013).

### Mitigating factors and spillback

Increased abundances of *L. salmonis* have repeatedly been observed on wild salmonids in coastal regions associated with salmon mariculture in Ireland, Norway and western Canada (Tully & Whelan 1993, Tully et al. 1999, Bjørn et al. 2001, Bjørn & Finstad 2002, Morton et al. 2004, Marty et al. 2010, Middlemas et al. 2010, 2013). Accordingly, Norway has implemented 'Temporary Protected Zones' and 'Norwegian Salmon Fjords' (Heuch et al. 2005, Bjørn et al. 2011, Serra-Llinares et al. 2014), in which there are restrictions to the development of new farms, and established farms must follow mandatory actions including scheduled reporting of lice numbers, synchronized treatments and fallowing within management areas to maintain lice levels below required limits (Bjørn et al. 2011, Ritchie & Boxaspen 2011). While larger protected areas can be effective in minimising levels of *L. salmonis* on farms, some protected areas may be too small due to increased local biomass densities or to increased external influences (Serra-Llinares et al. 2014). Other jurisdictions have implemented strategies to manage sea lice. In British Columbia (western Canada), the Sea Lice Management Strategy adopted in 2003 requires management action when total motile (adult and preadult) *L. salmonis* abundances exceed 3 per fish during the juvenile pink salmon juvenile migration between March and July (Saksida et al. 2011). Ireland has maintained a national Sea Lice Monitoring Programme for salmonid mariculture since 1991 (O'Donohoe et al. 2013) (O'Donohoe et al. 2013, p. 3). Data are published annually and serve in part 'to provide management information to drive the implementation of control and management strategies'. The 5 principal components of the programme are to separate generations, to fallow sites annually, to harvest early 2-sea-winter fish, to use targeted and synchronous treatment regimens and to use agreed husbandry practices.

Temporal patterns in the abundance of planktonic *L. salmonis* nauplii and copepodids in coastal and off-shore regions of a Scottish loch are correlated with treatment or relocation actions of farmed salmon within the same loch (McKibben & Hay 2004, Penston et al. 2008, Penston & Davies 2009, Murray et al. 2011, Penston et al. 2011). Similarly, infection pressure on sentinel salmon smolts is related to the abundance of ovigerous *L. salmonis* on adjacent populations of cultured salmon (Bjørn et al. 2011, Pert et al. 2014). Conversely, the coordinated proactive application of salmon louse treatments, regardless of louse abundance, was associated with reduced abun-

dances on juvenile Pacific salmon that migrate in adjacent waterways in British Columbia (Jones & Hargreaves 2009, Peacock et al. 2013, Rogers et al. 2013). Collectively, these studies recognise that spatial distributions of infective *L. salmonis* larvae near mariculture sites are governed by physical processes such as wind forcing which act locally and drive water flow (Amundrud & Murray 2009), and by the application of sea lice management strategies. Importantly, the failure of many treatment options due to reduced sensitivity within louse populations indicates a need for alternative management strategies (Jones 2009, Torrissen et al. 2013, Helgesen et al. 2014).

### Evidence for population-level effects related to spillback

The possibility that *L. salmonis* adversely impacts wild salmonid populations stems from evidence of disease caused by severe infestations on individual salmon combined with the observations that many populations of Atlantic salmon and sea trout have been declining throughout the North Atlantic Ocean since the late 1980s (Parrish et al. 1998, Chaput 2012). The extent to which the negative health effects of sea lice on individual juvenile salmon may be extrapolated to measurable changes in salmon population abundance has been explored using mathematical models (Krkošek et al. 2007, 2011) or meta-analyses (Ford & Myers 2008). Sea trout smolts may be particularly vulnerable because they occupy coastal marine habitats and therefore may be at greater risk of exposure associated with mariculture. In the Hardangerfjord, Norway, where annual production of maricultured salmon is over 80 000 t (Skaala et al. 2014a), sea trout have been infested with potentially lethal intensities of *L. salmonis* in 2008, 2010 and 2012 (Serra-Llinares et al. 2014). In this region there has been a decline in the number of mature sea trout in the River Guddalselva between 2000 and 2011 (Skaala et al. 2014b). Similarly, declining sea trout populations in western Ireland were associated with elevated sea lice infestations and proximity to mariculture (Tully et al. 1999). Effects of sea lice on Atlantic salmon populations have been investigated by treating smolts with emamectin benzoate and comparing the survival of treated and untreated salmon. Emamectin benzoate is toxic to *L. salmonis*, and these studies assumed that differences in survival are due to sea lice-associated mortality. The results of

similar long-term studies conducted in Ireland (Jackson et al. 2013a) and Norway (Skilbrei et al. (2013) are summarised in Torrissen et al. (2013). Both studies reported overall marine mortality of 95% or greater regardless of treatment, and there was considerable variability in the apparent efficacy of treatment among years and release dates. Nevertheless, the likelihood that treatment increased salmon survival, expressed as an odds-ratio, was calculated to range from 1.14:1 to 1.17:1 in the Irish and Norwegian studies, respectively. A meta-analysis of the Irish and Norwegian data, including those of Gargan et al. (2012), reported increased survival among treated salmon with an odds ratio of 1.29:1 (Krkošek et al. 2013). Although there is an ongoing debate regarding the quantitative outcome, these studies provide a glimpse into the magnitude of sea lice effects in wild salmonid populations. They also emphasise the challenges associated with attempting to quantify the incremental impact of a parasite within a population already experiencing >95% mortality.

### Risk assessment

The likelihood that disease mitigation strategies adopted by salmon mariculture influence the transmission of ISAV, SAV and *L. salmonis*, as conceptualised in Fig. 1, is summarised in Table 4. In the absence of mitigation, there is high confidence in the likelihood that zones of ISAV infectivity will extend beyond farms or farm clusters (Werkman et al. 2011), resulting in elevated risk of exposure among adjacent susceptible species. Mitigation of infectious salmon anaemia, including biosecurity measures, early detection and depopulation, is associated with a reduced likelihood of virus acquisition from neighbouring farms, resulting from reduced virus transmission by water, fish-to-fish contact or by biological or anthropogenic vectors (Table 4A). Conversely, mitigation practices in mariculture are unlikely to influence transmission of the virus from a wild reservoir. Similarly, while mitigation is expected to lessen the likelihood of ISAV spillback, the absence of effective surveillance of wild populations elevates the

Table 4. Estimates of likelihood and uncertainty surrounding the effects of mitigation on risk pathways associated with the introduction, dissemination and consequences of (A) infectious salmon anaemia virus, (B) salmon alphavirus and (C) the salmon louse *Lepeophtheirus salmonis* in mariculture. See Table 1 for mitigation measures

Pathway of effect	Description	With mitigation		Without mitigation	
		Likelihood	Uncertainty	Likelihood	Uncertainty
<b>(A) Infectious salmon anaemia virus</b>					
Introduction	Infection on farm derived from neighbouring farm	Unlikely	Low	Likely	Low
	Infection on farm derived from wild reservoir	Unlikely	High	Unlikely	High
Dissemination from farm	Water (including mucous, faeces)	Unlikely	Low	Likely	Low
	Fish-to-fish contact (including escaped fish)	Unlikely	Medium	Moderate	Medium
	Biological vectors (parasites, birds, etc.)	Unlikely	Medium	Moderate	Medium
	Equipment and personnel	Unlikely	Low	Likely	Low
Consequences	Spillback infection in wild host	Unlikely	High	Likely	High
	Disease in wild population	Unlikely	High	Unlikely	High
<b>(B) Salmon alphavirus</b>					
Introduction	Infection on farm derived from neighbouring farm	Unlikely	Low	Likely	Low
	Infection on farm derived from wild reservoir	Unlikely	Medium	Unlikely	Medium
Dissemination from farm	Water (including mucous, faeces)	Unlikely	Low	Likely	Low
	Fish-to-fish contact (including escaped fish)	Unlikely	Medium	Moderate	Medium
	Biological vectors (parasites, birds, etc.)	Unlikely	Medium	Moderate	Medium
	Equipment and personnel	Unlikely	Low	Likely	Low
Consequences	Spillback infection in wild host	Unlikely	High	Likely	High
	Disease in wild population	Unlikely	High	Unlikely	High
<b>(C) <i>Lepeophtheirus salmonis</i></b>					
Introduction	Infection on farm derived from neighbouring farm	Moderate	Low	Likely	Low
	Infection on farm derived from wild reservoir	Moderate	High	Moderate	High
Dissemination from farm	Water	Moderate	Low	Likely	Low
	Fish-to-fish contact (including escaped fish)	Unlikely	Medium	Unlikely	Medium
	Biological vectors (parasites, birds, etc.)	Rare	Medium	Unlikely	Medium
	Equipment and personnel	Unlikely	Low	Unlikely	Low
Consequences	Spillback infection in wild host	Moderate	High	Likely	Low
	Disease in wild population	Unlikely	High	Unlikely	High

uncertainty. Mitigation measures for SAV are similar to those for ISAV, resulting in a similar pattern in the likelihood and uncertainties of transmission pathways. The occurrence, geographic distribution and genetics of SAV in wild reservoirs, however, lessen the uncertainty of transmission to mariculture (Table 4B). Mitigation of sea lice results in an altered pattern in the likelihood of transmission pathways compared with the viruses: with mitigation there remains an elevated likelihood of sea lice transmission from neighbouring farms since treatments can be less than 100% effective, even less so when parasites display resistance to the medication (Table 4C). Similarly, the likelihood of sea lice spillback remains moderate, despite treatment.

## DISCUSSION AND CONCLUSIONS

A consistent finding of epidemiological investigations into the transmission of ISAV, SAV and *Lepeophtheirus salmonis* associated with mariculture is the risk posed to neighbouring farms as a function of distance (Aldrin et al. 2011, Salama & Murray 2013). The extent of this risk is site or area specific, and dependent on the biomass or density of the affected stock, the shedding rate and half-life of the pathogen and on hydrographic characteristics, which influence patterns of pathogen dispersal and can vary considerably among coastal regions (Suttle & Chen 1992, Foreman et al. 2012, Garver et al. 2013a, Asplin et al. 2014). These data have been used to estimate zones of risk for sea lice and ISAV, implying that neighbouring farms or any wild fish within defined zones are at elevated risk of exposure to the pathogen (Jarp & Karlsen 1997, Mardones et al. 2011, Werkman et al. 2011, Serra-Llinares et al. 2014). The consequences of this exposure will be determined by the magnitude and duration of the infectious dose and by factors intrinsic to the at-risk population such as density, age, overall health and natural susceptibility. These factors are relatively well characterised for cultured stock, which are therefore valuable in validating predictions of exposure, infection and possible disease consequences that result from pathogen transmission from neighbouring sites. The likelihood and uncertainty of pathogen transmission pathways were compared with and without farm-based disease mitigation strategies. Infections with ISAV or infectious haematopoietic necrosis virus (IHNV, see Saksida 2006) among maricultured Atlantic salmon tend to be acute with elevated mortality. Outbreaks of these infections trigger management responses which in-

clude early pathogen detection through the use of sensitive and specific diagnostic methods followed by cage- or site-specific depopulation. In addition, elevated biosecurity standards, including control over the movement of fish and the movement and disinfection of staff (including clothing and personal equipment) and larger equipment such as transport vehicles, have become widely adopted by industry. As a result, outbreaks of clinical ISA are now rare or absent in Scotland and New Brunswick in eastern Canada and a recent outbreak of IHN in western Canada was of shorter duration with lower mortalities compared with earlier outbreaks (Murray et al. 2010, ICES 2013). It is worth noting a possible difference between the epidemiology of ISAV and SAV. For ISAV, the wild reservoir of the HPR0 strain remains a potentially important source for continued outbreaks, in addition to HPR0 strains that persist in farmed populations (Lyngstad et al. 2011). By contrast, wild reservoirs no longer seem to play a part in the epidemiology of SAV. Biosecurity will minimise the spread of infections, and maintaining a high health status (through good water quality, vaccination, etc.) will minimise the likelihood of future disease emergence. New diseases inevitably have their origin in wild populations, but emergence is generally observed in farmed populations (Fig. 1); thus, a high health status in farmed fish will reduce their susceptibility to putative pathogens in wild populations (and possible subsequent back spill).

In comparison to the viruses, sea lice infections do not elicit similarly robust mitigation measures. Rather, they are readily counted and treatment or other management actions are often linked to parasite abundance relative to a treatment trigger level. Sea lice treatment trigger levels are management thresholds which aim to reduce infection pressure on adjacent farmed or wild host populations (Saksida et al. 2011). Where they exist, infection thresholds are legislated or adopted under industry codes of good practice (Murray 2014), and values differ within and among countries (Ritchie & Boxaspen 2011). In British Columbia, the adoption of management thresholds led to a transient increase in the quantity of emamectin benzoate used (Saksida et al. 2011). Generally, the increased use of a single medicine increases the risk of resistance in the target population, ultimately lessening the effectiveness of the treatment. Theoretically, to be most effective, trigger thresholds should be adjusted to reflect host biomass in an area (Ritchie & Boxaspen 2011). More data are required to assess the effectiveness of treatment triggers with respect to sea lice spillback to wild salmon. The continued release of

sea lice larvae resulting from reduced treatment efficacy and from sub-threshold infections argues for the continued application of integrated pest management strategies (Brooks 2009). The reliability with which sea lice populations in a given region can be screened for sensitivity to treatment chemicals or medicines and alternative treatments applied as required lessens the uncertainty surrounding the effectiveness of these measures.

Whereas epidemiological data from mariculture may be useful in estimating risk of exposure, they are limited in their ability to estimate infection and disease in adjacent wild populations. Thus, while evidence supports the theoretical occurrence of ISAV, SAV and salmon lice within a zone of risk associated with an infected mariculture site, there is little evidence of ISAV or SAV infections in wild fish in support of this claim, which may be a consequence of limited surveillance. Further, there are no data that permit interpretation of the consequences of ISAV or SAV infections in wild fish. The extent to which salmon lice contribute to measurable population-level effects is beginning to be explored, but there is uncertainty and spatial variation in the apparent effects (Krkošek et al. 2013). In the treated-smolt studies reported above, the extent to which the apparent louse effect is related to mariculture requires further work.

We have argued that the wealth of epidemiological data derived from salmon mariculture relative to its scarcity from wild populations, provides a reasonable basis for estimating pathogen interactions both among farmed populations and between farmed and wild populations. However, the existence of these data does not always equate with their availability for third party analyses. The following requirements are considered useful and possibly necessary to assist in the characterisation and mitigation of pathogen transmission from farmed salmonids.

(1) Systematic collection of disease-relevant data from cultured populations, including pathogen identification, prevalence, severity and mortality;

(2) Systematic collection of data related to farm species and biomass, seawater temperature and salinity and plankton density;

(3) Archival of mariculture-derived data in an accessible format and establishment of data sharing protocols;

(4) Development and application of coupled hydrodynamic and particle-tracking models to characterise hydrographic processes in mariculture coastal zones to estimate pathogen dispersion from farms or farm clusters;

(5) Establishment of epidemiologically isolated management zones for farm clusters. Management zones should incorporate limits to local biomass, and protocols for coordinated activities such as stocking, disease pathogen monitoring, harvesting, single age-class and sea lice treatments;

(6) Pathogen surveillance of adjacent wild populations to document marine reservoirs of infection and validate mariculture management practices.

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