



REVIEW

Developing models for investigating the environmental transmission of disease-causing agents within open-cage salmon aquaculture

N. K. G. Salama^{*,**}, B. Rabe^{**}

Marine Scotland Science, Marine Laboratory, Torry, Aberdeen, AB11 9DB, UK

ABSTRACT: Global aquaculture production continues to increase across a variety of sectors, including Atlantic salmon production in Scotland. One limitation to the expansion of open-cage aquaculture is disease-induced stock losses as well as the potential for disease agents from farms interacting with other farms and possibly with wild salmonids. Epidemiological studies of disease-agent transmission often omit environmental transmission of organisms, although this process is an integral part of parasite spread and incidence. Within the aquatic environment, water movements enable pathogens and parasites to potentially be transmitted over long distances. As pathogens and parasites are transported, their status can change; they can degrade or, in the case of sea lice, develop into an infectious stage. A combination of biological and physical models is required to understand the transmission of disease-causing organisms. Here we propose a set of components that have been implemented in a range of modelling studies of sea lice dispersal, and describe how such attributes have been used in developing a study in one of Scotland's largest fjordic systems. By developing descriptive simulation model frameworks, which are validated using physical and biological observations, alternative methods of integrated pest management can be investigated and developed. The identification of dispersal routes of sea lice and establishment of potential farm–farm connections can inform sea lice management.

KEY WORDS: Disease transmission · Environment · Modelling · Multi-disciplinary · Dispersion · Sea lice

INTRODUCTION

Globally, aquaculture production has increased at a rate of 6.9% yr⁻¹ to current levels of 63.6×10^6 t, and further increase is forecasted (FAO 2012). Salmonid species account for over a tenth of the production by value (FAO 2008), and within Scotland, Atlantic salmon *Salmo salar* dominates the production with over 158 000 t produced in 2011 (Walker et al. 2012). Total salmon production in Scotland has experienced a 5-fold expansion since the early

1990s, whilst over the last decade, the number of licensed sites has decreased, indicating that the total output per site is increasing. Currently, over 80% of Scotland's Atlantic salmon production occurs on farms licensed to stock over 1000 t. This trend for larger farm size is likely to continue as new production methods are continually being developed, enabling farms in Scotland to meet requirements for consents granted by the Scottish Environmental Protection Agency (SEPA) to stock up to 2500 t. Production methods also exist in Norway which make it

*Email: nabeil.salama@scotland.gsi.gov.uk

**Both authors contributed equally to this manuscript

possible for farms to stock more fish (Fiskeridirektoratet 2011). Within Scotland, there is an aspiration for a sustainable 50% increase in finfish aquaculture between 2009 and 2020 (Baxter et al. 2011). A dominating factor in restricting the increase of stocking on individual farms is their environmental impact, largely governed by dispersal conditions of the surrounding environment and the degradation of chemicals and waste associated with fish farming (SEPA 2011). This could be resolved by relocating production into areas where environmental impact is reduced due to the characteristics of the location (e.g. locations with greater flushing rates). However, relocating could lead to variation in disease transmission properties of the locality, and altered production systems (such as larger, more isolated sites) potentially leading to increased pathogen-induced production losses and altered disease risk due to increased pathogen transmission distances (Murray et al. 2005, Salama & Murray 2011).

Infectious disease has an impact on farmed salmon welfare (Turnbull et al. 2011), which subsequently affects fish productivity due to increased mortality or reduced growth rates. For example, infectious salmon anaemia (ISA) can cause 90% mortality over several months (Rimstad et al. 2011). This loss due to mortality can have significant productivity impacts and therefore economic consequences (Murray & Peeler 2005). Globally it was estimated that disease management across all aquaculture sectors costs €2.25 billion yr⁻¹ (Subasinghe et al. 2001), with outbreaks of notifiable diseases having additional costs due to a range of factors including those associated with destocking, surveillance and interruption in production. An estimated loss to the Scottish salmon industry of over €23 million was incurred due to an ISA outbreak in 1998–99 (Hastings et al. 1999), whilst the costs of the recent 2008/09 ISA outbreak in the Shetland Islands (Murray et al. 2010) are still to be established. The 2007–09 outbreak of ISA in Chile resulted in the economy losing an estimated €1.5 billion (Mardones et al. 2011). (Note that for consistency, currencies are converted at rates of 0.75 for USD, and 1.15 for GBP to €1.00, as of February 2013.)

Pathogens and parasites are ubiquitous in the natural environment and can be transmitted to farmed fish from wild sources (Murray 2009). Once an incidence occurs on a farm, if untreated, disease can spread through the farmed population. It can magnify the size of the infective agent population and create a greater infection pressure, which may then be transmitted back into the open environment where it could infect wild hosts (Murray 2009).

Fish pathogens and parasites have been reported as having impacts both on farmed (e.g. Mardones et al. 2011) and potentially on wild salmonid species (Costello 2009a, Krkošek et al. 2011) when they are present within the environment. Aquaculture companies make efforts to treat against pathogenic disease agents, e.g. by providing vaccination against viral diseases (Secombes 2011) and treatments against sea lice (Rae 2002). A range of integrated pest management (IPM) strategies are used to manage disease in salmon aquaculture, including biological controls such as using wrasse as 'cleaner fish' for lice reduction (Treasurer 2002, 2012) and undertaking production in designated aquaculture production zones, such as farm management areas (FMAs) as is the case in Scotland (CoGP Management Group 2010), Bay management areas (BMAs) in Canada (Chang et al. 2007), neighbourhoods in Chile (Kristoffersen et al. 2013) and Single Bay Management in Ireland (Jackson 2011), whereby farms coordinate production methods such as stocking, fallowing and applying treatments, termed chemical fallowing, to minimise disease transmission.

Predicting and assessing the potential risks from these disease-causing agents is a substantial challenge that requires considerable understanding of the biology of the agent and the host of interest, and their interaction with the physical environment, including the processes involved with transporting agents from sources to potential host populations. The development of coupled biological–physical models makes investigating such interactions possible. These can be used to predict dispersal patterns leading to exposure of susceptible individuals to infectious particles, assisting understanding of the host–disease agent system of interest, and aiding the development of more appropriate management practices in the aquaculture production of farmed fish. In order to build a modelling tool to investigate agent dispersal, a multi-disciplinary approach is required to develop and validate the model. The outcomes of the model can be used to direct field sampling efforts efficiently and to test management scenarios. Here we outline a possible framework for the development, assessment and use of such models to investigate the transmission of disease-agent dispersal by the physical environment.

FRAMEWORK COMPONENTS

The schematic in Fig. 1 (with examples in Table 1) represents important components to develop methods for investigating the environmental transmission

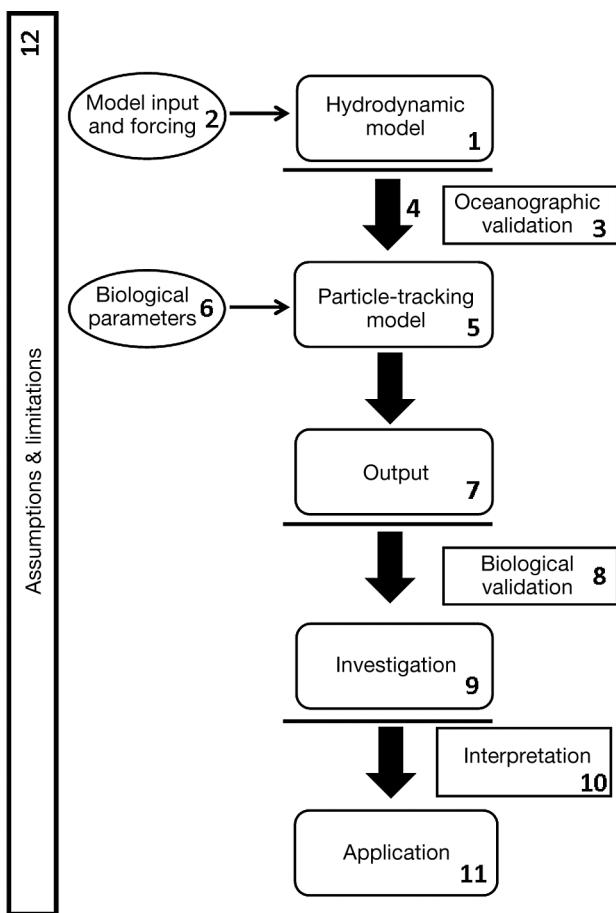


Fig. 1. Framework of components to develop methods for investigating the environmental transmission of disease-causing agents

of disease-causing agents. The hydrodynamic model (1) requires information relating to model forcing and input (2). Once a hydrodynamic model is created, it should be validated using oceanographic observations (3) to assess whether the model portrays the physical system. The hydrodynamic model is coupled (4) with a particle-tracking model (5), which accounts for the biological agent and as such requires biological parameterisation (6). Using this combined model will provide a range of computational outputs (7), which can highlight estimated locations or densities of biological particles within the model system. As with the simulated oceanographic estimates, the biological outputs also need validation (8). Should the model be fit-for-purpose, the system can be investigated (9) such as by measuring connectivity between sites within the system, and then interpreted (10) so that the simulated system is placed in context with the real world. Finally, the results of the simulation can be applied (11), e.g. by determining manage-

ment practices based on site relation. It must be noted that throughout and at each stage, assumptions and limitations (12) exist and sensitivity analyses need to be conducted. This paper reviews some of the methods which have been used in previous studies to develop environmental transmission models of disease agents of salmon produced by aquaculture. We demonstrate how we have adopted such principles in developing a biological and physical modelling approach with biological validation that can be used to assess the hydrodynamic movements of parasite particles and how such principles are being applied to study the dispersal of the ectoparasite *Lepeophtheirus salmonis* in a Scottish loch.

ROLE OF THE ENVIRONMENT IN DISEASE

Disease triangle

Disease is usually considered to be the result of the ecological interaction between at least 2 biological organisms (host and agent) and their abiotic environmental conditions (Fig. 2). However, the physical movement of agents in the environment plays an important role in infectious disease risk in aquaculture. Aspects of the host–disease agent interaction have long been investigated in fish cultivation through immunological, physiological and epidemiological studies. Much of the scientific work conducted within aquaculture infectious disease epidemiology concentrates on the relationship between host and pathogenic disease agents. Scales range from molecular (e.g. Schiøtz et al. 2008) to genetic (e.g. Vallejo et al. 2010), individual (e.g. Wagner et al. 2008) and population level, both empirically (e.g. Wallace et al. 2008) and theoretically (e.g. Werkman et al. 2011). However, anthropogenic factors (Murray et al. 2002) and aspects of the environment (Murray et al. 2010) are risk factors in transmission of pathogens such as *Infectious salmon anaemia virus* (ISAV) as well as other pathogens such as the disease agent of Pancreas Disease (PD; Viljugrein et al. 2009) and ectoparasitic sea lice (Amundrud & Murray 2009, Asplin et al. 2011, Stucchi et al. 2011).

The disease triangle (Fig. 2) (Stevens 1960) represents the interactions among host, disease agent (such as micro- or macroparasites) and the environment. The area covered by the intersection of all 3 represents the severity of the infection; thus, altering the intensity of any component alters the severity of disease expression. An interaction of a susceptible host with a pathogenic disease agent in favourable

Table 1. Summary of the components highlighted in Fig. 1 and how several studies have addressed such principles. Note that the assumptions and limitations are limited to 1 example, due to the vast array of implicit and explicitly described possibilities. T: temperature, S: salinity

| No. | Component | Region (modelling study) | | | | |
|-----|---------------------------|---|--|---|--|---|
| | | Scotland – Loch Linnhe (Salama et al. 2013) | Scotland – Loch Torridon & Shieldaig (Amundrud & Murray 2009) | Scotland – Loch Fyne (Adams et al. 2012) | Norway – Hardangerfjord (Asplin et al. 2011) | Canada – Broughton Archipelago (Stucchi et al. 2011) |
| 1 | Hydrodynamic model | Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS) | Georgia-Fuca system (GF8) model | Finite Volume Coastal Ocean Model (FVCOM) | Bergen Ocean Model (BOM) | Finite Volume Coastal Ocean Model (FVCOM) |
| 2 | Model input and forcing | Seasonal variation of T and S at open boundary; seasonal variation of freshwater input (adjoining lochs); tidal diamonds at open boundary; seasonal variation of atmospheric parameters; measured winds; bathymetry | Tidal elevations from POLCOMS; measured winds; freshwater input (river); densities from offshore conductivity, temperature and depth (CTD) samples; bathymetry | T and S nudging at open boundary; freshwater input (rivers); tidal forcing at open boundary; measured winds; bathymetry | Coastal Princeton Ocean Model/ Norwegian ecological model system; river runoffs; atmospheric model forcing; bathymetry | Tidal forcing from tide gauge records; North Pacific model at open boundaries; freshwater input (rivers); measured winds; initial 3-dimensional T and S fields; bathymetry |
| 3 | Oceanographic validation | Current, T, S, elevation data | UK hydrographic tide charts and current data | Current and S data | Current data | Current data |
| 4 | Model output | Surface velocities | Surface velocities | Upper layer velocities | Upper layer velocities | Surface velocities |
| 5 | Particle-tracking model | Amundrud & Murray (2009) | Simplified from Murray & Gillibrand (2006) | Amundrud & Murray (2009) | Ålandsvik & Sundby (1994) | Particle-tracking function in FVCOM |
| 6 | Biological parameters | Larvae maturation ($10\% h^{-1}$), Stien et al. (2005); larvae mortality ($1\% h^{-1}$), Stien et al. (2005) | Larvae maturation ($10\% h^{-1}$), Stien et al. (2005); larvae mortality ($1\% h^{-1}$), Stien et al. (2005) | Larvae maturation (more rapid development than Amundrud & Murray 2009); larvae mortality ($e^{-0.01t}$, no hosts die after 14 d), Adams et al. (2012) | Larvae maturation ($10\% h^{-1}$), Stien et al. (2005); avoid $S < 20$ (Heuch et al. 1995); limited to 10 m depth (Davidson et al. 2008); diel migration (Heuch et al. 1995) | Lice development coefficients, derived from Stien et al. (2005); lice mortality coefficient is salinity dependent (Johnson & Albright 1991b); vertical migration ($\pm 5.5\text{ m }h^{-1}$), Gillibrand & Willis (2007); limited to 10 m depth |
| 7 | Output | Particle location, age, trajectories; relative particle residency in each grid over simulation | Particle location, age, trajectories; relative particle residency in each grid over simulation | Source, destination and dispersal time of each successful particle | Particle locations | Copepodid concentration in the surface layer |
| 8 | Biological validation | Sentinel cages; plankton tows; lice counts from farms | Sentinel cages | Plankton tows; lice counts from farms | Sentinel cages | Plankton tows; wild fish survey |
| 9 | Investigation | Connectivity maps, connectivity probability | Role of variable winds in dispersal, role of mortality | Connection probability, graph/network analysis | None | None |
| 10 | Interpretation | Limitations, usefulness | Winds influence dispersal; mortality does not alter relative density | Caveats and limitations, future plans | Distance lice can travel from release | Spatial associations observed |
| 11 | Application | Model use in a larger system, policy advice | Principles used in further development for larger systems | Assisting in making management decisions relating to sites in Loch Fyne | Determining role of variable conditions in dispersing lice | Investigate credible sea lice interactions between wild and farmed salmon |
| 12 | Assumptions & limitations | Short model runs | Small study region | No diel movement | No plankton tows | No sentinel cage data |

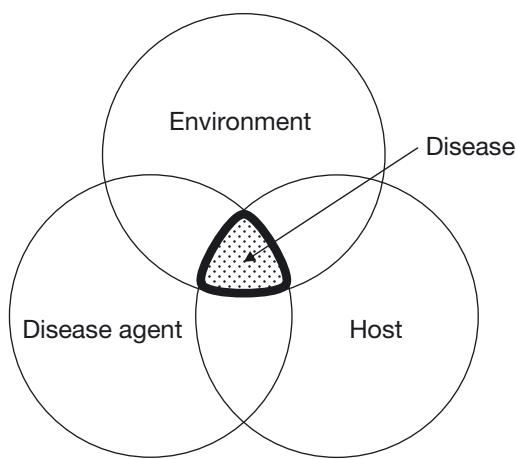


Fig. 2. Simple disease triangle demonstrating the relationships among host, disease agent and environment in causing disease (Stevens 1960)

environmental conditions is required for an expression of disease within a host. Therefore, by removing or minimising at least 1 of the segments of the triangle, disease is prevented. Whilst more widely used in phytopathology since its inception in the 1960s (Stevens 1960), the disease triangle has been applied to aquaculture (Snieszko 1973). This concept was amended to the disease pyramid or tetrahedron concept (e.g. Zadoks & Schein 1979) combining an axis for time and the anthropogenic interactions that lead to pathogenic disease progression (Scholthof 2007); both factors often simply alter the condition or state of the agent, host or environment. This framework is often seen as inappropriate in veterinary or human medicine, as the individual has the mobility to avoid inhospitable conditions and also due to the endothermic nature of humans and livestock with highly developed immune systems. This allows for mammals to mitigate environmental conditions to prevent disease transmission (Moore et al. 2011). Therefore, the environmental component is less important to disease progression. However, fish produced under aquaculture are held in pens, which restrict the individuals' ability to avoid exposure to pathogens and parasites but allow free flow of pathogens between them (Frazer 2009). Additionally, fish immune systems are less sophisticated than those of mammals (Tort et al. 2003) and therefore altering the host status aspect of the concept framework is less of an option in disease prevention in fish. Thus environmental conditions coupled with reduced immunological prevention play an important role in pathogenic disease progression in aquaculture fish production (Magnadottir 2010).

Environment

'Environment' is a broad term usually used to describe the physical and biological factors that, by working on host and pathogen, may influence disease incidence and severity, such as temperature (e.g. Becker & Speare 2004, Jokinen et al. 2011), salinity (e.g. Powell et al. 2001, Bricknell et al. 2006), water chemistry (e.g. Green et al. 2005), plankton blooms and nutrient availability (e.g. Leonardi et al. 2003). The environmental conditions can alter the predisposition of hosts to disease. A range of environmental impacts on the immune systems of commercial farmed fish is found in the literature (e.g. Bowden 2008, Magnadottir 2010) and as such would lead to altered disease status. Water temperature has been demonstrated to alter the leukocyte numbers in salmon smolts which will in turn alter the hosts' susceptibility to pathogenic diseases (Pettersen et al. 2005). Salmonids change growth hormone levels in response to varying salinity, temperature, pollutants and other stresses related to aquaculture (McGeer et al. 1991, Deane & Woo 2009). Changes in salinity can lead to susceptibility of salmon to amoebic gill disease due to changes in gill cell ionoregulation (Roberts & Powell 2003). Chemicals such as ammonia can increase susceptibility to disease in Chinook salmon *Oncorhynchus tshawytscha* (Ackerman et al. 2006), as can varying pH for infection in Coho salmon *O. kisutch* (McGeer et al. 1991). Atlantic salmon *Salmo salar* fry exposed to *Infectious pancreatic necrosis virus* (IPNV) suffer higher mortality levels as temperature increases between 12.5 and 15°C (Damsgård et al. 1998). In addition, other characteristics of an individual's environment that can lead to disease symptoms include stocking density, chemical environment, feed levels, genetic fitness/conditioning, disease condition and infection history (Snieszko 2006).

However, in aquatic ecosystems, the environment also transports, disperses and inactivates pathogenic agents which may initiate a disease. The environment is critical in the occurrence and persistence of infectious disease and may result in disease outbreaks far from the initial source. For example, marine pathogens have been reported as being transported up to 11 000 km yr⁻¹ (McCallum et al. 2003), causing far-reaching disease outbreaks. Scheibling & Hennigar (1997) and Scheibling et al. (2010) linked the transport of amoebic pathogens of sea urchins to large-scale oceanographic and meteorological processes. While this may be exceptional, transmission of pathogens over kilometres with water movement appears fairly common; for example, IPNV has been

isolated 19.3 km from its source at an infected hatchery (McAllister & Bebak 1997), and outbreaks of diseases such as PD and ISA are related to water currents (Aldrin et al. 2010).

The fluidity of the aquatic environment may result in greater connectivity between fish farm sites over large distance, much greater than those in terrestrial animal production systems. However, it must be noted that occasionally some airborne pathogens can be transmitted over large distances as was the case for *Foot-and-mouth disease virus* (Schley et al. 2009) and vector borne pathogens such as *Bluetongue virus* (Szmaragd et al. 2009). Within both terrestrial systems and aquaculture, infection occurs through the introduction of an infected individual and localised transmission. Transport pathways through hydrodynamic movements are able to transmit pathogenic agents between fish farms (Frazer 2009, Amundrud & Murray 2009) and also from wild fish to farms and vice versa (Johansen et al. 2011, Kurath & Winton 2011) over far-reaching distances. Hydrodynamic disease transmission between farms has been demonstrated as a risk factor for ISA (e.g. McClure et al. 2005, Gustafson et al. 2007, Aldrin et al. 2010, 2011) and PD (e.g. Kristoffersen et al. 2009, Viljugeein et al. 2009, Aldrin et al. 2010). Proximity is reported as being a risk factor for ISA transmission in Norway (Lyngstad et al. 2008), whilst the 2007–09 ISA outbreak in Chile demonstrated spatial clustering of infectious farms surrounding an initial outbreak farm (Mardones et al. 2009). Hydrodynamic transmission was shown to be important for sea lice transmission (e.g. Amundrud & Murray 2009, Salama et al. 2013).

The ability of disease agents within the environment to remain viable and cause disease changes depending on the environmental conditions. For example, sea lice *Lepeophtheirus salmonis* mature from nauplii to infective copepodids dependent on water temperature (Stien et al. 2005) and remain infective dependent on salinity (Bricknell et al. 2006), with lice exposed to salinities <30 having survivability described as being 'severely compromised'. Salinity has also been demonstrated as an environmental determination of viability for pathogens such as certain strains of *Viral haemorrhagic septicaemia virus* (VHSV), which survives longer in freshwater than seawater (Hawley & Garver 2008), as does a similar aquatic rhabdovirus *Infectious hematopoietic necrosis virus* (IHNV), which also degrades at a higher rate at higher temperatures (Barja et al. 1983). Salinity plays a role in pathogen viability such as IPNV degrading in conditions of

salinities >30 (Toranzo & Metricic 1982). *Aeromonas salmonicida* has higher degradation at high salinity (Rose et al. 1990), and *Salmonid alpha virus* (SAV) has been recorded to cause PD in salmon only at salinities between 16 and 34 (McLoughlin et al. 2003). Temperature also dictates the time for which VHSV remains infective, with temperature increased from 4 to 20°C leading to a decrease in viability (Hawley & Garver 2008). Graham et al. (2007) reported that the optimal temperature for SAV is within the range of 10 to 15°C, whilst it becomes inactive below 4°C and above 20°C. Additional aspects of the physical environment such as ultraviolet exposure lead to inactivation of pathogens such as ISAV, VHSV and IPNV, which at (mean ± SD) 33 ± 3.5, 7.9 ± 1.5 and 1188 ± 57 J m⁻², respectively, become no longer infective (Øye & Rimstad 2001). Exposure is sensitive to sunlight and to the mixing regime in surface waters (Suttle & Chen 1992, Murray & Jackson 1993). Exposure to ozone has been recorded to inactivate IPNV at 1944 (mg s) l⁻¹ and ISAV at 1.4 (mg s) l⁻¹ (Liltved et al. 2006). The pH of the aquatic environment also determines the viability of disease agents, for example as pH increases from 6.8 to 8, the degradation of IPNV becomes greater (Toranzo & Metricic 1982). The level of viability changes when the environmental factors are compounded, such as salinity and temperature in the case of IHNV (Barja et al. 1983) and *A. salmonicida* (McCarthy 1977).

Biological hazards also exist for pathogens in the aquatic environment. For example, bacteriophages play a role in altering the presence of microorganisms (Murray & Eldridge 1994), with bacteriophage numbers found to increase in water where *Aeromonas salmonicida* was present (Mackie et al. 1935). Viruses are sensitive to virucidal bacteria, grazing protozoa and filter feeding animals in the plankton (e.g. salps, Sutherland et al. 2010) or benthos (e.g. mussels, Faust et al. 2009). Such filter feeders can also consume bacteria and larval parasites such as sea lice (Molloy et al. 2011).

The elements of time and anthropogenic intervention are widely acknowledged in aquaculture by the use of fallowing strategies, treatment and harvesting times as described in the Code of Good Practice (CoGP) for Scottish finfish aquaculture (CoGP Management Group 2010). Anthropogenic intervention in disease transmission includes aspects such as therapeutic treatment, management intervention, stocking policy, harvesting and culling, pathogen and disease detection and control. Long-distance anthropogenic involvement in transmission of disease-causing

pathogens can occur, with shipping movements responsible for transport of viruses (Lawrence 2008), and well boats spreading ISAV more locally (Murray et al. 2010) as well as management practices influencing the transmission of IHNV in Pacific Canada (Saksida 2006). Trade movements are also a substantial contributor to disease transmission processes (e.g. Green et al. 2009). Although anthropogenic introduction of disease agents can have a substantial role in disease incidence, here we only concentrate on methods of investigating the introduction of disease agents through transport within the physical environment.

Localised dispersal through the environment has previously been recognised as a transmission route of ISAV and has led to the development of disease management areas (DMAs) partly based on simplified tidal excursion (TE) distances (Scottish Executive 2000), which categorise groups of farms in relation to their separation to another farm cluster where their TE distances do not overlap. During a recent ISA outbreak in the Shetland Islands (Murray et al. 2010), the application of DMAs was useful in controlling ISA transmission and prevented disease spread out with the initial outbreak area and subsequent eradication (Allan 2012). Simplified hydrodynamic model frameworks have demonstrated that the TE-based DMAs remain valid for rapidly degrading pathogens such as ISAV, although more conserved pathogens such as IPNV and *Aeromonas salmonicida* (Salama & Murray 2011), as well as sea lice (Murray et al. 2005), have the potential to be transmitted over much farther distances especially with increased tidal current speeds and where farms are increased in size (Salama & Murray 2013). Additionally, for control of non-colloidal or passively dispersed disease-causing agents such as salmon lice, FMA boundaries relate in part to the simple TE concept; however, basic hydrodynamic principles may not be appropriate because of the complexity of the characteristics of sea lice dispersal and infection.

An additional complexity when studying the role of the environment in disease transmission is its constant changes. These changes occur in the short term through weather events (Marcos-López et al. 2010); such as sunny periods altering predisposition to gill disease (Mitchell & Rodger 2011), seasonal and long-term climatic changes which are perceived to increase the risk of parasitic (Karvonen et al. 2010) and pathogenic (Peeler & Taylor 2011) infections in aquaculture. Therefore, long-term studies capturing environmental change and alterations in pathogen status are required.

These examples of the impact of the environmental conditions on the success of disease agents demonstrate that the role of the environment needs to be considered in developing transmission models, and highlights that it would be inappropriate to directly substitute a model developed for one specific agent directly for another. However, modifications of models can be undertaken as demonstrated by the development of a circulation model in Pacific Canada (Foreman et al. 2009) which has formed the basis for a study of IHNV dispersal (Foreman et al. 2012) and also sea lice (Stucchi et al. 2011).

MODELLING ENVIRONMENTAL TRANSMISSION OF DISEASE AGENTS

Overall principles

Models are a useful way to supplement information relating to systems where empirical observations and practical experimentation is unsuitable due to factors such as cost, ethical and methodological restrictions. Therefore, obtaining such data would be preferable but not always achievable. Models run diverse scenarios within a system and act as tools to reproduce interlinked processes under different conditions. They help us understand problems and questions relating to the system of interest. A model can represent a conceptual setting, verbal description, simplified physical representation or a description in quantitative mathematical relations (Jopp et al. 2011). Chassagnet & Verron (2006, p. 19) state that 'models provide an experimental apparatus for the scientific rationalization of (ocean) phenomena'. Jørgensen & Bendoricchio (2001) wrote that a model can offer a deeper understanding of the system than a statistical analysis. Therefore models yield a much better management plan for how to solve the focal environmental problem. They further stated that models are built on all available tools simultaneously, which include statistical analyses of data, physical-chemical-ecological knowledge, the laws of nature and common sense, among others.

Model development relies on a multi-disciplinary approach depending on the overarching questions. Sammarco & Heron (1994) stated that the multiple-team approach comprises the most effective means by which to solve a highly complex, multi-faceted scientific problem, such as dispersal in the marine environment. Large-scale modelling efforts require specialised scientists from different fields to work together to complement their statistical, geographi-

cal or computer science expertise (Jopp et al. 2011). Multi-disciplinary projects bring together different expertise to best evaluate and interpret questions and results.

Gallego et al. (2007, p. 125) wrote that 'models should be as simple as possible but as complex as necessary'. Murray (2008, after Jørgensen 1988) described a simple relationship: more complex models allow more detailed inference. However, this comes at a cost of additional parameters and increased uncertainty. Available data might motivate the choices and complexities. The challenge is to select the most appropriate model for your task, which will depend on forcing, boundary conditions or validation data. Gallego (2011) suggested that bio-physical models, for example, can be used to complement experimental and observational studies in the marine field since they do not suffer from some of the problems of observational methods like poor spatial or temporal coverage or instrumentation failure.

It is important to acknowledge that models can only represent reality up to a certain degree; they are simplified versions of the real world, include assumptions and limitations and require sensitivity analyses. Scenarios need to be validated for reliable results. The type of validation data, to ensure that the model generates robust results, depends on the model and will be described below. Also, an additional consideration is that the more detailed the model, the more computing power is required.

Murray (2008, 2009) provided summaries of various modelling approaches such as: susceptible infectious removed (SIR) type models, statistical models of surveillance, hydrodynamic models and network analysis. These can be used in addressing the transmission of pathogens in the aquatic environment.

Types of models

Types of models include, for example, conceptual or physical, stochastic or deterministic, and scientific or management models. Models can answer scientific questions, and their results can then be used as decision-support tools. In the case of disease transmission in the aquatic environment, we can apply epidemiological models (SIR models), structured population models, simple/specialised models (e.g. TE) or more complex models (e.g. coupled biological–physical models dispersing pathogens within a system under more realistic forcing conditions). Starting with disease dynamics, the model choice needs to consider how and if the model deals with

environmental transmission and whether classical SIR models are appropriate. Specialised models fill a niche while hydrodynamic models need to be introduced for physical–biological connections for more complex scenarios and studies. Outcomes can be interpreted and evaluated with results passed on to decision makers.

Epidemiological models

Models within epidemiological studies are used to inform prevention mitigation and control methods to restrict pathogen transmission between populations. This allows for key components to be identified and incorporated, and variables explored. The term modelling within an epidemiological context can describe the process of statistical modelling (using observed or experimentally derived data and simulation) or process modelling (informed through available data). Simulation modelling emphasis within traditional epidemiology has relied on direct contact or transmission (β) between infectious (I) and susceptible (S) individuals (Anderson & May 1979), which is often density dependent. The βSI infectious process does not necessarily account for the influence of the environment. Obviously the term β can encapsulate elements of the environment. The complexity of the role of the environment in disease transmission is highlighted by Ögüt (2001) who demonstrated that epidemiological model outcomes vary determined by changing the interactions of disease parameter values. Werkman et al. (2011) applied a stochastic SIS (Susceptible – Infectious – Susceptible) model to investigate spread of disease between farms, emphasizing the effects of local and long-distance contacts and different fallowing strategies. Murray (2009) analysed simple SIR epidemic models going beyond density-dependent transmission and concluded that appropriate models need to be selected depending, among other factors, on the disease. The general assumption of using such Kermack-McKendrick-based models (Kermack & McKendrick 1927) is that the agent is spontaneously transmitted from an infected individual to a susceptible individual through a probabilistic function.

In cases where infected and susceptible individuals do not come into direct contact, the transmissibility component between individuals by the environment can be undertaken using expansions of the Kermack-McKendrick-type models and allowing for an environmental component which becomes 'infected' and then 'infects' susceptible individuals. For example,

this has been applied to investigate the role of aquatic environments in human waterborne diseases. This approach has been considered as a secondary source of infection (e.g. Eisenberg et al. 2002, Tien & Earn 2010) in which the pathogen sheds from the population, accumulates in the water and decays with time. Further amendments to this model can be implemented whereby the environmental compartment undergoes movement using simplified hydrodynamic approximations (e.g. Murray et al. 2005, Salama & Murray 2011, 2013), to enable the establishment of general principles of the role of hydrodynamics and pathogen transmission and infection. However, to develop specific dispersal characteristics, the derivation of β can become complex and requires additional modelling. For example, establishing that the transmission of *Foot-and-mouth disease virus* was transmitted aerially in terrestrial animal production (Schley et al. 2009) required combining meteorology and epidemiology, whilst for specific dispersal in aquatic environments, detailed oceanographic particle dispersal models are required to, for instance, assess the dispersal of parasitic sea lice in a small sea loch, fjords and archipelagos (Amundrud & Murray 2009, Asplin et al. 2011, Murray et al. 2011, Stucchi et al. 2011). Using such methods highlights the potential long-distance dispersal of infectious agents, without the presence of an infected class of individuals in close proximity to a susceptible population, and allows for identification of where risk of transmission may occur, should a susceptible class be present.

Host-parasite modelling

SIR-type models applied for pathogens (viral, fungal, bacterial and oomycete agents) describe the status of the host in relation to the disease-causing agent (Anderson & May 1979); however, this modelling structure may be inappropriate for more complex macroparasite life cycles such as those of helminths (e.g. *Gyrodactylus salaris*) and arthropods (e.g. *Lepeophtheirus salmonis*). For such systems, the number of parasites determines the deleterious effects on the host and the level of transmission from the host. Additionally, it is likely that there is uneven distribution amongst the host population harbouring parasites, resulting in variable transmissibility from hosts within the population. Krkošek (2010) described that the key difference between the structure of models required for pathogens and parasites is that the models are required to account for the variation in

life cycle such that parasites tend to have a free-living phase. During this free-living phase, the organism (as discussed in the previous subsection) can undergo maturation and mortality and can be transported through the aquatic environment. These components of the life history require consideration in model development. The general structure of such models follows the principles described by May & Anderson (1979), whereby the model represents the population dynamics of the parasite (or stages of the parasite life cycle or components of the population important to transmission of the agent such as female stages), and includes the host population dynamics.

Such methods of coupled delayed-differential or differential equations models have been used in studying sea lice parasitism for approximately a decade with a simple lice population model developed by Tucker et al. (2002) parameterised using data obtained from experiments, as were stage-structured models accounting for pre-infective, infective, chalimus, pre-adult and adult stages (Stien et al. 2005). Models have also been developed to address questions relating to lice on farmed and wild fish, for example the transmission of lice from external sources (Krkošek et al. 2010) resulting in an assessment of the motile numbers of lice per farmed fish. Frazer et al. (2012) described a model representing the population dynamics of free living and all settled stages to establish potential host density thresholds influencing outbreaks. Revie et al. (2005) developed a stage-structured model for lice on farmed salmon accounting for mortality and time in stage as well as recruitment from external sources acting as an initiating condition and within farm population development. The model assesses the population progression of 4 classes within the population (chalimus, pre-adult, adult and gravid females) and takes account of treatment efficacies. This model was developed for an assessment of the Scottish industry and has since been applied to farms in Norway (Gettinby et al. 2011).

To account for an aspect of environmental transmission of lice through the environment, an alternate stage-structured model involving development through the copepodid, chalimus and motile stages was developed and takes into account spatial components of modelled transmission from farms to wild salmon (Krkošek et al. 2005) which was developed further by including host mortality and addresses the over-dispersion of lice loads on hosts (Frazer 2008).

May & Anderson (1979)-type models are not the only methods for estimating sea lice population dynamics on farmed fish; for example, there are empir-

ical models, such as those developed by Rogers et al. (2013), which determine the number of motile lice as a function of lice reproduction, environmental factors (temperature and salinity), management interventions and host surface area. Groner et al. (2013) recently developed a computational, agent-based approach to understanding sea lice parasitism and how this can be mitigated using cleaner fish.

Specialised, simple models

Aquaculture farms in Scotland, Norway, Chile, Canada and Ireland are mostly located in sea lochs, fjords or archipelagos which show estuarine circulation patterns due to their fjord-like features. Specialised, coarse, simplified models are usually run on smaller spatial and shorter temporal scales. Some models may be based on 30 d current measurements, to resolve the main tidal constituents, or do not include atmospheric forcing. Some simplistic dispersal models are only based on diffusion and tidal diamonds (symbols for direction and speed of tidal streams from British Admiralty charts) and give a general idea of particle dispersal without taking into account the larger area, dynamics and conditions (currents, wind) at the specific time and site. TE (Scottish Executive 2000) or simplified box models are examples (Gillibrand & Turrell 1997).

Previously, models on smaller scales for specific Scottish sea lochs have reproduced accurate patterns of hydrodynamics (e.g. Gillibrand 2002, Gillibrand & Amundrud 2007, Amundrud & Murray 2009). However, added detail may be required to reflect additional biological complications such as vertical movement in the water column, and a full 3-dimensional (3D) model may be necessary such as the case of sea scallop dispersal (Gilbert et al. 2010). Other animals, such as sea lice that we describe later on, remain predominantly in the surface layers (Hevroy et al. 2003).

Environmental assessment planning uses simplistic models within aquaculture. For example, maximum consented biomass in Scotland is determined using SEPA models (e.g. DEPOMOD, CODMOD, AutoDE-POMOD) that assess the benthic impact on the environment and the spread around farms (Cromey et al. 2009, Weise et al. 2009). Mayor et al. (2010) and Mayor & Solan (2011) demonstrated that the use of hydrodynamic dispersal of treatments and chemicals from fish farms can be used to ascertain the impact on the benthic community and demonstrated a threshold in farm size whereby further stocking size leads to no further degradation of the biota. These

passive dispersal models derived for chemical dispersal could be used to predict dispersal patterns for colloidal pathogens; however, for parasites with more complex ecology and biology, detailed coupled biological–physical models are required.

Coupled biological–physical models

The development of biological–physical models follows the general sequence displayed in Fig. 1. Not every step is required for every application, but a hydrodynamic and particle-tracking model, both influenced by forcing/parameters, lead to some output while validation of both models is essential. For pathogen modelling, connectivity analysis, interpretation thereof and applications (such as informing policy) are important parts.

General requirements for hydrodynamic circulation models (Component 1, see Fig. 1) (depending on varying complexities) are forcing and inputs (e.g. bathymetry) (2) and oceanographic validation data (3). Forcing for the hydrodynamic model can include seasonal variations of meteorological variables from climatologies or high-resolution wind models, freshwater input, tides, or realistic winds during specific validation periods (see Table 1 for specific examples for different study areas). Tides at the open boundaries can be derived from measurements, tidal diamonds from sea charts or fed in from coastal ocean models. For more complicated circulation patterns, a spin-up of the model (the time taken for an ocean model to reach a state of statistical equilibrium under applied forcing) might be necessary before certain scenarios are run. Hydrodynamic models can predict, among other variables, sea surface height, currents and water property distributions (e.g. temperature and salinity). Some examples of popular existing circulation models that are used by different research groups and can be set up for the relevant study area include POLCOMS (<http://cobs.noc.ac.uk/modl/polcoms/>), FJORDENV (Stigebrandt 2001) or the Finite Volume Coastal Ocean Model (FVCOM: <http://fvcom.smast.umassd.edu/FVCOM/>), to name a few. Depending on the desired outcome, time scales range from short event time scales to multi-annual. The physical oceanography component needs to be described accurately to provide a valid basis for the particle-tracking model. Model output needs to be validated against oceanographic measurements (3). These include, for example, current velocity (from moorings or drifters), sea surface height or temperature and salinity from different

suitable sites within the model domain. Measurements should preferably be made during the same time period that is being modelled, although historical data can fill in gaps.

Hydrodynamic model output (4) or simplified currents are the basis for particle-tracking models (5). In addition, knowledge of the biology of the particles (6) (e.g. plankton, larvae or pathogens) is required. If the particles do not have any swimming behaviour, then passive neutrally-buoyant particles are used. More complex models include locomotory abilities resulting in horizontal or vertical swimming, sinking or other behaviour within the water column. The implications of active particles would lead to a different spatial spread. Biological parameters representing life cycle behaviour need to be incorporated if necessary (e.g. the incorporation of temperature or salinity dependency). These biological-physical models represent the interplay between physical processes such as turbulent motion or advective processes resulting from currents generated by winds, tides and biological processes (Gallego 2011). To determine how hydrodynamics affect the transmission of material, particles need to be followed as they are moved around. Dispersal of pathogens can be modelled by tracking particles with the help of different algorithms. These particle-tracking models are widely used, and the term 'particle' is interchangeable with e.g. pathogen, larva, plankton or molecule. Particle-tracking models can be customised (Amundrud & Murray 2009) or developed using open-source codes like FVCOM. They are a well-established tool to determine dispersal of chemical discharges (e.g. Navas et al. 2011) and biological larval dispersal (e.g. North et al. 2008) but are less often used to evaluate the dispersal of disease-causing agents; however, the principles are similar.

Depending on the scenario, particles are released from a point source at once or continuously. Release sites can represent sources at farm sites, wild sources or fictional new locations of outbreaks. Knowledge of particle input is essential to obtain a realistic output for comparisons between model predictions and data observations. Each particle can be considered as a packet of particles or as a super-individual. Boundary conditions within discrete models must be designated to reflect the reality of the system. For example, boundaries can be absorbing (whereby particles that hit the boundary are removed causing a decrease of particles in the system) or reflecting (particles bounce back in to the system), or boundaries can be sticky such that accumulation occurs when currents push particles towards the shore (Soetaert &

Herman 2009). For example, open sea-sea boundaries could be absorbing representing particles being advected out of the system and leaving the model domain, whilst land-sea boundaries could be sticky boundaries as is the case for accumulation of zooplankton (Archambault et al. 1998) including sea lice in Scottish lochs (Penston et al. 2004). This is due to the no-slip condition of viscous flow and no flow along the boundary, which is widely described in the fluid dynamic literature (for example Goldstein 1965, Kundu & Cohen 2002).

The output of particle-tracking models (7) will show particle distributions, possibly different life stages after the set run-time or at intermediate time steps. Trajectories of particle movements can be plotted as well as areas of higher density (and therefore higher risk if evaluating diseases). Biological validation data (8) are a requirement to test the outputs of the model. Plankton samples or use of sentinel fish in the case of sea lice modelling will test the model results with respect to sea lice occurrence (Amundrud & Murray 2009, Penston & Davies 2009, Pert 2011). Interactions (connectivity) (9) between different sites can be evaluated and then be interpreted (10). These results can be applied (11), for example with regard to the effectiveness of management areas, if in existence.

Limitations (12) of coupled biological-physical models can include any or all of the below amongst many more: simplified reality with regard to coastline, bathymetry, currents, biology or behaviour; a lack of data on disease prevalence; effects of treatments on disease prevalence; effects of the difficulty in quantifying husbandry practices at farms (e.g. bio-security practices); effects of rare or difficult to predict events such as storms; unknown factors; varying time scales; or limited validation data. Uncertain model assumptions and parameters need to be evaluated to ensure confidence; therefore, sensitivity analyses to result in robust predictions are a requirement. Considerable work on the need to combine biological and physical models and reduce limitations has been done but more work is still required.

By combining these physical and biological modelling principles, it is possible to provide a structure that enables an assessment of the transmission and dispersal of pathogenic agents through the aquatic environment. To summarize: the main purpose of models in studying disease transmission in aquaculture is to predict the spatial and temporal spread of disease in order to help the industry and regulators. The study of the potential dispersal of the ectoparasitic sea lice, which is a concern to the salmon aqua-

culture industry, exemplifies the use of this modelling approach. Developing a modelling framework of sea lice transmission and investigating scenarios may aid an understanding of transmission characteristics and assist in informing future sea lice management.

SHARED PRINCIPLES TO STUDY SEA LICE TRANSMISSION

Ectoparasites which are of concern to the sustainability of both wild and farmed salmonid industries (Rosenberg 2008) are the ubiquitous copepodids of the family Caligidae, predominantly of the genera *Caligus* and *Lepeophtheirus*, commonly called sea or salmon lice. Sea lice management costs the global salmonid aquaculture industry in the region of €305 million yr⁻¹, which is some 6% of the overall salmon global production value (Costello 2009b). In Scotland, the species of concern are dominated by the salmonid specialist *L. salmonis* (Krøyer) and the generalist fish parasite *C. elongatus* (von Nordmann). Sea lice graze upon salmonid hosts causing skin abrasions which can lead to osmotic irregularities (Boxaspen 2006); there is also the potential that lice act as a vector for pathogens to cause secondary infections (e.g. Jakob et al. 2011). The cost to output ratio of sea lice management in Scotland is reported to be the highest of the salmon-producing countries at 0.25 € kg⁻¹ (Costello 2009b). Around 98% by volume of Scottish farms work towards a voluntary CoGP guideline (CoGP Management Group 2010) in order to minimise the numbers of lice settled on farmed fish, demonstrating the significance the industry places on mitigating against sea lice infection. The use of chemical pesticides and in-feed therapeutics represents the predominant cost associated with sea lice control. These have been used since the industrialisation of aquaculture in Scotland (Rae 2002).

Because lice are demonstrating aspects of resistance to some of these chemical applications (Murray 2011), alternative means of control need to be developed, in addition to wider issues related to the influence of pesticide use on the surrounding biota (e.g. Mayor et al. 2010). Such methods include developing alternate structural zones of production by positioning of farms in discrete management areas which has been demonstrated to aid disease control (Werkman et al. 2011) and can be used as a successful IPM tool for lice management (Brooks 2009). These structures can be informed through dispersal modelling. However, modelling is not the only intervention being

developed. For example, biological controls such as the use of cleaner fish, commonly wrasse species (Treasurer 2012), and the potential for using lice pathogens have been investigated (Treasurer 2002) as well as using integrated multi-trophic aquaculture approaches such as using mussels to filter planktonic larval lice (Molloy et al. 2011, Bartsch et al. 2013). Selective breeding (Jones et al. 2002) and genetic manipulation (e.g. Gjerde et al. 2011) for traits which enable salmon to be less susceptible to sea lice are alternate ways of minimising the risk posed by lice to farmed salmon. Methods such as fallowing (Bron et al. 1993) and single year class production (Butler 2002) have been demonstrated to diminish sea lice risk. The importance of alternative IPM strategies is evident by their inclusion in the CoGP, e.g. by designating separated FMAs of a single year class, with fallowing between cycles. Novel methods for the integration into IPM continue to be developed, such as using chemical layers on the water surface (Boxaspen & Holm 2001) and stimulating the jumping behaviour of salmon to aid with exposing lice to such chemicals (Dempster et al. 2011). A thorough review of the study of sea lice is provided in a work edited by Jones & Beamish (2011), and ongoing research is presented through international sea lice conference series and subsequent proceedings (Roth & Smith 2011, Boxaspen & Torrisen 2013).

Sea lice have complex characteristics compared to microparasites such as their life cycle and ability to remain predominantly near the surface (Hevrøy et al. 2003). The reported life cycle of *Lepeophtheirus salmonis* consists of 10 stages and 5 phases (Johnson & Albright 1991a); the nauplius (2 stages) and copepodid (1 stage) are planktonic phases, whilst the chalimus (4 stages), pre-adult (2 stages) and adult (1 stage) phases are completed on a host. The nauplius stage is non-pathogenic, whilst the copepodid phase poses a risk of infection to salmonids. *Caligus* species such as *C. elongatus* have a similar life cycle but lack a pre-adult phase (Piasecki 1996). However, a recent study has indicated that a *Lepeophtheirus* species shares a similar life cycle to that of *Caligus* species, which may indicate that there are corresponding life cycles across the family (Venmathi Maran et al. 2013). In terms of transmission of lice, both species are of interest during their nauplius and copepodid stages; however, the phases that cause harm to fish occur after attachment. The development through the phases is highly dependent on water temperature. Sea louse larval development time increases with lowering temperature (Johnson & Albright 1991a,b). The life cycle at 10°C ranges between 40

and 50 d for *L. salmonis* (Johnson & Albright 1991b), of which the nauplius stage lasts 3.6 d, and 40 d for *C. elongatus* (Piasecki & MacKinnon 1995), of which 3.8 d are as non-infectious nauplii. The mortality rate associated with copepodid stage lice appears to be strongly associated with salinity. Stien et al. (2005) reported that above a salinity of 30, mortality occurs at a rate of approximately 0.01 h^{-1} . However, Bricknell et al. (2006) estimated that at similar salinity, mortality is 0.058 h^{-1} , this doubles to around 0.1 h^{-1} at a salinity of 26 and to around a salinity of 0.5 h^{-1} at 25 and below. Johnson & Albright (1991b) estimated a mortality rate of 0.029 h^{-1} at 10°C and a salinity of 30.

Dispersal during the planktonic phase dictates the locations of lice accumulation, which may pose a risk to salmonids. As the lice are mainly in the surface layer, dispersal is strongly dictated by wind forcings as well as by tidal conditions and surface circulation (Amundrud & Murray 2009). Therefore, under varying conditions, accumulation could potentially occur near the source of lice or at some distance.

Applying the principles to sea lice

Over the last decade there has been a growing amount of research, through the combination of epidemiological and oceanographic methods, assessing the role of the aquatic environment in transporting disease agents (see Stephenson 2005). Although hydrodynamic connectivity is demonstrated to be a risk factor in the spread of various pathogenic diseases, to aid direct comparisons across a range of studies, we standardise by describing methods associated with investigating the dispersal of sea lice. In this manuscript, we consider sea lice dispersal studies of Asplin et al. (2011), Amundrud & Murray (2009), and Stucchi et al. (2011), which are compiled in a recent book edited by Jones & Beamish (2011), in addition to a recent study by Adams et al. (2012). Note that this is not a complete list of the sea lice dispersal modelling studies; there are others, such as the work in Ireland (Jackson et al. 2012), which are omitted merely in order to constrain this review. We apply the characteristics of the framework presented in Fig. 1 to highlight that, although different approaches have been used, the studies share common components as part of the development process. We then demonstrate how we applied such principles in undertaking an ongoing research project to study sea lice dispersal (Salama et al. 2013). Note that descriptions of each paper are kept to a minimum for brevity in Table 1.

Study comparison

Each of the studies used a hydrodynamic model with (FVCOM) being used for Broughton Archipelago (BA; Stucchi et al. 2011) and Loch Fyne (LF; Adams et al. 2012), Bergen Ocean Model (BOM) in Hardandgerfjord (HF; Asplin et al. 2011) and the eighth format of the Georgia-Fuca system (GF8) model of Loch Torridon (LT; Amundrud & Murray 2009). All hydrodynamic models are 3D models, which provide vectors for movements of parasite representative particles; however, they vary considerably in the methods of calculating these vectors and their structure. For example, there is a difference in the fixed grid used by the GF8 and BOM models versus the variable triangular grids of the FVCOM models. The fixed grid models vary in size, with $100 \times 100 \text{ m}$ for GF8 and $800 \times 800 \text{ m}$ for BOM. The FVCOM models vary, with the LF model comprising 943 nodes, whereas BA uses over 46 000 nodes, demonstrating the degree in difference in domain size of the various models. The models are also run for varying times. LT ran for 14 d, HF 20 d, BA 31 d and LF 1 mo for each month of the year between March 2011 and February 2012.

The models require input (e.g. bathymetry) and forcings (e.g. atmospheric data). HF uses an atmospheric model determined by meteorological data, a lower-resolution North Sea coastal model at the open boundary and over 60 freshwater river inputs. The LT and LF models use simplified tidal elevations at the open boundary, they have fewer river inputs, and LT is forced using uniform directional winds, whereas LF has measured winds and temperature and salinity nudging at the boundary. BA uses a similar number of recorded river flows as LT and LF; however, it is also supplemented with estimates for the other rivers in the system. The open boundary uses an open ocean model, and wind forcings are derived from several meteorological stations in the system.

The outputs of each of the models include estimates of the abiotic environment such as temperature, salinity and currents. To assess the modelled predictions, oceanographic observations are undertaken using methods such as current profilers as occurred in BA and HF, or conductivity, temperature, depth (CTD) measurements as used in LF.

Each of these studies used vectors obtained from the hydrodynamic model and input particles into the system which are monitored by using a particle-tracking algorithm. The format of the particle-tracking component has slight variations such that the LT study used a method described by Murray & Gilli-

brand (2006), also applied at LF. The BA study used a particle-tracking package as part of FVCOM, whilst the HF model incorporates a model presented in Ådlandsvik & Sundby (1994). The approaches also vary in the detail of biological parameters associated with the particles; each of the studies applied maturation conditions derived from Stien et al. (2005), but considered mortality in a range of ways. LT simply uses a constant mortality rate, LF uses the same mortality rate as Amundrud & Murray (2009) but after 14 d, a free living particle dies. The HF work does not include a mortality term, whereas BA uses variable mortality dependent on salinity and egg development as well as maturation between age stages. Furthermore, in HF and BA, particles avoid low salinity. Vertical migration of particles is included as part of the BA and HF models, but is omitted by LT and LF.

Each of the models produces relative particle concentrations and locations in the surface layer over the course of the simulation, which allows the potential for biological validation of the predictions. In LT, counts of lice on sentinel caged fish and plankton trawls demonstrated an increasing gradient of lice counts as predicted by the model. Similar use of caged fish was developed in HF, but comparison methods are still ongoing. Plankton trawls were attempted in LF and BA but resulted in low occurrences of planktonic lice and therefore could not be used to validate the models. However, non-0 counts were observed in regions predicted to have lice; similarly, the BA study also involved wild fish trapping, which resulted in 0 lice counts being observed in regions where modelled concentration were predicted to be low and thus demonstrate some correspondence of agreement between observations and model predictions.

The development of sufficiently accurate models allows for investigations of dispersal and transmission to be undertaken. For example, in LF, an assessment of the hydrodynamic connectivity among farms indicated distinct networks of groups of farms and also how the grid resolution impacts on the hydrodynamic simulations. Variable wind directions were investigated in LT to assess their influence on dispersal patterns; continual release versus single event release was investigated using the HF system, whilst in BA the diel migration of copepodid lice was considered to assess what role this may have on dispersal patterns.

The process of developing methods to investigate sea lice dispersal requires interpretation of outputs in order to make the model applicable. The results from BA indicate that the model predicted spatial differ-

ences in lice levels which could be assessed by the counts of lice corresponding to the spatial difference, as was the observation with LT. The results of LT indicate that wind direction has a strong influence on lice dispersion. In LF, relationships between farms were obtained and the most important nodes in the network were highlighted. HF demonstrated the potential dispersal distances of lice released from farms. The application of the results from LT and HF indicates that accumulation does not necessarily occur at the release point, allowing some assessment of the role of long-distance interaction that lice may have with wild fish populations. Such a model will allow for the potential capacity for lice in a region or system to be established and modes of transmission identified among farms in a system to aid sea lice mitigation measures. The highlighting of specific farms in LF as being important connections in a network could be applied to allow targeted treatments and surveillance at these influential sites. The results of the BA study are expected to contribute to large-scale/area-wide management strategies.

Model limitations

At each of the stages, there are assumptions which lead to limitations. For example, the resolution and grid structure of models may limit the accuracy of the hydrodynamic vectors, along with the vertical resolution of the model. There is a limitation on the collection/availability of wind data to force models. Likewise, gaining all the information on freshwater input can be highly resource intensive or inaccurate. The use of wider ocean models or tidal conditions at open boundaries depends on the study area, and various degrees of accuracy in space and time occur. In assessing the model predictions, biological and oceanographic recordings can only be taken at a limited number of locations and times, which could make the conclusions of any model to data assessments spurious; therefore, site location and replication must be an important consideration of study design. The biological parameters take account of reported means, whereas in reality there will be substantial variation within the population. With highly complex systems, computational efficiency becomes an issue; therefore, time resolution, particles tracked, and run time and number of iterations have to be considered, and it must be decided whether trade-offs in these could influence the simulation results. Assumptions have to be made when interpreting limited simulation times and applying

them to general system characteristics for applying management strategies. As with any investigation, the researcher needs to consider whether efforts are focused on important areas and do not ignore an unknown which may have more influence on the model output. Interpreting the modelling results to the real world with stochastic events needs caveats, especially within an area as controversial as sea lice on salmon (Bocking 2012) where public opinion is polarised. Although research is still ongoing, it could be the case that these developments will provide information to support sustainable aquaculture industries, such as developing management strategies, developing production zones, determining treatment timing and order and identifying critical treatment thresholds.

CASE STUDY OF LOCH LINNHE

Study system

In developing a study of sea lice dispersal model for Loch Linnhe, Scotland, Salama et al. (2013) used procedures consistent with the principles outlined in Fig. 1, using both complementary and alternative processes to those of previous studies.

The basis for undertaking a study of Loch Linnhe was to assess whether it was possible to scale-up the methods of Amundrud & Murray (2009), developed for the smaller Loch Torridon and Shieldaig system, to one of Scotland's largest fjordic systems (Fig. 3). This allows an assessment of whether these principles of biological–physical modelling of sea lice can be applied to other, more complex systems. Loch Linnhe has 2 FMAs (CoGP Management Group 2010) containing 10 active salmon farms with side lochs containing additional salmonid farms. The system contains farms that are consented to stock almost a tenth of Scotland's Atlantic salmon production output.

In the past, research in Loch Linnhe included physical oceanography (e.g. Allen & Simpson 1998), and it was the site of an extensive study in the early 1990s which incorporated simulation modelling (e.g. Ross et al. 1993) and plankton ecology (e.g. Heath 1995). It acted as a site for assessments of environmental change through anthropogenic activities such as the construction of artificial reefs (e.g. Wilding 2006) and industrialisation (e.g. Pearson 1975, Pearson et al.

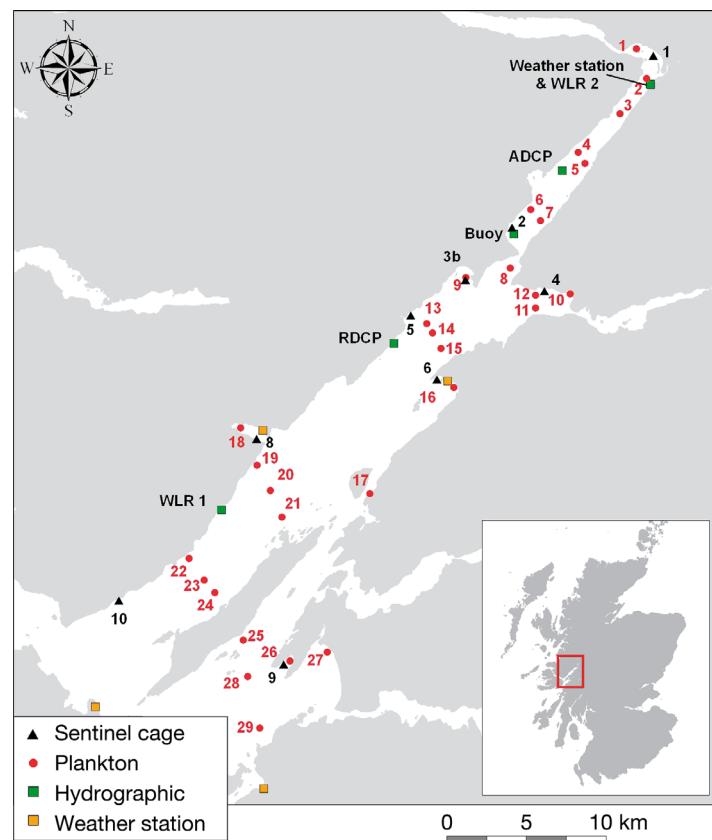


Fig. 3. Loch Linnhe on the west coast of Scotland, showing multi-disciplinary sampling stations for biological and physical model validations (WLR: water level recorder, ADCP: acoustic doppler current profiler, RDCP: recording doppler current profiler)

1982), whilst fish farms within Loch Linnhe have been used as trial sites for sea lice treatment investigations (Corner et al. 2008). A multi-disciplinary assessment of ectoparasitic sea lice is on-going in Loch Linnhe, and a brief description of the relevant model components applied in Loch Linnhe is provided below.

Model components

For the Loch Linnhe system, the Scottish Association for Marine Science ran and validated the hydrodynamic Proudman Oceanographic Laboratory Coastal-Ocean Model System (POLCOMS), differing from variable FVCOM applications and being similar in structure to BOM and GF8 (1), for different time periods (Ivanov et al. 2011). A 4 yr spin-up of this 3D hydrodynamic model established consistent density–velocity arrays. The model system with 365×488 nodes spans over 60 km from the Firth of Lorne and Sound of Mull in the SW to the opening of Loch Eil

near Corpach in the NE, catching the prevailing winds due to its SW–NE orientation. This 3D baroclinic model resolves 100 m in the horizontal and includes a variable vertical resolution with smaller steps in surface and bottom boundary layers (s-coordinates) to resolve the important surface layer where sea lice exist. Specific model scenarios for 1 test case and with a number of 2 wk validation periods have been run to date with time intervals ranging from 15 to 30 min.

Model forcing (2) during the model set-up included tides (tidal diamonds at the model boundary at the Firth of Lorne and Sound of Mull), seasonal variations of freshwater inputs from rivers and adjoining lochs (Lochs Etive, Creran, Leven, A'Choire and Eil), seasonal variations of temperature and salinity at the open boundary and seasonal variations of atmospheric parameters (e.g. wind speed and direction, pressure). Specific runs were forced using measured wind (speed and direction) from multiple weather stations around the loch (Fig. 3). These wind measurements were extrapolated onto a regular grid that then forced the hydrodynamic model for 2 wk validation periods. Since the complicated orography around Loch Linnhe channels air flows, wind measurements at different locations around the loch are essential for the most realistic wind forcing. Scenarios so far include four 2 wk periods in May and October 2011 and 2012, with further validation periods due to occur in 2013. Accurate bathymetry is required as part of the model input to represent e.g. the sills, near shore areas and islands. Good bathymetry data exist for Loch Linnhe, but the coarse model grid leads to some simplifications (see limitations below).

To develop dispersal models of sea lice, the surface layer velocities from the hydrodynamic model was combined post-simulation (4) to reduce computational overheads with a particle-tracking model (5), which not only followed the movements of lice particles, but had biological characteristics (6) of maturation, similar to all other mentioned models, and mortality, similar to all but the Norwegian study.

For the Loch Linnhe sea lice project, the particle-tracking model (5) follows an existing, tested model set-up (Murray & Amundrud 2007, Amundrud & Murray 2009) previously used in a smaller system in Loch Torridon. The outcomes from the POLCOMS runs (4), notably the surface currents, are used to move the particles that represent planktonic lice. Different model runs can be set up either using a point or continuous release from different source points. Surface current vectors, representing advection, are overlaid by diffusion. A fourth-order Runge-Kutta

solver for the Lagrangian equation of motion is used here including a random-walk stochastic element. Diffusion values are varied between 0.1 and 1 m² s⁻¹, a rate, which according to Turrell (1990), is representative of Scottish sea loch diffusion (for more details see Salama et al. 2013).

In addition, lice change due to maturation and mortality (6). In the Loch Linnhe dispersal model, nauplii mature to infectious copepodids at a default rate of 10 % h⁻¹. Maturation occurs at approximately 9.6 d at 5°C, 3.6 d at 10°C and 1.9 d at 15°C. Mortality depends on salinity, increasing rapidly as salinity drops to less than 29 (Bricknell et al. 2006). For Loch Linnhe, we use a default decay value of 1 % h⁻¹ (Johnson & Albright 1991a). For sea lice, the age status depends on development rates as a function of temperature. The model of Stien et al. (2005) is used here to describe the time for immature louse particles to become infectious mature particles. The Loch Linnhe model does not currently take realistic temperature and salinity into account due to computational overheads, but these could be implemented to provide more realism. The number of particles released at each site within the model domain and at the boundary was originally determined as a proportional function of farm-consented biomass; however, this has since been modified to account for lice input based on a voluntarily provided transformed weighting for farms. Limited data exist to determine the position of wild salmonids in the loch; therefore, randomly allocated release points are used to obtain distribution of lice from potential wild sources in addition to releases at freshwater boundaries where, due to salinity variation, lice on wild fish are likely to be dislodged. Model runs last for 2 wk, during which particles are released continuously. Ideally, longer releases and repeats of scenarios would be desirable and might be implemented in the future. A sticky wall is implemented at the interface between land and water which is consistent with passively dispersed material in sea lochs and an absorbing boundary at sea-sea interfaces. The age status of sea lice depends on development rates as a function of temperature, so we use the model of Stien et al. (2005) here to describe the time for immature louse particles to become infectious mature particles. Although there are suggestions that lice have the ability to undertake small-scale movements (Pike and Wadsworth 1999), the lice here are assumed to be passive and remain in the surface layer, as used with LT and LF, and do not undertake diel migration, as is the case in HF and BA.

The particle-tracking model produces particle distribution fields from different sources of lice as outputs (7). This helps to identify areas of varying risk for sea lice accumulation or potential interaction between lice and farmed/wild fish under different forcing conditions within Loch Linnhe.

The model produces particle tracks of each of the ~45 000 particles over the simulation and records their age. From this, we produce distribution maps (see an unvalidated example output in Fig. 4) presenting the relative particle-per-unit-time of each louse stage experienced at each grid cell over the entire simulation. As the input numbers into the system are relative, and not absolute, no prediction of numbers of lice can be made at each grid cell, merely the relative level compared to other grid cells.

To date it appears that there is a level of correspondence between model-simulated distributions (Salama et al. 2013) using farm-consented biomass as a proxy for input, and a similar correspondence assessment using weighted lice information provided by the farms (not presented). Using this model, we have investigated (9) the level of connectivity between farms in 2011, and this investigation for 2012 is ongoing to measure whether these connectivity patterns occur consistently. Should a regular network pattern arise, it could be possible to interpret (10) the relationships between groups of farms, and such information could be applied (11) to manage sea lice on farmed salmon in Loch Linnhe.

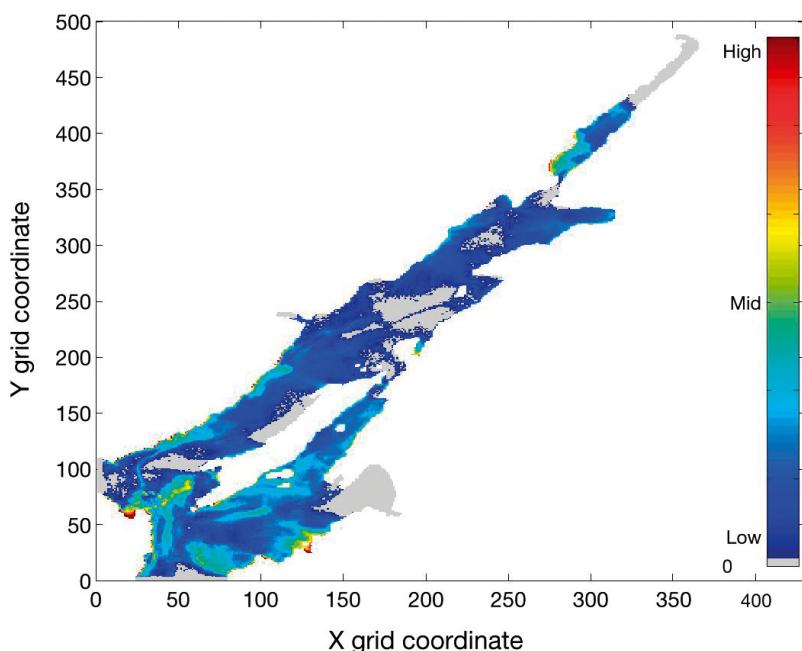


Fig. 4. Unvalidated results of Loch Linnhe particle dispersal showing high and low regions of particle density

Field validation

For the model to be informative, the simulation outputs need to be evaluated against field observations. A field work component to collect the relevant physical and biological data is included in this study (Fig. 3). To validate the hydrodynamic model output (3), measurements of currents, sea surface height, temperature and salinity were taken during the corresponding model validation periods by current profilers, CTDs, water level recorders and a multi-parameter data buoy. Drifters were deployed at a few sites to test the surface currents under realistic conditions. Within Loch Linnhe, the hydrodynamic model reproduces the hydrodynamic conditions well. Validation data are collected during the validation periods. Other studies (e.g. Adams et al. 2012) have used similar instrumentation and data from historical and recent measurements.

To assess the model and outputs of regions of the loch with higher and lower particle occurrence, accurate lice inputs are required. The particle distribution from a test scenario was used to identify areas potentially providing adequate variation in lice distributions. In those locations, plankton samples for passively dispersed lice (similar to BA, LT, LF) were collected, and sentinel caged salmon, using similar methods to HF, were deployed for sampling infective lice stages (8). Bongo nets were used to sample planktonic nauplii and copepodids in the surface

layer whilst sentinel cages were stocked with 50 smolts, and sea lice counts were taken after a 1 wk exposure. This procedure was repeated with a new batch of salmon for the second week (more details in Salama et al. 2013). These methods have proved useful in sampling plankton lice levels (e.g. Penston et al. 2011) and attached lice (Pert 2011) in Torridon and Shieldaig, and the latter is similar to sentinel cage fish work in Norway (Bjørn et al. 2011). A description of comparing observed sea lice data from tows and caged fish to simulated distributions is given by Salama et al. (2013).

As with all model studies, assumptions are made at each stage to minimise complexity whilst capturing important features; however, this may limit the accuracy of the outcome (12). For example, due to resolution constraints, all side lochs are omitted, except Loch A'Choire. Due to the 100 m horizontal model resolution, there is a small discrepancy between the model and reality

leading to a few features in the topography being simplified or omitted, for example Shuna Island. It is assumed that the surface velocities from the hydrodynamic model are accurately portrayed. This limits the likelihood of having lice disperse at different strata in the water column, which could lead to alternate dispersal patterns due to vertical variations in the current field. It is assumed that freshwater inputs and tides are replicated well for simulation times, although they are based on seasonal cycles and tidal diamonds at the open boundaries. This may limit the study, as stochastic or unusual events could occur during the study period of interest. The meteorological data collected from a few sites are used to extrapolate across the entire system, but could limit the study should the recordings be highly localised and not represent the far-field. These assumptions are not only made during the Loch Linnhe study, but are consistent with the assumptions in the previously described models. The time resolution is assumed to be an adequate trade-off between short-time resolving of the velocities, which would be computationally expensive, and unrealistic longer time steps. It is assumed that running the model to produce 2 wk simulations for each spring and autumn of 2011, 2012, 2013 will capture sufficient patterns that describe the consistent patterns experienced within Loch Linnhe. The oceanographic assessments made at several locations throughout the system are assumed to be reflective of the conditions throughout the loch and that the replication would capture any variation in modelled to observed conditions. The particle-tracking algorithm contains a defined stochastic element and fixed dispersive coefficients for ease of calculation, as was the case in previous studies. It is possible that this limits the accurate dispersal conditions by individual lice in the system which would experience variable dispersion. Sensitivity analyses were undertaken to evaluate a range of diffusivity parameters.

The biological components are simplified for a fixed growth and mortality rate based on the mean rates calculated from experimental studies; it is assumed that these results are valid in the field and that the fixed mean actually reflects the conditions experienced by individuals in nature. No level of variable mortality based on salinity- or temperature-induced maturation is included, as it is assumed that a mean rate will encapsulate the conditions experienced by the majority of lice individuals. Lice are also assumed to stay within the surface layer, and no diurnal movement is included. As it is

impossible to track the numerous eggs that are released from a gravid female, it is assumed that packets of lice can represent the dispersal distributions effectively without causing computational issues. This may result in not capturing sufficient variability of lice dispersal. The outputs of the model are assumed to portray the mean conditions experienced over the simulation, but it could be the case that transmission risk weighting could be applied at differing times of the simulation to reflect potential changes in risk, for example lower risk just after farm treatments. Such treatment may reduce the usefulness of the study should important features be omitted. The biological assessment can only be taken at a limited number of locations due to finite resources. It is assumed that the locations selected are not anomalies but reflect the likely conditions of the system.

Making interpretations based on limited replications could be spurious; therefore, this can be limited through replication over time. The potential applications of such dispersal results are assumed to not alter future dispersal, for example taking out an important node in the network through successful surveillance and treatment could alter the structure of the network and change the relationships between farms. However, although it will certainly be the case that the model over-simplifies and misses out possibly influential unknown characteristics and causes limitations in the possible accuracy of the dispersal characteristics experienced by sea lice in Loch Linnhe, it appears that the model has sufficient detail to allow for simulation outputs to be created which have a level of correspondence with the biological reports of planktonic and settled sea lice sampled from the environment (Salama et al. 2013).

This is an ongoing, multi-disciplinary project investigating sea lice dispersal within the large Loch Linnhe sea loch. It incorporates the characteristics of previous sea lice dispersal studies. Through the development of such modelling studies, it could be possible to develop accurate methods of studying transmission of pathogenic and parasitic organisms through the aquatic environment, which could be used in providing information for greater IPM approaches.

DISCUSSION

Here we have highlighted some principles that have been applied to developing and undertaking studies of the environmental transmission of sea lice,

and have demonstrated how the framework is applied to an ongoing study of sea lice dispersal in Loch Linnhe, Scotland. Although the framework could be applied to any disease agent of interest, here we concentrate on sea lice due to their importance to the aquaculture industry (control measures for sea lice are a substantial production cost, which can impact on the economic sustainability of salmon aquaculture). Furthermore, there is a long-standing debate about the role of sea lice with regard to the survivability and recruitment success of migratory Atlantic salmon (e.g. Jackson et al. 2013, Krkošek et al. 2013, Skilbrei et al. 2013), as well as the role of salmon farms in contributing to the levels of sea lice in the environment (e.g. Penston et al. 2011, Middlemas et al. 2013).

Although sea lice control is seen as an important issue by a substantial number of stakeholders and researchers from across broad disciplines, there are considerable gaps in knowledge related to sea lice management that are currently being explored (Box-aspen & Torrisen 2013). A range of IPM measures will be required, and sea lice dispersal models contribute to such approaches. Assessing the role of environmental variability on the dispersal and accumulation of lice in the environment is important as it will enable the ability to highlight areas where larval lice numbers and therefore likely the risk to salmon lice interactions is elevated. By identifying these regions, it may be possible to provide information on optimal locations of farms to minimise transmission of lice between sites. Additionally, connectivity assessments could highlight potential zonation information for aquaculture production, as regions where coordinated production strategies such as FMAs and BMAs have helped manage pathogenic and parasitic diseases. The network structure that arises from some connectivity assessment could help inform the order in which treatments occur, such as targeting the most highly connected nodes first to avoid re-infection through the system. Should it be the case that farm-derived lice have an impact on the success of out-migratory salmon, then it may be possible to use such models to help determine future farm site locations such that lice do not accumulate in areas where wild fish are known to congregate or along migration paths.

Substantial gaps must be overcome in order to thoroughly develop such models. All studies described short snap shots in time and did not address how the dispersal patterns may alter over longer time scales beyond the timeframes considered in the aforementioned studies, and general properties

may require further observations. Should the aim of such model developments be to aid the conservation of wild fish, then further information is needed as to where and how long migratory fish reside, and therefore field observations need to be incorporated. An additional requirement is that the implications of changes in production methods need to be incorporated, such as changes in chemical usage and efficacy, demand for production influencing stocking densities, and the removal and addition of new sites to systems, which may influence dispersal patterns. As such, studies need to account for these changes which could be innumerable and potentially highly influential.

In order to parameterise the model with more accuracy, biological and physical characteristics in the field need developing. For example, the sea lice behaviours used in previous studies are derived from laboratory trials and may not be reflected in the field. Likewise, these models are using parameters associated with *Lepeophtheirus salmonis* and may not be valid for other Caligidae species such as those in Chile. Additionally, the models do not thoroughly describe the life cycle of salmon lice, for example the Loch Linnhe project only attempts to describe 2 stages, nauplii and copepodids, and does not account for the other life stages. This requires the integration of biological population models with the coupled biological–physical models.

A major requirement is an assessment of whether the accumulation of larval lice in areas of higher concentration results in increased transmission risk to fish, and if so what effect this may have on fish health, and possibly mortality. It is difficult to currently determine the link between presence of dispersed lice and impact on health.

Oceanographic and atmospheric model developments are needed that include larger-scale ocean and atmospheric forcings, ideally in near-real time at high temporal resolution to achieve higher accuracy and link long-distance dispersal routes between systems. The smaller, fjord-based models may be restrictive in determining the possible transmission distances.

The characteristics highlighted (Fig. 1) and described (Table 1) demonstrate that although different methods exist for approaching environmental transmission modelling studies, there are shared principles. Highlighting these principles may act as a guide to develop best practices for studying environmental transmission of disease agents in order to provide information to help manage pathogenic and parasitic diseases.

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LITERATURE CITED

- Ackerman PA, Wicks BJ, Iwama GK, Randall DJ (2006) Low levels of environmental ammonia increases susceptibility to disease in Chinook salmon smolts. *Physiol Biochem Zool* 79:695–707
- Adams T, Black K, MacIntyre C, MacIntyre I, Dean R (2012) Connectivity modelling and network analysis of sea lice infection in Loch Fyne, west coast of Scotland. *Aquat Environ Interact* 3:51–63
- Ådlandsvik B, Sundby S (1994) Modelling the transport of cod larvae from the Lofoten area. *ICES Mar Sci Symp* 198:379–392
- Aldrin M, Storvik B, Frigessi A, Viljugrein H, Jansen PA (2010) A stochastic model for the assessment of the transmission pathways of heart and skeleton muscle inflammation, pancreas disease and infectious salmon anaemia in marine fish farms in Norway. *Prev Vet Med* 93:51–61
- Aldrin M, Lyngstad TM, Kristoffersen AB, Storvik B, Borgan Ø, Jansen PA (2011) Modelling the spread of infectious salmon anaemia among salmon farms based on seaway distances between farms and genetic relationships between infectious salmon anaemia virus isolates. *J R Soc Interface* 8:1346–1356
- Allan C (2012) Declaration from the UK of a compartment free from infectious salmon anaemia (ISA) in south west Shetland islands. The Scottish Government, Edinburgh
- Allen GL, Simpson JH (1998) Reflection of the internal tide in upper Loch Linnhe, a Scottish fjord. *Estuar Coast Shelf Sci* 46:683–701
- Amundrud TL, Murray AG (2009) Modelling sea lice dispersion under varying environmental forcings in a Scottish sea loch. *J Fish Dis* 32:27–44
- Anderson RM, May RM (1979) Population biology of infectious disease: Part 1. *Nature* 280:361–367
- Archambault P, Roff JC, Bourget E, Bang B, Ingram GR (1998) Nearshore abundance of zooplankton in relation to shoreline configuration and mechanisms involved. *J Plankton Res* 20:671–690
- Aspin L, Boxaspen KK, Sandvik AD (2011) Modelling the distribution and abundance of planktonic larval stages of *Lepeophtheirus salmonis* in Norway. In: Jones S, Beamish R (eds) Salmon lice: an integrated approach to understanding parasite abundance and distribution. Wiley-Blackwell, Oxford, p 31–50
- Barja JL, Toranzo AE, Lemos ML, Metcalf FM (1983) Influence of water temperature and salinity on the survival of IPN and IHN viruses. *Bull Eur Assoc Fish Pathol* 3:47–50
- Bartsch A, Robinson SMC, Liutkus M, Ang KP, Webb J, Pearce CM (2013) Filtration of sea louse, *Lepeophtheirus salmonis*, copepodids by the blue mussel, *Mytilus edulis*, and the Atlantic sea scallop, *Placopecten magellanicus*, under different flow, light and copepodid-density regimes. *J Fish Dis* 36:361–370
- Baxter J, Boyd I, Cox M, Donald A and others (eds) (2011) Scotland's marine atlas: information for the national marine plan. The Scottish Government, Edinburgh
- Becker JA, Speare DJ (2004) Impact of a water temperature shift on xenoma clearance and recovery time during a *Loma salmonae* (Microsporidia) infection in rainbow trout *Oncorhynchus mykiss*. *Dis Aquat Org* 58:185–191
- Bjørn PA, Sivertsgård R, Finstad B, Nilsen R, Serra-Llinares RM, Kristoffersen R (2011) Area protection may reduce salmon louse infection risk to wild salmonids. *Aquat Environ Interact* 1:233–244
- Bocking S (2012) Science, salmon, and sea lice: constructing practice and place in an environmental controversy. *J Hist Biol* 45:681–716
- Bowden TJ (2008) Modulation of the immune system of fish by the environment. *Fish Shellfish Immunol* 25:373–383
- Boxaspen K (2006) A review of the biology and genetics of sea lice. *ICES J Mar Sci* 63:1304–1316
- Boxaspen K, Holm JC (2001) The development of pyrethrum-based treatments against the ectoparasitic salmon lice *Lepeophtheirus salmonis* in sea cage rearing of Atlantic salmon *Salmo salar* L. *Aquat Res* 32: 701–707
- Boxaspen K, Torrisen O (2013) Sea lice 2012. *J Fish Dis* 36: 169
- Bricknell IR, Dalesman SJ, O'Shea B, Pert CC, Mordue Luntz JA (2006) Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. *Dis Aquat Org* 71:201–212
- Bron JE, Sommerville C, Wotten R, Rae GH (1993) Fallowing of marine Atlantic salmon, *Salmo salar* L., farms as a method for the control of sea lice *Lepeophtheirus salmonis* (Kroyer, 1837). *J Fish Dis* 16:487–493
- Brooks KM (2009) Considerations in developing an integrated pest management programme for control of sea lice on farmed salmon in Pacific Canada. *J Fish Dis* 32: 59–73
- Butler JRA (2002) Wild salmonids and sea louse infestations on the west coast of Scotland: sources of infection and implications for the management of marine salmon farms. *Pest Manag Sci* 58:595–608
- Chang BD, Page FH, Losier RJ, Lawton P, Singh R, Greenberg DA (2007) Evaluation of bay management area scenarios for the southwestern New Brunswick salmon aquaculture industry. Aquaculture Collaborative Research and Development Program final project report. Can Tech Rep Fish Aquat Sci 2722:1–69
- Chassagnet EP, Verron J (2006) Ocean weather forecasting: an integrated view of oceanography. Springer, Amsterdam
- CoGP (Code of Good Practice) Management Group (2010) A code of good practice for Scottish finfish aquaculture. <http://bit.ly/z5LzYv> (accessed 22 October 2012)
- Corner RA, Marshall J, Hadfield B, Gowrie K and others (2008) A review of the sea lice bath treatment dispersion model used for discharge consenting in Scotland. Final Report to the Scottish Aquaculture Research Forum. Project No. SARF 023, University of Stirling
- Costello MJ (2009a) How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proc R Soc Lond B Biol Sci* 276:3385–3394
- Costello MJ (2009b) The global economic cost of sea lice to

- the salmonid farming industry. *J Fish Dis* 32:115–118
- Cromey CJ, Nickell TD, Treasurer J, Black KD (2009) Modelling the impact of cod (*Gadus morhua* L.) farming on the marine environment – CODMOD. *Aquaculture* 289: 42–53
- Damsgård B, Mortensen A, Sommer AI (1998) Effects of infectious pancreatic necrosis virus (IPNV) on appetite and growth in Atlantic salmon, *Salmo salar* L. *Aquaculture* 163:185–193
- Davidson JG, Plantalech Manel-la N, Økland F, Diserud OH and others (2008) Changes in swimming depths of Atlantic salmon *Salmo salar* post smolts relative to light intensity. *J Fish Biol* 73:1065–1074
- Deane EE, Woo NYS (2009) Modulation of fish growth hormone levels by salinity, temperature, pollutants and aquaculture related stress: a review. *Rev Fish Biol Fish* 19:97–120
- Dempster T, Kristiansen TS, Korsøen OJ, Fosseidengen JE, Oppedal F (2011) Technical note: modifying Atlantic salmon (*Salmo salar*) jumping behavior to facilitate innovation of parasitic sea lice control techniques. *J Anim Sci* 89:4281–4285
- Eisenberg JNS, Brookhart MA, Rice G, Brown M, Colford JM (2002) Disease transmission models for public health decision making: analysis of epidemic and endemic conditions caused by waterborne pathogens. *Environ Health Perspect* 110:783–790
- FAO (Food and Agriculture Organization of the United Nations) (2008) World review of fisheries and aquaculture. FAO, Rome
- FAO (2012) The state of world fisheries and aquaculture - 2012. FAO, Rome
- Faust C, Stallknecht D, Swayne D, Brown J (2009) Filter-feeding bivalves can remove avian influenza viruses from water and reduce infectivity. *Proc R Soc Lond B Biol Sci* 276:3727–3735
- Fiskeridirektoratet (2011) Registre knyttet til akvakultur. Available at www.fiskeridir.no/fiskeridir/akvakultur/registre (accessed 8 March 2012)
- Foreman MGG, Czajko P, Stucchi DJ, Guo M (2009) A finite volume model simulation for the Broughton Archipelago, Canada. *Ocean Model* 30:29–47
- Foreman MGG, Stucchi DJ, Garver KA, Tuel D and others (2012) A circulation model for the Discovery Islands, British Columbia. *Atmos Ocean* 50:301–316
- Frazer LN (2008) Sea-lice infection models for fishes. *J Math Biol* 57:595–611
- Frazer LN (2009) Sea cage aquaculture, sea lice, and declines of wild fish. *Conserv Biol* 23:599–607
- Frazer LN, Morton A, Krkošek M (2012) Critical thresholds in sea lice epidemics: evidence, sensitivity and subcritical estimation. *Proc R Soc Lond B Biol Sci* 279:1950–1958
- Gallego A (2011) Biophysical models: an evolving tool in marine ecological research. In: Jopp F, Reuter H, Brecking B (eds) *Modelling complex ecological dynamics*. Springer, Heidelberg, p 279–289
- Gallego A, North EW, Petitgas P (2007) Introduction: status and future of modelling physical-biological interactions during the early life of fishes. *Mar Ecol Prog Ser* 347: 121–126
- Gettinby G, Robbins C, Lees F, Heuch PA, Finstad B, Malkenes R, Revie CW (2011) Use of a mathematical model to describe the epidemiology of *Lepeophtheirus salmonis* on farmed Atlantic salmon *Salmo salar* in the Hardangerfjord, Norway. *Aquaculture* 320:164–170
- Gilbert CS, Gentleman WC, Johnson CL, DiBacco C, Pringle JM, Chen C (2010) Modelling dispersal of sea scallop (*Placopecten magellanicus*) larvae on Georges Bank: the influence of depth-distribution, plankton duration and spawning seasonality. *Prog Oceanogr* 87:37–48
- Gillibrand PA (2002) Observations and model simulations of water circulation and transport in Loch Fyne, a Scottish fjord. Report NO 07/02. FRS Marine Laboratory, Aberdeen
- Gillibrand PA, Amundrud TL (2007) A numerical study of the tidal circulation and buoyancy effects in a Scottish fjord: Loch Torridon. *J Geophys Res* 112:5530–5553, doi: 10.1029/2006JC003806
- Gillibrand PA, Turrell WR (1997) The use of simple models in the regulation of the impact of fish farms on water quality in Scottish sea lochs. *Aquaculture* 159:33–46
- Gillibrand PA, Willis KJ (2007) Dispersal of sea louse larvae from salmon farms: modelling the influence of environmental conditions and larval behaviour. *Aquat Biol* 1: 63–75
- Gjerde B, Odegard J, Thorland I (2011) Estimates of genetic variation in the susceptibility of Atlantic salmon (*Salmo salar*) to the salmon louse *Lepeophtheirus salmonis*. *Aquaculture* 314:66–72
- Goldstein S (1965) Modern developments in fluid dynamics: an account of theory and experiment relating to boundary layers, turbulent motion and wakes, Vol 2. Dover, New York, NY
- Graham DA, Staples C, Wilson CJ, Jewhurst HL, Cherry K, Gordon AW, Rowley HM (2007) Biophysical properties of salmonid alphaviruses (SAV)—influence of temperature and pH on virus survival. *J Fish Dis* 30:533–543
- Green TJ, Powell MD, Harris JO, Butler R (2005) Effects of dissolved organic carbon and hardness in freshwater used to treat amoebic gill disease. *Aquacult Res* 36: 398–404
- Green DM, Gregory A, Munro LA (2009) Small-and large-scale network structures of live fish movements in Scotland. *Prev Vet Med* 91:261–269
- Groner ML, Cox R, Gettinby G, Revie CW (2013) Use of agent-based modelling to predict benefits of cleaner fish in controlling sea lice, *Lepeophtheirus salmonis*, infestation on farmed Atlantic salmon, *Salmo salar* L. *J Fish Dis* 36:195–208
- Gustafson LL, Ellis SK, Beattie MJ, Chang BD and others (2007) Hydrographics and the timing of infectious salmon anemia outbreaks among Atlantic salmon (*Salmo salar* L.) farms in the Quoddy region of Maine, USA and New Brunswick, Canada. *Prev Vet Med* 78:35–56
- Hastings T, Olivier G, Cusack R, Bricknell I, Nylund Å, Binde M (1999) Infectious salmon anaemia. *Bull Eur Assoc Fish Pathol* 19:286–288
- Hawley LM, Garver KA (2008) Stability of viral hemorrhagic septicemia virus (VHSV) in freshwater and seawater at various temperatures. *Dis Aquat Org* 82:171–178
- Heath MR (1995) Size spectrum dynamics and the planktonic ecosystem of Loch Linnhe. *ICES J Mar Sci* 52: 627–642
- Heuch PA, Parsons A, Boxaspen K (1995) Diel vertical migration: a possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids. *Can J Fish Aquat Sci* 52:681–689
- Hevroy EM, Boxaspen K, Oppedal F, Taranger GL, Holm JC (2003) The effect of artificial light treatment and depth on the infestation of the sea louse *Lepeophtheirus salmonis*.

- nis on Atlantic salmon (*Salmo salar* L.) culture. Aquaculture 220:1–14
- Ivanov V, Dale A, Inall M (2011) A high-resolution baroclinic model of Loch Linnhe. Geogr Res Abs 13:4461 (Abstract)
- Jackson D (2011) Ireland: the development of sea lice management methods. In: Jones S, Beamish R (eds) Salmon lice: an integrated approach to understanding parasite abundance and distribution. Wiley-Blackwell, Oxford, p 177–204
- Jackson D, O'Donohoe P, Kane F, Kelly S and others (2012) Result of an epidemiological study of sea lice infestations in South Connemara, West of Ireland. Aquaculture 364–365:118–123
- Jackson D, Cotter D, Newell J, McEvoy S and others (2013) Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar* L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. J Fish Dis 36:273–281
- Jakob E, Barker DE, Garver KA (2011) Vector potential of the salmon louse *Lepeophtheirus salmonis* in the transmission of infectious haematopoietic necrosis virus (IHNV). Dis Aquat Org 97:155–165
- Johansen LH, Jensen I, Mikkelsen H, Bjørn PA, Jansen PA, Bergh Ø (2011) Disease interactions and pathogens exchange between wild and farmed fish in populations with special reference to Norway. Aquaculture 315:167–180
- Johnson SC, Albright LJ (1991a) The developmental stages of *Lepeophtheirus salmonis* (Krøyer 1837) (Copepoda: Caligidae). Can J Zool 69:929–950
- Johnson SC, Albright LJ (1991b) Development, growth and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. J Mar Biol Assoc UK 71:425–436
- Jokinen IE, Salo HM, Markkula E, Rikalainen K, Arts MT, Browman HI (2011) Additive effects of enhanced ambient ultraviolet B and increased temperature on immune function, growth and physiological conditions of juvenile (parr) Atlantic salmon, *Salmo salar*. Fish Shellfish Immunol 30:102–108
- Jones CS, Lockyer AE, Verspoor E, Secombes CJ, Noble LR (2002) Towards selective breeding of Atlantic salmon for sea lice resistance approaches to identify trait markers. Pest Manag Sci 58:559–568
- Jones S, Beamish R (eds) (2011) Salmon lice: an integrated approach to understanding parasite abundance and distribution. Wiley-Blackwell, Oxford
- Jopp F, Reuter H, Breckling B (2011) Modelling complex ecological dynamics. Springer, Heidelberg
- Jørgensen SE (1988) Fundamentals of ecological modelling. Developments in environmental modelling Vol 9. Elsevier, Amsterdam
- Jørgensen SE, Bendoricchio G (2001) Fundamentals of ecological modelling. Developments in environmental modelling Vol 21. Elsevier Science, Oxford
- Karvonen A, Rintamaki P, Jokela J, Volonen ET (2010) Increasing water temperatures and disease risks in aquatic systems: climate change increases the risk of some, but not all diseases. Int J Parasitol 40:1483–1488
- Kermack WO, McKendrick AG (1927) A contribution to the mathematical theory of epidemics. Proc R Soc Lond A 115:700–721
- Kristoffersen AB, Viljugrein H, Kongtorp RT, Brun E, Jansen PA (2009) Risk factors associated with pancreas disease (PD) outbreaks in farmed Atlantic salmon and rainbow trout in Norway during 2003–2007. Prev Vet Med 90:127–136
- Kristoffersen AB, Rees EE, Stryhn H, Ibarra R, Campisto JL, Revie CW, St-Hilaire S (2013) Understanding sources of sea lice for salmon farms in Chile. Prev Vet Med 111:165–175
- Krkošek M (2010) Host density thresholds and disease control for fisheries and aquaculture. Aquacult Environ Interact 1:21–32
- Krkošek M, Lewis MA, Volpe JP (2005) Transmission dynamics of parasitic sea lice from farm to wild salmon. Proc R Soc Lond B Biol Sci 272:689–696
- Krkošek M, Bateman A, Proboszcz S, Orr C (2010) Dynamics of outbreak and control of salmon lice on two salmon farms in the Broughton Archipelago, British Columbia. Aquacult Environ Interact 1:137–146
- Krkošek M, Connors BM, Morton A, Lewis MA, Dill LM, Hilborn R (2011) Effects of parasites from salmon farms on productivity of wild salmon. Proc Natl Acad Sci USA 108:14700–14704
- Krkošek M, Revie CW, Gargan PG, Skilbrei OT, Finstad B, Todd CD (2013) Impacts of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proc R Soc Lond B Biol Sci 280:20122359
- Kundu PK, Cohen IM (2002) Fluid mechanics. Academic Press, London
- Kurath G, Winton J (2011) Complex dynamics at the interface between wild and domestic viruses in finfish. Curr Opin Virol 1:73–80
- Lawrence JE (2008) Furtive foes: algal viruses as potential invaders. ICES J Mar Sci 65:716–722
- Leonardi M, Sandino AM, Klempau A (2003) Effect of a nucleotide-enriched diet on the immune system, plasma cortisol levels and resistance to infectious pancreatic necrosis (IPN) in juvenile rainbow trout (*Oncorhynchus mykiss*). Bull Eur Assoc Fish Pathol 23:52–59
- Liltved H, Vogelsang C, Modahl I, Dannevig BH (2006) High resistance of fish pathogenic viruses to UV irradiation and ozonated seawater. Aquacult Eng 34:72–82
- Lyngstad TM, Jansen PA, Brun E, Sindre H (2008) Epidemiological investigations of infectious salmon anaemia (ISA) outbreaks in Norway 2003–2005. Prev Vet Med 84:213–227
- Mackie TJ, Arkwright JA, Pryce-Tannatt TE, Mottram JC, Johnston WD, Menzies WJM (1935) Furunculosis Committee final report. HM Stationery Office, Edinburgh
- Magnadottir B (2010) Immunological control of fish diseases. Mar Biotechnol 12:361–379
- Marcos-López M, Gale P, Oidtmann BC, Peeler EJ (2010) Assessing the impact of climate change on disease emergence in freshwater fish in the United Kingdom. Transbound Emerg Dis 57:293–304
- Mardones FO, Perez AM, Carpenter TE (2009) Epidemiologic investigation of the re-emergence of infectious salmon anemia virus in Chile. Dis Aquat Org 84:105–114
- Mardones FO, Perez AM, Valdes-Donoso P, Carpenter TE (2011) Farm level reproduction number during an epidemic of infectious salmon anemia virus in southern Chile in 2007–2009. Prev Vet Med 102:175–184
- May RM, Anderson RM (1979) Population biology of infectious diseases: Part II. Nature 280:455–461
- Mayor DJ, Solan M (2011) Complex interactions mediate the effects of fish farming on benthic chemistry within a region of Scotland. Environ Res 111:635–642
- Mayor DJ, Zuur AF, Solan M, Paton GI, Killham K (2010)

- Factors affecting benthic impacts at Scottish fish farms. Environ Sci Technol 44:2079–2084
- McAllister PE, Bebak J (1997) Infectious pancreatic necrosis virus in the environment: relationships to effluent from aquaculture facilities. J Fish Dis 20:201–207
- McCallum H, Harvell D, Dobson A (2003) Rates of spread of marine pathogens. Ecol Lett 6:1062–1067
- McCarthy DH (1977) Some ecological aspects of the bacterial fish pathogen *Aeromonas salmonicida*. Aquat Microbiol 6:299–324
- McClure CA, Hammell KL, Dohoo IR (2005) Risk factors for outbreaks of infectious salmon anemia in farmed Atlantic salmon, *Salmo salar*. Prev Vet Med 72:263–280
- McGeer JC, Baranyi L, Iwama GK (1991) Physiological response to challenge tests in six stocks of coho salmon (*Oncorhynchus kisutch*). Can J Fish Aquat Sci 48: 1761–1771
- McLoughlin MF, Peeler E, Foyle KL, Rodger HD, O'Ceallachain D, Geoghegan F (2003) An epidemiological investigation of the re-emergence of Pancreas Disease in Irish farmed Atlantic salmon (*Salmo salar* L.) in 2002. Mar Environ Health Ser 14:1–47
- Middlemas SJ, Fryer RJ, Tullett D, Armstrong JD (2013) Relationship between sea lice levels on sea trout and fish farm activity in western Scotland. Fish Manag Ecol 20:68–74
- Mitchell SO, Rodger HD (2011) A review of infectious gill disease in marine salmonid fish. J Fish Dis 34:411–432
- Molloy SD, Pietrak MR, Bouchard DA, Bricknell I (2011) Ingestion of *Lepeophtheirus salmonis* by the blue mussel *Mytilus edulis*. Aquaculture 311:61–64
- Moore D, Robson GD, Trinci APJ (2011) Fungi as pathogens of plants. In: Moore D, Robson GD, Trinci APJ (eds) 21st century guide to fungi. Cambridge University Press, Cambridge, p 367–391
- Murray AG (2008) Existing and potential use of models in the control and prevention of disease emergencies affecting aquatic animals. Rev Sci Tech Off Int Epizoot 27:211–228
- Murray AG (2009) Using simple models to review the application and implications of different approaches used to simulate transmission of pathogens among aquatic animals. Prev Vet Med 88:167–177
- Murray AG (2011) A simple model to assess selection for treatment-resistant sea lice. Ecol Model 222:1854–1862
- Murray AG, Amundrud TL (2007) Using coupled biophysical–particle tracking models of sea lice in Loch Torridon. Proceedings of the International Congress on Modelling and Simulation. Christchurch, New Zealand, December 2007, p 2848–2853
- Murray AG, Eldridge PM (1994) Marine viral ecology: incorporation of bacteriophage into the microbial plankton food-web paradigm. J Plankton Res 16:627–641
- Murray AG, Gillibrand PA (2006) Modelling salmon lice dispersal in Loch Torridon, Scotland. Mar Pollut Bull 53: 128–135
- Murray AG, Jackson GA (1993) Viral dynamics II: a model of the interaction of ultraviolet light and mixing processes on virus survival in seawater. Mar Ecol Prog Ser 102: 105–114
- Murray AG, Peeler EJ (2005) A framework for understanding the potential for emerging diseases in aquaculture. Prev Vet Med 67:223–235
- Murray AG, Smith RJ, Stagg RM (2002) Shipping and the spread of infectious salmon anemia in Scottish aquaculture. Emerg Infect Dis 8:1–5
- Murray AG, Amundrud TL, Gillibrand PA (2005) Models of hydrodynamic pathogen dispersal affecting Scottish salmon production: modelling shows how Scotland eradicated ISA, but not IPN. Bull Aquacult Assoc Can 105:1: 79–86
- Murray AG, Munro LA, Wallace IS, Berx B, Pendrey D, Fraser DI, Raynard RS (2010) Epidemiological investigation into the re-emergence and control of an outbreak of infectious salmon anaemia in the Shetland Islands, Scotland. Dis Aquat Org 91:189–200
- Murray AG, Amundrud TL, Penston MJ, Pert CC, Middlemas SJ (2011) Abundance and distributions of larval lice in Scottish coastal waters. In: Jones S, Beamish R (eds) Salmon lice: an integrated approach to understanding parasite abundance and distribution. Wiley-Blackwell, Oxford, p 51–81
- Navas JM, Telfer TC, Ross LG (2011) Application of 3D hydrodynamic and particle tracking models for better environmental management of finfish culture. Cont Shelf Res 31:675–684
- North EW, Schlag Z, Hood RR, Li M, Zhong L, Gross T, Kennedy VS (2008) Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Mar Ecol Prog Ser 359:99–115
- Öğüt H (2001) Modeling of fish disease dynamics: a new approach to an old problem. Turk J Fish Aquat Sci 1:67–74
- Øye AK, Rimstad ER (2001) Inactivation of infectious salmon anaemia virus, viral haemorrhagic septicaemia virus and infectious pancreatic necrosis virus in water using UVC irradiation. Dis Aquat Org 48:1–5
- Pearson TH (1975) Benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on west coast of Scotland. IV. Changes in benthic fauna attributable to organic enrichment. J Exp Mar Biol Ecol 20:1–41
- Pearson TH, Stanley I, Stanley SO (1982) Degradation of organic pollutants in near shore marine-sediments. 1. Breakdown of pulp-mill fiber. Mar Environ Res 7: 195–210
- Peeler EJ, Taylor NG (2011) The application of epidemiology in aquatic animal health—opportunities and challenges. Vet Res 42:94
- Penston MJ, Davies IM (2009) An assessment of salmon farms and wild salmonids as sources of *Lepeophtheirus salmonis* (Krøyer) copepodids in the water column in Loch Torridon, Scotland. J Fish Dis 32:75–88
- Penston MJ, Mckibben MA, Hay DW, Gillibrand PA (2004) Observations on open-water densities of sea lice larvae in Loch Shieldaig, Western Scotland. Aquacult Res 35: 793–805
- Penston MJ, McBeath AJA, Millar CP (2011) Densities of planktonic *Lepeophtheirus salmonis* before and after an Atlantic salmon farm relocation. Aquacult Environ Interact 1:225–232
- Pert CC (2011) The lifecycle and infection dynamics of *Lepeophtheirus salmonis* (Krøyer 1837), on typical and atypical hosts in marine aquaculture areas. PhD thesis, University of Aberdeen
- Pettersen EF, Bjørlo I, Hagland TJ, Wergeland HI (2005) Effects of seawater temperature on leucocyte populations in Atlantic salmon smolts. Vet Immunol Immunopathol 106:65–76
- Piasecki W (1996) The developmental stages of *Caligus elongatus* von Nordmann, 1832 (Copepoda: Caligidae). Can J Zool 74:1459–1478

- Piasecki W, MacKinnon BM (1995) Life cycle of a sea louse, *Caligus elongatus* von Nordmann, 1832 (Copepoda, Siphonostomatoidea, Caligidae). *Can J Zool* 73:74–82
- Pike AW, Wadsworth SL (1999) Sealice on salmonids: their biology and control. *Adv Parasitol* 44:233–337
- Powell MD, Parsons HJ, Nowak BF (2001) Physiological effects of freshwater bathing of Atlantic salmon (*Salmo salar*) as a treatment for amoebic gill disease. *Aquaculture* 199:259–266
- Rae GH (2002) Sea louse control in Scotland, past and present. *Pest Manag Sci* 58:515–520
- Revie CW, Robbins C, Gettinby G, Kelly L, Treasurer JW (2005) A mathematical model of the growth of sea lice, *Lepeophtheirus salmonis*, populations on farmed Atlantic salmon, *Salmo salar* L., in Scotland and its use in assessment of treatment strategies. *J Fish Dis* 28:603–613
- Rimstad E, Dale OB, Dannevig BH, Falk K (2011) Infectious salmon anaemia. In: Woo PTK, Bruno D (eds) *Fish diseases and disorders*, Vol 2: viral, bacterial and fungal infections. CAB International, Wallingford, p 143–165
- Roberts SD, Powell MD (2003) Comparative ionic flux and gill mucous cell histochemistry: effects of salinity and disease status in Atlantic salmon (*Salmo salar* L.). *Comp Biochem Physiol A Mol Integr Physiol* 134:525–537
- Rogers LA, Peacock SJ, McKenzie P, DeDominicis S and others (2013) Modelling parasite dynamics on farmed salmon for precautionary conservation management of wild salmon. *PLoS ONE* 8:e60096
- Rose AS, Ellis AE, Munro ALS (1990) The survival of *Aeromonas salmonicida* subsp. *salmonicida* in sea water. *J Fish Dis* 13:205–214
- Rosenberg AA (2008) Aquaculture: the price of lice. *Nature* 451:23–24
- Ross AH, Gurney WSC, Heath MR, Hay SJ, Henderson EW (1993) A strategic simulation of a fjord ecosystem. *Limnol Oceanogr* 38:128–153
- Roth M, Smith P (2011) Sea lice 2010—the 8th international sea lice conference. *Aquaculture* 320:147–148
- Saksida SM (2006) Infectious haematopoietic necrosis epidemic (2001 to 2003) in farmed Atlantic salmon *Salmo salar* in British Columbia. *Dis Aquat Org* 72:213–223
- Salama NKG, Murray AG (2011) Farm size as a factor in hydrodynamic transmission of pathogens in aquaculture fish production. *Aquacult Environ Interact* 2:61–74
- Salama NKG, Murray AG (2013) A comparison of modelling approaches to assess the transmission of pathogens between Scottish fish farms: the role of hydrodynamics and site biomass. *Prev Vet Med* 108:285–293
- Salama NKG, Collins CM, Fraser JG, Dunn J, Pert CC, Murray AG, Rabe B (2013) Development and assessment of a biophysical dispersal model for sea lice. *J Fish Dis* 36: 323–337
- Sammarco PW, Heron ML (eds) (1994) The bio-physics of marine larval dispersal. Coastal estuarine studies. American Geophysical Union, Washington, DC
- Scheibling RE, Hennigar AW (1997) Recurrent outbreaks of disease in sea urchins *Strongylocentrotus droebachinensis* in Nova Scotia: evidence for a link with large-scale meteorologic and oceanographic events. *Mar Ecol Prog Ser* 152:155–165
- Scheibling RE, Feehan C, Lauzon-Guay JS (2010) Disease outbreaks associated with recent hurricanes cause mass mortality of sea urchins in Nova Scotia. *Mar Ecol Prog Ser* 408:109–116
- Schiøtz BL, Jørgensen SM, Rexroad C, Gjøen T, Krasnov A (2008) Transcriptomic analysis of responses to infectious salmon anemia virus infection in macrophage-like cells. *Virus Res* 136:65–74
- Schley D, Burgin L, Gloster J (2009) Predicting infection risk of airborne foot-and-mouth disease. *J R Soc Interface* 6: 455–462
- Scholthof KB (2007) The disease triangle: pathogen, the environment and society. *Nat Rev Microbiol* 5:152–156
- Scottish Environmental Protection Agency (2011) Marine cage fish farm CAR licence review. Available at <http://goo.gl/krpY3> (accessed 21 June 2013)
- Scottish Executive (2000) Final report of the joint government/industry working group on infectious salmon anaemia (ISA). Scottish Executive, Aberdeen
- Secombes CJ (2011) Fish immunity: the potential impact on vaccine development and performance. *Aquacult Res* 42: 90–92
- Skilbrei OT, Finstad B, Urdal K, Bakke G, Krogland F, Strand R (2013) Impact of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 1997–2009. *J Fish Dis* 36:249–260
- Snieszko SF (1973) Recent advances in scientific knowledge and developments pertaining to diseases of fishes. *Adv Vet Sci Comp Med* 17:291–314
- Snieszko SF (2006) The effects of environmental stress on outbreaks of infectious diseases of fishes. *J Fish Dis* 6: 197–208
- Soetaert K, Herman PMJ (2009) A practical guide to ecological modelling: using R as a simulation platform. Springer, New York, NY
- Stephenson RL (2005) Water movement and aquatic animal health workshop. *Bull Aquacult Assoc Can* 105:1:3–4
- Stevens RB (1960) Cultural practices in disease control. In: Horsfall JG, Dimond AE (eds) *Plant pathology, an advanced treatise*, Vol 3. Academic Press, New York, NY, p 357–429
- Stien A, Bjørn PA, Heuch PA, Elston DA (2005) Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. *Mar Ecol Prog Ser* 290:263–275
- Stigebrandt A (2001) FjordEnv: a water quality model for fjords and other inshore waters. C40 2001. Earth Sciences Centre, Göteborg University, Göteborg
- Stucchi DJ, Guo M, Foreman MGG, Czajko P, Galbraith M, Mackas DL, Gillibrand PA (2011) Modelling sea lice production and concentrations in Broughton Archipelago, British Columbia. In: Jones S, Beamish R (eds) *Salmon lice: an integrated approach to understanding parasite abundance and distribution*. Wiley-Blackwell, Oxford, p 117–150
- Subasinghe RP, Bondad-Reantaso MG, McGladdery SE (2001) Aquaculture development, health and wealth. In: Subasinghe RP, Bueno P, Phillips MJ, Hough C, McGladdery SE, Arthur JR (eds) *Aquaculture in the third millennium*. Tech Proc Conf Aquacult Third Millennium, Bangkok, Thailand, 20–25 February 2000. NACA, Bangkok, and FAO, Rome, p 167–191
- Sutherland KR, Madin LP, Stocker R (2010) Filtration of sub-micrometer particles by pelagic tunicates. *Proc Natl Acad Sci USA* 107:15129–15134
- Suttle CA, Chen F (1992) Mechanisms and rates of decay of marine viruses in seawater. *Appl Environ Microbiol* 58: 3721–3729
- Szmaragd C, Wilson AJ, Carpenter S, Wood JLN, Mellor PS, Gubbins S (2009) A modeling framework to describe the

- transmission of bluetongue virus within and between farms in Great Britain. PLoS ONE 4:e7741
- Tien JH, Earn DJD (2010) Multiple transmission pathways and disease dynamics in a waterborne pathogen model. Bull Math Biol 72:1506–1533
- Toranzo AE, Metricic FM (1982) Comparative stability of two salmonid viruses and poliovirus in fresh, estuarine and marine waters. J Fish Dis 5:223–231
- Tort L, Balasch JC, Mackenzie S (2003) Fish immune system: a crossroads between innate and adaptive responses. Immunología 22:277–286
- Treasurer JW (2002) A review of potential pathogens of sea lice and the application of cleaner fish in biological control. Pest Manag Sci 58:546–558
- Treasurer JW (2012) Disease of north European wrasse (Labridae) and possible interactions with cohabited farmed salmon, *Salmo salar* L. J Fish Dis 35:555–562
- Tucker CS, Norman R, Shinn AP, Bron JE, Sommerville C, Wootten R (2002) A single cohort, time delay model of the life cycle of the salmon louse (*Lepeophtheirus salmonis*) on Atlantic salmon *Salmo salar*. Fish Pathol 37: 107–118
- Turnbull JF, Berrill IK, Green DM, Kaye R and others (2011) Applied epidemiology with examples from UK aquaculture. Aquacult Res 42(Suppl 1):21–27
- Turrell WR (1990) Simulation of advection and diffusion of released treatments in Scottish sea lochs. Scottish Fisheries Working Paper No 16/90. Marine Laboratory, Aberdeen
- Vallejo RL, Wiens GD, Rexroad CE III, Welch TJ and others (2010) Evidence of major genes affecting resistance to bacterial cold water disease in rainbow trout using Bayesian methods of segregation analysis. J Anim Sci 88: 3814–3832
- Venmathi Maran BA, Moon SY, Ohtsuka S, Oh SY and others (2013) The caligid life cycle: new evidence from *Lepophtheirus elegans* reconciles the cycles of *Caligus* and *Lepeophtheirus* (Copepoda: Caligidae). Parasite 20:15
- Viljugrein H, Staalstrøm A, Molvaer J, Urke HA, Jansen PA (2009) Integration of hydrodynamics into a statistical model on the spread of pancreas disease (PD) in salmon farming. Dis Aquat Org 88:35–44
- Wagner GN, Fast MD, Johnson SC (2008) Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. Trends Parasitol 24:176–183
- Walker AJ, Wallace IS, Munro LA (2012) Scottish fish farm production survey: 2011 report. The Scottish Government, Edinburgh
- Wallace IS, Gregory A, Murray AG, Munro ES, Raynard RS (2008) Distributions of infectious pancreatic necrosis virus (IPNV) in wild marine fish from Scottish waters with respect to clinically infected aquaculture sites producing Atlantic salmon, *Salmo salar* L. J Fish Dis 31:177–186
- Weise AM, Cromey CJ, McKindsey CW, Callier MD, Archambault P (2009) Shellfish-DEPOMOD: modelling the biodeposition from suspended shellfish aquaculture and assessing benthic effects. Aquaculture 288:239–253
- Werkman M, Green DM, Murray AG, Turnbull JF (2011) The effectiveness of fallowing strategies in disease control in salmon aquaculture. Prev Vet Med 98:64–73
- Wilding TA (2006) The benthic impacts of the Loch Linnhe artificial reef. Hydrobiologia 555:345–353
- Zadoks JC, Schein RD (1979) Epidemiology and plant disease management. Oxford University Press, Oxford

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