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Modelled salmon lice dispersion and infestation patterns in a sub-arctic fjord

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Salmon lice infestation is a major challenge for the aquaculture industry in Norway, threatening wild salmonid populations and causing welfare problems for farmed salmon. Lice dispersion and infestation patterns are simulated by combining a high-resolution hydrodynamic model for the Norwegian coast and fjords with an individual-based model for salmon lice. We here present results from Altafjorden, a sub-arctic fjord with large stocks of wild salmonids, where the inner part is protected as a National Salmon Fjord. The outer part of the fjord hosts several fish farms, and our simulations demonstrate how ocean currents can disperse lice between farms as well as into the protected part of the fjord. The relative contributions from the farms in the different parts of the fjord depends on their locations relative to the currents and circulation patterns in the fjord. Knowledge of how the highly variable water currents disperse salmon lice within fjord systems is necessary for managing farm locations and production quotas, if the goal is to minimize infestation pressure on wild salmonids and between fish farms.

Keywords: Alta, aquaculture, currents, individual-based model, Northern Norway, numerical ocean model, partickle tracking, physical oceanography, ROMS, sea lice

Introduction

The salmon louse (*Lepeophtheirus salmonis*) is a parasite naturally present in the Norwegian coastal waters, but in areas with intensive salmon farming the elevated number of available hosts has increased the amounts of lice far beyond natural levels (Costello, 2009b; Serra-Llinares *et al.*, 2014; Taranger *et al.*, 2015; Thorstad *et al.*, 2015; Serra-Llinares *et al.*, 2016). Salmon lice epizootics can represent a welfare issue for the farmed fish, and the repeated delouse treatments of farmed fish to keep the lice level under the permitted level cause significant economic losses to the industry. Further, the salmon lice are regarded as a serious threat for wild anadromous salmonids (Ashley, 2007; Costello, 2009a, b; Forseth *et al.*, 2017). The Norwegian government has chosen mortality on wild salmonids due to salmon lice infestation as the index of carrying capacity for environmentally sustainable growth of the aquaculture industry (Anon., 2014–2015; Taranger *et al.*, 2015; Vollset *et al.*, 2018). Aquaculture production will not be allowed to increase in areas where the salmon lice reaches concentrations that have population-reducing effects on wild salmonid stocks, including Atlantic salmon (*Salmo salar*) that migrate quickly through coastal areas to the ocean, and sea trout (*Salmo trutta*) and arctic char (*Salvelinus alpinus*) that spend their whole sea-feeding migration period in coastal areas (Klemetsen *et al.*, 2003).

Aquaculture activity is projected to continue to grow substantially in the future (Anon., 2014–2015). Most of this growth will occur in Northern Norway where there is still available space, as well as favourable growth conditions for farmed salmon. This can create serious conflicts of interest, as Northern Norway is also a very important region for wild Atlantic salmon populations (Anon., 2016; www.nasco.int/convention.html). So far, the lice infestation pressure has been relatively low during the migration period of the wild salmon post-smolts (June–July) in Finnmark, the northernmost county of Norway, due to relatively low aquaculture activity (Svåsand *et al.*, 2017). In addition, the fjords in Finnmark exchange water with the southern, Atlantic-influenced part of the Barents Sea and can therefore be regarded as sub-arctic. The low water temperatures lead to slower generation cycles of the lice (Samsing *et al.*, 2016b), and the wild salmon populations in Finnmark have been relatively unaffected by the salmon farming industry (Bjørn *et al.*, 2007; Svåsand *et al.*, 2017). This in contrast to the situation on the west coast of Norway, where the long-standing intensive aquaculture industry combined with higher water temperatures have caused concentrations of lice that may have contributed to a serious decimation of wild Atlantic salmon stocks (Skaala *et al.*, 2014; Taranger *et al.*, 2015; Svåsand *et al.*, 2016; Forseth *et al.*, 2017).

Sustainable growth in the aquaculture industry in Northern Norway without a decimation of the wild salmonid stocks, requires governing policies based on sound knowledge of any population-reducing effects of lice, as well as protective measures that are accurate and effective. The knowledge needed when planning farm locations, quotas for salmon production, and protected areas, must therefore include the dynamics of salmon lice dispersal by the highly variable currents in the fjords and coastal areas. Due to the long-lasting planktonic phase of the lice after hatching (~2 weeks), the ocean currents can disperse the lice over several tens of kilometres from their hatching locations (Asplin *et al.*, 2014). The variable fjord circulation, resulting from many different forcing agents acting on stratified water over complex topography, requires 3-D modelling efforts to get realistic dispersion statistics for planktonic copepodids. The present work, focusing on Altafjorden in Finnmark, is the first high-resolution (160 m) modelling study of salmon lice growth and dispersion for the northernmost part of Norway. The river Altaelva that drains into Altafjorden, hosts one of the last large wild salmon stocks in the world (Anon., 2016). While the outer part of the fjord hosts several fish farms, the inner part is protected as a National Salmon Fjord (Aasetre and Vik, 2013; Sønvinsen, 2003). Thus, the salmon juveniles (post-smolts) migrate through both the protected area and the aquaculture areas on their seaward feeding migration from the river to the ocean. Therefore, a successful post-smolt migration requires low lice levels in both inner and outer parts of the fjord during the migration period, typically lasting for ca. 2–4 weeks in June–July (Ugedal *et al.*, 2008). In contrast, the more stationary sea trout and arctic char that reside close to their home rivers during their sea feeding migration (Klemetsen *et al.*, 2003) need low lice levels throughout the whole summer season.

The aim of this paper is to quantify the potential for dispersion of salmon lice in the different parts of Altafjorden; the connectivity between farms, and the potential for infestation of the protected area. We use a state-of-the-art individual-based model for lice growth and dispersion (Ådlandsvik and Sundby, 1994; Johnsen *et al.*, 2014; Sandvik *et al.*, 2016a) with equal release of particles from all farm locations to quantify the potential dispersion of lice caused by the fjord circulation during summer conditions. In addition, we simulate "realistic" dispersion and concentrations of lice by including reported lice numbers from salmon farms, and we present model estimates of lice concentrations in a scenario where all farms experience relatively high but allowed levels of lice infestation. Finally, we discuss the effect of protecting the inner part of the fjord from aquaculture activity, and how increased future aquaculture production can affect the infestation pressure in the region.

Methods

Study area

Altafjorden (70–70.4°N; 22.2–23.6°E, Figure 1) is 450 m deep and ~30 km long. The fjord is connected to the Barents Sea through three inlets; Stjernsundet (sill depth ~200 m), Rognsundet and Vargsundet (sill depths ~50 m). The largest source of freshwater to the fjord is the river Altaelva, from which the discharge can exceed 1000 m^3/s in May–June (Røhr *et al.*, 2003). The brackish surface layer in the fjord is typically 5–10 m thick in summer, with temperature varying between 5 and 16°C throughout summer, with monthly mean temperature of 10°C in August (Eilertsen and Skarðhamar, 2006; Mankettikkara, 2013). Below the upper brackish layer, the salinity is relatively high (>33) everywhere. In summer the monthly mean surface salinity is 31–32 in the outer part of the fjord and 19–32 in the inner part of the fjord, but the shorter-term variability is large, ranging from below 7 to above 34 (Mankettikkara, 2013). Altafjorden experiences a semidiurnal tide with sea level difference between 1.5 and 2.5 m. The tidal wave propagates from the south to the northeast along the Norwegian coast, and enters the three inlets of Altafjorden with a phase lag of a few minutes, 7 min from Stjernsundet to Rognsundet, and 17 min from Rognsundet to Vargsundet (Svendsen, 1995). The currents respond differently to the tides in the three inlets. In Vargsundet the currents change direction with the tidal phase, while in Stjernsundet and Rognsundet other forcing than tides can dominate, and the current speed may vary with the tidal phase without necessarily changing the current direction (Svendsen, 1995). This causes complex and variable current patterns in the outer part of the fjord where the three inlets interact. The fjord is wide enough for its circulation being affected by the Earth's rotation, thus the current direction often varies across the fjord (Svendsen, 1995; Davidsen *et al.*, 2009, 2013). The combination of all the forcing agents and the bathymetry of Altafjorden results in a fjord circulation that are much more complex than the simplified, traditional two-layer estuarine circulation model often used in fjord studies. Therefore, for assessing the dispersion of lice (and other planktonic matter) numerical modelling that includes all relevant forcing agents is necessary.

Numerical model

The numerical modelling experiments were performed with a general ocean circulation model simulating the currents and hydrography in the fjord system, combined with a particle tracking model with built-in individual-based model of salmon lice behaviour and growth. Model experiments were performed with equal release of particles from all farm locations, to estimate the relative potential infestation between farms and into the protected area of the fjord. We also included the reported lice numbers to model "realistic" dispersion of lice for a summer situation. The model output consists of hourly fields of spatial distribution of particles representing salmon lice copepodids in the sea, and can be analysed at two levels: (i) "general" analysis of particle dispersion, depending on oceanographic conditions, age (degree days) and vertical behaviour only, and (ii) "realistic" analysis where also reported lice numbers on each farm are included (see "Input data to the salmon lice particle tracking model" section).

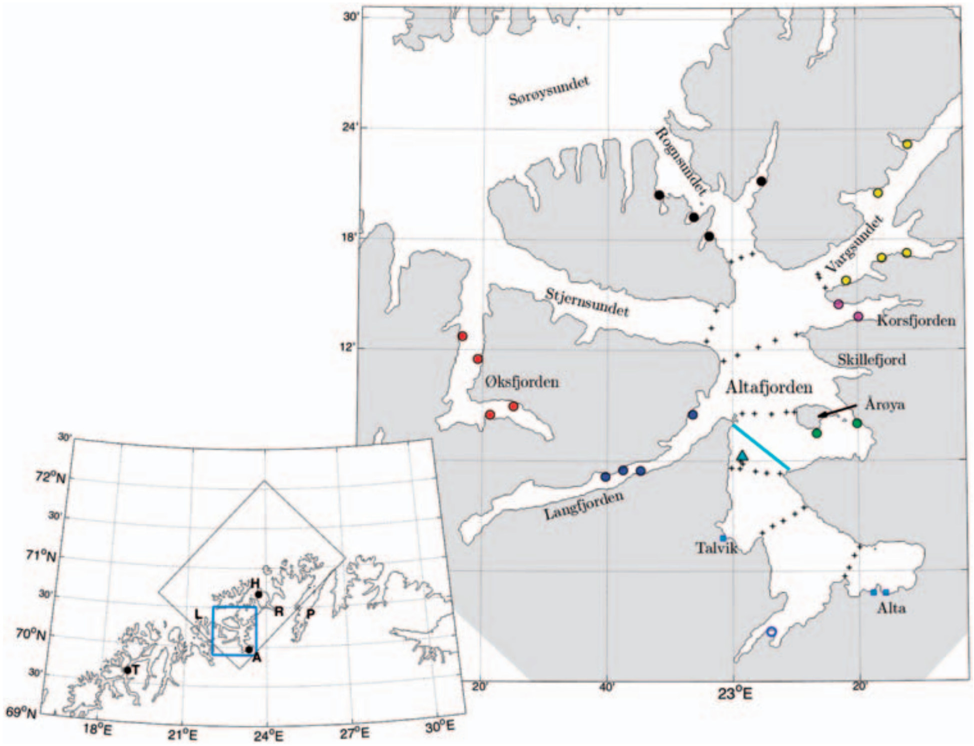

Figure 1. Map of the fjord system Altafjorden in Norway. Aquaculture sites included in the analysis are marked with coloured circles (farms reporting lice in 2015), CTD stations are marked with +, and the current metre mooring location is marked with a solid triangle. The farms are located in Øksfjorden, Langfjorden, Årøya, Korsfjorden, Vargsundet and Rognsundet. The solid blue line shows the border of the protected area (National Salmon Fjord), and the open circle south in the fjord shows the location of a salmon slaughterhouse. The positions of rivers mouths where hydrological discharge measurement data were used instead of climatological discharge (used elsewhere in the model grid) in the model are marked with blue small squares. The town Alta is located near the river mouth of the largest river, Altaelva. The left panel shows the northern Norwegian coast with a frame around the model domain (160 m grid) and a smaller blue frame displaying the locality of the fjord system Altafjorden shown in the main panel. The largest towns are marked in the left panel; T, Tromsø; A, Alta and H, Hammerfest. The other letters denote other place names mentioned in the text; L, Loppa; R, Repparfjord and P, Porsanger.

Salmon lice particle tracking model

The particle tracking model, simulating salmon lice advection and growth, is based on the Lagrangian advection and diffusion model (LADIM) (Ådlandsvik and Sundby, 1994), coupled offline to an ocean circulation model (see “Hydrodynamic ocean circulation model” section). The particles are given a vertical behaviour to represent the planktonic stages of the salmon louse, swimming downward to avoid low salinity water ($S < 20$) and up toward surface light as described in Johnsen *et al.* (2014). Vertical mixing is included with a constant mixing coefficient, keeping the particles vertically distributed in the water column, although restricted to the upper 20 m in the model. Horizontally, the lice drift passively with the currents, with a random movement component representing sub-grid-scale processes (Johnsen *et al.*, 2014). The growth of the individual louse is temperature dependent and is parameterized as a function of degree days. The infective copepodid stage of the lice has been assumed to be between 50 and 150 degree days (Stien *et al.*, 2005), but recent research has shown that the start and duration of the infective stage vary with temperature (Samsing *et al.*, 2016b): 40–170 degree days at temperature 10°C and 50–135 degree days at 7°C. As the modelled mean temperature of the upper 5 m in Altafjorden was between 8 and 12°C from mid-June to September, which is the period where the lice numbers increase in the area, we use 40–170 degree days as the infective age for the whole period. This will lead to an overestimation of the lice dispersion in the spring and early summer, but as the lice numbers are low before mid-June, this is a reasonable approach. The mortality rate of salmon lice nauplii and copepodids is kept constant at 17% per day (Stien *et al.*, 2005).

Input data to the salmon lice particle tracking model

In this study, we used input data of lice numbers from 21 locations that reported lice numbers to the Norwegian Food Safety Authority (NFSA, www.mattilsynet.no) during the summer of 2015 (marked in Figure 1). The locations are situated within six geographical areas (fjord arms, bays, inlets) named Øksfjorden, Langfjorden, Årøya, Korsfjorden, Vargsundet and Rognsundet (see Figure 1). There were additional one or two fallowed farm locations in each of these farming areas in 2015. We expect dispersion from these locations to be comparable to the dispersion from their neighbouring locations. Locations outside the fjord system were not included here (west of Øksfjorden, in Sørøysundet, and east of Vargsundet).

We estimated the number of hatched lice eggs released to the sea from each farm based on the number of farmed fish from monthly reports of biomass from the farmers to the Norwegian Directorate of Fisheries (NDF, www.fiskeridir.no), and weekly

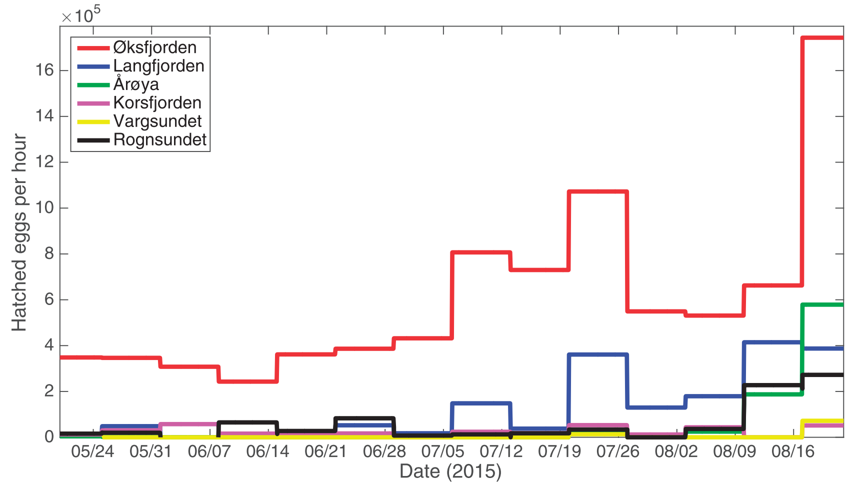

Figure 2. Temporal development of hatched salmon lice eggs used as input data to the salmon lice particle tracking model. The graphs show the total number of lice eggs released hourly from all farms within each of six parts of the fjord system. The numbers are calculated as described in the text and Stien *et al.* (2005) (see online version for colours).

reports to the NFSA of average number of mature female lice per fish and water temperature at 3 m depth. The data were reported weekly and we calculated the average hourly number of eggs hatched on each farm, as described by Stien *et al.* (2005) (we assume 150 eggs per egg string from each female louse). In the model, we released five super particles at each farm position every hour, each super particle representing 1/5 of the hourly release of hatched eggs per hour at that site. Figure 2 shows the estimated, hourly values of lice released from the farms in the different parts of Altafjorden. In June, there were relatively low numbers varying from none in Vargsundet to ca. 400 000 eggs per hour from the three farms in Øksfjorden (in total), increasing in July to above 10^6 eggs per hour (Figure 2). The lice particle model was run for 90 days, from 20 May to 18 August 2015.

Hydrodynamic ocean circulation model

The open-source Regional Ocean Modelling System (ROMS) [Shchepetkin and McWilliams (2005); Haidvogel *et al.* (2008), http://myroms.org] is a state-of-the-art, three-dimensional, free-surface, hydrostatic, primitive equation ocean model using generalized terrain-following s-coordinates in the vertical. The s-coordinate levels are specified relative to the total water depth between the free surface and the bottom, keeping a fixed number of vertical levels in all horizontal grid cells. Our simulation applied 35 s-levels with an enhanced resolution in the upper ∼50 m. The high-resolution model was established with grid cell size 160 m × 160 m covering Altafjorden and the surrounding coast and fjords from Loppa (21.4°E) to Porsanger (26.7°E) (see Figure 1). The bathymetric data were obtained from the online data source Norge Digitalt (http://www.norgedigitalt.no) established by the Norwegian Mapping Authority, the Hydrographic service (Statens Kartverk Sjø) having an original resolution of about 50 m on an irregular grid. The forcing along the open boundaries was obtained from the 800 m × 800 m resolution coastal model NorKyst800 (Albretsen *et al.*, 2011) at hourly temporal resolution. NorKyst800 also applies ROMS and covers the whole Norwegian coast. NorKyst800 was run from 1 January 2015 and provided initial fields to the 160 m-model from 1 March 2015. The lateral boundary values for the NorKyst800 were obtained from the Norwegian Meteorological Institute's operational Nordic Seas 4 km × 4 km resolution model (http://thredds.met.no), and included daily mean sea level, currents, salinity and temperature at fixed depths. Tidal forcing was imposed along the boundary of the NorKyst800 and was based on the global inverse barotropic model of ocean tides (TPXO7.2; Egbert and Erofeeva, 2002).

The river runoff was primarily based on daily climatology from estimated discharge data provided by the Norwegian Water Resources and Energy Directorate (NVE; Beldring *et al.*, 2003), but we used measured river runoff data from the rivers Altaelva, Halselva and Tverrelva (see locations in Figure 1), also provided by the NVE. The Alta river is by far the largest river in this region with an approximate mean runoff of 200 m^3/s for the summer season (May–September), and with enhanced discharge during the spring melting of snow in May/June. The maximum discharge in 2015 was 700 m^3/s at the beginning of June and the mean runoff for May–September was 220 m^3/s, which is within one standard deviation from the mean runoff for the period 1990–2015.

It is well-known that the near-surface winds are highly influenced by the local topography, and that sufficiently high model resolution is required to predict local winds (Sandvik and Furevik, 2002; Ágústsson and Ólafsson, 2007). Previous work has also shown that increased resolution of the atmospheric forcing improves the ocean circulation in fjords significantly (Skogseth *et al.*, 2007; Myksvoll *et al.*, 2012). High-resolution atmospheric forcing was provided by applying the Weather Research and Forecasting model (WRF, http://www.wrf-model.org/) on a 3-km resolution grid, sufficient to resolve the topography well. A detailed description of the WRF model can be found in Skamarock *et al.* (2008). The WRF model domain was initialized with analysis of upper air and surface data from the European Centre for Medium Range Weather Forecasts (ECMWF). The lateral boundary values were included every 6 h during the integrations. The output was stored every third hour and in addition to wind, mean sea level pressure, air temperature, air specific humidity,

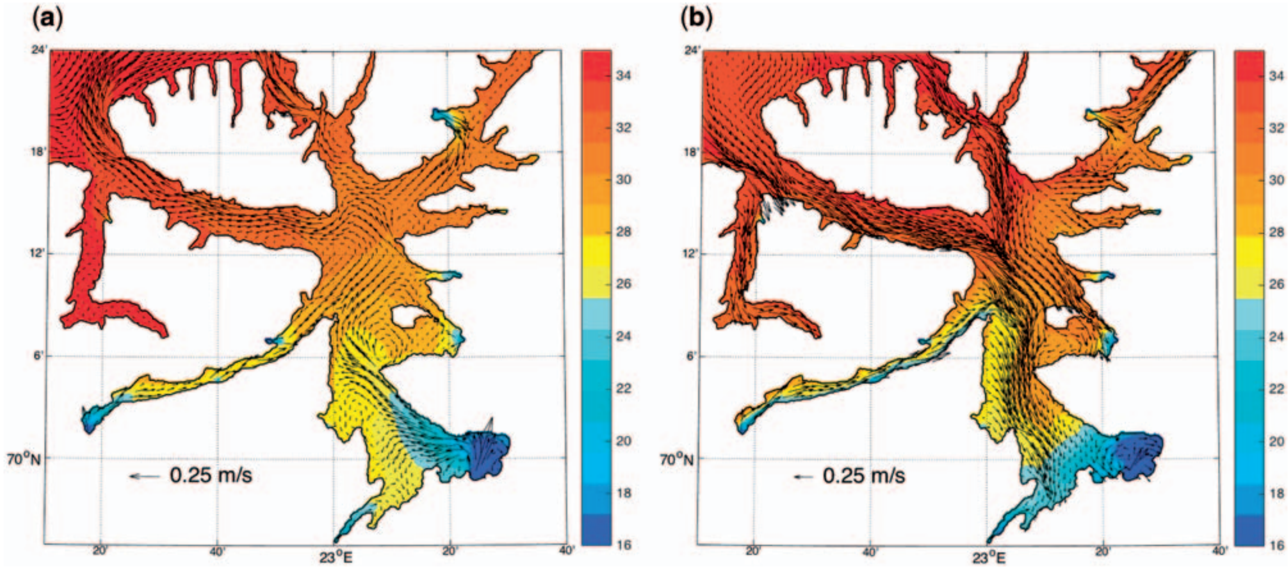

Figure 3. Simulated surface currents (vectors) and surface salinity in Altafjorden, averaged for (a) two summer months (June–July 2015) and (b) 1 day (24 h, 29 June 2015).

cloud cover and precipitation were applied in the 800 m and the 160 m ocean model simulations.

All variables, such as temperature, salinity, current speed and current direction, from the hydrodynamic model were saved every hour and provided input to the particle tracking model. Neither data assimilation nor surface relaxation was applied.

Field measurements

A moored Acoustic Doppler Current Profiler (ADCP) was deployed on the western side of the fjord (Figure 1) in the period 21 May – 19 July 2015. The ADCP measurements were sampled at 10-min intervals and averaged over 1 m bins in the upper 40 m of the water column. The measurements have been de-spiked using |2 m/s| as the limit. Due to the side lobe effect from reflectance of the three-angled sound beams at the surface, the current in the proximity of the surface will not be calculated correctly (overestimated) and the upper four bins (shallower than 4 m depth) are not used in the analysis.

Vertical profiles of temperature and salinity were measured in the upper 30–50 m of the water column with a SAIV STD/CTD SD204 along sections across the fjord basin and straits, see Figure 1 for positions, at the following dates: 21 May, 1–2 July and 18–19 July 2015. The upper bound of accuracy of the SD204 is $\pm 0.01^{\circ}$C for temperature and 0.02 for salinity, which is sufficient for fjord waters where variations in temperature and salinity are typically large, i.e. $\sim$1 or larger on the unit scale.

Datasets

Atmospheric data were obtained from the Norwegian Meteorological Institute (www.eklima.no); six-h measurements of wind speed and direction (10 m) and air temperature (2 m) for the period 2000–2015 from Alta airport in Alta to Hasvik airport in north-western Sørøysundet. Data on *river runoff* from major rivers draining into the Altafjorden system were provided by the Norwegian Hydrographic Service (NVE). *Hydrographic* measurements of temperature and salinity profiles at the Ingøy fixed coastal hydrographic station were downloaded from the Institute of Marine Research (IMR) database (http://www.imr.no/forskning/forskningsdata/stasjoner).

Results

Fjord hydrography and circulation

The fjord waters in Alta are layered in summer, with a relatively warm (10–14°C in July) and reduced salinity surface layer of thickness 5–10 m, overlaying more saline and colder waters, as seen both in the model and measurements. The modelled salinity is typically 22–30 in the main fjord basin of Altafjorden, and less than 20 in the inner part of the fjord and fjord arms near river mouths. The river water from Altaelva form a low-salinity layer that spread out along the eastern side of the fjord most of the time, but are sometimes also pushed by the wind over to the western side of the fjord basin. The vertical salinity gradients are strong within the surface layer, and the salinity increases to 32 at 5–10 m depth. We focus on the upper 20 m in the following, since this is the depth interval where the lice are present. The modelled surface currents averaged over two summer months show a classic fjord circulation pattern with strongest outflowing currents along the eastern shore in the inner part of the fjord (Figure 3a). The averaged surface currents have an offshore direction trough Rognsundet and Stjernsundet, while there is a net inflow through Vargsundet. In Stjernsundet, the averaged current is strongest along the northern side of the sound. However, in shorter periods the circulation pattern can be quite different; Figure 3b shows one example of daily averaged surface currents directed southwards in the main fjord basin, with inflow through Stjernsundet and Rognsundet and outflow through Vargsundet, i.e. a reversal relative to the summer-mean flow. During the following two days when the winds were weak, the surface waters flowed northwards and out through all three inlets (not shown). The daily averaged modelled currents revealed periods of all combinations of in- and outflow through the three inlets, typically lasting from one to three days (not shown). The model results indicate large variations in the fjord circulation on time scales from hours to days and weeks, including both horizontal and vertical velocity shear. In the main part of Altafjorden and in Stjernsundet, the surface currents can be oppositely directed across the fjord/inlet. The strong mean surface currents shown in Figure 3a were confined to the upper 5 m on the eastern side and shallower (< 1 m) on the western side of the fjord basin, while the currents below 5 m depth were headed in the opposite direction (not shown). During other periods the surface layer flowed in one direction, overlaying a circulation with inflow on one side and outflow on the other side. Hence, the classical assumption of a steady-state fjord circulation is not sufficient to resolve the dynamics relevant for the lice dispersion.

Comparing modelled and measured hydrography and currents

The model reproduced the known general water mass distribution in Altafjorden, with a low-salinity upper layer covering the fjord and lowest salinities most often along the eastern shore. This was confirmed by the observations from the three short (1–2 days) CTD surveys carried out during calm wind conditions (Figure 4c and d). Furthermore, the model reproduced the seasonal heating from May to July (not shown). Although the observed water mass distribution supported the model results, the model vertical temperature gradients were weaker than observed overall (Figure 4b and d). The model temperatures below the surface layer were on average 1–2.5°C higher than the observed temperatures (Figure 5, right panels). The temperature variability was high in both model and observations in July, when the modelled temperatures were on average 1°C lower than the observed temperature at the surface (Figure 5, right panels). The modelled vertical salinity gradients were weaker than those observed (Figure 4a and c), and the model salinity had a positive bias throughout the water column (Figure 5, left panels); the observed salinity below the surface layer was about 1 unit lower than modelled, while the difference in surface salinity varied between stations.

The model shows mainly a north-south direction of the current at the ADCP position, in agreement with the observations (Figure 6). However, the model tends to underestimate the current speed at the mooring position, especially toward the north, both at 5 m depth (Figure 6) and deeper below (not shown). A comparison between modelled and observed current speed and direction throughout the upper 40 m of the water column (disregarding the current observations from the upper 4 m due to reflectance in the observations near the surface) shows that the model biases are close to zero (Figure 7a), while the root-mean-square error (RMSE) reveals that the sign of the model—observation differences varies in time (Figure 7b). The biases and the RMSE are not sensitive to whether we choose daily or hourly-sampled de-tided currents. Yet, we find significant correlations ($p < 0.05$) between modelled and observed current speed between 5 and 10 m water depth, and between modelled and observed current direction between 5 and 15 m water depth (Figure 7c and d).

Particle tracking and salmon lice modelling

The particle tracking results were analysed in two ways. First, we present results from the model run where an equal number of particles were released from the farm locations. Thus, the results of infestation of *particles* depend on the oceanographic

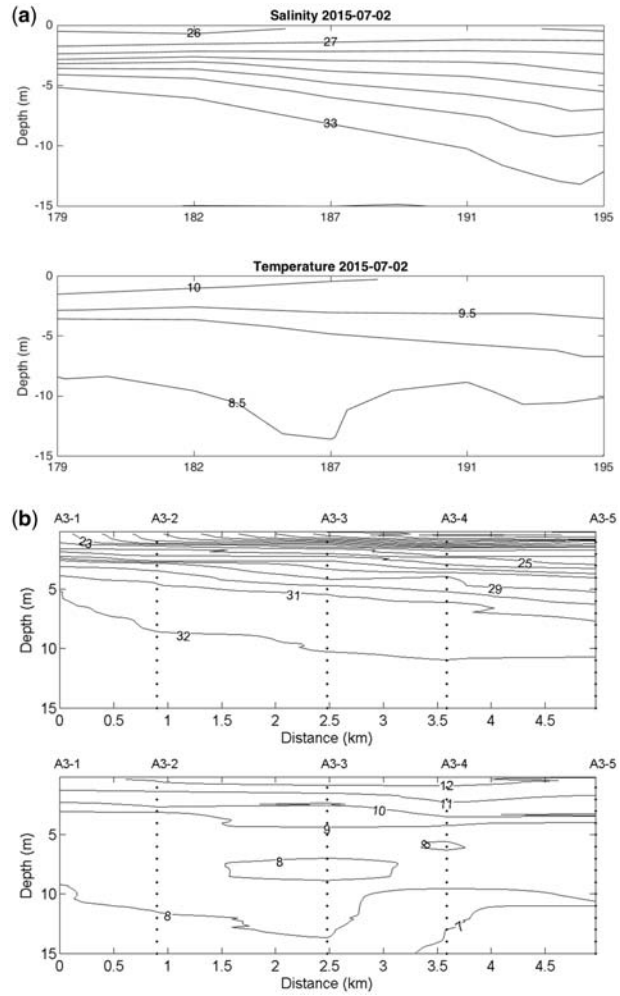

Figure 4. Modelled (a, b) and measured (c, d) salinity (a, c) and temperature (b, d) distribution across Altafjorden 2 July 2015 close to the mooring location and south of the border of the protected area, see Figure 1. West is left and East is right along the *x*-axis. The vertical stipled lines (c, d) marks the CTD stations.

conditions, and not on the actual salmonid production and presence of lice. Second, we present a quantification of realistic infestation, where the actual number of *lice* present in the farms in summer 2015 were used as input data (see Figure 2).

A connectivity matrix based on the equal amounts of particles released at each of the 21 farming sites (Figure 1) is shown in Figure 8. The matrix shows the number of particles (not lice) present during 90 days in the grid cells covering farm sites. The farms are located at the six geographical areas: Øksfjorden, Langfjorden, Årøya, Korsfjorden, Vargsundet and Rognsundet (see Figure 1). The connectivity matrix shows that the potentially highest farm-to-farm infestation was between farms within each of these geographical areas. To quantify the potential for local and regional infestation for the different areas, the number of particles arriving each farm site (1 grid cell) within the different areas were counted. The proportion of these particles originating from farm sites within that local area represent the local infestation, while particles originating from other parts of the fjord system represent the regional infestation. The regional infestation was largest

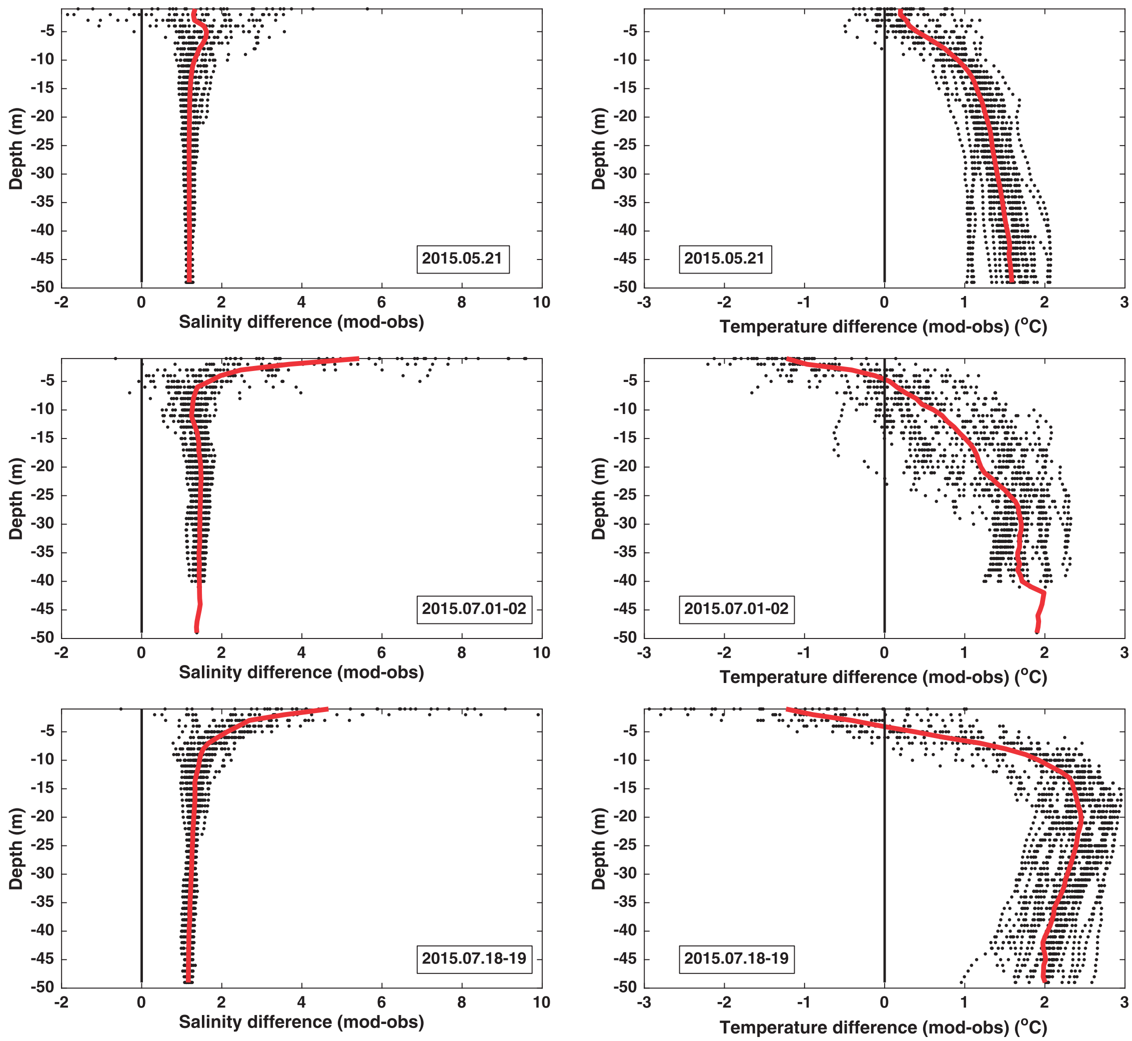

Figure 5. Difference between modelled and measured salinity (left panels) and temperature (right panels) on CTD stations surveyed on three cruises in May and July 2015 in Altafjorden. Each panel shows all CTD stations combined for one cruise. The solid red curves show the average bias for each cruise, while the black dots show the difference for all profiles.

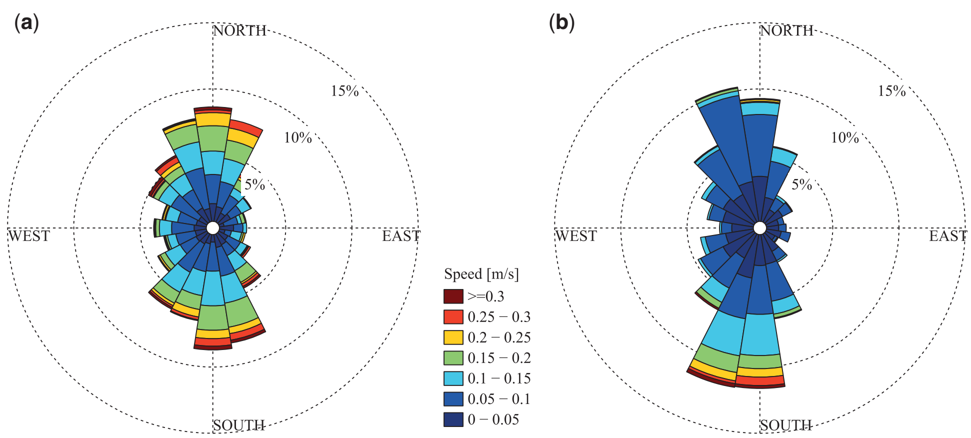

Figure 6. Frequency distribution of currents on the western side of Altafjorden based on 1-h resolution data of (a) measured and (b) modelled currents at 5 m water depth summer 2015. See Figure 1 for location of the current metre mooring. The sectors (each spanning 15°) represent the percentage (dashed circles) of currents toward each direction. For example, the sector pointing toward North from origo means northward currents, i.e. flowing out of the fjord. The colour scale denotes current speed (m/s) (see online version for colours).

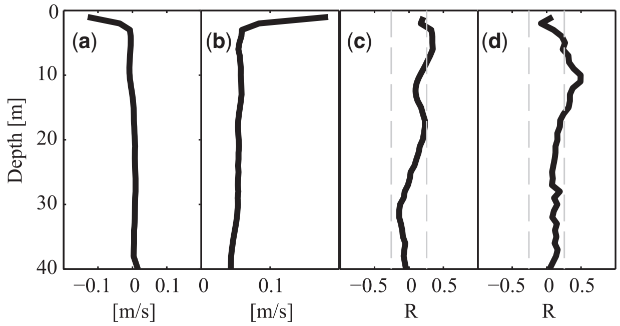

Figure 7. Comparison between modelled and observed ocean currents at the site of the moored ADCP (see Figure 1 for position). (a) Model current speed bias; (b) model current speed RMSE; (c) correlation between modelled and observed current speed. Dashed grey lines show 95% confidence level; (d) similar to (c), but showing for current direction. Both the model and observation data were interpolated to 1 m vertical resolution prior to the analysis. The large bias and RMSE in the upper 4 m is due to the noise from reflectance at the surface in the observational data.

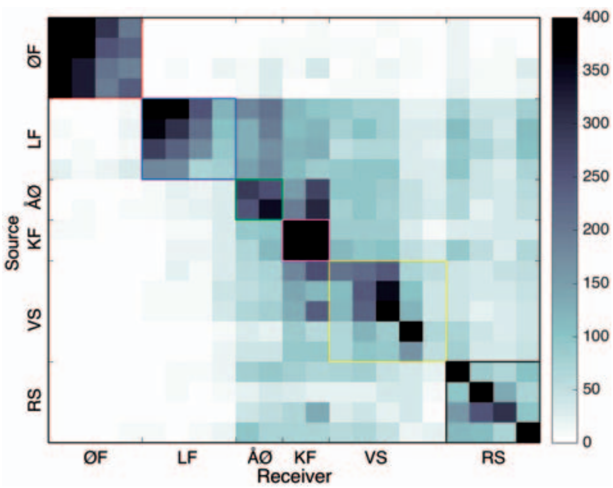

Figure 8. Model connectivity matrix of how the salmon farms potentially affect each other with salmon lice infestation. The grey-shaded colour scale denotes number of model particles, representing infestive copepodid stage, present in grid cells at farm locations integrated over 90 days (20 May–18 August 2015). The farms are grouped geographically around the fjord, and assigned by ØF (Øksfjord), LF (Langfjord), ÅØ (Årøya), KF (Korsfjorden), VS (Vargsundet) and RS (Rognsund). The *y*-axis lists the source of particles or lice, affecting the sites along the *x*-axis. The gray colour scale is limited to 400 to illustrate the pattern, but the largest values are > 1000 in ØF, KF and RS. The parts of the matrix representing local infestation within each of the geographical areas are squared with the same colours as used in Figure 1 (see online version for colours).

along the eastern side of the fjord (Årøya and Korsfjorden) and the sounds Vargsundet and Rognsundet (Figure 9a). Langfjorden contributed to infestation of the other areas, especially Årøya and Korsfjorden, but received relatively few particles (Figure 8). Øksfjorden is less connected to the other areas.

The ratio between local and regional infestation varied between the different geographical areas (Figure 9a). In Øksfjorden and Langfjorden, local infestation dominated, i.e. more than 90% and

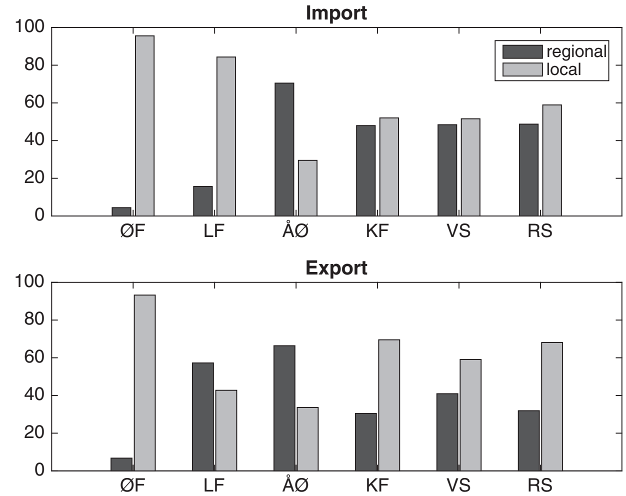

Figure 9. Simulated potential import (a) and export (b) infestation of salmon lice in different parts of Altafjorden: ØF (Øksfjorden), LF (Langfjorden), ÅØ (Årøya), KF (Korsfjorden), VS (Vargsundet) and RS (Rognsundet). (a) For each of the six parts of the fjord, the number of particle arrivals at farm sites were counted. The bargraph shows the percentage of these particles that originated from local farm sites (grey) versus farms sites in other parts of the fjord (black). (b) Out of the particles released from each part of the fjord, the number of particle arrivals at farm sites were counted. The bargraph shows the percentage of these particles arriving at local farm sites (grey) versus farm sites in other parts of the fjord (black). The simulation is based on equal hourly release of particles from all farms. The "age" of the particles represents the infestive copepodid stage of salmon lice (40–170 degree days) during the simulation period 20 May-18 August 2015. NB: Particles originating from other areas than those listed along the *x*-axis are not included in this analysis. See Figure 1 for locations of aquaculture sites.

80% of the particles arriving the farms had local origin. At Årøya more than 70% of the hits were by particles from other parts of the fjord, thus regional infestation dominated. In Korsfjorden and in the sounds the ratio was nearly one to one, with a slight dominance of local infestation.

To quantify how the farms in different parts of the fjord system potentially contribute to the export of particles to other areas, we counted how many of the particles released from the different farms that reached farm sites in other parts of the entire fjord system (regional infestation) compared with the local infestation. We found that farms in Øksfjorden contributed least to infestation of farms in other areas (Figure 9b); of those Øksfjord particles reaching a farm site, less than 10% of the hits were at farms outside Øksfjorden and thus contributing to regional infestation. In contrast, the farm sites at Årøya and Langfjorden contributed more to regional infestation (ca. 65% and 55%, respectively) than to local infestation. From Korsfjorden, Vargsundet and Rognsundet 30–40% of the hits were in other areas than the source area.

All areas contribute with particles drifting into the inner part of Altafjorden protected as a National Salmon Fjord (see Figure 1 and Table 1). The simulations show that 31–58% of the particles released within the main body of Altafjorden (Langfjorden, Årøya and Korsfjorden) drifted into the protected part of the fjord at ages representing the infective stage of the salmon lice (Table 1). A total of 18–20% of the particles released in the sounds, and 5% of the particles released in Øksfjorden reached the protected part of

Table 1. Proportion (%) of particles released from the different aquaculture areas of Altafjorden (Øksfjorden, Korsfjorden, Årøya, Langfjorden, Rognsundet, Vargsundet) reaching each of the protected National Salmon Fjord areas.

Release area	Alta	Repparfjord	Porsanger
Øksfjorden	5	< 1	0.1
Langfjorden	41	2	0.1
Årøya	58	3	<0.1
Korsfjorden	31	3	<0.1
Vargsundet	20	14	0.2
Rognsund	18	2	0.2

See Figure 1 for locations. Equal number of particles were released from each aquaculture site and tracked hourly on for 90 days (period 20 May–18 August 2015). Only the particles representing the infectious copepodid stage of salmon lice were counted within the salmon fjords. The number of particles reaching copepodid age (40–170 degree days) from each farm was 10 340$\pm$20.

Altafjorden while being infective (40–170 degree days). The other two National Salmon Fjords in western Finnmark, Repparfjorden and Porsanger, also received particles representing infective salmon lice from the aquaculture locations in Altafjorden. Repparfjorden received 14% of the particles released in Vargsundet, and 2–3% of the particles released elsewhere in Altafjorden, and less than 1% of the particles released in Øksfjorden. Porsanger, located 200 km downstream, did receive a few particles from all the areas in Altafjorden, but the share was of order 0.1%.

Figure 10 shows the potential influence area of copepodid particles from six parts of the fjord system, i.e. the integrated number of particles (not lice) of age 40–170 degree days per grid cell over a 90-days simulation, representing the spatially variable potential infestation from different sources in the fjord system. The colour scale is chosen to show the variation of particle distribution relative to release area. We see that particles may spread everywhere in the fjord system from all release locations, but the different farming areas do affect different parts of the fjord with high concentrations of particles. The maps show that particles released in Øksfjorden mostly affect locally and in Stjernsundet (Figure 10a), while the other areas affect the main part of Altafjorden and all three inlets. The bay south of Årøya obtains high numbers of particles independently of where the particles are released (except Øksfjorden). The inner, protected part of Altafjorden obtain large numbers of particles released in Langfjorden and Årøya. Although Øksfjorden has a weaker connection to the other areas, episodes of infestation from Øksfjorden to Altafjorden are likely to occur. There are two pathways for particles drifting from Øksfjorden and into Altafjorden: directly through Stjernsundet, or through Rognsundet via Sørøysundet, depending on the current direction along the coast and through the sounds. In periods when surface waters are piled up in Øksfjorden (onshore winds and currents), particles are aggregated here and can reach high concentrations in the surface waters. In a following period of outflowing water from the fjord, particles can be flushed out, and high concentration patches can be advected rapidly through Stjernsundet or around Stjernøya and into Rognsundet to Altafjorden. This mechanism may lead to episodes of unexpected and sudden infestation of lice in farms far away from Øksfjorden. Alternation between piling up of water and flushing of high concentration patches of particles are also seen in the fjord arms Korsfjorden and Langfjorden, and in the bay at Årøya. Particles aggregated in these areas can in periods be flushed through the sounds, or into the inner part of Altafjorden, depending on the currents and circulation at that time. Lice particles from all farming sites may be advected into Altafjorden, and the bay at Årøya in periods act as an accumulation area of particles from most farms, before the currents redistribute the particles as described above.

The spatial distribution of the total numbers of particles released from all farming sites (releasing an equal number of particles from all locations) is shown in Figure 11. The map shows that the highest numbers are found in the fjord arms, the bay at Årøya, and in the central part of the Altafjorden, also within the protected parts of Altafjorden.

For comparison with observations of lice pressure, the modelled lice abundance (using the actual number of lice based on reports from the farms as input data) were extracted for the two periods used in the monitoring programme for salmon lice on wild salmonids (Svåsand *et al.*, 2016). Figure 12 shows the abundance of infective copepodids in the upper 2 m of the water column, expressed as daily averaged numbers of lice per m^2 integrated over two 2-weeks periods; in July (weeks 27–28) and August (weeks 32–33). We use the scaling by Sandvik *et al.* (2016a) to classify the modelled concentrations as high or low. They found that model concentrations of 1.5 lice/m^2 (over time within an area covering 80% of 3 $\times$ 3 grid cells) represent conditions where post-smolts will get more than 10 lice attached, which is considered lethal for small fish (Finstad and Bjørn, 2011; Finstad *et al.*, 2011). Lice were present in all grid cells of the fjord in both periods, but only Øksfjorden had high levels of lice in the first period (Figure 12a). In the second period, the lice levels increased around Årøya and in the fjord arms on the eastern side of the fjord, and high levels ($>$1.5) were reached in the inner part of Korsfjorden (Figure 12b).

We then assume that all farms release the same number of lice as the farm releasing the most lice nauplii within each of the two periods. Note that the reported levels of lice at this farm were below the allowed upper limit of 0.5 lice/fish during both the two periods and the two preceding weeks. The resulting lice distribution shows relatively high concentrations of lice in the inner part of the fjord, and $>$ 1.5 lice/m^2 at Årøya, in Øksfjorden, Korsfjorden and other fjord arms during the first period (Figure 13a). During the second period, the areas experiencing lethal concentrations of lice ($>$ 1.5 lice/m^2) are larger, now also including the protected part of the fjord (Figure 13b).

Discussion

We have presented results from the first high-resolution modelling study of salmon lice growth and dispersal in a fjord under typical summer conditions in Finnmark, the northernmost part of Norway. In the following we discuss results from of our model system with respect to available observations (see "Representativeness of model results and observations" section), the modelled connectivity and infestation dynamics (see "Salmon lice dispersion and infestation patterns" section), and the implications of our findings for managing a potential growth of the salmonid aquaculture in the Altafjord region (see "Implications" sections).

Representativeness of model results and observations

It is not straightforward to interpret comparisons between observations and model results, because observations are snapshots in

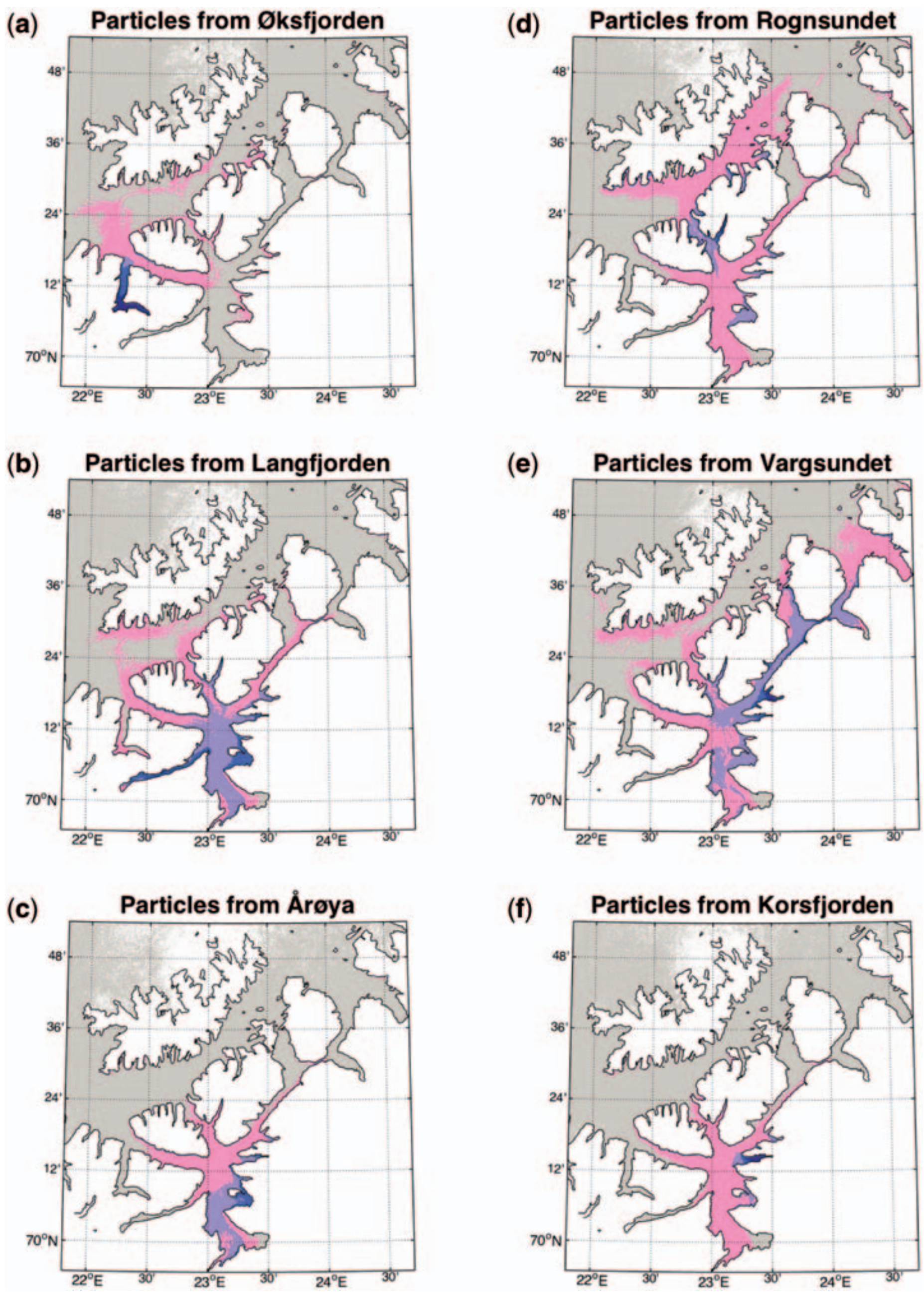

Figure 10. Potential influence area of each farming area. Spatial distribution of particles of age 40–170 degree days, originating from the different regions of the fjord system. The same number of particles (5) were released on each farm location every hour, regardless of the number of lice reported. The spatial distribution is integrated over 90 days. The colours show the number of particles per grid cell, integrated over 90 days: grey represents 1–50, pink 50–200, violet 200–500, blue 500–1000, and dark blue > 1000 (see online version for colours). See Figure 1 for locations of the farms.

either time or space, or both, often with an unknown error of representativeness, while model results represent average conditions over a volume continuous in time (Sandvik *et al.*, 2016b). The ROMS hydrodynamic circulation model has been evaluated in several studies from Norwegian waters by comparing with hydrographic and current measurements, both in regional, open-ocean applications (Lien *et al.*, 2013a, b, 2014; Skarðhamar *et al.*, 2015; Hattermann *et al.*, 2016; Lien *et al.*, 2016) and coastal applications (Myksvoll *et al.*, 2012; Asplin *et al.*, 2014; Johnsen *et al.*, 2014). Furthermore, ROMS has been utilized for drift studies and evaluated through comparisons with drifter observations as well as observations of ichthyoplankton dispersion (Vikebø *et al.*, 2011; Langangen *et al.*, 2014; Myksvoll *et al.*, 2014; Johnsen *et al.*, 2016; Sandvik *et al.*, 2016b, c). Generally, these studies conclude that the model hydrography, ocean currents, and particle drift and dispersion agree with observations with respect to general patterns, mean state, and variability on spatial scales resolved by the model. Simulations of salmon lice dispersion have shown that the model system used in this study is able to reproduce the lice infestation levels reported from the fish farms (Samsing *et al.*, 2016a) and through the national monitoring programme on wild salmonids (Sandvik *et al.*, 2016a).

Our model simulations of Altafjorden reveals the 3-D circulation and highly dynamic current regime described from field measurements in previous publications (Davidsen *et al.*, 2009, 2013; Svendsen, 1995). Similarly, our comparison between model and observations shows that the model reproduces the general pattern of the observed hydrography and currents in Altafjorden, including mean state and variability on spatial scales resolved by the model. However, as we have current measurements from one single location only, we do not know how the main current is positioned relative to this location, and how it varies spatially. Thus, the error of representativeness, which is unknown, may be significant for the measurements. We acknowledge that the information provided by the measurements is therefore limited and to be considered as indicative of the model performance. Thus, given the variable conditions in the fjord and the scarce data coverage of hydrography and currents in time and space, respectively, we cannot expect the modelled and measured variability to agree exactly in time and space on a detailed level, e.g. spatial scales smaller than ∼1 km. However, the model represents the water mass distribution, currents, and circulation in the fjord system within realistic ranges of variability.

The weaker vertical stratification in the model implies that the modelled surface layer is less decoupled from the water below the pycnocline compared with the observations. It is therefore likely that the model is underestimating the wind-driven vertical velocity shear in the upper few meters of the water column, i.e. that the model is underestimating the surface currents. We therefore consider the surface particle drift to be conservative regarding drift distance. The lower average surface temperatures in the model compared with the observations indicate that the period in which the salmon lice are infective is about one day too long in the model for lice near the surface, based on Samsing *et al.* (2016b). Similarly, the higher than observed model temperature below 5 m depth may reduce the infective period with approximately 1 day for lice deeper down. We consider the overall effect of biased temperature on the duration of the infective period to be minor, because 1 day accounts for less than 10% of the infective period, and the salmon lice are drifting in the depth interval 0–20 m.

We have investigated observations and modelling results from the summer of 2015. While we acknowledge the limitations by

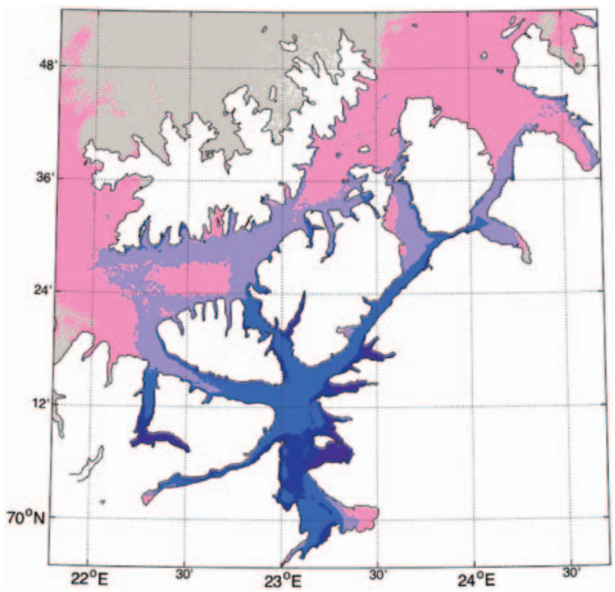

Figure 11. Spatial distribution of particles of age 40–190 degree days, released from the 21 farm sites shown in Figure 1. The same numbers of particles (5) were released on each farm site every hour. The colour scale shows the number of particles per grid cell, integrated over 90 days: grey represents 1–50, pink 50–200, violet 200–500, blue 500–1000, and dark blue > 1000.

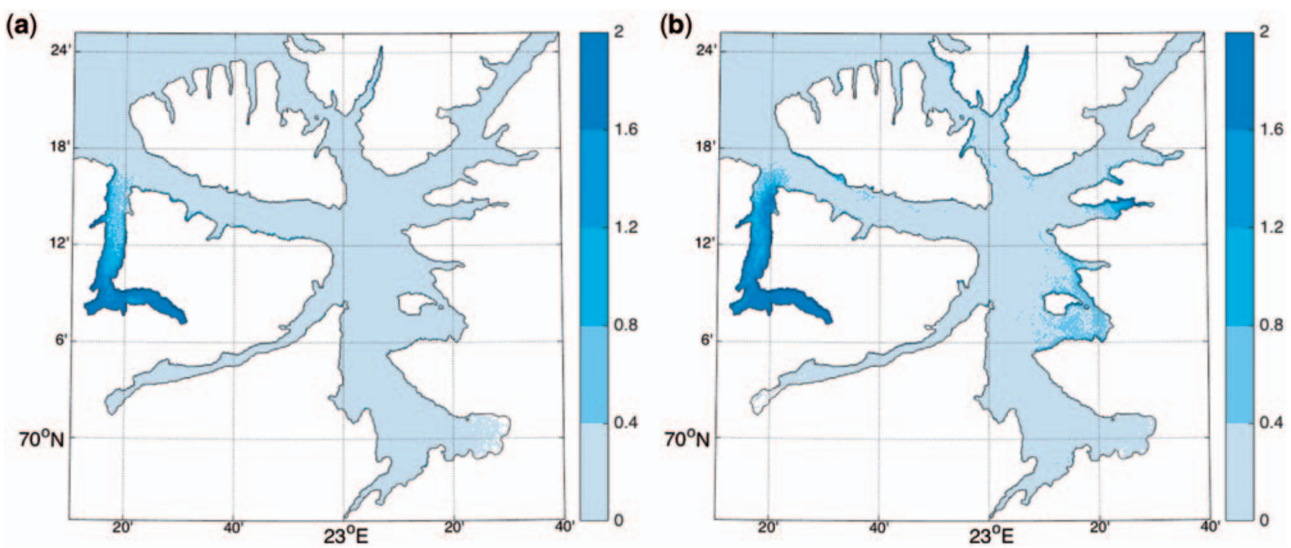

Figure 12. Modelled spatial distribution of infective salmon lice copepodids in (a) weeks 27–28 and (b) weeks 32–33 in 2015 in Altafjorden, corresponding to the periods of the salmon lice monitoring of wild salmonids, see Svåsand *et al.* (2016). The lice concentrations are modelled based on reported lice numbers from all fish farms and locations in Finnmark. The colour denotes number of lice copepods per m^2 within one grid cell of 160 m × 160 m (daily averaged values integrated over 14 days and at depth 0–2 m). Note that the maximum lice abundance exceeds the range of the colour scale.

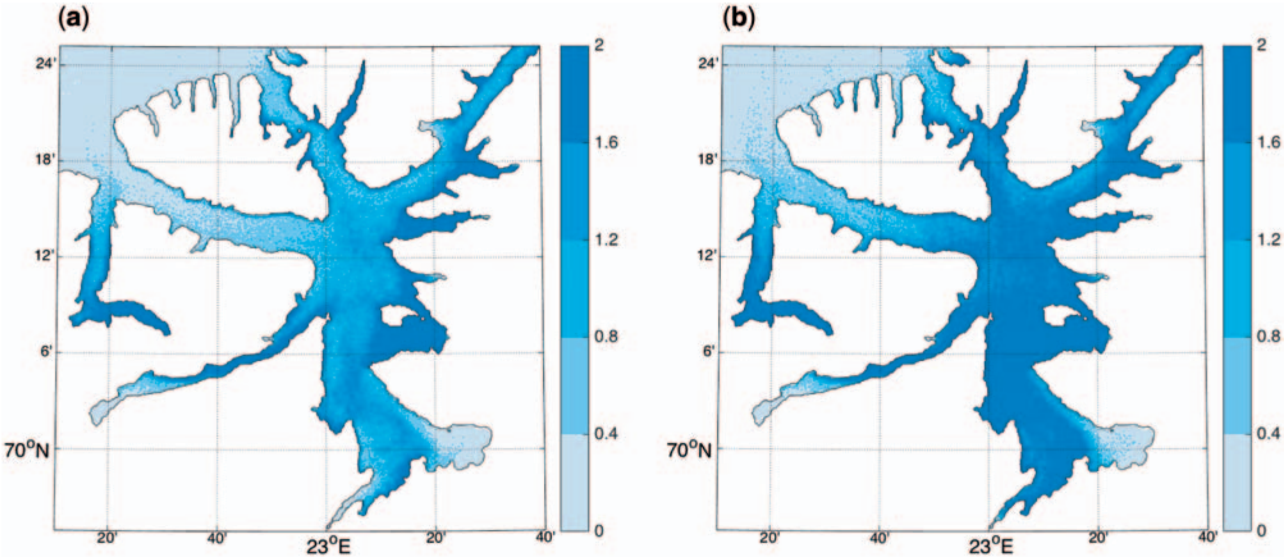

Figure 13. Modelled bad case scenarios with equal release of lice particles from 21 farm locations in Alta (see Figure 1), based on reported lice numbers from the farm with highest estimated lice production in the shown periods and the preceding 2 weeks. This farm reported lice below the allowed limit (<0.5 lice/fish) within both timeframes and the preceding 2 weeks. The maps show modelled spatial distribution of infective salmon lice copepodids in Altafjorden in (a) weeks 27–28 and (b) weeks 32–33 in 2015. The colour scale denotes numbers of lice copepodids per m^2 within grid cells of 160 m $\times$160 m (daily averaged values integrated over 14 days and at depth 0–2 m).

this approach, we argue that this period is representative of summer conditions with regard to hydrography and circulation in Altafjorden. The river discharge in 2015 was within one standard deviation of the 1990–2015 average. A modelling study of the coastal hydrographic conditions of Norway showed surface layer temperature below average on the coast in July 2015, and that the total runoff in western Finnmark was above average in spring and below average in June–July 2015 (Albretsen and Asplin, 2017), indicating an early spring flood and dry summer. Furthermore, hydrographic observations at Ingøy, located offshore of Altafjorden and in the Norwegian Coastal Current, show temperatures one standard deviation warmer than the long-term average from 20 m depth to the bottom during the summer of 2015. These coastal waters feed directly into Altafjorden through the three inlets. The modelled below-average surface layer temperatures agree with observations of air temperature at Alta airport, while air temperatures at the mouth of Altafjorden were close to average (not shown). Hence, the anomalies in both the temperature and salinity in summer 2015 would tend to weaken the vertical stratification compared with the climatological average. The wind conditions, as represented by mean and variance of wind speed, were close to the 2000–2015 average both in the inner and outer parts of Altafjorden (not shown), and the 2015 wind direction variability resembled the general pattern of wind direction variability for the period 2000–2015, both in the inner and outer parts of the fjord (not shown). Hence, we consider the modelling results for particle drift and the analysis for potential infestation between the different regions in summer 2015 to be representative for summer conditions.

Salmon lice dispersion and infestation patterns

Our results show connectivity, albeit to a varying degree, between all aquaculture farm locations in the area. The widespread dispersion of salmon lice with a fluctuating dispersion pattern and inter-farm connectivity agrees with previous studies showing that infective copepodids can spread several tenths of kilometres away from the source (Adams *et al.*, 2012, 2016; Salama *et al.*, 2013; Asplin *et al.*, 2014; Johnsen *et al.*, 2016; Samsing *et al.*, 2016a; Patursson *et al.*, 2017). Indeed, there are two planktonic non-infective nauplius stages prior to the copepodid stage, and coupled with the relatively strong and variable currents in the Norwegian fjords, the salmon lice are clearly designed to travel far away from its hatching area.

The set of ocean current forcing factors create retention areas and transient flushing events in Altafjorden. Together with the long planktonic life of the lice copepodids, typically 2 weeks under summer conditions in Finnmark, this gives rise to large spatio-temporal variability in lice concentration due to the potential for advection of high-concentration patches. Thus, infestation from Øksfjorden to farms in Altafjorden is related to episodes of inflowing currents through Stjernsundet, advecting large amounts of lice copepodids within a short time frame. This potentially leads to sudden infestation of farms in regions other than the source region. Hence, if a farm is unable to keep the lice at a low level, an epizootic may rapidly spread to other parts of the fjord. Such rapid variability due to environmental conditions has also been shown by Asplin *et al.* (2014), Adams *et al.* (2016), Johnsen *et al.* (2016) and Salama *et al.* (2016), and illustrates that transportation of water masses inside the Norwegian fjords are episodic with typical periods from hours to several days, and governed by the variability of the stratified water masses of the coastal current outside the fjords and episodic winds associated with passing atmospheric low-pressure systems (Asplin *et al.*, 1999, 2014; Stigebrandt, 2012). Thus, the relatively high-frequency tidal currents are important for transportation over shorter distances only, typically on the order of a few kilometres.

The model parametrizations of salmon lice growth, development and behaviour are based on scientifically published knowledge, and will be updated when new knowledge on salmon lice biology is made available in peer-review literature. A recent improvement in the model was the change in temperature dependent duration of the copepodite phase (Samsing *et al.*, 2016b). We expect that new knowledge of infestation efficiency and mortality rate will be gained in the future, and the model parametrizations of these will be refined accordingly. Vertical migration, as response to light and salinity, is included in the model, and is important for the lateral dispersion of lice when the horizontal currents vary with depth (Johnsen *et al.*, 2014). Although the vertical positioning of the lice during the planktonic stages is not fully understood, the vertical distribution of model lice has been shown to coincide well with experimental studies of lice levels on fish (Samsing *et al.*, 2016a). The swimming speed of salmon lice (Gravil, 1996; Fields *et al.*, 2017) is much lower than typical horizontal current velocities, and the lice are not able to significantly influence their positioning in the horizontal. No swimming in the horizontal by the lice is therefore implemented in the model. Changes to the parametrizations of salmon lice biology, as described above, can affect the modelled lice abundance and concentrations quantitatively. However, based on earlier studies where the model results are compared with observations (Samsing *et al.*, 2016a; Sandvik *et al.*, 2016a), it is reasonable to assume that the spatio-temporal dispersion patterns presented here will likely be similar.

Juvenile salmon (post-smolts) migrate from the Alta river at the innermost part of the fjord and follow the surface currents to the ocean (Davidsen *et al.*, 2009) in June/July. A programme monitoring the salmon lice assessed the risk of lice-induced mortality for salmonid post-smolts to be low during the first half of July 2015 (weeks 27–28) and high for trout and char in August (weeks 32–34) (Svåsand *et al.*, 2016). A similar seasonal pattern of low to moderate risk for post-smolts during their migration in June–July, followed by increased risk for trout and char from mid-July and in August due to higher temperatures and faster lice development and reproduction, has been shown also for other years (Bjørn and Finstad, 2002; Bjørn *et al.*, 2007). Thus, for the present conditions in Altafjorden, the wild salmon post-smolts can migrate with relatively low risk of being infested by salmon lice in the fjord and the inlets (Bjørn and Finstad, 2002; Svåsand *et al.*, 2017).

When we use the actual lice counts from the farm locations as initial conditions, our model system reproduces the pattern of lower lice concentrations in June and July and increased concentrations in late summer on the eastern side of Altafjorden, in accordance with the observed high level of infestation on wild salmonids reported here (Svåsand *et al.*, 2016). However, the reported high level of infestation in Talvik in the protected part of Altafjorden in late summer (Svåsand *et al.*, 2016) was not reproduced in the model. While the model could be underestimating the currents and subsequently the transport into the fjord and a potential retention area in this part of the fjord, another possible explanation is a salmon slaughterhouse located in Alta (see Figure 1). Here, salmon is kept in open storage cages in the sea before being slaughtered, without requirement to report lice counts. Thus, the salmon lice that are not accounted for in the model initialization may explain the discrepancy between modelled and observed lice concentrations.

Implications

To prevent decimation of wild salmonid populations, the authorities have imposed an allowance of up to 0.5 adult female lice/fish on average per cage. A new regulation (2017) lowered this limit to 0.2 lice/fish during weeks 21–26 in Northern Norway. Most farms in the Altafjorden area reported lice counts below, and many farms far below, the allowed limit of 0.5 lice/fish during summer 2015. To investigate a scenario where all farms experience relatively high lice levels, we performed a simulation using salmon lice input data from the farm with the largest production of lice eggs (estimated from reported lice numbers and salmon biomass) for all farms in Altafjorden. The reported numbers were 0.14-0.32 lice/fish, i.e. well below the allowed limit of 0.5 lice/fish. In this model scenario, a substantial part of the fjord, including parts of the protected area, experienced lice concentrations considered to be lethal to wild post-smolts, following Sandvik *et al.* (2016a). Furthermore, concentrations where negative effects may start to occur were found throughout large parts of the fjord during the migration period (June–July). Hence, under the current regulation regime, the infestation risk could become severe for wild salmonids even when all farms keep their lice concentrations below the allowed limit. Also, any growth in the total number of farmed salmon could further add to the infestation risk. These findings do question the effectiveness of applying a regulation based on allowed number of lice per fish rather than an upper limit to the total number of lice nauplii release allowed within a given production area. Furthermore, our results show that the effect of protecting the inner part of the fjord may be limited, even during conditions where all farms keep their number of lice per fish within the allowed limit. This corroborates the findings of Serra-Llinares *et al.* (2014), who concluded that protected areas less than 30 km across have limited effects. Indeed, our results show that even the downstream fjord Repparfjorden, also a National Salmon Fjord, is affected by lice from Altafjorden, although the impact is limited.

If the number of salmon farm locations in Altafjorden and/or the production quotas on the existing locations are increased in the future, we can expect that the total number of hatched lice will increase. Subsequently, the risk of population-reducing effects caused by salmon lice on wild salmonids will likely increase, even when farmers keep the number of lice within the presently allowed limit of 0.5 lice/fish.

Our results underscore the need for a revision of the current regulation regime, which is based on a simple rule of a maximum allowed number of lice per fish disregarding how many fish the farm carry or where it is located. Rather, our results call for assessing the total salmon lice pressure within a given geographical area by considering geographical connectivity and exchanges of water masses. Furthermore, the complex and unpredictable nature of the spatio-temporal variability of lice distribution arising from the physical factors determining lice dispersion, calls for a precautionary approach to management and regulation. Especially the regulation of the regions adjacent to any protected area needs to be carefully considered in order to obtain the desired effect of protection.

Acknowledgements

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