



The effect of a warmer climate on the salmon lice infection pressure from Norwegian aquaculture

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Climate change can hamper sustainable growth in the aquaculture industry by amplifying and adding to other environmental challenges. In Norway, salmon lice-induced mortality in wild salmonid populations is identified as a major risk factor for further expansion. Higher temperatures will induce increased production of salmon lice larvae, decreased developmental time from non-infective nauplii to infectious copepods, and higher infectivity of copepodids. In a warmer climate, a modelling exercise shows how these three factors lead to a significant increase in the infection pressure from farmed to wild salmonids, where the infectivity of copepodids is the term with the highest sensitivity to temperature changes. The total infection pressure gradually increases with increasing temperature, with an estimated twofold if the temperature increases from 9°C to 11°C. Thus, making it even harder to achieve a sustainable expansion of the industry with rising water temperature. This study demonstrates how bio-hydrodynamic models might be used to assess the combined effects of future warmer climate and infection pressure from salmon lice on wild salmonids. The results can be used as an early warning for the fish-farmers, conservation stakeholders and the management authorities, and serve as a tool to test mitigation strategies before implementation of new management plans.

Keywords: aquaculture, climate change, Hardangerfjord, *Lepeophtheirus salmonis*, temperature, salmon lice

Introduction

Climate change is altering the marine environments throughout the world (IPCC, 2014) projecting an increase in global mean surface air temperature between 1°C and 4°C by year 2100 dependent on the greenhouse gas emission scenario chosen. Finfish aquaculture is an increasingly important source of protein production for human consumption (FAO, 2018), contributes to food security (Pradeepkiran, 2019) and is responsible for more than half of the global seafood production as a growing population creates an increased demand for food. Due to over-exploitation of wild fish stocks (FAO, 2018), it is expected that aquaculture will be even more important in the future. However, this industry is becoming increasingly scrutinized in terms of environmental impact, sustainability and, for salmonid aquaculture, consequences for conservation for wild salmonid populations.

Norway is one of the largest producers of Atlantic salmon in the world with a political ambition to further increase, from 1.3 in 2018 to 5 million metric tons by 2050 (Statistics Norway, <https://www.ssb.no/fiskeoppdrett>). To support a predictable and environmentally sustainable growth in salmon aquaculture, the Norwegian government has implemented a science-based management system where the coast is divided into 13 production zones (see Figure 1). In this management system, popularly named the “traffic light (green-yellow-red) system” (Norwegian White Paper: St. Meld. 16, 2014–2015), the sustainability status within each zone is assessed every year. Salmon lice has been identified as one of the main risk factors for a further increase in Norwegian salmon farming (Taranger *et al.*, 2015), and salmon lice-induced mortality in wild salmonid populations is currently used as the key sustainability indicator in the traffic light system (Vollset *et al.*, 2019).

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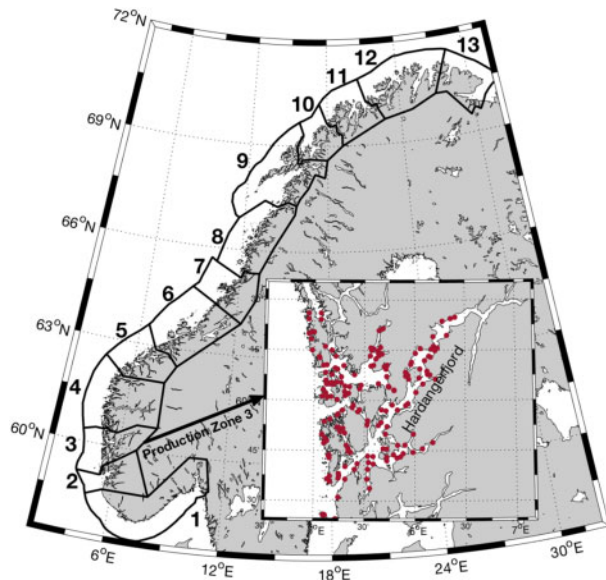


Figure 1. The 13 aquaculture production zones along the Norwegian coast, with Production Zone 3 and Hardangerfjord highlighted. The red dots in the zoomed-in area show the location of sea farms in Production Zone 3.

Salmon louse (*Lepeophtheirus salmonis*) is a naturally occurring ectoparasite, which parasitize salmonid fish [in Norwegian water: Atlantic salmon (*Salmo salar*), Sea trout (*Salmo trutta*), and Arctic charr (*Salvelinus alpinus*)]. The number of hosts for salmon lice has increased dramatically in parallel with the expansion of Atlantic salmon farming, and an imbalance has developed between lice abundance and susceptible wild hosts (Serra-Llinares *et al.*, 2014, 2018; Vollset *et al.*, 2014; Thorstad *et al.*, 2015; Fjørtoft *et al.*, 2017, 2019). Salmon lice have been correlated to reductions in wild populations of both sea trout and Atlantic salmon (Vollset *et al.*, 2018; Forseth *et al.*, 2019; Bøhn *et al.*, 2020; Serra-Llinares *et al.*, 2020), and therefore limits the ability of Norway 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/convention.html and the law of nature biodiversity §8). Finally, salmon louse can represent a welfare problem for farmed salmon due to delousing methods (Overton *et al.*, 2019; Bui *et al.*, 2019). To successfully estimate the salmon lice infection pressure on wild and farmed salmonids, a good and science-based understanding of parameters that influence the distribution and biology of the planktonic stages of lice are needed.

Salmon lice eggs carried by the mature females hatch directly into the water masses and develop through three non-feeding planktonic stages: two nauplius stages and the infective copepodid stage. Lice larvae that do not locate a host fish in time will die from starvation or predation. The duration of the planktonic stages depends on the ambient water temperature lasting up to 35 and 10 days at 5°C and 15°C, respectively. Thus, lice larvae can potentially drift several tens of kilometres away from the source (Asplin *et al.*, 2014; Johnsen *et al.*, 2014; Samsing *et al.*, 2015), and therefore contribute to an elevated infection pressure over a large geographic area. Hydrodynamic models are a widely used tool for simulating dispersion of planktonic matter (Stucchi *et al.*, 2011; Adams *et al.*, 2016; Salama *et al.*, 2018; Cantrell *et al.*,

2020b; Rabe *et al.*, 2020; Toorians and Adams, 2020). Combined with individual-based models (IBMs) where known behaviour and development parameters have been implemented, it is possible to quantify the number of salmon lice and their infectivity with high resolution in both space and time (Sandvik *et al.*, 2016, 2020c; Myksvoll *et al.*, 2018; Johnsen *et al.*, 2020a). Based on such a coupled model system, a warning system describing areas with elevated lice infection pressure [the relative operating characteristic (ROC), see “Relative operating characteristic” section], was first presented in Sandvik *et al.* (2016), and further developed in Sandvik *et al.* (2020c). This method is currently an operational part of the Norwegian traffic light management system. Such models are well suited to perform simulations and do theoretical assessments of the infection pressure from salmon louse on wild salmonids. In this way, e.g. mitigation strategies can be tested before management plans are implemented, both through manipulating environmental factors and the magnitude of nauplii releases from fish farms (Sandvik *et al.*, 2020b).

In this study, the main objective has been to investigate the combined effect of two of the major challenges to Norwegian aquaculture: increased temperatures due to climate change and salmon lice. The focus has been to investigate and decipher three known temperature impacts on salmon lice: number of hatched eggs (Stien *et al.*, 2005), copepodid infectivity (Skern-Mauritzen *et al.*, 2020), and larval (nauplii and copepodid) mortality (Stien *et al.*, 2005) that are all expected to give a positive feedback on the infection pressure in a warmer climate. The study on temperature impacts is general and will be valid for all farming of Atlantic salmon. In addition, an assessment of the temperature induced changes in infection pressure from the aquaculture industry on wild salmonids has been exemplified for the Hardangerfjord area using the ROC method (Sandvik *et al.*, 2020c) and year 2019 as a reference.

Material and methods

Production zones and study area

Since 2017, the Norwegian coast has been divided into the 13 production zones based on an analysis of the dispersion of lice between the aquaculture sites. The boundaries between the zones were drawn where there was minimum cross-dispersion (Ådlandsvik, 2015). This zoning approach using connectivity implies that lice released from farms within one production zone are likely to stay within that production zone, making it beneficial to consider each zone as an independent management unit.

The Hardangerfjord system is located in Western Norway (Production Zone 3), south of Bergen. The fjord system stretches 179 km from the coast into the mountainous interior of Norway. It consists of a number of large and small fjord arms and has several connections to the open sea, thus the circulation pattern is relatively complicated with large spatial and temporal variability. A detailed description of the fjord physics can be found in Asplin *et al.* (2014), Johnsen *et al.* (2014), Asplin *et al.* (2020), and Dalsøren *et al.* (2020).

In Production Zone 3 around 170 locations are approved for aquaculture production (2012–2020), producing ~80 000 tons of salmon annually. The production cycle generally lasts 15–18 months, and legislation rules say that the locations must be fallowed between cycles. Thus, not all farms are active and in the same stage of the production cycle at a given time. In the targeted

period (1 April to 31 August 2019) 107 farms had reported mandatory measures on numbers of fish (around 60 million), lice and temperature in 3-m depth to the authorities. From the recent evaluation, based on data from 2018 and 2019 (Ministry of Trade, Industry and Fisheries, 4 February 2020), the environmental impact of salmon lice on wild salmonid stocks in Production Zone 3 was classified as medium (yellow) in the Norwegian traffic light system (Vollset *et al.*, 2019).

Salmon lice dispersion model

The density of infective salmon lice was computed using a bio-hydrodynamic lice dispersion model system (Johnsen *et al.*, 2014, 2016; Myksvoll *et al.*, 2018; Sandvik *et al.*, 2016, 2020c). In this system, an IBM with known behaviour and life development for salmon louse is coupled to an ocean model system based on the Regional Ocean Modelling System (www.myroms.org; Shchepetkin and McWilliams, 2005; Haidvogel *et al.*, 2008), implemented for the Norwegian coast and fjords (Albretsen *et al.*, 2011; Asplin *et al.*, 2020; Dalsøren *et al.*, 2020). The salmon lice advection and growth model is based on the Lagrangian Advection and Diffusion Model and the code is available in an online repository (LADiM; Ådlandsvik, 2019). As the salmon lice model is used in management, it is updated regularly as new biological knowledge is available. For this work the LADiM model was implemented with biological parameters using the salmon lice plugin, version 1.2 (Sævik, 2020). In the vertical, the water column is divided into 35 sigma levels, and the horizontal quadratic grid cell size is 160×160 m. The biology and life history of the lice are handled with an IBM using the super-individual (SI) approach (Scheffer *et al.*, 1995). The model is initiated without any salmon lice SI, while new louse SIs are added hourly as newly hatched nauplii at a rate of five SI/farm/hour with the internal number of each SI scaled to represent the estimated (Stien *et al.*, 2005) reported egg numbers that week. The model output consists of 3D hourly fields of spatial distribution and density of salmon lice copepodids in the sea. The developmental rate of an individual louse is purely temperature dependent and is parameterized as a function of degree-days (Hamre *et al.*, 2019).

The results from the lice dispersion model are publicly available weekly (www.lakselus.no) and as an archive from 2012 to 2019 (Sandvik *et al.*, 2020a). Similar approaches to predict salmon lice density in the water masses have been widely used in the scientific community (Adams *et al.*, 2012, 2015, 2016; Salama *et al.*, 2013, 2018; Kough *et al.*, 2015; Samsing *et al.*, 2017; Cantrell *et al.*, 2018; Kristoffersen *et al.*, 2018; Kragestein *et al.*, 2018; Samsing *et al.*, 2017).

Hatching rate, mortality, infectivity, and temperature

All active Norwegian Sea farms are obliged to report water temperatures at 3-m depth and the average number of adult female lice pr. fish from their site every week to the management authorities. The total number of fish on their site is reported once a month. The daily number of hatching eggs is temperature dependent and was calculated using a formula from Stien *et al.* (2005), assuming that the adult females were continuously producing batches of eggs in paired egg strings, with each string containing 150 eggs (Johnsen *et al.*, 2016):

$$N_{egg} = N_{fish} \cdot N_{female} \cdot 0.17 \cdot (T + 4.28)^2, \quad (1)$$

where T is the temperature, N_{fish} is the number of fish and N_{female} is the number of adult female lice pr. fish.

The larvae develop to infective copepodids after 40 degree-days and die after 170 degree-days if they are not successful in finding a host (Samsing *et al.*, 2016a). The planktonic larvae mortality is assumed to be constant in time and space at 17% per day (Stien *et al.*, 2005). Thus, given a batch of eggs the temperature, and thereby also the time spent from hatching and through the infective period, will decide the number of infective copepodids at a given time.

$$N_{cop} = N_{egg} \cdot e^{-0.17 \cdot \frac{A}{4}}, \quad 40 \leq A \leq 170, \quad (2)$$

where A is the age in degree-days (= temperature · time). At 15°C, the infective period (A) will start after 2.7 days and last until day 11.3, whereas at 5°C the infective period will start later but last three times longer. Beginning with 1000 nauplii at 15°C the number of individuals will thus be reduced to 636 as they become infective (at 40 degree-days) and further reduced to 145 after 170 degree-days, whereas at 5°C the corresponding numbers are 256 and 3.

The infection pressure (IP) for a given position and time is the number of infective salmon lice copepodids (N_{cop}) multiplied by their infectivity (I) such that:

$$IP = N_{cop} \cdot I. \quad (3)$$

Based on laboratory experiments at 5°C, 10°C, and 15°C, Skern-Mauritzen *et al.* (2020) estimated the infectivity, I , as a function of temperature and age as:

$$\begin{aligned} \ln(I) = & -34.660 + 2.306 \cdot T - 2.585 \cdot 10^{-2} \cdot T^2 + 7.156 \cdot 10^{-1} \cdot A \\ & - 5.354 \cdot 10^{-3} \cdot A^2 + 1.191 \cdot 10^{-5} \cdot A^3 - 3.577 \cdot 10^{-2} \cdot A \cdot T \\ & - 2.526 \cdot 10^{-4} \cdot A^2 \cdot T - 5.541 \cdot 10^{-7} \cdot A^3 \cdot T. \end{aligned} \quad (4)$$

The infectivity (I) can then be calculated from:

$$I = \frac{e^{\ln(I)}}{1 + e^{\ln(I)}}, \quad 5^\circ\text{C} \leq T \leq 15^\circ\text{C}. \quad (5)$$

Relative operating characteristic

The ROC is a graph of the hit rate, H , against the false alarm rate, 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 salmon lice density by stepping through different forecast systems, each system generating a 2×2 contingency table and values of H and F (Mason, 1982). For a forecast system with zero skill, $H = F$, whereas in a perfect system, $H = 1$ and $F = 0$. Based on observations from sentinel cages for the years 2012–2017, a ROC was developed to predict the potential salmon lice infection pressure (Sandvik *et al.*, 2016, 2020c). The system uses three categorical events (high, medium, and low) for a potential lice infection

pressure, and is at present in use as one of the components of the “Traffic light system” for a sustainable management of Norwegian salmon farming. In the present work using the ROC-parameters $R=0.50$ lice/m² in 9 out of 9 ($=3 \times 3$) neighbouring points as thresholds between red (> 10 salmon lice per smolt) and yellow (between 1 and 10 salmon lice per smolt), and $R=0.22$ in 6 out of 9 points between yellow and green (<1 salmon lice per smolt), the method’s skill score (red to yellow) becomes 0.12 (Skern-Mauritzen *et al.*, 2020). For more details on the ROC method see Sandvik *et al.* (2020c).

The ROC-products constitutes a combination of: (i) salmon lice infestation maps in three colours (hereinafter named ROC-maps), where the colours indicate the local severity of salmon lice-induced mortality on wild salmonids, and where a subjective assessment is performed based on overlap between areas with elevated salmon lice pressure and assumed salmon post-smolt migration routes, and (ii) a time series of an index (hereinafter named ROC-index) defined for 30 days periods and calculated as a weighted mean of these categorical areas relative to the total area using this formula from Sandvik *et al.* (2020b):

$$ROC_{index} = \frac{Area_{red} + 0.5 \cdot Area_{yellow}}{Area_{red} + Area_{yellow} + Area_{green}} \cdot 100, \quad (6)$$

where $Area_{red}$ is the size of the red area, and similar for the other colours.

In this work, the total infection pressure is defined as the value of the ROC-index from the estimated date that 50% of salmon post-smolts would have migrated (Production Zone 3: 21 May) and 30 days thereafter. This period is covering a large part of the salmon smolt migration period and the early feeding period for Sea trout and Arctic charr. In the traffic light evaluation the ROC-index is defined to be low ($ROC_{index} < 10$), moderate ($10 < ROC_{index} < 30$) and high ($ROC_{index} > 30$). Thus, if only a small area within the production zone has elevated salmon lice pressure (i.e. $ROC_{index} < 10$), this method will suggest that the production zone should be categorized as having a low risk for salmon lice-induced mortality on the wild fish population (green colour), while if there is a large portion of the area with elevated salmon lice infection

pressure (i.e. $ROC_{index} > 30$) the indicator will suggest that the production zone should be categorized as having a high risk of mortality in the wild fish population (red colour).

Results

In our model experiments, the nauplii become infective copepods after 40 degree-days and die after 170 degree-days (Samsing *et al.*, 2016a) if they are not successful in finding a host, thus the total infection pressure (IP_T) from a batch of eggs can be considered to be the integral of the infection pressure IP [Equation (3)] through this period. For a given temperature, the total infection pressure (IP_T) from a batch of eggs becomes:

$$IP_T = \int_{40}^{170} IP dA = I_H \cdot I_M \cdot I_I = N_{egg} \cdot \int_{40}^{170} e^{-0.17 \frac{A}{T_0}} \cdot \frac{e^{ln(I)}}{1 + e^{ln(I)}} dA, \quad (7)$$

when combining Equations (1), (2), and (5). Omitting the number of fish (N_{fish}) and number of female lice per fish (N_{female}) in Equation (1), the total infection pressure for $5^\circ\text{C} \leq T \leq 15^\circ\text{C}$ is given in the left panel of Figure 2, normalized by setting $IP_T = 1$ at 5°C . IP_T increase from 1 to 55 going from 5°C to 15°C , and with a factor 2 when the temperature increases from 9°C to 11°C .

In the right panel of Figure 2, the individual contributions from each of the three temperature dependent terms in Equation (7) are estimated separately. The temperature effect of the first term (I_H) (the batch size N_{egg}), is computed from Equation (1). For a given number of fish and adult female lice, the number of hatched eggs increases with a factor 4.3 when the temperature increases from 5°C to 15°C , and with 30% from 9°C to 11°C . The effect from this is shown in the right panel of Figure 2, again setting $I_H = 1$ at 5°C .

The second term in Equation (7), I_M , accounts for the number of infective copepodites from the mortality of 17% per day [Equation (2)]. The mortality is temperature independent, but as the infective period is given in degree-days the time window and thereby the number of infective salmon lice will depend on the actual temperature. The effect from mortality due to the length of the infective period and the number of salmon lice (I_M) is also shown in the right panel of Figure 2. Again, the numbers are

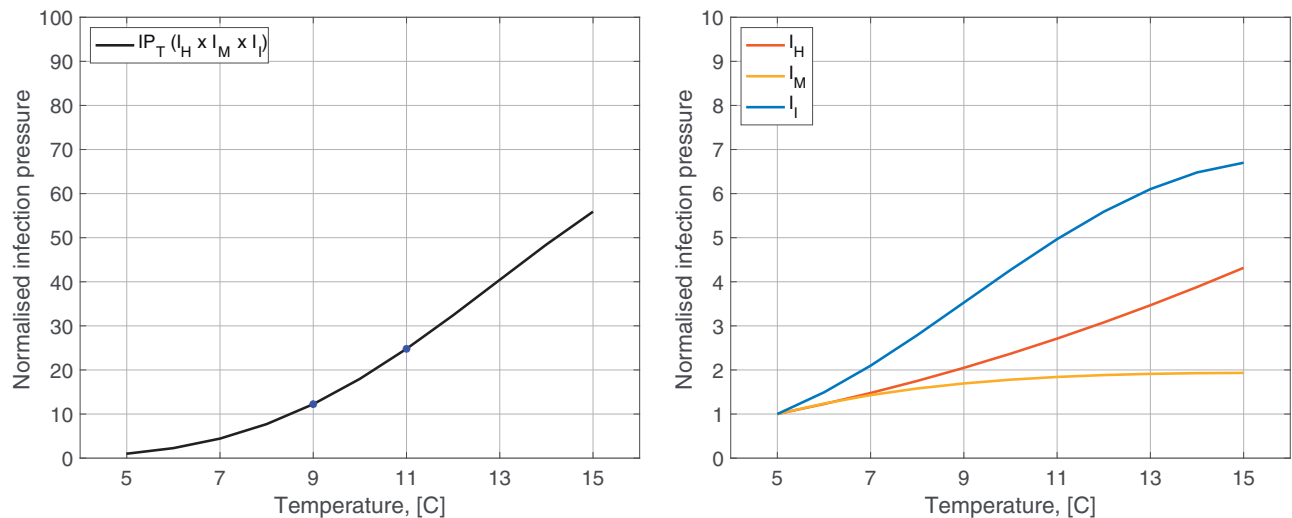


Figure 2. Normalized total infection pressure, IP_T , for temperatures 5–15°C relative to 5°C (left panel) and the different infectivity components: hatching rate (I_H), mortality (I_M) and infectivity (I_I) also normalized to 5°C (right panel).

normalised so that $I_M = 1$ at 5°C . I_M is lower than I_H with an increase of a factor 1.9 when going from 5°C to 15°C , and with a 9% increase when the temperature goes from 9°C to 11°C .

Finally, using a constant temperature, Equations (4) and (5) can be used to compute the temperature dependent infectivity (I_I) between 40 and 170 degree-days, which is the third term of Equation (7). This line is again given in Figure 2 normalized to 1 at 5°C . I_I shows the largest temperature dependency of the three terms, increasing with a factor 6.7 when going from 5°C to 15°C , and 40% from 9°C to 11°C . In total, when isolating the three different temperature dependency terms of the total infectivity pressure on wild salmonids, the largest, I_b , equals the sum of the two others (I_H and I_I) when the temperature increases.

The spatio-temporal variability in the total infectivity pressure is large, as is the estimated mortality on wild salmon post-smolt populations migrating from the rivers (Johnsen *et al.*, 2020a). How much the salmon-lice-induced mortality on wild salmonids will increase in a future warmer climate, is to our knowledge not established. We therefore show an example on how the infection pressure changes using the ROC-method for a regional area (Production Zone 3) in a specific year (2019). In Figure 3, the ROC-map for Production Zone 3 (the Hardangerfjord area, reference case) is shown together with the effect of a 2°C increase in the temperature for a stepwise inclusion in the different temperature dependent processes above for three different simulations:

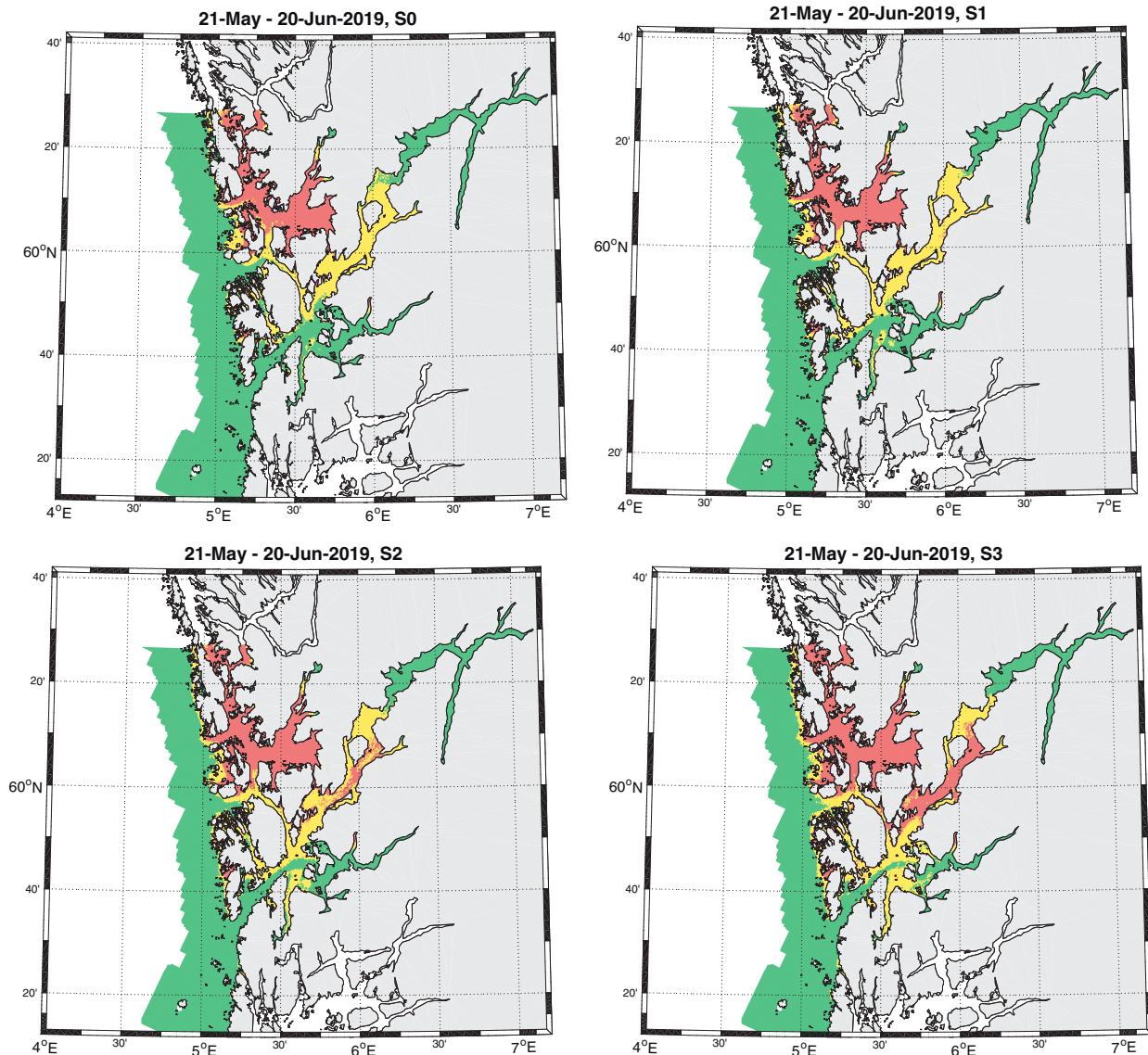


Figure 3. ROC maps that display areas where wild salmonids, occupying the area for the given time period, are expected to be infected by more than 10 lice (red colour), between 1 and 10 lice (yellow colour), and less than 1 lice (green colour). Outcomes are shown for the four different simulations in the Hardangerfjord area 2019 as defined in the “Results” section. Reference (upper left), S1 (upper right), S2 (lower left), and S3 (lower right).

Table 1. ROC-index [Equation (6)] for the four different simulations.

	Reference	S1	S2	S3
ROC-index	21.9	23.2	26.5	30.9

S1: Effect of increased temperature in the mortality [2nd term in Equation (7)].

S2: S1 and effect of increased temperature in infectivity [2nd + 3rd term in Equation (7)].

S3: S2 and effect of increased temperature in the nauplii production [all terms of Equation (7)].

Note that, it is only in the salmon lice calculations that temperature has been changed, while the temperature in the circulation model, and thus the hydrodynamics is the same in all four simulations. As seen in Figure 3 only a slight increase in the yellow area from the reference case to S1 can be detected. When going from S1 to S2 there is a slight further increase in the yellow area, but in addition, a part of the central Hardangerfjord is changing from yellow to red. For S3 most of the central Hardangerfjord becomes red. The ROC-index for the four different simulations is given in Table 1. The index shows a slight increase from the references to S1, and a further increase as successively more of the temperature dependent terms are included in the salmon lice dispersion model. The final assessment for the area goes from yellow (ROC-index between 10 and 30) to red (higher than 30) with such an increase of the temperature with 2°C.

Discussion

Three different temperature-dependent processes and their impacts on the total salmon lice infection pressure from parasites on farmed fish in aquaculture to wild salmonids have been investigated: the number of hatched eggs produced, the infectivity of the copepodid, and the larval (nauplii and copepodid) mortality. In a warmer climate, all three processes lead to negative effects and are likely to lead to a large increase in the total infection pressure. Due to the non-linearity in the temperature dependent infectivity, the effect of a warmer climate will differ between seasons and the geographical areas where aquaculture activity is present. The infection pressure is estimated to increase by a factor two going from 9°C to 11°C, and the relative impact of a 2°C increase will be highest at low temperatures (factor 4.4 from 5°C to 7°C) with a decreasing trend towards the highest temperatures (factor 1.4 from 13°C to 15°C; Figure 2, left panel). With an equal number of fish and equal number of female lice per fish, the infection pressure is estimated to increase by a factor 55 over the temperature window we have examined (5°C to 15°C). The annual variability in water temperature at 3-m depth (as reported from the sea farms) in Production Zone 3 is around 10°C (6–18°C in 2019, with a SD of 1.2°C for both the minimum winter temperature and the maximum summer temperature in the period 2012–2020), thus the seasonal variability in infectivity is higher than that from the projected climate change. However, this temperature increase will be on top of the seasonal cycle, and its consequences should therefore be considered separately.

The projected annual mean sea surface temperature increase in the North Sea area by the end of the century is in the range 1–3°C for the A1B greenhouse gas emission scenario (IPCC, 2014), with

the highest projected increase in spring (Schrum *et al.*, 2016). Thus, a temperature increase in the order 2°C is within a realistic window. A bio-hydrodynamic model was used to estimate the heterogeneous increase in the salmon lice infection pressure, and the ROC-index was further used to objectively quantify how such a projected temperature increase might change the sustainability assessment. As seen from the results, the ROC-index increases from 21.9 to 30.9 (40%), which is a substantial increase keeping in mind that values below 10 are considered as low in the traffic light evaluation. However, a 40% increase is less than the direct effect on the infectivity (Figure 2), indicating that the ROC-index has a relatively low sensitivity to changes in the infection pressure. The main reason for this is the definition of the ROC-index (Sandvik *et al.*, 2020c) and that the ROC-index only changes when there is a change in the assessment level (colour) in a given position. Due to a high (but variable) freshwater runoff, the salinity in the inner part of the Hardangerfjord is generally low (Dalsøren *et al.*, 2020). The combination of salmon lice avoidance to low salinity (Crosbie *et al.*, 2019) and the low number of fish farms in this area (Figure 1) will generally result in low (green) salmon lice infection pressure on wild salmonids here. There is also a relatively large green area at the coast, which in most cases will continue to be green under different scenarios and years due to the geographical localization of the farms (Figure 1) and local currents. These areas will act as a buffer and efficiently prevent the ROC-index from reaching 100. On the other hand, if an area already is red, it will not change even if the infection pressure increases. From a biological point of view, there is however a difference between areas with high infection pressure (few fish will survive) to very high infection pressure, where no fish are expected to survive. In the present assessment example (Production Zone 3, 2019), the main area of interest for changes is limited to the middle and outer part of the fjord. This is also an important area as salmon post-smolt from many rivers must migrate through here on their way towards the open ocean (Halttunen *et al.*, 2018; Johnsen *et al.*, 2020a). Parts of this area change from yellow to red, also changing the ROC-method assessment of Production Zone 3 from moderate to high impact (Table 1).

Uncertainties in the three infection pressure terms

In this study, the sensitivity to the temperature increase was highest in the infectivity term [term three (I_H) of Equation (7)]. This term is estimated as a function of both temperature and age, with newly moulted copepodids being less infective than those having matured 1–2 days ago followed by a decline of infectivity towards the end of their life expectancy (Brooker *et al.*, 2018; Skern-Mauritzen *et al.*, 2020). In the experiments in Skern-Mauritzen *et al.* (2020) the infectivity was investigated for three different temperatures (5°C, 10°C, and 15°C). Over the infective period the total infectivity increased with a factor four from 5°C to 10°C, and another factor 1.5°C to 15°C (Figure 2, right panel, blue line). Similarly, other studies confirm infectivity as a function of temperature, but with variable sensitivity: Samsing *et al.* (2016a) showed that the infectivity is an order of magnitude higher at 10°C compared with 5°C (and slightly higher than the success at 20°C), and Dalvin *et al.* (2020) found that the infectivity increased from 20% at 3°C to 50% at 10°C. In accordance with the findings of (Samsing *et al.*, 2016a), I_I seems to level out above 15°C, indicating that higher temperatures will limit the

infectivity. However, more experiments are needed to estimate infectivity at such high temperatures. In the future, more infectivity profiles and potential temperature adaptations should be established in laboratories, and the results from all these studies should be analyzed and included in a common model for salmon louse infectivity.

The effect of temperature on production of eggs has not been thoroughly explored but appears to affect both qualitative and quantitative parameters (Brooker *et al.*, 2018; Skern-Mauritzen *et al.*, 2020). Based on reports from the fish farms (water temperature, adult female lice per fish, and number of fish) the number of nauplii released into the water masses from each farm was calculated using a published formula from Stien *et al.* (2005). In this study, each pair of egg strings on the female lice was assumed to contain 300 eggs (150 eggs in each of 2 egg strings). This is a conservative estimate considering that numbers of eggs produced per female lice commonly varies in the range of 300–600 eggs per female at intermediate temperatures (Ritchie *et al.*, 1993; Heuch *et al.*, 2000; Stien *et al.*, 2005; Samsing *et al.*, 2016b) with extreme cases reporting more than 900 eggs per batch of egg strings originating from wild fish (Jackson and Minchin, 1992). Although Heuch *et al.* (2000) observed no difference in fertility at 9°C and 12°C and despite the large variability in absolute numbers of eggs produced at intermediate temperatures there does appear to be a systematic temperature driven component in fecundity. For instance, a seasonal temperature-correlating variability in fecundity is evident in Ritchie *et al.* (1993) and a decrease in number of eggs between 5°C and 15°C has been reported by (Samsing *et al.*, 2016b). Such systematic variability is also expressed at the daily production rate level where, at 6°C, 12°C, and 18°C, daily production is estimated to be 18, 45, and 84 by Stien *et al.* (2005), and 30, 81, and 91 by Hamre *et al.* (2019) at the same temperatures. However, in this work, we are only focusing on the relative changes, thus as long as a fixed egg string length is used the effect from fecundity would be the same. Samsing *et al.* (2016b) suggest a temperature dependence in the egg string length. Using this formulation, the total effect from fecundity on the infection pressure would have been less for high temperatures.

The mortality term was found to be the least important (Figure 2), but is probably also the term supported with the least biological evidence. The daily mortality rate from Stien *et al.* (2005) of 17% day⁻¹ is not directly dependent on temperature, rather the temperature dependence is indirect and due to the longer development time at lower temperatures. The large seasonal and environmental variability in high latitude spring bloom systems, leads to a large difference in survival of plankton (Eiane and Ohman, 2004). There is no reason to believe that this is different for salmon lice, thus the use of a constant mortality rate is an oversimplification that should be refined in the future. Johnson and Albright (1991a) estimated the mean survival time of infective copepodids, and found no clear trend with increasing temperature, but a slightly higher mean mortality rate of 22% day⁻¹ was estimated. An increased daily mortality rate will decrease the total infection pressure as the number of infective copepodids will be lower, but the temperature dependency curve, I_M , will be almost unchanged.

Further refinements of the salmon lice dispersion model

Validation of the salmon lice dispersion model against available data has shown that it is able to reproduce the observed lice level

on salmonid fish (Sandvik *et al.*, 2016, 2020c; Myksvoll *et al.*, 2018). However, it has also been shown that vertical distribution of the lice larvae might have a large influence on the horizontal distribution (Heuch, 1995; Johnsen *et al.*, 2014). The salmon lice larvae are known to have a vertical behaviour where they swim towards the surface light and sink to avoid low-salinity water (Bron *et al.*, 1991; Heuch, 1995; Heuch *et al.*, 1995; Flamarique *et al.*, 2000; Crosbie *et al.*, 2019), and both these responses are implemented in the IBM. Nevertheless, laboratory experiments show large individual variability in these responses, and the salinity in the surface layer in many fjords are in the range where only a proportion of the lice is swimming/sinking downwards (salinity between 23 and 31; Sandvik *et al.*, 2020c). In addition, Coates *et al.* (2020) recently showed that the planktonic larvae also respond to hydrostatic pressure, which will increase if larvae sinks out of low salinity surface water. The final vertical response of salmon lice larvae should therefore be determined integrating all these three factors, and further experiments and sensitivity simulations should be performed to reduce the uncertainty in the modelled vertical behaviour.

As discussed in Sandvik *et al.* (2016) and Myksvoll *et al.* (2018) the observed temperature and number of female lice are reported weekly (with week number as the time reference), whereas the number of fish in the farms are reported monthly (with month as time reference). Thus, there is a temporal uncertainty in calculations of the number of salmon lice larvae released into the water masses, which could have been reduced with a more precise time information and a higher frequency. In addition, the accuracy of lice counts is hampered by the difficulty of reliable counting based on the small size of the parasite, the conditions for counting and the large number of fish that needs to be inspected (Heuch *et al.*, 2011; Thorvaldsen *et al.*, 2019; Dalvin *et al.*, 2020). The vertical temperature gradient within a cage might be several degrees (Johnsen *et al.*, 2020b), and the salmon (and thereby also the attached female lice and their eggs) often swim deeper to find their preferred temperature. Thus, the present legislation routines (temperature at 3-m depth only) is likely to give an underestimation of egg and larvae production in winter and overestimation in summer for a range of sites (Johnsen *et al.*, 2020b).

The infection efficiency of salmon lice is influenced by several factors such as salinity, temperature, water currents, and the age of the copepodid (Hevrøy *et al.*, 2003; Brooks, 2005; Genna *et al.*, 2005; Bricknell *et al.*, 2006; Samsing *et al.*, 2015, 2016b; Skern-Mauritzen *et al.*, 2020). Quantitative relationships between the factors are only known in part, and in this study only temperature and age were considered. When better knowledge on the other terms is available, these relationships should also be included in the model. Also, some data indicate that preexisting lice infections makes fish more vulnerable to new infections (Ugelvik *et al.*, 2017).

Other climate change impacts on salmon lice

There are several other factors that have not been taken into consideration when investigating the impact of temperature on the infectivity of salmon lice on wild salmonids. In addition to the effect that the infection pressure is likely to increase as fewer lice will die before development to the infective copepodid stage, development time from copepodids to reproducing adult females will decrease Hamre *et al.* (2019). At 6°C development to adult females lasted 432 degree-days, but was significantly shorter at

higher temperatures with an almost linear decrease to only 271 degree-days at 21°C.

A warmer climate will also change the hydrology with more precipitation and an earlier snow-melt (Hanssen-Bauer *et al.*, 2017). As the salmon louse tries to avoid the brackish surface layer (Crosbie *et al.*, 2019; Cantrell *et al.*, 2020a), more freshwater will potentially give a deeper infective zone, change dispersion and decrease the surface infection pressure. However, with a mismatch between the spring-flood and the time when the salmon-smolt migrates towards the sea, there is also a possibility for an increased salmon lice exposure.

The main driver for climate change is the increased concentration of pCO₂ in the atmosphere. Due to this, the average pH of the surface waters of the global oceans has decreased from ~8.2 before the onset of the industrial revolution to a present average of ~8.1 (Orr *et al.*, 2005). Studies of biological consequences of ocean acidification indicate that large groups of organisms will confer induced stress or reduced success rate in seawater with reduced pH (Fabry *et al.*, 2008). However, Thompson *et al.* (2019) investigated the effects of increased pCO₂ on growth and metabolic rates in the planktonic stages of salmon louse from eggs to copepodids. The results indicate that salmon louse have mechanisms to compensate for increased concentration of pCO₂ and that populations will be tolerant of projected future ocean acidification scenarios.

With increasing temperature it is expected that climatic barriers in northern polar regions will weaken, and enabling an exchange of Pacific and Atlantic species, including salmonid fishes (Wisz *et al.*, 2015). Riding their backs, literally, we can expect the Atlantic *L. salmonis salmonis* and Pacific *L. salmonis oncorhynchii* subspecies (Skern-Mauritzen *et al.*, 2014) to reunite. The size of adults and development time of planktonic stages of Pacific (Skern-Mauritzen *et al.*, 2014) and Atlantic salmon lice appear to be comparable (Johnson and Albright, 1991b; Schram, 1993; Stien *et al.*, 2005) whereas post infestation development of Pacific salmon lice may exhibit a slower rate of development (Johnson and Albright, 1991a; Hamre *et al.*, 2019). The latter observation was potentially caused by the study on the Pacific lice being conducted using Atlantic salmon (*S. salar*) as host. Reported fecundity of salmon lice is highly variable (Brooker *et al.*, 2018) but reported egg production and rate of maturation of the two subspecies are comparable (Johnson and Albright, 1991a; Samsing *et al.*, 2016b; Hamre *et al.*, 2019). Hence, data on fecundity and development do not suggest that the modelled results should be invalid for migrant *L. salmonis oncorhynchii* or introgressive hybrids (Skern-Mauritzen *et al.*, 2014) with *L. salmonis salmonis*.

Other climate change impacts on fish farming

In addition to the changed infection pressure from salmon louse, climate change will affect Norwegian aquaculture in general as southern sites already experience temperatures that are higher than optimal for the currently farmed species during summer months. Optimal farming conditions for Atlantic salmon occurs between 10°C and 18°C, decreasing significantly above 18°C (Handeland *et al.*, 2008). In the future, temperatures might be so high that they would pose considerable risk to production (Falconer *et al.*, 2020), and farm management strategies and feed composition may have to adjust to changes in temperature affecting feed utilization, metabolism, disease treatment, and growth (Handeland *et al.*, 2000). Warmer water will also reduce the

dissolved oxygen levels. Due to this the fish will prefer to stay deeper, and to avoid crowding the farmers will need to build even deeper cages or compensate by pumping oxygen rich water from depth to surface. As salmon lice are mainly found in the upper metres of the water column (Heuch, 1995; Johnsen *et al.*, 2014) this will lead to a decrease in infection pressure on farmed fish and subsequently less transfer to wild fish.

Concluding remarks

A warmer climate will significantly increase the salmon lice infection pressure from fish in aquaculture to wild salmonids. This may hamper a further sustainable growth in Norwegian fish farming. A shorter developmental time from eggs to infective copepodids, will also alter the pattern of transportation of salmon lice from the fish farms resulting in areas with increased infection pressure to be closer to the farms where releases occurs, which has to be considered in future management plans.

A good management plan is therefore necessary to ensure environmental sustainability and further growth in the Norwegian aquaculture industry in a warmer climate. To mitigate the increasing infection pressure on wild salmonids with higher temperatures, there is a need to minimize the release of salmon lice from farmed fish. Today the lice level in many production zones are critically high (Vollset *et al.*, 2019; Sandvik *et al.*, 2020b), and closed cages, lice skirts, and submerged cages are among the innovative solutions, which are tested to reduce the encounter rates between wild fish and the parasitic salmon lice (Barrett *et al.*, 2020).

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Data Availability Statement

The data underlying this article will be shared on reasonable request to the corresponding author.

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