

Available online at www.sciencedirect.com



Marine Pollution Bulletin 53 (2006) 128-135

MARINE POLLUTION BULLETIN

www.elsevier.com/locate/marpolbul

Modelling salmon lice dispersal in Loch Torridon, Scotland

A.G. Murray ^{a,*}, P.A. Gillibrand ^b

^a Fisheries Research Services, Marine Laboratory, P.O. Box 101, 375 Victoria Road, Aberdeen, Scotland AB11 9DB, UK ^b Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll PA37 1QA, UK

Abstract

A particle transport model is described that is being used to simulate the dispersal of salmon lice (*Lepeophtheirus salmonis*) larvae in the waters of Loch Torridon. A hydrodynamic model, forced by tides and winds, drives the transport model. Particle movements are strongly influenced by winds, which can lead to formation of lice concentrations in coastal areas several kilometres from the source. Idea-lised constant wind simulations have been used to locate areas that larval lice may potentially reach from given source locations. Detailed analysis of simulations forced with real wind data is required to assess areas that larval lice from these sources are likely to reach. Further field and experimental work on the viability of lice is required to assess infection risk.

Keywords: Sea loch; Hydrodynamic model; Particle transport model; Sea lice larvae

1. Introduction

The physical oceanographic processes that generate currents play a major role in many biological processes in marine environments. For example, currents drive processes such as advection of larvae (Siegel et al., 2003) or dispersal of pollutants such as oil spills (Elliott et al., 1992) or from sewage outfalls (Murray et al., 2001). In coastal environments, such as estuaries, where biological gradients (both on-shore–offshore and along shore) are strong and point sources (e.g. sewage discharges) are most common, horizontal dispersal and advection are particularly biologically significant.

One important class of estuaries are the fjordic systems that are found in places such as Norway, western Scotland, the North American North-West Pacific coast and New Zealand (Dyer, 1997). Fjords are often quite different to drowned valleys, with features such as over deepened basins, shallow sills and rivers that are small relative to the fjord; this leads to different oceanographic processes generating different current patterns (Dyer, 1997). Compared with estuaries such as drowned valleys, these areas have historically tended to be less populated and less developed and hence have attracted less study. However, in recent years fjordic environments have proven highly suitable for salmon farming and so have attracted considerable development; in the UK alone, annual farmed salmon production exceeds 130,000 tonnes (Stagg and Smith, 2003). In order to understand interactions between farms, and interactions between farms and the environment, it is necessary to understand the dispersal processes driving these interactions.

Marine fish farms typically consist of net pens that exchange their contents easily with the environment. Released material includes nutrients, organic waste, pathogens and medicines used to treat those pathogens. Currents disperse these materials and transport them around the fjord. They can become a problem either because total carrying capacity is exceeded, i.e. average concentration is dangerously high, or because they may cause local problems if advected to other areas without dispersal. The latter may apply at a much lower average concentration than the former.

A pathogen of particular interest to salmon farmers is the salmon louse *Lepeophtheirus salmonis*. This ectoparasitic

^{*} Corresponding author. Tel.: +44 1224 876544; fax: +44 1224 295511. *E-mail address:* murrays@marlab.ac.uk (A.G. Murray).

⁰⁰²⁵⁻³²⁶X/\$ - see front matter @ 2005 Elsevier Ltd. All rights reserved. doi:10.1016/j.marpolbul.2005.09.013

copepod attaches to salmonid fish in marine waters (Pike and Wadsworth, 1999). In northern European waters the hosts are both farmed and wild salmon and sea trout, in the north Pacific a range of other Pacific salmon species are affected; salmon lice may occasionally use non-salmonid fish as temporary hosts.

Salmon lice became a serious problem for farmed salmon soon after aquaculture was established (Rae, 2002); they reduce production and at high intensity of infection may cause death. The annual loss to salmon farmers in Scotland has been estimated at £15-30M (Pike and Wadsworth, 1999). Because farmed salmon biomass is so high, lice on these fish represents a very large component of salmon lice production even when lice levels per fish are low (Heuch and Mo, 2001). Lice from farms are believed to have contributed to the decline of wild sea trout populations, although the exact role is controversial (McVicar, 1997) and sea trout began to decline before salmon farming started. Conversely, wild fish can act as a source of lice to farmed fish and, as lice on wild fish cannot be controlled, a farm that is cleared of lice can soon be re-infected (Rae. 2002).

Salmon lice larvae disperse in the plankton; after hatching there are two development stages as nauplius I and



Fig. 1. Map of north-west Scotland, showing location of the Loch Torridon model domain (including the central basin of Loch Shieldaig) and the meteorological station at Glascarnoch. Axes are latitude and longitude. The location of the seabed pressure data, used to provide tidal forcing to the model, is marked (\blacktriangle) .

nauplius II, followed by a third infectious copepodid stage; this pattern of pre-competent and competent phases is typical of planktonic larvae (Siegel et al., 2003). They are not entirely passive, tending to keep in surface water so that most infection occurs at depths of 0-4 m (Hervøv et al., 1997). In the copepodid phase, they are capable of actively contacting host fish over short distances. But dispersal is likely to be largely controlled by surface currents as they are only capable of swimming slowly relative to advection currents. It is this dispersal that largely controls interaction between farmed and wild fish and between different farms. Understanding the dispersal of lice may therefore help to understand which farm locations may pose a risk to fish entering rivers that host significant salmonid populations. It may also be important to understanding how lice populations on different farm sites interact, thus allowing efficient co-ordinated fallowing strategies to be developed.

In this paper we describe a particle dispersal model used to simulate dispersal of salmon lice larvae in Loch Torridon, a sea loch (fjord) on the west coast of Scotland (Fig. 1). The model uses current fields generated by a separate hydrodynamic model to explore scenarios of environmental forcing aimed at evaluating the interaction between louse producing sites and adjacent areas.

2. Methods

Because of the relatively limited anthropogenic pressures on sea lochs, these systems have been perhaps less intensively studied and modelled than other types of estuaries. Indeed, much of the early modelling of sea lochs treated them as large mesocosms, small patches of enclosed coastal sea that can be intensively studied, with inputs and outputs quantified. Models of fjordic ecosystems have been developed with the aim of understanding larger shelf sea ecosystem processes (e.g. Tett, 1986; Ross et al., 1993).

With the advent of fish farming, more detailed models have been required to assess the dispersal of dissolved effluent. Two-dimensional, laterally integrated numerical models have been used to understand and quantify exchange rates in Scottish fjord basins (Gillibrand et al., 1995; Gillibrand, 2001). However, understanding exchanges of pathogens requires a knowledge of how specific sites interact. Advection processes may lead to high concentrations occurring at considerable distances from their source. To understand such processes requires a full three-dimensional hydrodynamic model, generating current velocities in response to external forcing, and a coupled particle transport model that simulates the movement of particles under these current fields.

2.1. Hydrodynamic model

The hydrodynamic model is the first of the two models that have been developed to simulate the movement of sea lice larvae. In this paper we concentrate on the particle transport model, and do not detail the internal processes of the hydrodynamic model, concentrating on its outputs that are used by the particle transport model and on inputs used to force different scenario outputs.

The hydrodynamic model used is a version of the GF8 model (Stronach et al., 1993) developed for the St. Lawrence Estuary by Saucier and Chasse (2000). Full details of the mathematical framework and solution methods are provided in those publications. In the present application, the model is run in barotropic mode, with tidal and wind forcing only. Horizontal viscosity is calculated using the Smagorinsky (1963) equation as in Saucier and Chasse (2000), but the vertical turbulent viscosity A_v is parameterised based on the depth-mean flow field, i.e.

$$A_{\rm v} = c(\overline{U}^2 + \overline{V}^2)^{1/2}h$$

where c = 0.0025, *h* is the water depth, and *U* and *V* are the depth-mean currents (e.g. Young et al., 2001).

Boundary forcing consists of calculated time series of sea surface elevation at the mouth of the loch, generated with tidal analysis and prediction software (Foreman, 1977) using bottom pressure data collected outside the mouth of Loch Torridon during 2000 and 2001 (Fig. 1). At the surface, wind data from the meteorological station at Loch Glascarnoch (Fig. 1) are used. Wind stress is calculated with a variable drag coefficient (Lavelle et al., 1991). Although baroclinic effects are not included in these simulations, tidal and wind forcing are thought to provide the strongest influence on the dispersal of planktonic larvae in the surface layers and the barotropic model configuration should therefore capture the main features of the lice dispersal.

The model calculates three-dimensional flow fields in Loch Torridon in response to the external forcing conditions. The current field is resolved vertically into 15 layers, the bases of which are located at depths of 4, 8, 12, 16, 20, 25, 30, 40, 50, 60, 80, 100, 150, 200 and 250 m. Because we assume that sea lice remain within surface waters (Hervøy et al., 1997) only predicted currents from the uppermost layer (0–4 m) are passed to the particle transport model. Abandoning vertical structure allows more horizontal and temporal resolution to be achieved in the output file.

The standard output from the model consists of two arrays of two-dimensional surface current speeds, resolved at 100 m intervals in the X and Y dimensions. The model grid is not aligned to compass directions (so X and Y do not correspond to north-south and east-west), but rather is aligned to create the minimum size grid that can accommodate the entire loch. This minimises the number of land grid squares that would otherwise have to be incorporated as null elements in the array. The current velocities are defined at half hourly time intervals for 720 time steps (15 days).

Predicted tidal currents have been calibrated and validated against observed water level and current data. The former were collected during 1999–2001 using Aanderaa WLR-7 bottom pressure sensors. Current data were collected between 1999 and 2001 using a moored upwardlooking 307 kHz RDI ADCP, a Sontek Argonaut MD acoustic current meter, and Aanderaa RCM-7 current meters, deployed at various locations in the loch.

Different sets of output have been generated for the model assuming different external forcing. The basic input is tidal forcing, using tidal elevation at the mouth of Loch Torridon. To this, in other scenarios, is added wind forcing. Four simulations applied wind forcing from the cardinal directions: north-west, north-east, south-west and south-east. These cardinal winds were assumed to blow at the average speeds observed (at Loch Glascarnoch) for winds from these directions: 5.25 m s^{-1} (NW), 5.05 m s^{-1} (NE), 5.93 m s⁻¹ (SW) and 4.2 m s⁻¹ (SE). Further model scenarios used observed wind velocities for specific periods. Finally, although forcing with freshwater input has not been added because river discharge is relatively low in Loch Torridon, it may be important for incorporation of future work on salmon lice biology as larval behaviour and survival are sensitive to salinity (Pike and Wadsworth, 1999).

2.2. Particle transport model

The predicted currents from the hydrodynamic model are used to calculate movements of particles in the particle transport model. The particle tracking technique is an established tool in ocean science and such models have many applications for both physical (e.g. Hunter, 1987; Elliott et al., 1992) and biological (e.g. Gallego et al., 1999; Siegel et al., 2003) dispersion. This model finds the current velocity at a given point in space and time where a particle is located, and uses this to move the particle to another point. At this second point the appropriate local current is found and the particle moved on again. By following the particle over many time steps a trajectory can be built up. This shows which grid squares the particle occupied and hence in which grid square a fish would potentially be at risk of being infected by the louse. By following multiple particles the areas in which fish might be put at risk can be found. This simple situation requires some significant calculation, because advective currents may have to be interpolated in space and time and diffusive turbulent displacements must also be determined.

The problem of interpolation arises because the velocity predictions are defined at a 100 m grid interval, which is inadequate to accurately define the movement of particles, particularly local to features of interest. Instead the particle has an exact location, defined by integer grid square coordinates (X and Y) and real intra-grid square co-ordinates (x and y) lying between 0 and 1. If the particle is not at the centre of the grid square (x = y = 0.5) then the current velocity it experiences is influenced by the velocities in adjacent grid squares (Fig. 2). The velocities of these adjacent currents are weighted by the inverse square of distance; thus particles near the centre of the grid are only very weakly affected by neighbours, but as they approach the corners of the grid square the influence becomes more equal.



Fig. 2. Velocities of currents not located at the grid centre are subjected to interpolated currents dependent on velocities defined in neighbouring grid squares, weighted by the inverse square of distance. Particle o_1 will be little influenced by currents in neighbouring grid squares, while o_2 will be almost as strongly influenced by currents at x_3 , x_5 and x_6 as by its own grid centre x_2 .

Movement depends not just on large scale advection, but also on smaller scale turbulence. The model calculates a turbulent diffusion coefficient on the basis of velocity gradient according to the Smagorinsky formula

$$D = C \Delta x \Delta y \sqrt{[u_x^2 + v_y^2 + (u_y + v_x)^2/2]}$$

(after Gallego et al., 1999). Here u and v are the components of velocity in the X and Y directions, and the subscripts x and y denote differentiation along those dimensions. Here C is the Smagorinsky constant (C = 0.2 for all the simulations presented here) and Δx and Δy are the grid steps in the X and Y dimensions. For current velocities expressed within the program in units of grid squares per time step the grid step = 1.

The diffusion coefficient is used to generate stochastic movements so that particles move apart with time, even though they start at the same location and are subject to the same currents. The movements due to diffusion depend on six times the root of diffusion divided by time period over which movement occurs, Δt . It also depends on a stochastic element *m* or *n* lying between -1 and +1 (Gallego et al., 1999).

 $u_p = m\sqrt{[6D/\Delta t]}$ $v_p = n\sqrt{[6D/\Delta t]}$

This stochastic diffusive motion is added to the deterministic advection.

As a particle moves it enters areas where current velocities are different to those that applied at its point of origin. The use of velocity at the point-of-origin could lead to overall velocity being seriously miscalculated; in particular it is possible that particles caught in high velocity currents near coasts could be driven ashore if this high velocity is used for an entire half-hour time step. We have used a simple means to avoid this problem: if the calculated movement of a particle in a time step is greater than a given fraction of a grid square, then the time step is broken up into sub-time steps. For a fast-moving particle the model could be seen as having a fixed spatial movement and variable time step. This use of fixed movement ensures numerical stability and that particle velocity is always calculated with an appropriately local current.

However, there is one serious problem with the variation of time steps. Movement by advection varies linearly with time, while diffusive movement varies with the square root of time (Berg, 1993). This means that if the time step were reduced to one-quarter of its original value, then advection falls to a quarter, but diffusive movement is only halved. This complication results in further computational overheads and the need to keep diffusive and advective motion separate, until the particle's movement is completed.

Finally the model keeps track of the particles age and development stage. Development depends on temperature and age; however in the absence of data from the hydrodynamic model, or direct specification, a temperature of $10 \,^{\circ}$ C is assumed. This allows non-infectious naupuli (pre-competent) and infectious copepodid (competent) stages to be distinguished.

2.3. The Loch Torridon system

The models have been set up to study the Loch Torridon system by using appropriate local hydrography. Loch Torridon is a moderately large sea loch system on the west cost of Scotland. The loch is approximately 25 km long, and consists of three basins separated by relatively shallow sills (Fig. 3). These basins are Outer Loch Torridon, Inner Loch Torridon, and between these Loch Shieldaig. Both outer Loch Torridon and Loch Shieldaig contain basins of over 100 m depth, and Inner Loch Torridon reaches depths of nearly 100 m. Freshwater inputs occur from a number of small rivers, such as the Torridon River, the River Balgy and the Shieldaig River.

Little previous research on the hydrodynamics of Loch Torridon has been conducted. Current meter and acoustic Doppler current profiler (ADCP) data collected during the present project exhibit circulation features typical of fjordic



Fig. 3. Map of Loch Torridon showing the three basins into which the system is divided. Depth contours are at 20 m intervals. The model grid consists of $100 \text{ m} \times 100 \text{ m}$ cells. Also shown are the locations of two sites from which particles are released in model simulations and of the River Shieldaig, which supports a population of wild sea trout.

estuaries (e.g. Dyer, 1997) i.e. a net seaward flowing surface layer overlying a compensating landward-flowing intermediate layer with isolated deep basin water decoupled from this circulation. Oscillatory tidal currents are superimposed on this net circulation and currents in the surface layer are strongly influenced by wind forcing to the extent that the seaward flow can be temporarily reversed. The tidal range in the loch ranges from 1 m at neap tides to 5 m at springs. Stratification in the loch is generally weak because of the small drainage area; the surface-to-bottom density difference is typically about 1 kg m⁻³.

Loch Shieldaig, the central basin, has been an area of particular interest to the FRS Freshwater Laboratory, because the sea trout population of the Shieldaig River has been the subject of an on-going study (McKibben and Hay, 2004; Penston et al., 2004). This population has been enhanced using artificial stocking, but high mortality occurs in the marine phase of the sea trout life-cycle (McKibben and Hay, 2004) and the population has been slow to recover. One possible reason for this poor survival was believed to be increased sea lice infestation caused by the presence of salmon farms in the Loch Torridon system. The FRS Freshwater laboratory sampled Loch Shieldaig for larval sea lice, which were found in high numbers in the vicinity of the Shieldaig River in 2001 when local farms were in the second year of a production cycle, but not in 2000 when they were in the first year (McKibben and Hay, 2004). Lice larvae were previously found to be abundant in 1999, the second year of the previous cycle.

An understanding of hydrodynamic dispersal in Loch Torridon is important to determine whether these observed larval lice could have come from fish farms, and if so which ones. It is also important in determining how these farms might interact, and so how effective co-ordinated fallowing might be expected to be. Understanding of this dispersal alone is not sufficient to understand local sea lice dynamics, but it is a necessary component of that understanding.

3. Results

Results from example scenarios run in the Loch Torridon model are presented to indicate the model's outputs. They are selected to show general processes that distribute lice larvae and the importance of wind-generated currents. Wind directions that maximise interactions are chosen. Further biological work on the infectivity of lice is required to turn this information into true risk distribution. In all scenarios discussed here, 1000 particles were released at a steady rate of 20 per time step from the source location for the first 50 time steps (i.e. 25 h) of the transport simulation. This ensured that there was no tidal bias in the results. Recorded outputs are the number of time steps that particles occupy a given grid square, summed for all particles in a simulation. Only infectious copepodid particles are recorded in these simulations, thus giving a relative infection risk for fish in different model grid square.

The mean current vector fields for two of the simulations discussed here are presented for illustration (Fig. 4). In both cases, the mean flows on either side of the narrows between Loch Shieldaig and Upper Loch Torridon are strongly influenced by tidal rectification, resulting in strong mean flows into the centre of both basins. Under northwesterly winds, a net landward flow developed in the surface waters of Loch Shieldaig, potentially transporting buoyant (or passive) biota directly toward the River Shieldaig (Fig. 4a), although predicted flows in the headwaters of the loch were very weak. Under the observed wind forcing of July 2000 (Fig. 4b), mean flows were much weaker (apart from the currents induced at the narrows). There remained a slight landward tendency in the outer loch and in Loch Shieldaig.

The hydrodynamic model used to generate these fluxes did not include freshwater inputs and resultant stratification. Freshwater inputs to the Loch Torridon system are relatively small, with a terrestrial drainage basin only about the same size as the surface area of the loch. However, ongoing developments of the model do include incorporation of freshwater flows for full baroclinic simulations.

Examples of particle dispersal scenarios are presented for lice released at two locations referred to as farm 1





Fig. 4. Predicted mean surface velocity vectors in Loch Shieldaig for (a) steady north-westerly wind forcing of 5.25 m s^{-1} , and (b) observed wind speed and direction during 1–21 July 2000.

(Fig. 5) and farm 2 (Fig. 6). The currents used for these scenarios are forced by either constant or real winds from July 2000.

For farm 1 three scenarios are presented: these are forced by constant north-west (Fig. 5a) or south-west (Fig. 5b) wind or by real winds (Fig. 5c). These scenarios



Fig. 5. Results of model scenarios in which 1000 particles are released from model site 1 (triangle); only copepodids shown with units of particle time steps per grid square. These particles are subject to north-west (a), south-west (b) or observed (c) winds.



Fig. 6. Results of model scenarios in which 1000 particles are released from model site 2 (triangle). These particles are subject to north-east (a), south-east (b) or observed (c) winds. Units are as for Fig. 5.

are chosen because the north-west wind maximised lice transport to the vicinity of the Shieldaig River, while the south-west wind maximised transport into upper Loch Torridon, and hence to the vicinity of farm 2. It can be seen that with favourable north-west winds there is considerable risk of transfer to the vicinity of the river Shieldaig, where lice concentrations have been observed (McKibben and Hay, 2004). Under south-west winds there is considerable transfer into Upper Loch Torridon, indeed some lice may be transferred the full length of this basin. Under the real winds scenario (Fig. 5c), concentrations are distributed throughout Loch Shieldaig. If the particles are followed time step by time step (not shown) it is observed that although lice occasionally do disperse generally there exists a small patch in which high concentration occurs, and the location of this patch moves considerably with time.

Lice released from farm 2 are subjected to easterly winds, as these are most likely to lead to transfer into Loch Shieldaig, and hence maximise interactions with both farm 1 and the River Shieldaig. Scenarios are thus forced using north-east (Fig. 6a) and south-east (Fig. 6b) winds. In both cases the results are quite similar, with concentrations occurring in the strait connecting Upper Loch Torridon and Loch Shieldaig, with a secondary concentration occurring in northern Loch Shieldaig. This concentration is slightly further south under north-east winds, and hence more likely to pose a risk to farm 1. Under the real wind scenario (Fig. 6c) lice larvae are mostly found in southern Upper Loch Torridon, with secondary concentration in Loch Shieldaig, but in this case small numbers of lice are distributed throughout Loch Shieldaig, a very small proportion reaching the vicinity of the Shieldaig River.

4. Discussion and conclusions

The model described is a tool for assessing the transport of substances released at a given location. Hence the model can be used to obtain a more detailed picture of environmental risks and the key physical processes behind movements of substances. The specific results are preliminary, but do indicate the importance of wind-driven transport in assessing affected areas.

With north-west winds, sea lice larvae may be transported from site 1 to the immediate vicinity of the River Shieldaig. Analysis of the wind data from 2000 and 2001 reveals that north-westerly winds were prevalent for about 30% of the time; this may explain the high concentrations observed in the vicinity of this river. Under the real wind conditions of July 2000, larval lice did reach the River Shieldaig from site 2, but only in relatively small numbers. For significant numbers to reach the river mouth, either optimal wind conditions, or some other factor beyond wind forcing, would be needed.

The modelled currents have been validated by tracking the movement of buoys. Individual lice particles cannot be tracked directly, but modelled concentrated patches are consistent with observed copepodid distributions. Wind generated currents produce patches of elevated concentrations of lice in coastal areas. These model-generated patches appear consistent with observations of patches of copepodids (Costelloe et al., 1998; McKibben and Hay, 2004), and with aggregated patterns of infestation of lice numbers on sea trout (Murray, 2002).

The results shown are for copepodids, which form patches that may be distant from their source. Naupuli are relatively more likely to be observed near the farms where infected fish are found (Penston et al., 2004), and the model generates this pattern too (not shown).

Inter-farm site exchange in Loch Torridon may occur under suitable winds, both north-east and south-east winds may mean lice from farm 2 pose a risk of infection to farm 1, while south-west winds may transport lice larvae from farm 1 to farm 2. Therefore farms 1 and 2 should be treated as a unit for fallowing purposes; i.e. the farms should be harvested and left without fish for a few weeks at the same time. However, most lice remain in the basin that they are released in even under these winds. Because transport depends on the exact nature of the wind forcing, many scenarios are required to asses the likely extent of interactions between farm sites and hence the value of synchronous fallowing.

Because winds are important in assessing exchanges of lice larvae, analysis of the risks of such exchanges occurring requires the use of real wind data and extensive analysis of situations where wind direction changes. This presents considerable computational and data-gathering costs. However, the pattern of risk is very different to that generated under tidal exchange alone. Tidal exchanges have been used to develop the tidal excursion model which is used to assess risk, e.g. to devise control regions to limit the spread of Infectious Salmon Anaemia (JGIWG, 2000). This wind-driven exchange indicates that more sophisticated approaches may be required in future.

The predicted dependence on winds is consistent with the weakness of linkage between lice levels on salmon farms and on adjacent populations of wild sea trout (Mac-Kenzie et al., 1998; Marshall, 2003). Variable wind based dispersal, and concentration, is consistent with the large regions of low larval lice abundance observed between areas of high concentrations at farms and at river mouths (Costelloe et al., 1998). When a large number of locations were compared a relationship was found, though with large standard deviations (Tully et al., 1999). If the dispersal of larval lice from farms is dependent on the wind then, because the wind is so variable, the risk to specific population will be only weakly related to conditions on particular farms. A tidal excursion model would produce risks that were essentially constant, i.e. sites within the tidal excursion zone would be exposed with every tidal cycle.

One caveat, the fact that larval lice may reach a particular area does not necessarily mean they present a risk of infection. The degree of risk depends not only on the numbers of lice, but also their viability. A model that generates appropriate movements of larval lice purely in response to currents could equally describe the movement of dead or live lice. Experimental assessment of the effect of the survival of lice, and field assessment of their viability, are required to determine risk.

Results from our model are in broad agreement with results recently presented from a model of a much larger Norwegian fjord (Asplin et al., 2004). In that study sea lice dispersed over distances of many kilometres, but also tended to form concentrations at particular location, as in the Loch Torridon model. Indeed distances of dispersal were sometimes greater than in our model, up to 100 km, due to stronger currents and lower temperatures in the Norwegian fjord.

Acknowledgements

We are grateful to F.J. Saucier for providing the code for the hydrodynamic model, and are greatly indebted to J.-F. Dumais for his efforts in developing and configuring the initial version of the Torridon model. The wind data from Loch Glascarnoch was supplied by the UK Meteorological Office through the British Atmospheric Data Centre.

References

- Asplin, L., Boxaspen, K., Sandvik, A.D., 2004. Modelling distribution of salmon lice in a Norwegian fjord. ICES CM 2004/P:11.
- Berg, H.C., 1993. Random Walks in Biology, New, expanded edition. Princeton University Press, Princeton, New Jersey.
- Costelloe, M., Costelloe, J., O'Donohoe, G., Coghlan, N.J., Oonk, M., Van Der Heijden, Y., 1998. Planktonic distribution of sea lice larvae, *Lepeophtheirus salmonis*, in Killary Harbour, west coast of Ireland. Journal of the Marine Biological Association of the UK 78, 853–874.
- Dyer, K.R., 1997. Estuaries: A Physical Introduction, second ed. John Wiley & Sons, London, 195pp.
- Elliott, A.J., Dale, A.C., Proctor, R., 1992. Modelling the movement of pollutants in the UK shelf seas. Marine Pollutution Bulletin 24, 614– 619.
- Foreman, M.G.G., 1977. Manual for tidal heights analysis and prediction. Pacific Marine Science Report 77-10, Inst. Ocean Sciences, Victoria, BC, Canada, 58pp.
- Gallego, A., Mardaljevic, J., Heath, M.R., Hainbucher, D., Slagstad, D., 1999. A model of the spring migration into the North Sea by *Calanus finmarchicus* overwintering off the Scottish continental shelf. Fisheries Oceanography 8, 107–125.
- Gillibrand, P.A., 2001. Calculating exchange times in a Scottish fjord using a two-dimensional laterally integrated numerical model. Estuarine Coastal and Shelf Science 53, 437–449.
- Gillibrand, P.A., Elliott, A.J., Turrell, W.R., 1995. Deep-water renewal in the Upper Basin of Loch Sunart, a Scottish Fjord. Journal of Physical Oceanography 25, 1488–1503.
- Hervøy, E.M., Holm, J.C., Boxaspen, K., 1997. The effect of swimming depth, speed and artificial light treatment in Atlantic salmon (*Salmo* salar) culture on the infestation of the copepod *Lepeophtheirus* salmonis. In: Cultivation of Cold Water Species: Production, Technology and Diversification. European Aquaculture Society, Trondheim.
- Heuch, P.A., Mo, T.A., 2001. A model of salmon louse production in Norway: effects of increasing salmon production and public management measures. Diseases of Aquatic Organisms 45, 145–152.

- Hunter, J.R., 1987. The application of lagrangian particle-tracking techniques to modelling of dispersion in the sea. In: Noye, J. (Ed.), Numerical Modelling: Applications to Marine Systems. Elsevier, Amsterdam, The Netherlands, pp. 257–269.
- JGIWG, 2000. Final Report of the Joint Government/Industry Working Group on Infectious Salmon Anaemia (ISA) in Scotland. Scottish Executive, FRS Marine Laboratory, Aberdeen, UK, 141pp.
- Lavelle, J.W., Cokelet, E.D., Cannon, G.A., 1991. A model study of density intrusions into and circulation within a deep silled estuary: Puget Sound. Journal of Geophysical Research, C 96, 16779–16800.
- MacKenzie, K., Longshaw, M., Begg, G.S., McVicar, A.H., 1998. Sea lice (Copepoda: Caligidae) on wild sea trout (*Salmo trutta* L.) in Scotland. ICES Journal of Marine Science 55, 151–162.
- Marshall, S., 2003. The incidence of sea lice infestation on wild sea trout compared to farmed salmon. Bulletin of the European Association of Fish Pathologists 23, 72–79.
- McKibben, M.A., Hay, D.W., 2004. Planktonic distribution of sea lice *Lepophtheirus salmonis* larvae in inter-tidal planktonic samples in Loch Shieldaig, western Scotland in relation to local salmon farm production cycles. Aquaculture Research 35, 742–750.
- McVicar, A.H., 1997. Disease and parasites, implications for the coexistence of wild and cultured Atlantic salmon populations. ICES Journal of Marine Science 54, 1093–1103.
- Murray, A.G., 2002. Using observed load distributions and simple models to analyse the epidemiology of sea lice (*Lepeophtheirus salmonis*) on sea trout (*Salmo trutta*). Pest Management Science 58, 585–594.
- Murray, A.G., Parslow, J.S., Walker, S.J., 2001. Modelling treated waste disposal in Port Phillip Bay and Bass Strait: biogeochemical and physical removal. Environment International 27, 249–255.
- Penston, M.J., McKibben, M., Hay, D.W., Gillibrand, P.A., 2004. Observations of sea lice larvae distributions in Loch Shieldaig, western Scotland. Aquaculture Research 35, 793–805.
- Pike, A.W., Wadsworth, S.L., 1999. Sealice on salmonids: their biology and control. Advances in Parasitology 44, 231–337.
- Rae, G.H., 2002. Sea louse control in Scotland, past and present. Pest Management Science 58, 515–520.
- Ross, A.H., Gurney, S.C., Heath, M.R., Hay, S.J., Henderson, E.W., 1993. A strategic simulation of a fjordic ecosystem. Limnology and Oceanography 38, 128–153.
- Saucier, F.J., Chasse, J., 2000. Tidal circulation and buoyancy effects in the St. Lawrence Estuary. Atmosphere-Ocean 38, 505–556.
- Siegel, D.A., Kinlan, B.P., Gaylord, B., Gaines, S.D., 2003. Lagrangian descriptions of marine larval dispersion. Marine Ecology Progress Series 260, 83–96.
- Smagorinsky, J., 1963. General circulation experiments with primitive equations. I. The basic experiment. Monthly Weather Review 91, 99– 164.
- Stagg, R.M., Smith, R.J., 2003. Scottish Fish Farms Annual Production Survey 2002. Fisheries Research Service, Aberdeen, 53pp.
- Stronach, J.A., Backhaus, J.O., Murty, T.S., 1993. An update on the numerical simulation of oceanographic processes in the waters between Vancouver Island and the mainland: the GF8 model. Oceanography and Marine Biology Annual Review 31, 1–86.
- Tett, P., 1986. Physical exchange and the dynamics of phytoplankton in Scottish sea lochs. In: The Role of Freshwater Outflow in Coastal Marine Ecosystems. In: Skreslet, S. (Ed.), NATO ASI Ser. G, vol. 7. Springer, pp. 205–218.
- Tully, O., Gargan, P., Poole, W.R., Whelan, K.F., 1999. Spatial and temporal variation in the infestation of sea trout (*Salmo trutta* L.) by the caligid copepod *Lepeophtheirus salmonis* (Krøyer) in relation to sources of infection in Ireland. Parasitology 119, 41–51.
- Young, E.E., Brown, J., Aldridge, J.N., 2001. Application of a large area curvilinear model to the study of the wind-forced dynamics of flows through the North Channel of the Irish Sea. Continental Shelf Research 21, 1403–1434.