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Original Article

Prediction of the salmon lice infestation pressure in a Norwegian fjord

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A further growth in the Norwegian aquaculture industry might potentially be hampered by the conclusion that it is not environmentally sustainable. As direct measurements of the lice induced mortality on wild salmonids are impossible, the management is based on a set of highquality and well-documented sustainability indicators. These indicators combine observations from the national Norwegian salmon lice monitoring programme with salmon lice models. Here, we have documented the quality of one of these models used to identify areas where the impact from farmed to wild salmonids is over the prescribed limit. The Hardangerfjord area has been used as a test area, but the model is general and, therefore, suitable for the rest of the coast. It is shown that the model system is robust and also can be used to test whether new knowledge gained from laboratory experiments improves the model. New findings on salmon lice behaviour at low salinities have been incorporated and the new model, consisting of a high-resolution hydrodynamic model coupled with an individual-based salmon lice model and forced with realistic input of salmon lice larvae from aquaculture farms, represents the best realization of the local potential infestation pressure on wild fish.

Keywords: biophysical model, Hardangerfjord, LADiM, ROC, salmon lice dispersion, sentinel cage, sustainability, traffic-light system.

Introduction

Norway is one of the largest producers of Atlantic salmon in the world; however, the production volume has stagnated around the 2012-level of approximately 1.2 million tons (Statistics Norway, https://www.ssb.no/fiskeoppdrett, last accessed 24 December 2019). The political ambition is to increase the aquaculture production to 5 million tons in 2050, presuming an environmentally sustainable production. Salmon louse has been identified as one of the main risk factors for a further increase in salmon farming in Norway (Taranger et al., 2015). Lice epidemics are assumed to reduce populations of wild salmonids in large geographical areas (Skilbrei et al., 2013; Serra-Llinares et al. 2014; Vollset et al., 2014, 2017; Taranger et al., 2015; Thorstad et al., 2015; Anonymous, 2015), and therefore, limiting Norway's ability to fulfil its responsibility for the conservation of wild salmon stocks (Convention for the Conservation of Salmon in the North Atlantic Ocean, 1982, www.nasco.int/conven tion.html and the law of nature biodiversity §8).

The Norwegian government has, therefore, implemented a management system using traffic lights (green-yellow-red) to control the growth in an environmentally sustainable way (Vollset et al., 2017; Myksvoll et al., 2018). So far, the only indicator for sustainability is the effect of parasitic salmon lice, released from salmon farms, on the mortality of wild salmonid fish. The entire Norwegian coast is divided into 13 production areas and based on the indicator, each area is classified as high (red), moderate (yellow), or low (green) risk of salmon lice induced mortality on wild fish. The assessment is done bi-annually by an expert group, and the consequence for production is either 6% reduction (red), freeze (yellow), or 6% growth (green). The qualitycontrolled advice provided by the expert group includes several data and model sources, providing a knowledge-based foundation for the management authorities to make a decision. This management system was applied for the first time in 2017 and will be fully implemented in 2019, also including the possibility for a

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International Council for the Exploration of the Sea reduction in production, which will have major implications for the aquaculture industry.Salmon louse (Lepeophtheirus salmonis) is a natural ectoparasite, which needs a salmonid fish [in Norwegian water: Atlantic salmon (Salmo salar), Sea trout (Salmo trutta), and Arctic charr (Salvelinus alpinus)] to reproduce. Salmon farming in open cages has increased the host density substantially, which in turn affects the salmon lice population dynamics (Jansen et al., 2012). The infestation pressure caused by salmon lice is several orders of magnitude higher in farm intensive areas compared to farm-free areas. Salmon lice hatch directly into the water masses and develop through two naupliar stages before they become infective copepodids and remain pelagic until they find a host. The nauplii become infective copepodids after 40 degree-days and die after 170 degree-days if they are not successful in finding a host (Samsing et al., 2016). The lice are transported long distances during the pelagic phase (Asplin et al., 2014), and they can adjust their vertical positioning depending on external stimuli (Johnsen et al., 2014, 2016; Crosbie et al., 2019). To successfully estimate the salmon lice pressure on wild and farmed salmonids, we need a good and knowledge-based understanding of the environmental parameters that influence the distribution of the planktonic stages of lice in the water column. Several studies have been performed during the last years, and recently new knowledge on the influence of low salinity and salinity gradients was achieved by Crosbie et al. (2019).

Hydrodynamic models are widely used tools for dispersion of planktonic matter and waterborne infection, like salmon lice (Gillibrand and Willis, 2007; Salama et al., 2013; Asplin et al., 2014; Johnsen et al., 2014, 2016; Sandvik et al., 2016; Myksvoll et al., 2018). The main advantages with these types of models are their high spatial and temporal resolution. The Institute of Marine Research (IMR) has developed a national operational model that quantifies the number of infective salmon lice with high resolution in both space and time through the coupling of a state-of-the-art hydrodynamic model to a particle tracking model, capable of simulating pelagic salmon lice behaviour (Asplin et al., 2004, 2011, 2014; Johnsen et al., 2014; Sandvik et al., 2016; Myksvoll et al., 2018). Such models are particularly suitable for computation of salmon lice infection pressure, since the source of salmon lice is assumed to be known as the total number of fish is reported monthly and the number of adult female lice and the temperature are reported weekly by all active salmon farms in Norway [formula given by Stien et al. (2005) for details]. The model system was validated through a comparison with lice in sentinel cages in Sandvik et al. (2016). By nature, hydrodynamic models are simulating the dispersion and advection of particles such as salmon lice, giving their density or concentration in the water masses. It is, therefore, an extra challenge to compare the direct model results (dose) to an indirect observation such as lice on fish in the sentinel cages (response) without having exact information on the dose-response relationship. To overcome the problem of model validation in such cases, new methods, from numerical weather prediction, such as fuzzy verification has been developed (Ebert 2008) and used (Sandvik et al., 2016). The main purpose with operating such a complex model is to provide a warning system to the government on areas with elevated lice infestation pressure. Sandvik et al. (2016) developed a binary forecast system that "translates" the direct model output, being copepodids per metre square, into high and low lice densities based on observations in sentinel cages. This forecast system provides the opportunity to monitor the entire Norwegian coast

a red zone according to the traffic-light management system. High-quality observations of salmon lice directly in the water masses are hampered by both the spatial and temporal heterogeneity in planktonic matter induced by patchiness due to high concentrations in fronts and eddies (Martin 2003; Lévy et al., 2018). Skarðhamar et al. (2019) and refs therein have shown relatively low abundance of salmon lice (typically less than one ind. m^{-3}), in accordance with published concentrations of salmon lice in Scottish and Faeroes open waters, compared to other species of similar size range (Penston et al., 2004, 2011; á Nordi et al., 2015, 2016). The methods for direct sampling, therefore, need to be substantially improved before this can be considered as a suitable method for monitoring. Indirect measurements of lice attached to wild salmonids and smolts in sentinel cages have traditionally been the observational part of the Norwegian salmon lice monitoring programme. Whilst cages are deployed at known times and locations, wild fish data are hampered with uncertainties both in time and space. Thus, counting of salmon lice on smolts in sentinel cages is used as a proxy for lice infestation pressure on wild salmonid fish in the present work. We have used data from lice on fish in sentinel cages for the years 2012-2017 to calibrate the modelled salmon lice density in the Hardangerfiord.

tation pressure, where there is a higher risk for being classified as

In the present study, the main objective was to document the quality and the set-up of an operational modelling system, which is one of the main components of the "Traffic-light system". The binary forecast system proposed in Sandvik *et al.* (2016) has been further developed and constitute now of three categories (green, yellow, and red). In addition, the method is a suitable tool to investigate whether new knowledge gained from, for example, empirical, laboratory, or field studies will improve the model product when implemented in the model. This has been exemplified through the implementation of the results from a recent publication by Crosbie *et al.* (2019), that showed a gradual avoidance of the salmon lice from low saline water.

The robustness of the method has been investigated through a cross-validation (CV) scheme. This is a further development of the method presented in Sandvik *et al.* (2016), where data from 2012 to 2014 were used to make the model, and data from 2015 were used for validation. Observations from the Hardangerfjord on the Norwegian west coast have been used to parameterize the method, but the new forecasting system is general, and the findings can be transferred to other areas along the Norwegian coast.

Material and methods Study area

The long and branched Hardangerfjord is located in western Norway, south of Bergen (Figure 1). It stretches 179 km from the coast into the mountainous interior of Norway. The sill depth is about 170 m, and the fjord has several deep basins with a maximum depth of 850 m. Because the Hardangerfjord system consists of a number of large and small fjord arms and has several connections to the open sea, the current pattern is relatively complicated with large spatial and temporal variability. A detailed description of the fjord physics (currents, temperature, and salinity) can be found in Asplin *et al.* (2014) and Johnsen *et al.* (2014).



Figure 1. Map showing position and numbering of the 18 sentinel cages in the Hardangerfjord (left) and frequency diagram of the observations (mean abundance in the 216 cages; right).

Release of salmon lice from fish farms

There are around 100 salmon/salmonid farms (red dots shown in Figure 1) in the Hardangerfjord system, producing \sim 80 000 tons of salmon annually (www.fiskeridirektoratet.no).

The adult female sea louse extrudes a pair of egg strings and the planktonic nauplii stages hatch directly into the water column. The number of hatched lice larvae (nauplie) has been calculated using formula in Stien et al. (2005), and numbers of fish, female lice, and water temperature have been made available from all salmon farms along the Norwegian coast. More details on this calculation can be found in Myksvoll et al. (2018). As discussed in Sandvik et al. (2016) and Myksvoll et al. (2018), the observed temperature and number of female lice are reported weekly by Tuesday the following week, while the number of fish in the farms is reported monthly. Thus, there is a temporal uncertainty in calculations of the number of salmon lice larvae released into the water masses, which has to be taken into account in the analysis of the results. The quality of these estimates might suffer from both the coarse and imprecise time resolution, as well as the uncertainty in the lice counts and the temperature, which is taken from only one depth in the cages.

Observation by sentinel cages

Sentinel cages stocked with hatchery-reared Atlantic salmon smolts were used to gather independent observational data of salmon lice infestation pressure in different parts of the Hardangerfjord system.

During a 6-year (2012–2017) study period, 18 sentinel cages (diameter 0.8 m, height 0.9 m, covered with a knotless mesh 1×1 cm) were deployed annually at 0.5 m depth at fixed locations along the fjord (see Figure 1, left panel). The methodology for the mooring system is described by Bjørn *et al.* (2011) and has also been used in Scotland (Salama *et al.*, 2013; Pert *et al.*, 2014). The cages are assumed to give an integrated measure of the local lice infestation pressure over the period of their deployment. Two consecutive trials were performed in 2012–2013 and three trials

in 2014-2017 (Sandvik et al., 2016). In each trial, 30 salmon smolts were placed in each of the sentinel cages and kept at sea for ~ 3 (or 2) weeks at a time (Table 1), after which all fish were gently removed from the cages, euthanized by an overdose of anaesthetic (MS-222), placed in individual plastic bags and kept on ice until inspected for lice at the laboratory within the following 48 h. In the laboratory, the salmon lice were identified and counted on a morphological basis according to Johnson and Albright (1991); Schram (1993), and recently also Hamre et al. (2013). In the following, we have used the mean abundance defined as total number of lice divided by the total number of fish as a measure of the infestation level in the cage. This was assumed to be the most suitable metrics for the coarse-scale classification of infestation pressure used in the following. Due to the uncertainty of the observational date of the reported numbers of fish and lice per fish in the fish farms, which only refer to week number (not date), we consider a trial length of 2 weeks to be too short. In the analysis, we have, therefore, combined the two last trial periods in 2014–2017 (Sandvik et al., 2016). This resulted in 216 data points from the observations by sentinel cages. Thirtyfour of these possible observations were not used. Cage number 12 was omitted as it was placed in a narrow part of the fjord not resolved by the model (800 m horizontal resolution), and in addition, 22 observations were rejected in cases where the cage was not deployed or due to technical problems with the cage. A frequency diagram of the remaining valid observations is shown in the right panel of Figure 1.

Based on extensive experience and field observations of lice abundance in hatchery-reared and sentinel-caged smolts over several years and large areas along the coastline (Asplin *et al.*, 2011; Bjørn *et al.*, 2011, 2012, 2013; Nilsen *et al.*, 2014; Karlsen *et al.*, 2015; Svåsand *et al.*, 2016), the sentinel cage infestation have been divided into four classes as low (0–1 louse per fish), moderate (1–5 lice per fish), medium (5–10 lice per fish), and high (>10 lice per fish). To better reflect the classes used in the traffic-light system (low, medium, and high), classes 2 and 3 have been

 Table 1. Time periods for sentinel cages deployed in the

 Hardangerfjord 2012–2017.

Year	Period 1 (P1)	Period 2 (P2)	Period (P3)
2012	8/5-29/5	29/5-20/6	-
2013	13/5-5/6	5/6-26/6	-
2014	8/5-22/5	22/5-5/6	5/6-21/6
2015	12/5-27/5	27/5-9/6	9/6-23/6
2016	11/5-24/5	24/5-7/6	7/6-20/6
2017	8/5-23/5	23/5-6/6	6/6-21/6

merged in the present study, thus 10 lice per fish is used to classify the limit of high infestation pressure and 1 louse per fish is used to separate low and medium infestation pressure.

Salmon lice dispersion model

The salmon lice advection and growth model is based on the Lagrangian Advection and Diffusion Model (LADiM; Ådlandsvik, 2019). Physical forcing fields (three-dimensional currents and hydrography) are provided by the ocean model system NorKyst800 (Albretsen *et al.*, 2011), based on the Regional Ocean Modelling System (ROMS, www.myroms.org; Shchepetkin and McWilliams 2005; Haidvogel *et al.*, 2008). The horizontal quadratic grid cell size is 800×800 m, and realistic forcing of the ocean model from atmosphere, tides, and rivers are included as described by Asplin *et al.* (2014) and Johnsen *et al.* (2014).

The vertical distribution of the lice larvae might have a large influence on the horizontal distribution (Heuch 1995; Johnsen et al., 2014). The larvae are known to have a vertical behaviour where they swim up towards the surface light and downwards to avoid low-salinity water (Bron et al., 1991; Heuch 1995; Heuch et al., 1995; Flamarique et al., 2000). To mimic the drift of the three planktonic salmon louse stages (the two non-infective nauplius I and II and the infective copepodid), four different parameterizations of this vertical behaviour as a function of salinity and stage have been tested. In all experiments, a vertical swimming speed of 0.5 mm s⁻¹ directed upwards towards the surface when the light level exceeds a critical level of $2 \times 10^{-5} \mu mol$ photon s^{-1} m⁻² (nauplii) and 0.392 µmol photon s^{-1} m⁻² (copepodid) was used (Johnsen et al., 2014). When exposed to low-salinity levels and light conditions, the low-salinity avoidance was assumed to be the strongest trigger, and the lice swam down according to:

- (A1) Downward swimming of all lice when the salinity <20 [identical to Sandvik *et al.* (2016)]
- (A2) Downward swimming of all lice when the salinity <25.
- (A3) Downward swimming of gradually more lice as the salinity is in the range between 23 and 31 [probability decreasing linearly from 1 (all swimming downward) when the salinity is <23 to 0 (none swimming downward) when the salinity is >32, based on laboratory experiments described in Crosbie *et al.* (2019)]
- (A4) As A3 but adding that for the nauplii stages they are all swimming downward when the salinity is <34 (Crosbie *et al.*, 2019).

Horizontally, the salmon lice larvae passively drift with the currents (Asplin *et al.*, 2014; Johnsen *et al.*, 2014). The biology and life history of the lice are handled with an individual-based model (IBM) using the super-individual (SI) approach (Scheffer *et al.*,

Table 2. Schematic contingency	table for	r categorical forecasts	of a
binary event.			

	Observed							
Forecast	Yes	No	Total					
Yes	а	b	a + b					
No	с	d	c + d					
Total	$\mathbf{a} + \mathbf{c}$	$\mathbf{b} + \mathbf{d}$	a + b + c + d = n					

The numbers of observations in each category are represented by a, b, c, and d, and n is the total. Redrawn from Mason (2003).

1995). The growth of an individual louse is purely temperaturedependent and is parameterized as a function of degree-days. Following Samsing *et al.* (2016), we assume the infective copepodid stage to be between 40 and 170 degree-days. The model is initiated without any salmon lice, while new louse SIs are added hourly as nauplii at a rate of 5 SI/farm/hour with the internal number of each SI scaled to represent the reported egg numbers that week. The lice mortality is assumed to be constant in time and space at 17% per day (Stien *et al.*, 2005). The model output consists of hourly fields of spatial distribution and density of salmon lice copepodids in the sea.

Relative operating characteristic

For discontinuous fields with high spatiotemporal variability and a skewed distribution, commonly used measures such as root mean square difference and correlation coefficients can give poor scores even if both intensity and area extent are correct but are slightly displaced in space and/or time (e.g. Ebert, 2008). For skewed distributions, extreme values will also have undue influence on the values of standard measurements. For multicategorical data series that are not normally distributed, the probability of detection (POD) is a robust and well-suited estimate of the forecast skill (Wilks, 1995). POD is defined as the number of events correctly forecasted divided by the total number of events. However, to give a measure of the quality of a forecast it is better to combine the hit rate with the false alarm rate. The hit rate, H, for a random binary forecast (categorical forecast with only two categories) which, for example, is the case if we only consider the risk of salmon lice density above a given threshold, is the number of such predicted values divided by the number of observed ones. The false alarm rate, F, is defined as the number of events predicted but not confirmed by observations, divided by the total number of events predicted. Both of them can take any value between 0 and 1. In such a binary forecast system (Table 2), these ratios simply become: $POD = \frac{a+d}{a+b+c+d}$, $H = \frac{a}{a+c}$ and $F = \frac{b}{b+d}$

The relative operating characteristic (ROC) is a graph of H against F for different decision thresholds (Mason, 2003). Assuming a binary forecast system, the ROC becomes a pure index of accuracy that gives quantitative estimates of the probabilities of forecast outcomes for any decision threshold that the system might use, and the trade-offs between these probabilities as the decision threshold varies. An empirical ROC can be plotted from forecasts of elevated density by stepping through different forecast systems, each system generating a 2×2 contingency table (Table 2) and values of H and F (Mason, 1982). For a forecast system with zero skill, H = F, while in a perfect system, H = 1 and

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F=0. The score of the ROC can be defined as the distance between the perfect solution and the actual solution. In the present work, the score of the ROC has been defined using the 2-norm: $\text{ROC}_{\text{score}} = \sqrt{(1-H)^2 + F^2}$, where a perfect solution is recognized when $\text{ROC}_{\text{score}} = 0$.

We used the ROC score to test whether the model was capable of correctly predicting high lice infestation levels in sentinel cages. Two binary classification schemes were used. In the first classification scheme, high infestation level was defined as more than 10 lice per fish, and in the second scheme, the limit was set to 1 louse per fish. These limits coincide with those used by the Norwegian traffic-light system to distinguish between low, intermediate, and high infestation level.

To obtain a binary forecast from the modelled sea lice concentration keeping in mind the natural patchiness of the salmon lice field, we first computed the time-averaged lice concentration in the upper 2 m of all nine grid cells (3 × 3) surrounding each cage. A high infestation level was predicted if at least *N* of the nine grid cells exceeded a threshold value of *R* (lice m⁻²), where *N* and *R* are adjustable parameters. We computed the hit rate *H* and false alarm rate *F* for variable combinations of *N* and *R*. The combination that yielded a minimum ROC score was selected as the optimal threshold values. This was repeated for each of the four lowsalinity avoidance models (A1–A4) described above.

Table 3. ROC integration methods (A1–A4) for high infestation pressure.

	R	#N/9	Score	Н	F	MHCH	MHCL	MLCH	MLCL	POD
A1	2.2	7	0.17	0.96	0.17	24	26	1	131	0.85
A2	2.0	9	0.13	0.92	0.10	23	16	2	141	0.90
A3	1.8	9	0.10	0.92	0.06	23	9	2	148	0.94
A4	1.7	7	0.14	0.88	0.07	22	11	3	146	0.92

R denotes threshold level in model field (lice m⁻²), N denotes the number of model values above threshold within the 3 \times 3 = 9 matrix, Score is the dis-

tance $\sqrt{(1-H)^2 + F^2}$ to the perfect solution (lowest value is best score), *H* is the hit rate and *F* the false alarm rate, MHCH is the number of cages where ModelHighCageHigh, etc., while POD is the probability of detection.

Results

We first present the results for the binary classification scheme where 10 lice per fish were used as the limit between observed high and low lice abundance. Using the 2012–2017 observations and the corresponding model fields, H and F were computed for all combinations of threshold parameters R and N, and several sub-optimal ($H \le 1$, $F \ge 0$) solutions were found. The 34 NA observations were excluded from the analysis.

Using the four different vertical behaviour algorithms, details for the best resulting integration methods from the ROC are listed in Table 3 as A1–A4, and their performance is also shown in the left panel of Figure 2 that illustrates how all methods are close to the perfect solution (H=1, F=0) in the upper left corner of the figure. There is a clear improvement of the model performance when including a less restrictive and more detailed description of the vertical behaviour of the salmon lice larvae as a function of salinity (A1–A3), while there is a slight decrease when using an alternative approach for the nauplii stages.

As stated, the ROC is a method to quantify skills from a family of methods, and how the performance of such methods varies as a function of different thresholds is illustrated in Table 4 where nine members of the A3 family is given as S1-S9. In this table, the best solution, S6, is identical to the best solution, A3, in Table 3. In the right panel of Figure 2, it is illustrated how all these possible solutions are close to the perfect solution (H=1, F=0). However, Table 4 clearly also shows the difference in characteristics between them. With a low lice per metre square threshold, the model overestimates the number of high values compared to the sentinel cages (MHCL). This number decreases when increasing this threshold, but the price for this decrease is an increase in the number of observed high values not given by the model (MLCH). A similar picture is seen when varying the proportion of grid cells above the lice per metre square threshold (as exemplified with integration methods S4-S6), where the price for a decrease in MHCL when increasing this proportion is a corresponding increase in MLCH. Except for method S9, the score shows little variations between the methods. The best score is found for integration method S6, with a proper balance between the hit rate and the false alarm rate.



Figure 2. Left panel: ROC-plot of the possible solutions (A1 to A4—circles) and (L1 to L4—crosses) detailed in Tables 3 and 6, together with mean skill and standard deviation of *H* and *F* from the experiment with 10 000 permutations of the cages (solid square). Right panel: methods (S1–S9) detailed in Table 4. Note the full value space (left) and zoomed view (right) to better highlight the different integration methods. Perfect solution (F = 0, H = 1) is in the upper left corner at point (0, 1), while the diagonal H = F represents zero skill.

The integration method with the best performance (S6) has a POD of 0.94 (171 of 182 hits) but predicts high infestation pressure in nine cages where the observed mean abundance is below 10 lice per fish (MHCL) and misses two cages with high infestation pressure (MLCH). To get a full overview of the hits and misses, the mean observed lice abundance from all periods and cages are given in Table 5, together with a colour coding to show where model and observations disagree. Out of the nine MHCL data points, 6 observations have a mean lice abundance between 5 and 10 (5 between 6 and 10). These are elevated model points that are also indicating an observed high lice density from the sentinel cages. Of the remaining three observations, one observation in the first period of 2015 and one observation in the second period of 2016 stands out. These observations are 2.2 and 2.8, respectively, indicating only a low-to-moderate observed lice infestation pressure. The two incidents where the model misses an observed high infestation pressure are cage number 14 in the

Table 4. Example ROC integration methods for high infestation pressure.

	R	#N/9	Score	Н	F	мнсн	MHCL	MLCH	MLCL	POD
S 1	1.5	9	0.13	0.92	0.10	23	16	2	141	0.90
S2	1.7	6	0.14	0.92	0.12	23	18	2	139	0.89
S 3	1.7	9	0.11	0.92	0.08	23	12	2	145	0.92
S4	1.8	6	0.13	0.92	0.10	23	16	2	141	0.90
S5	1.8	7	0.12	0.92	0.09	23	14	2	143	0.91
S6	1.8	9	0.10	0.92	0.06	23	9	2	148	0.94
S7	1.9	6	0.15	0.88	0.09	22	14	3	143	0.91
S8	1.9	9	0.13	0.88	0.06	22	9	3	148	0.93
S9	2.1	9	0.24	0.76	0.04	19	6	6	151	0.93

R denotes threshold level in model field (lice m⁻²), *N* denotes the number of model values above threshold within the $3 \times 3 = 9$ matrix, Score is the distance $\sqrt{(1-H)^2 + F^2}$ to the perfect solution, *H* is the hit rate and *F* the false alarm rate, MHCH is the number of cases where ModelHighCageHigh, etc., while POD is the probability of detection.

second period of 2015 and cage number 2 in the second period of 2017.

The traffic-light system separates into three different classes, and 1 louse per fish is used to distinguish between observed low and medium lice infestation pressure from the sentinel cages. In a similar way, an ROC can be developed using this as the limit in a binary forecast. Repeating the same procedure for all different algorithms for salinity-dependent vertical behaviour with this limit gives the integration methods (L1–L4) detailed in Table 6 and the score is shown in Figure 2. The integration method L3 (corresponding to A3) gives a model threshold of 0.7 lice m⁻² in at least 6/9 of the points in the 3 × 3 neighbourhood of each of the cages. This method has a skill score of 0.32, with *H*, *F*, and POD of 0.70, 0.11, and 0.76, respectively. By combining A3 (S6) and L3, a model forecast system with three classes (low, moderate, and high) can then be given. Two example maps (period 1 of 2015 and period 2 of 2016) are shown in Figure 3.

Validation of the ROC

The model has a clear predictive skill far from random. This can be illustrated through a simple experiment with a redistribution of the cages. By randomly permuting the sequence of cage data and using the simulated louse distribution from A3, the ROC algorithm has been used to fit the best method (lowest score) and corresponding hits and false alarms. By repeating this experiment 10 000 times, we get a mean score of 0.66 (H=0.54, F=0.45) with a minimum score of 0.41 and a maximum score of 0.90. The full distribution of these scores is shown in Figure 4. The mean point is marked with a black square in the left panel of Figure 2 together with the standard deviation of H and F. The point is very close to the "no-skill-line" (H=F), showing the predictive skill of the model.

When constructing an integration method, there is always a chance that a bad model can gain high skill through a special

Table 5. Overview of the mean lice abundance in the sentinel cages used in the analysis.

	12-1	12-2	13-1	13-2	14-1	14-2	15-1	15-2	16-1	16-2	17-1	17-2
#1	1.3	1.6	NA	1.5	0.1	0.9	2	6.5	0.6	0.8	1.0	4.3
#2	2.5	5.3	0.1	3.7	0.3	2.7	4.8	15.7	1.1	5.2	3.9	11.0
#3	0.7	6.6	0.3	4.2	0.2	1.6	4.9	16	1.1	3.4	2.8	9.9
#4	NA	3.7	0.1	6.7	0.3	2.2	4.4	19.2	NA	2.8	2.1	9.7
#5	NA	4.4	0.3	5.7	0.1	2	5.9	16.4	NA	3.9	3.5	NA
#6	NA	5.7	0.1	5.3	NA	1.9	5.2	13.1	1.5	6.2	3.9	11.4
#7	1.1	3.8	0.1	NA	0.1	2.1	3.6	18	NA	2.7	1.9	8.3
#8	0.7	3.2	0.4	4	0.3	3.2	4.8	12.6	0.6	6.1	3.0	8.6
#9	0.5	18.3	0.2	NA	0.9	8.5	2.5	6.3	NA	11.1	2.4	5.0
#10	0.1	3.9	0	1	0.1	NA	0.8	2.8	0.6	11.8	0.2	2.8
#11	0.3	12.1	0	0.7	0.2	16.7	0.4	1.6	0.3	17.5	0.3	1.1
#12	NA											
#13	0.5	5.6	0.2	1.1	0.1	12.5	2.6	7.2	1.0	8.9	0.7	2.2
#14	1.2	7.7	0.4	1.3	0.2	19.5	5.2	13.0	1.1	17.9	2.6	3.3
#15	0.3	17.2	0.1	1.3	0.8	8.8	2.3	3.8	0.9	14.1	0.7	3.6
#16	0.4	13.4	0.1	0.3	0.2	19.5	0.7	4.2	0.3	10.5	0.4	0.8
#17	NA	NA	NA	0.9	0.4	0.6	2.2	4.5	NA	0.4	0.3	2.5
#18	NA	NA	NA	1.8	0.2	1.2	2.8	13.4	NA	NA	1.8	4.7

One row per cage (1–18), and one period per column (2012 period 1 to 2017 period 2). The nine red cells indicate the cages and period where the S6 ROC integration method in Table 2 proposes a high value while the corresponding observation in the cage indicates a low level (MHCL in Table 2). The two orange cells are the occurrences where S6 give a low value where the observation indicated a high value (MLCH in Table 2). In the remaining cells, the model and observed level high/low is the same (MHCH and MLCL) (Colour version of this table is available at *ICES Journal of Marine Science* online.).



Figure 3. Modelled traffic-light forecast (red = high, yellow = moderate, green = low lice infestation pressure) for period 1 in 2015 (left) and period 2 in 2016 (right). Circles are the position of the cages.



Figure 4. Probability density function (score vs. frequency) counted in 0.05 bins for the 10 000 experiments with redistribution of the cages. For comparison, the vertical dotted line is the score of integration method A3.

distribution in the data. Therefore, we also validated our model using a CV framework (Bergmeir and Benítez, 2012). The CV process randomly splits the data series into two disjoint subsets: (i) the training subset used to run the ROC procedure to evolve an integration method to approximate the lice abundance; (ii) the validation subset used to evaluate the approximation capability of the Integration method. Since the validation subset is not involved in the training phase, the generalization capability of an Integration method is defined through the error obtained by predicting the values of the target variable of the validation subset, and the stability of the parameters in the integration method. As the observation data used contains both a spatial and a temporal

Table 6. ROC integration methods (L1–L4) for low infestation pressure (1 louse per fish).

	R	#N/9	Score	Н	F	MHCH	MHCL	MLCH	MLCL	POD
L1	0.8	6	0.32	0.73	0.16	87	10	33	52	0.76
L2	0.8	6	0.33	0.71	0.16	85	10	35	52	0.75
L3	0.7	6	0.32	0.70	0.11	84	7	36	55	0.76
L4	0.5	6	0.32	0.75	0.19	90	12	30	50	0.77

R denotes threshold level in model field (lice m^{-2}), N denotes the number of model values above threshold within the 3 \times 3 = 9 matrix, Score is the dis-

tance $\sqrt{(1-H)^2 + F^2}$ to the perfect solution (lowest value is best score), *H* is the hit rate and *F* the false alarm rate, MHCH is the number of cages where ModelHighCageHigh, etc., while POD is the probability of detection.

dimension, the data partition was done through randomization instead of blocks. The CV was run 10 000 times. Each time 80% of the observations were chosen randomly to become the training subset, while the remaining 20% of the observations became the validation subset. Each time the ROC integration method with the best score was chosen and used to predict the salmon lice infestation pressure and corresponding error statistics using the validation subset. For the selection of integration method, a threshold of R = 1.8 lice m⁻² was chosen in 80% of the cases (1.9 in 16%), while the proportion of grid cells above the threshold (N/9) was 9/9 in 97% and 8/9 in 2.5% of the cases. Mean skill, H, F, and POD for both the training and validation subset are given in Table 7. Doing the CV analysis for the low lice abundance (1 louse per fish) conclude that close to 62% of the runs give a threshold of R = 0.7 (31% for 0.5), and 77% gives a fraction (N/ 9) of 6/9 (21% for 9/9). Further results for this CV exercise are also given in Table 7. Through the high stability of the parameters

Table 7. Error statistics (mean score, hit rate, false alarm rate, and probability of detection) for the training and validation subsets after 10 000 runs of the CV.

	Score	н	F	POD
High/low = 10: training subset	0.10	0.92	0.06	0.94
High/low = 10: validation subset	0.16	0.87	0.06	0.93
High/low = 1: training subset	0.32	0.72	0.14	0.76
High/low = 1: validation subset	0.37	0.70	0.17	0.74

in the integration method, we conclude that the high skill of the proposed method is not through a special distribution in the data.

Discussion

Based on observations from sentinel cages for the years 2012–2017, an ROC has been used to suggest a prediction method for salmon lice infestation pressure in the Hardangerfjord. Using the binary method twice, a system with three categorical events (high, medium, and low) is also suggested. The method has clear predictability skills ($H \gg F$). Through the stepwise process with different integration methods (A1–A4), it has also been demonstrated that the ROC enables an objective way of quantifying the performance of these methods when combining models and observations. This can easily be repeated if the salmon louse IBM is further refined; thus, the ROC also serves as a benchmark system to assess the quality of future updates of the system.

Through a stepwise process (A1–A4), the vertical behaviour in the salmon lice IBM has been improved compared to the first implementation of a forecast method based on the ROC (Sandvik et al., 2016). The results from Sandvik et al. (2016) indicated that the model had too many false alarms in areas with low salinity, and a clear improvement was gained simply by adjusting the strict salinity avoidance threshold from 20 (A1) to 25 (A2) psu. A comprehensive testing of salinity avoidance has been done in a recent laboratory study and reported by Crosbie et al. (2019). Their results show how the relative avoidance changes with salinity, and this has been implemented for all particles in A3 through a randomization of behaviour as a function of salinity. Salinity avoidance was also tested in Crosbie et al. (2019). In that study, salinity avoidance was formulated using an equal salinity-dependent swimming speed for all larvae. This resulted in a too strong avoidance of surface water with low salinity, a deeper vertical distribution and shorter horizontal dispersion, which was most pronounced in areas with strong stratification (inner fjords), and an almost absence of lice larvae in the upper 2 m, even in areas with observations of lice on wild and farmed fish. In the present work to ensure an avoidance of (but not complete absence from) water masses with low salinity, the salinity avoidance was, therefore, parameterized using a probability function. The clear improvement in performance from A2 to A3 confirms the sensitivity to salinity found in the laboratory experiments, while the inclusion of a stricter salinity avoidance for the nauplii stages (A4) results in a slightly worse score. The main difference from A1 to A2 and A3 is how likely the copepodites are to move away from the surface layer where the sentinel cages are placed at 0.5 m depth. The difference between A3 and A4 is how this avoidance is done for the nauplii. There is no impact for the infestation pressure as it will only alter the drift pattern of the particles during the first 40 daydegrees. As wind-induced current generally weakens with depth, the dispersion of particles is less in A4 than in A3, which is also seen with the increase in false alarms. In addition to the salinity avoidance, it is also known that the nauplii will swim up towards the surface light (Bron *et al.*, 1991). How the balance between these two acts in nature is not known. With its best performance, A3 is, therefore, kept as the preferred algorithm. The score of the corresponding algorithms for the low limit of 1 louse per fish (L1–L4) are almost identical varying between 0.32 and 0.33 (Table 6). However, despite this, there are some variability in the performance shown in *H* and *F*. The chosen method L3 is characterized by the lowest number of false alarms (F=0.11), meaning that this method is likely to have a slight less yellow area compared to the other three.

The suggested method to separate between high and low infestation pressure (S6 and A3), misses two of the elevated cages and give nine false alarms. A proper examination of these inconsistencies between model and observations is necessary. The reason there are more false alarms than missed high-value cages is the distribution of the data set with fewer high values (above 10 lice per fish) than low values (below 10), and the definition of H and F (using these total numbers) that implies that the price for a false alarm is less than that for a missed cage. The two missed cages are cage 14 in period 2-2015 and cage 2 in period 2-2017 (see Table 5). The first occurrence (cage 14) is the outermost cage in the fiord. The model includes data on salmon lice from all fish farms in the area. However, there are also other potential sources. Next to cage 14, there is a harvest cage (open cage where the salmon is stored before slaughtering) that is not required to report salmon lice. A possible explanation for the high infestation level in cage 14 is, therefore, salmon lice originating from this site. In the future, also information on number of fish and lice in harvest cages should be reported as this might have an impact on the total lice pressure. The second incident (cage 2 in period 2-2017) is to the north of Varaldsøy in the inner part of the fjord. The neighbouring cages to the north, further into the fjord (1, 17, and 18), all have low infestation levels, while the nearest cages further out the fjord (3-7) all have high or close to high levels. Again, close to cage 2, there is a harvest cage, and as the infestation level in both model and observations in sentinel cages agree in all neighbouring locations, a likely explanation is that the difference between model and observations in this position is due to this harvest cage.

Of the nine false alarms, seven cages are reporting an elevated lice level above 4.9 and will not be discussed further. However, the two remaining cages (cage 17 in period 1-2015 and cage 4 in period 2-2016) need a thorough examination. In the first period of 2015, the model forecast a few small red areas in the inner part of the fjord (left panel in Figure 3). One of these coincided with cage 17. Two of the nearby fish farms were reporting high lice levels in this period; thus, it is likely that there are somewhat more lice in the area than what was recorded in the cage. The model also shows a rather patchy field in this area (Figure 3, left panel), which again supports uncertainty in the observations here due to patchiness. Cage 4 is situated in the narrow sound west of Varaldsøy, and in the model (right panel of Figure 3), the entire sound and a small strip along land south of it (including cage 6) are coloured red. From the figure, the origin of the salmon lice causing the modelled high infestation level in this area seems to be the outer part of the fjord where several cages are red both in the observations and in the model. A possible explanation for the too high level in the model at this site is, therefore, too strong advection, which can also explain the elevated model level at nearby cage 6 in the same period, combined with too coarse resolution locally in the 800 m model.

It should be noted that the infestation efficiency of salmon lice is influenced by several factors such as salinity, temperature, water currents, and the age of the copepodite (Hevrøy et al., 2003; Brooks, 2005; Bricknell et al., 2006; Samsing et al., 2015, 2016), relationships that are only partly known. It is also unclear whether fish are less resistant to further lice infestation if it is already weakened by existing lice infestation. In the present work, we have assumed a linear dose/response relationship where the infestation efficiency is only dependent on the concentration of infective larvae in the water masses. Samsing et al. (2016) showed that the infestation success is an order of magnitude higher at 10°C compared to 5°C (and slightly higher than the success at 20°C), while experiments by R.Skern-Mauritzen et al. (pers. comm.) suggest an increased efficiency from 5°C to 10°C, and an even higher success rate at 15°C. All fish farms are reporting temperatures at 3 m depth weekly. In the period when the cages have been deployed, the mean temperature in the Hardangerfjord is typically between 8.5°C (week 19) and 13°C (week 25). In such a limited temperature window, a linear response appears to be a good approximation. However, when running the model in early spring and late summer a temperature dependence should be added to the ROC. An interesting observation is that in the two periods where the ROC has the highest number of false alarms (period 1-2015 and 2-2016), the modelled temperatures are among the extremes (second lowest in period 1-2015 and highest in period 2-2016).

Concluding remarks

Facing the problems caused by salmon lice from the aquaculture industry, a reliable forecasting system is essential for a further sustainable development of fish farming. Using the binary method twice, a system with three categorical events (high, medium, and low) for a potential lice infestation pressure is suggested, and it is demonstrated through a random permutation of the cages and a CV that the system is robust and has clear predictability skills. The main driver for advection and dispersion of salmon louse is the ocean physics, and this is well-represented using a highresolution ocean model. The system also includes an IBM for salmon louse, where known behaviour and life development has been implemented. It has also been shown how model performance has improved through the inclusion of new results on salmon louse behaviour from laboratory experiments. The suggested model system can, therefore, also serve as a benchmark to assess the performance of future updates of the salmon louse IBM based on updated experimental knowledge. The system has been developed for the Hardangerfjord, but the method is general and can be applied to all Norwegian fjords, and the ROC is at present in use as one of the main components of the "Traffic-light system" for a sustainable management of Norwegian salmon farming.

The model system uses inputs on reported fish biomass and lice densities from all aquaculture sites in the area. These numbers are only reported by week number, and with the well-known high variability of the hydrodynamics within the fjords, this is a clear and uncontrolled weakness of the model system. In addition, the harvest cages also represent an uncontrolled weakness, but always an underestimation of the model predicted salmon lice infestation. The combination of observations and models is valuable and high-quality products depend on proper use of both. Therefore, the ROC has been developed and performance has been assessed using the best available and controlled observations on salmon louse densities in the Hardangerfjord represented by the number of lice on fish in sentinel cages. The cages are assumed to give an integrated measure of the local lice infestation pressure over the period of their deployment, but this has never been proven. This kind of indirect measurement can be influenced by biofouling, the quality and size of the smolt, the handling of the fish, and the counting of the lice, but are still considered to be the most suitable data set for the present coarse-scale analysis. A number of studies has shown that "particles" transported in the ocean rarely constitute smooth continuous fields but rather establish patchy patterns with strong gradients (Mackas et al., 1985). This non-uniformity in the integrated field has, for example, been shown through a deployment of several cages in close vicinity to each other resulting in a relatively large difference in numbers of salmon lice between individual cages (Svåsand et al., 2015). The lack of a comprehensive study to understand the impact of shortterm variability and patchiness on the representativeness and quality of observations from the sentinel cages is a clear limitation in the use of such data. We, therefore, believe that a high-resolution model with well-validated hydrography and a realistic representation of the salmon louse biology based on all available knowledge represents the best realization of the local potential infestation pressure on wild fish.

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References

- á Nordi, G., Simonsen, K., Danielsen, E., Eliasen, K., *et al.* 2015. Abundance and distribution of planktonic *Lepeophteirus salmonis* and *Caligus elongatus* in a fish farming region in the Faroe Islands. Aquaculture Environment Interactions, 7: 15–27.
- á Nordi, G., Simonsen, K., and Patursson, Ø. 2016. A method of estimating *in situ* salmon louse nauplii production at fish farms. Aquaculture Environment Interactions, 8: 397–405.
- Ådlandsvik, B. 2019. LADiM documentation. https://ladim.readthe docs.io (last accessed 27 December 2019).
- Albretsen, J., Sperrevik, A. K., Staalstrøm, A., Sandvik, A. D., Vikebø, F., and Asplin, L. 2011. NorKyst-800 report no. 1: User manual and technical descriptions. IMR Res Rep Ser Fisken og Havet 2/2011. Institute of Marine Research, Bergen.
- Anonymous. 2015. Innstilling til Stortinget fra næringskomiteen Meld. St. 16 (2014 – 2015). Innstilling fra næringskomiteen om forutsigbar og miljømessig bærekraftig vekst i norsk lakse- og ørretoppdrett. Stortinget, Oslo.
- Asplin, L., Boxaspen, K., and Sandvik, A. D. 2004. Modelled Distribution of Salmon Lice in a Norwegian Fjord. ICES Document CM 2004/P: 11, 12pp
- Asplin, L., Boxaspen, K. K., and Sandvik, A. D. 2011. Modeling the distribution and abundance of planktonic larval stages of *Lepeophtheirus salmonis* in Norway. *In* Salmon Lice: An Integrated Approach to Understanding Parasite Abundance and Distribution, pp. 31–50. Ed. by S. Jones and R. Barnes Wiley-Blackwell, Oxford.

- Asplin, L., Johnsen, I. A., Sandvik, A. D., Albretsen, J., Sundfjord, V., Aure, J., Boxaspen, K. K., *et al.* 2014. Dispersion of salmon lice in the Hardangerfjord. Marine Biology Research, 10: 216–225.
- Bergmeir, C., and Benítez, J. M. 2012. On the use of cross-validation for time series predictor evaluation. Information Sciences, 191: 192–213.
- Bjørn, P. A., Nilsen, R., Serra Llinares, R. M., Asplin, L., Boaspen, K,K., Finstad, B., Uglem, I. *et al.* 2012. Lakselusinfeksjonen på vill laksefisk langs norskekysten i 2012. Sluttrapport Til Mattilsynet. Rapport Fra Havforskningen 31-2012. Institute of Marine Research, Bergen.
- Bjørn, P. A., Nilsen, R., Serra Llinares, R. M., Asplin, L., et al. 2013. Lakselusinfeksjonen på vill laksefisk langs norskekysten i 2013. Sluttrapport Til Mattilsynet. Rapport Fra Havforskningen 32-2013. Institute of Marine Research, Bergen.
- Bjørn, P. A., Sivertsgård, R., Finstad, B., Nilsen, R., Serra-Llinares, R. M., and Kristoffersen, R. 2011. Area protection may reduce salmon louse infection risk to wild salmonids. Aquaculture Environment Interactions, 1: 233–244.
- Bricknell, I. R., Dalesman, S. J., O'S, S., Pert, C. C., and Mordue Luntz, A. J. 2006. Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. Diseases of Aquatic Organisms, 71: 201–212.
- Bron, J. E., Sommerville, C., Jones, M., and Rae, G. H. 1991. The settlement and attachment of early stages of the salmon louse, *Lepeophtheirus salmonis* (Copepoda, Caligidae) on the salmon host, *Salmo salar*. Journal of Zoology (London), 224: 201–212.
- Brooks, K. M. 2005. The effects of water temperature, salinity, and currents on the survival and distribution of the infective copepodid stage of sea lice (*Lepeophtheirus salmonis*) originating on Atlantic salmon farms in the Broughton Archipelago of British Columbia, Canada. Reviews in Fisheries Science, 13: 177–204.
- Crosbie, T., Wright, D. W., Oppedal, F., Johnsen, I. A., Samsing, F., and Dempster, T. 2019. Effects of step salinity gradients on salmon lice larvae behavior and dispersal. Aquaculture Environment Interactions, 11: 181–190.
- Ebert, E. E. 2008. Fuzzy verification of high-resolution gridded forecasts: a review and proposed framework. Meteorological Applications, 15: 51–64.
- Flamarique, I. N., Browman, H. I., Belanger, M., and Boxaspen, K. 2000. Ontogenetic changes in visual sensitivity of the parasitic salmon louse *Lepeophtheirus salmonis*. Journal of Experimental Biology, 203: 1649–1657.
- Gillibrand, P. A., and Willis, K. J. 2007. Dispersal of sea louse larvae from salmon farms: modelling the influence of environmental conditions and larval behavior. Aquatic Biology, 1: 63–75.
- Haidvogel, D. B., Arango, H., Budgell, W. P., Cornuelle, B. D., Curchitser, E., Di Lorenzo, E., Fennel, K., et al. 2008. Ocean forecasting in terrain-following coordinates: formulation and skill assessment of the Regional Ocean Modeling System. Journal of Computational Physics, 227: 3595–3624.
- Hamre, L. A., Eichner, C., Caipang, C. M. A., Dalvin, S. T., Bron, J. E., Nilsen, F., Boxshall, G., *et al.* 2013. The salmon louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) life cycle has only two chalimus stages. PLoS One, 8: e73539.
- Heuch, P. A. 1995. Experimental evidence for aggregation of salmon louse copepodids (*Lepeophtheirus salmonis*) in step salinity gradients. Journal of the Marine Biological Association of the United Kingdom, 75: 927–939.
- Heuch, P. A., Parsons, A., and Boxaspen, K. 1995. Diel vertical migration: a possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? Canadian Journal of Fisheries and Aquatic Sciences, 52: 681–689.
- Hevrøy, E. M., Boxaspen, K., Oppedal, F., Taranger, G. L., and Holm, J. C. 2003. The effect of artificial light treatment and depth on the infestation of the sea louse *Lepeophtheirus salmonis* on Atlantic salmon (*Salmo salar* L.) culture. Aquaculture, 220: 1–14.

- Jansen, P. A., Kristoffersen, A. B., Viljugrein, H., Jimenez, D., Aldrin, M., and Stien, A. 2012. Sea lice as a density-dependent constraint to salmonid farming. Proceedings of the Royal Society B, 279: 2330–2338.
- Johnsen, I. A., Asplin, L., Sandvik, A. D., and Serra-Llinares, R. M. 2016. Salmon lice dispersion in a northern Norwegian fjord system and the impact of vertical movements. Aquaculture Environment Interactions, 8: 99–116.
- Johnsen, I. A., Fiksen, Ø., Sandvik, A. D., and Asplin, L. 2014. Vertical salmon lice behavior as a response to environmental conditions and its influence on regional dispersion in a fjord system. Aquaculture Environment Interactions, 5: 127–141.
- Johnson, S. C., and Albright, L. J. 1991. Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda, Caligidae) under laboratory conditions. Journal of the Marine Biological Association of the United Kingdom, 71: 425–436.
- Karlsen, Ø., Bjørn, P. A., Johnsen, I. A., Skarðhamar, J., et al. 2015. Risikovurdering Lakselus – 2014. Pages 16-49 in Risikovurdering norsk fiskeoppdrett 2014., Svåsand, T., Boaspen, K. K., Karlsen, Ø., Kvamme, B. O., Stien, L. H., og Taranger, G. L. (eds). Fisken Havet særnummer 2-2015. Institute of Marine Research, Bergen. http://hdl.handle.net/11250/281780 (last accessed 27 December 2019).
- Lévy, M., Franks, P. J. S., and Smith, K. S. 2018. The role of submesoscale currents in structuring marine ecosystems. Nature Communications, 9: 4758.
- Mackas, D. L., Denman, K. L., and Abbott, M. R. 1985. Plankton patchiness: biology in the physical vernacular. Bulletin of Marine Science, 37: 652–674.
- Martin, A. P. 2003. Phytoplankton patchiness: the role of lateral stirring and mixing. Progress in Oceanography, 57: 125–174.
- Mason, I. B. 1982. A model for assessment of weather forecasts. Australian Meteorological Magazine, 30: 291–303.
- Mason, I. B. 2003. Binary events. *In* Forecast Verification. A Practitioner's Guide in Atmospheric Science, pp. 37–76. Ed. by I. T. Jolliffe and D. B. Stephenson. John Wiley & Sons, Chichester.
- Myksvoll, M. S., Sandvik, A. D., Albretsen, J., Asplin, L., Johnsen, I. A., Karlsen, Ø., Kristensen, N. M., et al. 2018. Evaluation of a national operational salmon lice monitoring system—from physics to fish. PLoS One, 13: e0201338.
- Nilsen, R., Bjørn, P. A., Serra-Llinares, R. M., Asplin, L., *et al.* 2014. Lakselusinfeksjonen på vill laksefisk langs norskekysten i 2014. Sluttrapport Til Mattilsynet. Rapport Fra Havforskningen 36-2014. Institute of Marine Research, Bergen.
- Penston, M. J., McBeath, A. J. A., and Millar, C. P. 2011. Densities of planktonic *Lepeophtheirus salmonis* before and after an Atlantic salmon farm relocation. Aquaculture Environment Interactions, 1: 225–232.
- Penston, M. J., McKibben, M. A., Hay, D. W., and Gillibrand, P. A. 2004. Observations on open water densities of sea lice larvae in Loch Shieldaig, Western Scotland. Aquaculture Research, 35: 793–805.
- Pert, C. C., Fryer, R. J., Cook, P., Kilburn, R., McBeath, S., McBeath, A., Matejusova, I., *et al.* 2014. Using sentinel cages to estimate infestation pressure on salmonids from sea lice in Loch Shieldaig, Scotland. Aquaculture Environment Interactions, 5: 49–59.
- Salama, N. K. G., Collins, C. M., Fraser, J. G., Dunn, J., Pert, C. C., Murray, A. G., Rabe, B., *et al.* 2013. Development and assessment of a biophysical dispersal model for sea lice. Journal of Fish Diseases, 36: 323–337.
- Samsing, F., Johnsen, I., Stien, L. H., Oppedal, F., Albretsen, J., Asplin, L., Dempster, T., *et al.* 2016. Predicting the effectiveness of depth-based technologies to prevent salmon lice infection using a dispersal model. Preventive Veterinary Medicine, 129: 48–57.
- Samsing, F., Solstorm, D., Oppedal, F., Solstorm, F., and Dempster, T. 2015. Gone with the flow: current velocities mediate parasitic

infestation of an aquatic host. International Journal for Parasitology, 45: 559–565.

- Sandvik, A. D., Bjørn, P. A., Ådlandsvik, B., Asplin, L., Skarðhamar, J., Johnsen, I. A., Myksvoll, M., *et al.* 2016. Toward a model-based prediction system for salmon lice infestation pressure. Aquaculture Environment Interactions, 8: 527–542.
- Scheffer, M., Baveco, J. M., DeAngelis, D. L., Rose, K. A., and van Nes, E. H. 1995. Superindividuals a simple solution for modeling large populations on an individual basis. Ecological Modelling, 80: 161–170.
- Schram, T. A. 1993. Supplementary descriptions of the developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). *In* Pathogens of Wild and Farmed Fish: Sea Lice, pp. 30–47. Ed. by D. E. Boxshall and D. Defaye. Ellis Horwood, Chichester.
- Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M., and Asplin, L. 2014. Almon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. Aquaculture Environment Interactions, 5: 1–16.
- Shchepetkin, A. F., and McWilliams, J. C. 2005. The regional oceanic modeling system (ROMS): a split-explicit, freesurface, topography-following-coordinate oceanic model. Ocean Modelling, 9: 347–404.
- Skarðhamar, J., Fagerli, M. N., Reigstad, M., Sandvik, A. D., and Bjørn, P. A. 2019. Sampling planktonic salmon lice in Norwegian fjords. Aquaculture Environment Interactions.11:701-715. https:// doi.org/10.3354/aei00342.
- Skilbrei, O. T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F., and Strand, R. 2013. Impact of early salmon louse (*Lepeophtheirus salmonis*) infestation, and differences in survival and marine growth

of sea-ranched Atlantic salmon (*Salmo salar*) smolts 1997-2009. Journal of Fish Diseases, 36: 249–260.

- Stien, A., Bjørn, P. A., Heuch, P. A., and Elston, D. A. 2005. Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. Marine Ecology Progress Series, 290: 263–275.
- Svåsand, T, Boxaspen, KK, Karlsen, Ø, Kvamme, BO, Stien, LH, Tarranger, GL (Eds). 2015. Riskikovurdering Norsk fiskeoppdrett 2014. Technical report, Fisken og Havet særnummer 2-2015, Institute of Marine research, Pb1870 Nordnes, Bergen Norway, 175 pp. In Norwegian.
- Svåsand, T., Karlsen, Ø., Kvamme, B. O., Stien, L. H., Taranger, G. L., and Boxaspen, K. K. 2016. Risikovurdering norsk fiskeoppdrett 2016. Fisken Havet 2-2016. Institute of Marine Research, Bergen.
- Taranger, G. L., Karlsen, Ø., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., Kvamme, B. O., *et al.* 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES Journal of Marine Science, 72: 997–1021.
- Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., *et al.* 2015. Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta*—a literature review. Aquaculture Environment Interactions, 7: 91–113.
- Vollset, K. W., Barlaup, B. T., Skoglund, H., Normann, E. S., and Skilbrei, O. T. 2014. Salmon lice increase the age of returning Atlantic salmon. Biology Letters, 10: 20130896.
- Vollset, K. W., Dohoo, I., Karlsen, Ø., Halttunen, E., Kvamme, B. O., Finstad, B., *et al.* 2017. Disentangling the role of sea lice on the marine survival of Atlantic salmon. ICES Journal of Marine Science. 75: 50–60.
- Wilks, D. S. 1995. Statistical Methods in the Atmospheric Sciences. Elsevier, New York, NY.

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