



Optimal estimation of lice release from aquaculture based on ambient temperatures

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ABSTRACT: Models for mapping and forecasting infective pressure from salmon louse *Lepeophtheirus salmonis* larvae are of major importance in the Norwegian government's management of salmonid aquaculture. These models use site-reported temperature and number of egg-producing female adult lice present within cages to calculate how many lice eggs and larvae are released from individual farms. The reported temperature is critical in this calculation, as temperature influences both frequency of 'spawnings' and egg developmental time until hatching. Farms report temperature measured at 3 m depth, as defined by regulation. However, the salmon themselves, and therefore also the attached female lice and their eggs, often swim deeper to meet their preferred temperature within the water column. This study compares calculated lice egg production based on reported temperature at 3 m depth to calculated lice egg production based on a hydrodynamic ocean model of temperature stratification and salmon-preferred temperature in the modelled stratifications. The results clearly show that present legislated routines with farm site temperature measurements at 3 m depth lead to underestimation of egg and larvae production in winter and overestimation in summer for a range of sites. Future mitigating management and models of lice output should use the temperature measured or modelled for the depths the salmon predominantly occupy.

KEY WORDS: *Lepeophtheirus salmonis* · Marine parasites · Aquaculture · Marine epidemiology · Vertical behaviour

1. INTRODUCTION

The salmon louse *Lepeophtheirus salmonis* (Krøyer, 1837) is a major limiting factor for further salmon aquaculture growth in Norway (Torrissen et al. 2013, Taranger et al. 2015). According to legislation, all Norwegian production sites must ensure that the average lice infestation level remains below 0.2 adult female lice per fish in spring and early summer (during the migration period of wild Atlantic salmon *Salmo salar* L.) and below 0.5 adult female lice per fish the rest of the year (NFD 2012). Still, with almost 1000 times more farmed salmonid fish than returning wild salmon (Vitenskapelig råd for lakseforvaltning

2014, SSB 2018), the natural parasite–host interaction is distorted. At a regional scale, even legal densities of salmon lice on the fish can produce conditions exceeding carrying capacity of wild Atlantic salmon and sea trout *Salmo trutta trutta* (Skaala et al. 2014, Skarðhamar et al. 2018).

Based on calculated lice dispersion along the coast, the Norwegian coastline is divided into 13 salmonid aquaculture production areas (NFD 2017a). To evaluate in which production areas the aquaculture industry can grow sustainably with respect to the environment, a new regulation has been implemented (NFD 2017b). This regulation is popularly termed the 'traffic light' system, as it grades areas according to the

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colours green (growth is allowed), yellow (no growth is allowed) and red (production must decrease). The colour classification is based on an expert group's evaluation of likely impacts on wild salmon and sea trout (NFD 2015, Vollset et al. 2017). This evaluation is, to a large extent, based on models mapping infestation pressure from salmon lice larvae on wild Atlantic salmon and sea trout. These models have therefore become of major management importance.

The number of fish in the sea cages of salmon and trout farms are required to be reported monthly by fish farmers to the Norwegian Directorate of Fisheries (NFD 2008). Farmers must also report the average number of adult female lice weekly to the Norwegian Food Authorities, along with temperature as measured at 3 m depth (NFD 2012). These numbers are used in the current lice models to predict the number of nauplii released from farms. Further, the distribution of the estimated lice release is calculated using a hydrodynamical model system to estimate the concentration of infestive salmon lice larvae along the coast (Asplin et al. 2014, Johnsen et al. 2014, Sandvik et al. 2016, Samsing et al. 2017). Both the number of eggs produced per egg-string and the development time of salmon lice eggs are strongly temperature-dependent (Samsing et al. 2016b, Hamre et al. 2019). The relationship between temperature and development time is non-linear, and alterations

in the temperature cause especially large differences in development time at low temperatures ($<10^{\circ}\text{C}$) (Samsing et al. 2016b, Hamre et al. 2019).

The reported temperatures at 3 m depth have a major impact on model calculations, but there are often steep vertical gradients in temperature (thermoclines) along the Norwegian coast and especially in inner parts of fjords (Farmer & Freeland 1983, Cottier et al. 2010, Inall & Gillibrand 2010). The size, direction and position of thermoclines depend on local hydrodynamic conditions, weather and season. Typically, the water is colder near the surface during the winter and warmer near the surface during summer (e.g. modelled temperature gradients in 2 fjords: Fig. 1). Salmon position themselves according to these gradients, with several studies showing a strong preference towards a temperature of about 16°C (e.g. Oppedal et al. 2011a,b, Stien et al. 2014, 2016, Oldham et al. 2017) and avoidance of higher or lower temperatures (e.g. Oppedal et al. 2001, 2011a,b, Folkedal et al. 2012, Dempster et al. 2016, Stehfest et al. 2017). When temperature profiles are reasonably homogeneous (i.e. $<1^{\circ}\text{C}$ temperature difference within a cage), temperature does not strongly influence the salmon's vertical distribution (Juell et al. 2003, Juell & Fosseidengen 2004, Stien et al. 2014). Without vertical temperature gradients, fish are more spaced out and choose their swimming depth by other parameters, such as deeper swim-

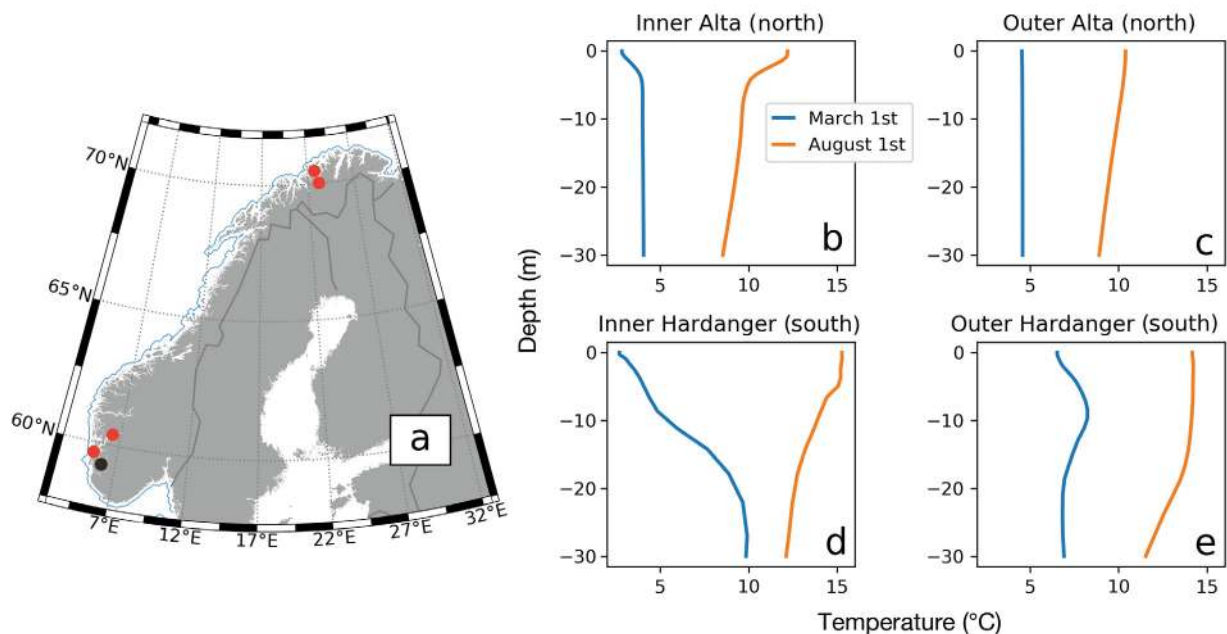


Fig. 1. (a) Scandinavian Peninsula. Blue line: Norwegian coastline, with the shortest distance to this line used for gridding of data. Black dot: fish farm Langavika. Red dots: geographical positions of the vertical temperature profiles in (b–e). (b–e) Temperature profiles from 1 March and 1 August in (a,b,c) northern and (d,e) southern fjord

ming during the day and shallower at night, tighter 'schooling' during the day and more disperse 'shoaling' at night, attraction towards artificial light sources at night and coming to the surface when hungry or during feeding (reviewed in Oppedal et al. 2011a, Stien et al. 2013). Caged salmon may avoid surface waters in daytime under significant wave heights of 2–2.5 m (Dam 2015); however, knowledge of nighttime behaviours in wavy conditions are lacking, and salmon are known to migrate towards the surface layers during nighttime (Oppedal et al. 2011a). With increased current speeds, salmon group structure gradually changes from only circular swimming to standing on the current maintaining a fixed position (Johansson et al. 2014, Hvas et al. 2017), while no indications have been made of a change in vertical position.

Behavioural temperature preferences of farmed salmon in a vertically stratified water column are likely to reduce the reliability of estimates of salmon lice egg developmental rates if the temperature measured at 3 m depth is unrepresentative of the temperature that the lice eggs actually experience. It is therefore likely that the rate of hatching of salmon lice will be better estimated if the models incorporate information of the temperature at the swimming depth of the host fish. One possible solution is to use the temperature gradients from the ocean model (Albretsen et al. 2011) and use the salmon's preferred temperature in these gradients as the temperature input instead of temperature at 3 m depth.

The present study compares predictions of salmon lice larval production using (1) model data of temperature and modelled preferred swimming depth of salmon to (2) actual data from a salmon production aquaculture site where we have both temperature–depth profiles and partial data on vertical position of the fish. First, we compare how the ocean model simulated temperatures compare with the observed temperatures. Second, we propose a model estimate of the temperature representative for depth where the farmed fish reside. Finally, we present the seasonal effect of this estimated temperature on the estimated lice release from all approved farm locations along the Norwegian coastline.

2. MATERIALS AND METHODS

2.1. Farm observations

A dataset from a previous project was used in which we had monitored water temperature and fish

behaviour in a cage from sea transfer to slaughter (Stien et al. 2009). On 9 May 2007, ~70 000 Atlantic salmon smolts were transferred to a sea cage (24 × 24 m, 20 m deep) at the Centre for Aquaculture Competence, a large-scale research facility in Langavika, Rogaland, Norway (59.23° N, 6.01° E; Fig. 1a). The vertical distribution of the fish within the cage was observed continuously using a PC-based echo integration system (Lindem Data Acquisition) until 31 December 2007. The transducer was facing upwards with a 42° acoustical beam angle and positioned at ~23 m depth in the centre of the cage. A mean value of echo observations (60 pings min⁻¹) was recorded at 0.5 m depth intervals from 0.5 to 20 m. Fish distribution was estimated by the relative echo strength per half metre (Bjordal et al. 1993). Temperature was measured continuously at 1, 7 and 20 m depths (Akvasmart, AKVA Group) and recorded as daily mean values per depth. In addition, a vertically profiling CTD (SD204, SAIV AS) connected to an automatic winch (HF5000, Belitronics) provided detailed temperature profiles for selected time periods. The fish were harvested from the cage on 26–29 November 2008.

2.2. Temperature from the ocean model

The temperature input was obtained from a numerical coastal model covering the whole Norwegian coast with 800 × 800 m horizontal resolution and 35 vertical layers (Shchepetkin & McWilliams 2005, Albretsen et al. 2011). The model includes tides, runoff from land, heat exchange with the atmosphere and is coupled with a 4 km horizontally resolved ocean model at the open boundary. The model outputs hourly values including temperature, salinity and currents. To evaluate the correspondence between modelled and observed temperature, we compared the corresponding daily temperatures at 1, 7 and 20 m depths from the model predictions versus the observations from the Langavika site. Further, a full vertical temperature gradient from the model was used to estimate a temperature representative for the periods with observed vertical distribution of the fish.

Monthly averages of the vertical temperature distribution were calculated from a 10 yr simulation (2005–2015) for all sites along the coast. The monthly temperatures were used to evaluate seasonal differences between the estimated lice release from fish farms based on temperature from 3 m depth and the temperatures representative for the fish distribution (see below).

Table 1. The 4 modelled temperature estimates used in this study to obtain a proxy temperature for when the vertical positioning of fish is unknown

Modelled temp.	Depth	Comment
Estimate 1	3 m	Corresponds to the temperature currently used to estimate salmon lice production at farm sites
Estimate 2	0–40 m	Average temperature in the upper 40 m of the water column. This is the typical depth of net pens and corresponds to the vertical depth available for farmed fish
Estimate 3	Variable	Temperature weighted by a Gaussian curve centred on the maximum temperature <16°C, having a fixed standard deviation of 4 m
Estimate 4	Variable	Temperature weighted by a Gaussian curve centred on the thermocline, with a fixed standard deviation of 4 m

2.3. Estimates of representative temperatures

To obtain a proxy temperature for use when the vertical positioning of the fish is unknown, we selected 4 alternative temperature estimates from the model (Table 1: fixed depth, vertical mean depth and 2 dynamic alternatives). By comparing each of the estimates to the mean value weighted by the normalised observed vertical distribution of the fish at Langavika, herein referred to as the fish weighted average (FWA) temperature, we evaluated how representative the estimates are in calculating the development time of salmon lice eggs on fish farms. The estimates are compared to the FWA temperature by calculating the Pearson correlation coefficient (PCC) and root mean square deviation (RMSD), which gives the linear correlation and the difference between the 2 datasets. A perfect linear fit between 2 datasets would give PCC = 1 and RMSD = 0.

We used the temperature estimate that was closest to the FWA temperature at the Langavika site, i.e. the temperature experienced by the fish and lice. This estimate was compared to the temperature modelled at 3 m depth (Estimate 1: current practice) for all approved farm sites in Norway (per August 2018). To investigate seasonal variability in the temperature field, modelled monthly averages of the temperature in the period 2005 to 2015 were used. The temperature differences were spatially clustered in a grid, with distance from coastline along one axis and latitude along the other axis. The coastline, for this calculation, was defined as the line with no land within 10 km, shown by the blue line in Fig. 1a. The resolution of the spatial grid was set to 10 km in the distance from the coast and 0.5° along the latitudinal dimension. The temperature difference between the most realistically modelled estimate and the mod-

elled 3 m temperature was used to calculate the corresponding changed production of salmon lice larvae, i.e. the altered hatch rate of lice by using Estimate 4 compared to Estimate 1 (Table 1).

RMSD, correlation coefficients, and linear regressions were calculated using the `scipy.stats` function in Python (<https://docs.scipy.org/doc/scipy/reference/stats.html>).

2.4. Estimating the salmon lice release

The number of salmon lice released per adult female (hatch rate) was estimated for all approved farm locations (per August 2018). The hatch rate was estimated from previous studies and combines a calculated number of lice per egg-string and the number of days between hatching, both being a function of temperature.

The number of eggs (N_{eggs}) per egg-string was calculated using Eq. (1) from Samsing et al. (2016b):

$$N_{\text{eggs}} = e^{\{\beta_0 + \beta_1 \times \frac{t}{t_c} + \beta_2 \times [\ln(\frac{t}{t_c})]^2\}} \quad (1)$$

where $\beta_0 = 5.6$, $\beta_1 = -0.43$, $\beta_2 = -0.78$, t = the salmon lice ambient temperature and t_c is a temperature constant set to 10°C.

Further, the number of days between hatching (D_{hatch}) was calculated using Eq. (2), from Hamre et al. (2019):

$$D_{\text{hatch}} = 0.25 \times \left[\frac{5.0}{(\alpha_0 \times t^2 + \alpha_1 \times t + \alpha_2)} \right] \quad (2)$$

Here, t still denotes the ambient temperature, $\alpha_0 = 4.85 \times 10^{-4}$, $\alpha_1 = 8.667 \times 10^{-3}$, and $\alpha_2 = 3.75 \times 10^{-3}$. Adult female salmon lice develop eggs in 2 egg-strings, and we assumed no time between egg

batches. Hence the hatch rate per female louse per day was calculated following Eq. (3):

$$\text{Hatch rate} = 2 \times N_{\text{eggs}} / D_{\text{hatch}} \quad (3)$$

The calculated hatch rate per adult female per day (from Eq. 3) at temperatures ranging from 3 to 18°C is shown in Fig. 2. Mate limitation was previously calculated to reduce the release rate of salmon lice eggs, when the average number of lice on the fish is below 0.2–0.5 per fish (Krkošek et al. 2012, Stormoen et al. 2013). In the present study, we considered the potential hatch rate of salmon lice at different temperatures, and no mate limitation is considered in the calculation.

3. RESULTS

3.1. Observed and simulated temperature

The simulated temperatures at 1, 7 and 20 m depths from the ocean model were in good agreement with the observed temperatures at the farm when looking at the 512 overlapping daily values (Fig. 3). However, the model slightly underestimated the vertical temperature gradient, where the model on average predicted lower temperatures compared to the observations at 1 and 7 m depths, and higher temperatures at 20 m depth. The averaged difference and RMSD between modelled and observational values can be seen in Table 2. Temperature fluctuations were apparent at seasonal scale, as were fluctuations on a scale of a few days (Fig. 3). These short-term fluctuations are caused by water exchange between the fjord and the open ocean. The range of the temperature oscillations decreased with depth, and the seasonal fluctuations were delayed deeper in the column. As the temperature fluctuates with the season, a transition occurred late September 2007, with the warmest layer changing from the surface to deeper in the water column. This lasted until the beginning of April 2008. The shaded area in Fig. 3 denotes the time periods when the water was warmer at 20 m depth compared to the water at 1 and 7 m depths.

3.2. Vertical fish distribution

The observed vertical distribution of fish changed through the seasons where data were available (Fig. 4). During summer, most of the fish resided close to the warmest surface waters. During autumn, some salmon swam deeper in the water column, and at times the fish preferred 2 different vertical layers. From late autumn and into the winter (November

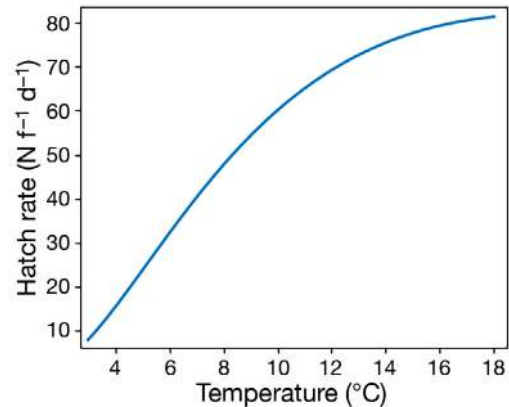


Fig. 2. Calculated hatch rate of salmon louse eggs per adult female salmon louse per day as a function of ambient temperature

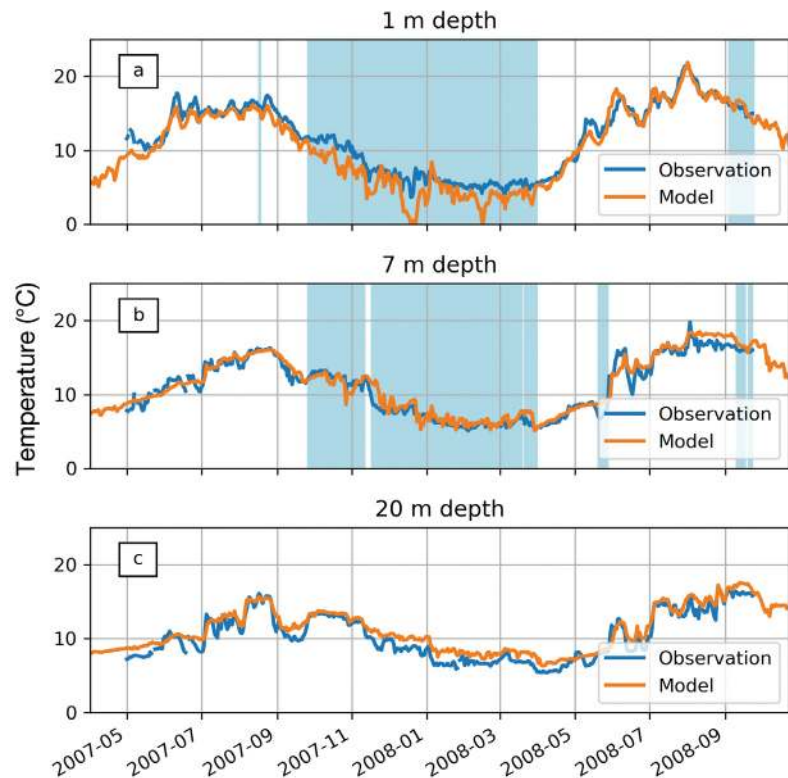


Fig. 3. Observed and simulated temperatures at (a) 1 m, (b) 7 m and (c) 20 m depth at farm site Langavika. Shaded areas: time periods when temperature was higher at 20 m than at 1 or 7 m depth

Table 2. Mean difference and root mean square deviation (RMSD) between modelled and observed temperature at 3 depths

Depth (m)	Mean difference (°C) (observation – model)	RMSD
1	1	1.6
7	0.4	2.7
20	0.4	3.8

onwards), a large proportion of the fish swam deeper, away from the colder surface water. The observational dataset gave us 187 days of observed vertical distribution of fish that was used for the analysis.

3.3. Estimating fish distribution from temperature gradient

In accordance with previous studies, where salmon migrated vertically to obtain favourable conditions

(up to 16°C), the fish at Langavika resided close to the observational depth of 3 m when the temperature was >10°C. Hence the daily temperature at 3 m depth (Estimate 1) was close to the FWA temperature at times when temperatures were approximately 10–17°C (Fig. 5). This means that the 3 m temperature is a suitable measure of the temperature experienced by the fish when the water is relatively warm (data were available only up to 17°C). Overall, there was a high correlation between temperature series, but in the lower temperature end (FWA temperature <10°C), the 3 m temperature estimates were too low (average 0.9°C lower and up to 4.2°C lower). The linear regression between the FWA and the 3 m temperatures shows that the relationship between the 2 is not 1:1, with an intercept <0 and slope >1 (Table 3). This temperature difference underestimated the lice production on average by 11 % and by a maximum of 44 % when the FWA temperature was <10°C.

In Estimate 2, the fish were assumed to migrate homogeneously in a 40 m deep pen. The average

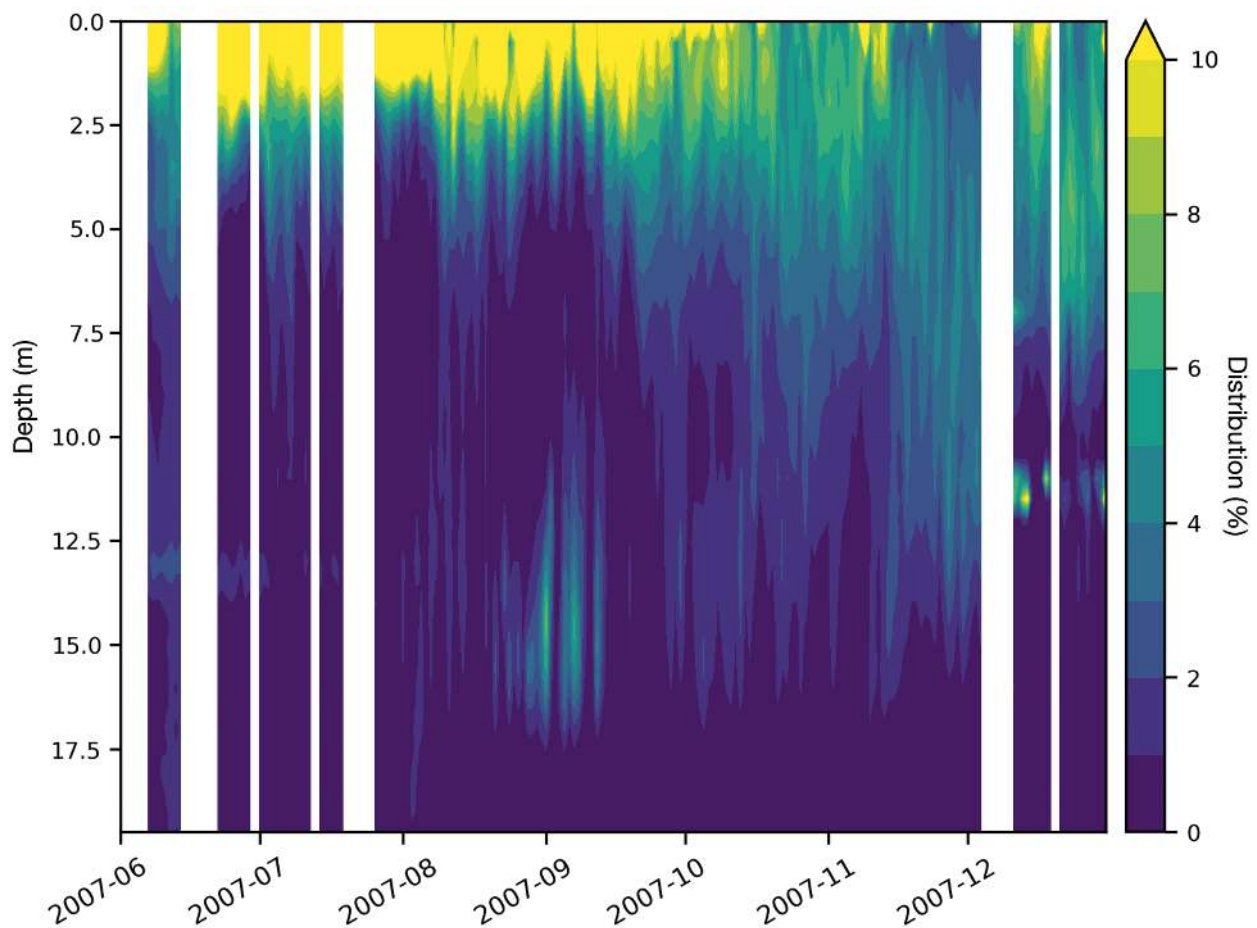


Fig. 4. Daily, relative vertical distribution of salmon observed at Langavika from June throughout December 2007 in 1 representative cage. White areas: data lacking

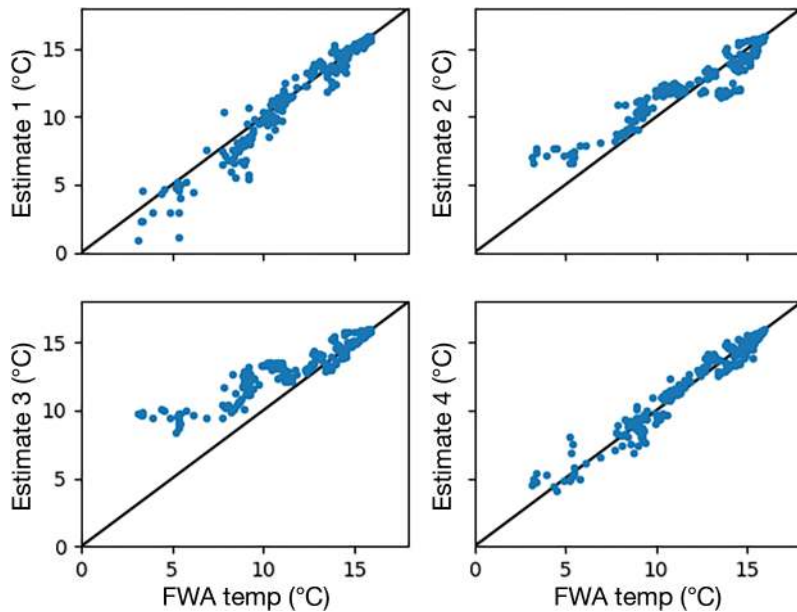


Fig. 5. Fish weighted average (FWA) temperature by the observed vertical distribution of salmon, plotted against 4 different estimated temperatures from the model. Daily values are plotted

temperatures in the upper 40 m was lower than the FWA temperature during summer, but higher during winter. More specifically, Estimate 2 was on average 1.6°C higher than FWA temperature and at most 4.3°C higher when the FWA temperatures were <10°C. Also in Estimate 3, where the fish were assumed to reside close to the maximum temperature, the temperatures were overestimated during winter compared to FWA temperature in winter conditions. The overestimate of the temperature using Estimates 2 and 3 is reflected by the linear slope <1 and intercept >0 (Table 3, Fig. 5).

The modelled distributions from Estimates 3 and 4, from 1 July and 1 December, are plotted, along with the observed vertical distribution on the corresponding day (Fig. 6). In summer, stratification within both modelled estimates predicts the fish distribution to be aggregated towards the surface. In December, a typical winter stratification with colder surface water above warmer water masses is apparent. In the winter stratification, the fish were observed to reside relatively close to the surface, contrary to earlier findings in the literature (Oppedal et al. 2011a). This was a persistent pattern throughout our observation period.

By calculating the weighted average temperature in a layer centred on the thermocline depth (where the temperature gradient is steepest; in Estimate 4), the seasonal difference to the FWA temperature found in Estimates 1, 2 and 3 was eliminated (Fig. 5). Thus, the

linear regression of Estimate 4 has the slope closest to 1 and intercept closest to 0 of the 4 estimated temperatures.

The PCC, RMSD between the linear slope and intercept between Estimates 1–4 versus the FWA temperature can be seen in Table 3. The temperature weighted by the Gaussian curve was tested by iteration using different values for the standard deviation of the Gaussian curve, and a standard deviation of ± 4 m was the best fit. As such, the standard deviation in Estimate 4 was set at 4 m for the further calculations.

3.4. Geographical and seasonal differences in temperature and hatch rates

To identify the areas and seasons where the vertical positioning of the salmon has the strongest influence on lice egg hatching rates, we calculated lice hatching using the monthly means of the modelled temperature along the Norwegian coastline. For this work, we did not have data on the vertical distribution of salmon. We therefore assumed that the temperature calculated from the Gaussian curve around the thermocline (Estimate 4) is the best estimated temperature for where the fish reside. This temperature was then compared to the temperature at 3 m depth (Estimate 1), as this is the current practice for calculating the release of salmon lice from fish farms.

The temperature difference between the weighted mean temperature at the thermocline and the 3 m temperature (Estimates 4 and 1) for all approved salmon farm locations (per August 2018) is shown in Fig. 7. The temperature where the fish are assumed

Table 3. Pearson correlation coefficient (PCC), root mean square deviation (RMSD), slope and intercept of the linear regression between 4 different ways of selecting temperature in a vertical gradient and the mean temperature weighted by observed vertical salmon distribution (fish weighted average [FWA] temperature)

Estimate	PCC	RMSD	Linear slope	Intercept
Estimate 1	0.97	0.68	1.12	-1.63
Estimate 2	0.94	1.15	0.69	4.05
Estimate 3	0.93	1.72	0.55	6.83
Estimate 4	0.97	0.56	0.94	0.76

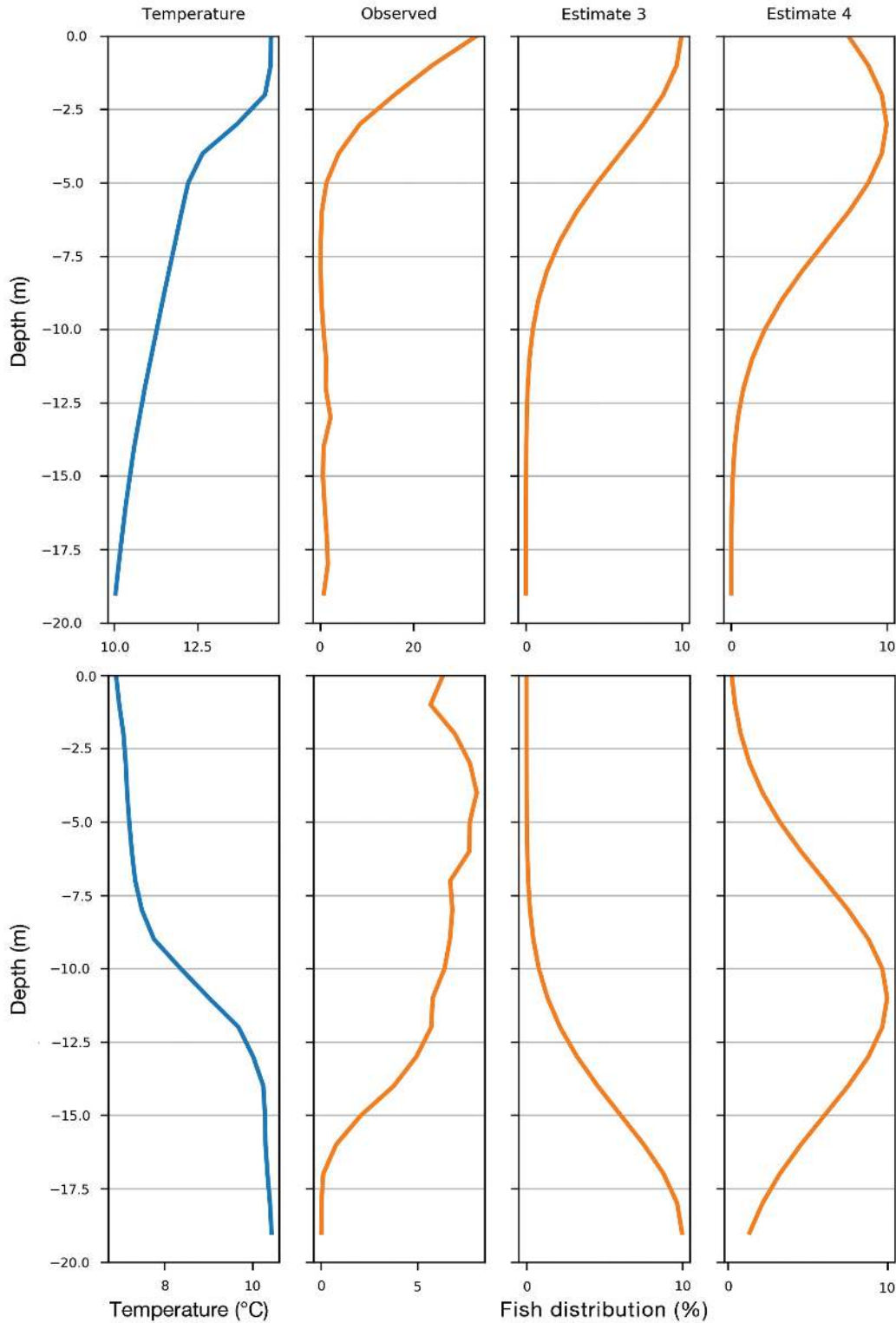


Fig. 6. Modelled vertical temperature gradient from Langavika on 1 July (upper panel) and 1 December (lower panel), observed vertical distribution of salmon and modelled fish distribution from Estimates 3 and 4

to reside is higher than the reported 3 m temperature from September to April. The difference is largest in the south of the country, and in particular inside the long fjords found along the west coast of Norway,

with a maximum difference in January of 2.1°C. In May, the temperature where the fish are assumed to reside (Estimate 4) is roughly the same as the temperature at 3 m depth, but from June to August, the tem-

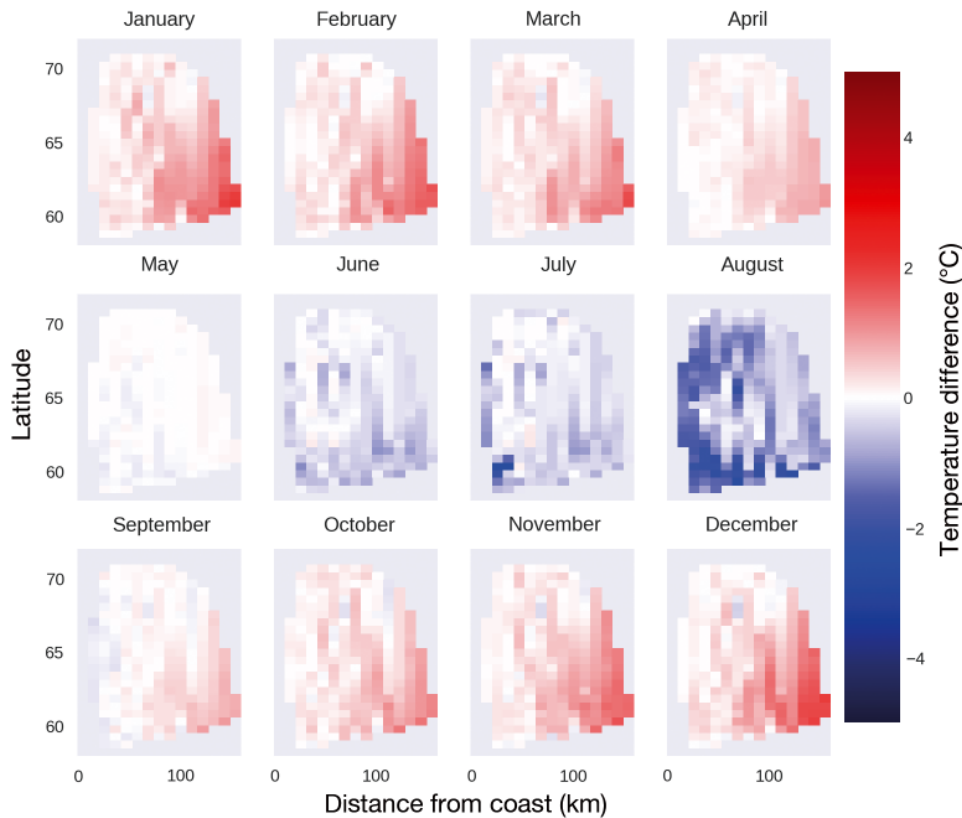


Fig. 7. Difference between the modelled monthly mean temperatures where we assume that the salmon reside (Estimate 4) and from 3 m depth (Estimate 1). The temperature differences are from all approved farm locations in Norway and clustered into spatial grids (distance from the coast and geographic latitude of the farm). Red: areas where the temperature at the assumed fish location is warmer than the temperature measured at 3 m depth; blue: areas where the opposite is the case

perature where the fish is estimated to reside (Estimate 4) is lower than the reported temperature at 3 m depth. This distance is greatest for the farm locations positioned close to the coast, where the maximum difference of 2.5°C was found in July.

As the lice hatching rate is not linearly dependent on the temperature, we calculated the relative increase in lice release using the temperature at the assumed fish position, compared to the temperature at 3 m depth (Fig. 8, Table 4). This is the percentage increase or decrease in lice production due to the new temperature. Lice release was calculated for all approved aquaculture farm positions and gridded as for temperature in the previous section. By using the temperature where the fish are assumed to reside (Estimate 4), the calculated lice release increased from September through April relative to the current practice based on the temperature at 3 m depth (Estimate 1). The difference was highest in February and for the locations positioned inside the longest fjords. The largest difference occurred in February, with an average of 28% and maximum of 158% increase. During May, the calculated lice release was similar between the 2 temperatures. From June through August, slightly fewer lice were calculated to hatch from aquaculture sites using Estimate 4 compared to

Estimate 1. In August, Estimate 4 predicted on average 4% less lice production compared to Estimate 1, with a maximum decreased lice production of 14%. The difference in hatching rate between the temperature estimates was smaller during the summer stratification (June, July and August) compared to the rest of the year (Fig. 8).

4. DISCUSSION

This work highlights the importance of using representative temperatures, i.e. the surrounding water temperature of farmed salmon, in the calculation of lice egg production on farmed salmon. Presently, legislation in Norway requires that temperature measurements at farm sites be taken at 3 m depth. This underestimates egg production in winter and overestimates it slightly in summer. Observations of fish positioning in the vertical structured water column would improve the accuracy of calculations of salmon lice release. However, although such instrumentation is available and relatively inexpensive, it is not in general use, nor reported, in the present system (Noble et al. 2018). Future management should use the temperature at the main depth salmon occupy.

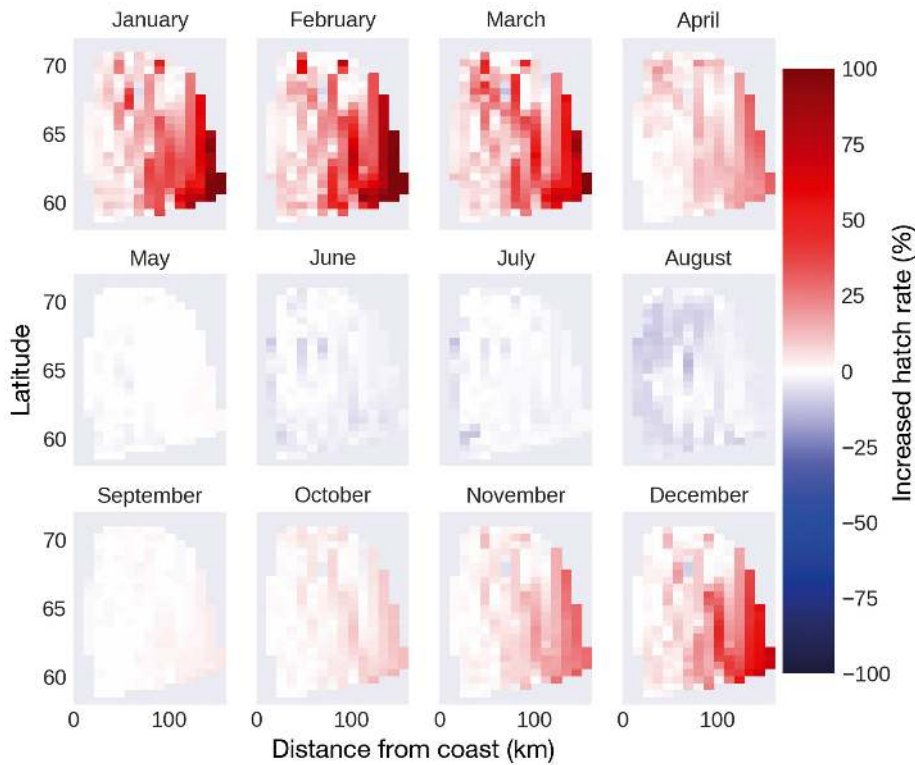


Fig. 8. Relative difference in calculated egg hatch rate per adult female salmon louse between where we assume that the salmon reside (Estimate 4) and the current practice of temperature at 3 m depth (Estimate 1). The calculated lice releases are calculated for all approved aquaculture sites in Norway and are clustered into spatial grids (distance from the coast and geographic latitude of the farm). Red: areas where Estimate 4 increased the calculated salmon lice production compared to Estimate 1; blue: areas with decreased estimated lice production by Estimate 4 compared to Estimate 1. The maximum difference in the increased hatch rate was 158%; however, the scale is cut off at 100% to more clearly illustrate the differences

In the absence of observations, simulated estimates should be considered.

With the limited dataset obtained from part of the production cycle at the Langavika site in 2007, weighting the vertical temperature using a Gaussian curve around the thermocline gave a better fit in late summer and early winter with the temperature actually experienced by the bulk of the biomass in the sea

Table 4. Difference between salmon louse hatch rate where temperature from 3 m depth (Estimate 1) and temperature from where we assume that farmed salmon reside (Estimate 4) is used. Positive (negative) values show when Estimate 4 is greater (less) than Estimate 1

Month	Mean difference (%)	Maximum difference (%)
January	22	134
February	28	158
March	22	128
April	8	32
May	0	3
June	-2	-9
July	-2	-11
August	-4	-14
September	1	5
October	3	14
November	8	32
December	14	72

cage. Despite the limited observational dataset of the vertical positioning of farmed fish in this study, the results are supported by and in accordance with previous findings (e.g. Oppedal et al. 2011a, Oldham et al. 2017, Stehfest et al. 2017) where salmon were found to avoid the cold surface waters in winter and the warmest (approximately $>16^{\circ}\text{C}$) layers in late summer. The farmed fish were observed to divide into 2 schools residing at different depths on some occasions—our best Estimate 4 did not capture this feature. However, the estimated temperature coincided well with the observed FWA temperature without systematic seasonal deviations. In the future, more farm data on vertical fish distribution over years, including east-west and north-south variability, may provide better knowledge of where fish reside vertically. Improved estimates of fish vertical positioning should allow even more accurate modeling of the experienced water temperature.

As the adult lice are attached to fish residing within a vertical temperature gradient, the vertical position of the fish influences the developmental rate and total lice release from aquaculture sites. Until now, the calculation of the lice release from the farms has been made using the observed temperature at 3 m depth. Much of the simulation of salmon lice has been done to evaluate the influence of lice from aquaculture sites on wild fish in the fjords, primarily

from May to August (Sandvik et al. 2016, 2020, Myksvoll et al. 2018). During this period, the difference in lice production based on the 2 estimated temperatures is small. However, the model has also been used to investigate inter-farm infestations and dispersal networks, and to maximise the efficiency of preventive measures at and between salmon farms (Johnsen et al. 2016, Samsing et al. 2016a, 2017, Skarðhamar et al. 2018). For this purpose, accurate year-round estimates of salmon lice release from farms is of great interest. In this paper we have illustrated how the temperature from 3 m depth will underestimate the number of lice released from aquaculture sites during winter conditions and overestimate the release during summer.

Both the number of eggs per egg-string and the development time of salmon lice eggs have a non-linear relationship with ambient temperatures (Samsing et al. 2016b, Hamre et al. 2019). So, temperature differences will have stronger effects on the lice hatch rate at lower temperatures compared to higher temperatures. For example, the daily hatch rate of an adult female louse increased from 23 to 40 eggs d^{-1} (~70%), while a temperature increase from 15 to 17°C increased the hatch rate from 78 to 80 eggs d^{-1} (~4%) (calculations from Eq. 3). This non-linear relationship between egg development time and temperature explains why the largest differences in lice production between the 2 temperature estimates were found during winter stratification, despite the largest absolute temperature differences occurring during summer stratification in August.

The stratification of the water is strongest in the fjords and close to rivers, in particular during the spring melt, but the depth of the pycnocline is also shallower during spring. As a result, the estimated salmon distribution around the thermocline (Estimate 4) was relatively close to the 3 m layer during May. During winter, due to the large sensitivity in egg development at low temperatures and with a deeper location of the thermocline, the difference between the estimates was about an order of magnitude larger in February than in May. In particular, the difference was more pronounced inside the longest fjords, where the stratification is stronger than at coastal sites with more homogeneous oceanic waters. Moreover, the dispersion of salmon lice from farms located in inner fjords has been shown to have a greater impact on the surrounding environment, as the lice are distributed to a narrow, limited area (Johnsen et al. 2016). Farms positioned closer to the coast disperse lice to a larger area, where the dilution is greater. The simulated concentration of salmon lice will therefore be especially sen-

sitive to the calculated number of lice released in the model at fjord locations.

The present study highlights the importance of using the temperature at the residence depth of the fish in modelling temperature-related processes. When calculating the development time of salmon lice, the observation of the fish vertical position would be valuable, but is seldom measured and never reported. However, by combining information on the physical properties of the water column and salmonids' preferred environmental conditions, we estimated realistic temperatures experienced by developing salmon lice. The estimated temperature was close to the temperature for the observed fish distribution, without any systematic seasonal deviation. Hence, the model approach suggested in this paper will estimate the salmon lice release from aquaculture sites in better accordance with the actual lice release than by using the legislated temperature observations from 3 m depth.

Acknowledgements. This research combines work from various projects, including the EU project 022720 FASTFISH, the Research Council of Norway Project 267664 REGFISH-WELH and the Institute of Marine Research internal Salmon lice surveillance program funded by the Norwegian Department of Trade, Industry and Fisheries (internal project no. 14650). Thanks to the anonymous referees for constructive inputs and Luke Barrett for improving the English language.

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*Editorial responsibility: Bengt Finstad,
Trondheim, Norway*

*Submitted: November 22, 2019; Accepted: March 6, 2020
Proofs received from author(s): April 21, 2020*