





## The development of a sustainability assessment indicator and its response to management changes as derived from salmon lice dispersal modelling

Anne D. Sandvik \*, Samantha Bui , Mats Huserbråten, Ørjan Karlsen, Mari S. Myksvoll, Bjørn Ådlandsvik, and Ingrid A. Johnsen

Institute of Marine Research, Nordnes 5817 Bergen, Norway

\*Corresponding author: tel: +47 4740 8020; e-mail: [anneds@hi.no](mailto:anneds@hi.no).

Sandvik, A. D., Bui, S., Huserbråten, M., Karlsen, Ø., Myksvoll, M. S., Ådlandsvik, B., and Johnsen, I. A. The development of a sustainability assessment indicator and its response to management changes as derived from salmon lice dispersal modelling. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsab077.

Received 23 November 2020; revised 10 March 2021; accepted 26 March 2021.

Aquaculture is providing an increasingly larger proportion of the world's protein for human consumption; however, its environmental impact is a bottleneck for sustainable expansion. In Norway, the government has enacted a framework where salmon lice-induced mortality in wild salmonid populations is used for assessing the environmental sustainability in production zones. Direct measurements of the level of lice-induced mortality on wild salmonids are difficult to acquire, thus comprehensive sustainability assessments are based on a set of evidence-based proxies. One such proxy is the infestation pressure from a bio-hydrodynamic model, from which we develop an index that summarize the sustainability of aquaculture in terms of lice infestation. This index is based on the proportion of areas with elevated lice loads, and is a novel approach used to investigate how sustainability could be achieved through scenario testing of different management strategies. The analyses identified a mismatch between legal and sustainable lice levels, but also a beneficial effect of reducing lice levels on farms. This study's approach demonstrated how bio-hydrodynamic models might be used to assess sustainability and to predict the necessary reduction of lice larvae from farms to classify the entire Norwegian aquaculture industry as environmentally sustainable.

**Keywords:** bio-hydrodynamic model, infestation, *Lepeophtheirus salmonis*, management, ROC-method, wild salmonids

### Introduction

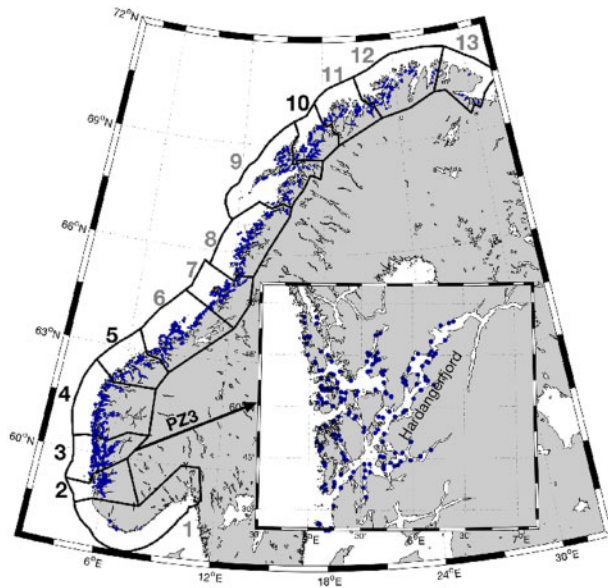
Aquaculture of finfish is an increasingly important source of protein for human consumption, however there is a sharp focus on the environmental impact and sustainability of the industry. In Norway, conventional aquaculture of salmonid fish in fjords and along the coast uses open net-pens that allow the transfer of pathogens and parasites between wild and farmed fish (Fjørtoft *et al.*, 2017, 2019). Existing in parallel with the aquaculture industry, Norway has approximately one third of world's population of wild Atlantic salmon (*Salmo salar*, consisting of more than 400 local stocks), and numerous anadromous local populations of sea trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*). Thus,

Norway has an international responsibility of preserving wild salmon stocks (Hindar *et al.*, 2010; Forseth *et al.*, 2019) while simultaneously carrying a political ambition of sustainable growth in aquaculture production. The balance in achieving both goals is challenging (Liu *et al.*, 2011; Johnsen *et al.*, 2021), and the priority of conservation creates a conflict with the objective of industry growth.

The salmon louse (*Lepeophtheirus salmonis*) is a naturally occurring ectoparasite on salmonids in the northern hemisphere, and infects both farmed and wild salmonids. However, as the number of hosts for salmon lice has increased dramatically in parallel with the expansion of Atlantic salmon farming (Barrett

© International Council for the Exploration of the Sea 2021.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.



**Figure 1.** The 13 aquaculture PZs along the Norwegian coast, with PZ3 and Hardangerfjord highlighted. PZs evaluated in this article were marked with black numbers (others with grey), and blue dots mark the aquaculture locations.

*et al.*, 2020), an imbalance has developed between lice abundance and susceptible wild hosts (Penston *et al.*, 2011; Skilbrei *et al.*, 2013; Serra-Llinares *et al.*, 2014, 2018; Vollset *et al.*, 2014; Thorstad *et al.*, 2015; Fjørtoft *et al.*, 2017, 2019; Serra-Llinares, 2020).

Salmon lice begin life with larval stages hatched directly into the water masses and dispersed by local ocean currents. They have three planktonic stages, with development rate as a function of the ambient water temperature (Hamre *et al.*, 2013, 2019; Samsing *et al.*, 2016). Thus, the lice larvae can potentially drift far away (100 km) from the hatching source (Johnsen *et al.*, 2014; Samsing *et al.*, 2015), and therefore contribute to an elevated infestation pressure over a large geographic area.

Salmon lice have been identified as one of the main risk factors of further growth of salmon farming (Taranger *et al.*, 2015; Forseth *et al.*, 2017). In Norway, the coast is divided into 13 production zones (PZs; Figure 1; Ådlandsvik, 2015), and the sustainability status within each zone is evaluated separately every year in the popularly named “traffic light system” (Anon 2020). From the recent evaluation, based on data from 2018 and 2019, the environmental impact of salmon lice on wild salmon stocks was classed as low (green) in nine PZs, medium (yellow) in two and high (red) in two (Vollset *et al.*, 2019).

As farmed salmon is Norway’s second largest export industry (next to oil and gas), the outcome from this management evaluation scheme has a potentially huge economic impact. Thus, the fish-farmers, as well as the conservation stakeholders and the management authorities, have high motivation to find solutions that can ensure environmentally sustainable growth.

Direct measurements of lice infestation and the corresponding lice-induced mortality on wild salmonids is difficult to achieve over large geographical areas. Therefore, the traffic light system has adopted a set of high quality and well-documented datasets to serve as proxies for the impact of lice on wild salmonid survival. Information from a dispersion model (Sandvik *et al.*,

2020a) provides input data for one of the proxies (ROC, relative operating characteristic; Sandvik *et al.*, 2016, 2020b), whereby the lice density in the water masses (infestation pressure) and the number of lice on wild salmonids is estimated through a calibration against the observed number of lice on salmonid fish kept in small sentinel cages. Thus, the model product (ROC) can be interpreted as the result from numerous simulated sentinel cages in a fine mesh network along the entire coast. In accordance with the results from the real sentinel cages, these “virtual” smolt cages can be used both to estimate the mortality on wild salmonids and to test scenarios of mitigation strategies before new management plans are implemented.

Based on the ROC-method, described in Sandvik *et al.* (2016, 2020b), we define the proportion of the PZ with elevated lice loads through an index, which is further used to give a quantitative assessment of the effect of different management strategies. The method is novel in its approach and act as a straightforward and objective way for assessment of salmon lice management effectiveness. The main objective of this work is to use the suggested ROC-indexes to find a sustainable level of salmon lice larvae originating from farmed fish in Norwegian fjords and coastal waters, in terms of their projected impact on wild salmonid populations.

The ROC-index is estimated for all 13 PZs covering the Norwegian coast, and scenarios are tested in those where the ROC-index shows unacceptable impact (PZs 2–5, and 10).

To find the management approach that would achieve a low environmental impact classification in the target PZs, seven scenarios were tested to determine when the mortality-related effect of aquaculture would be acceptable.

## Material and methods

### Study area and PZs

More than 1000 locations are approved for aquaculture production along the Norwegian coast and fjords. The production cycle is generally 15–18 months, and the locations must be fallowed between cycles. Thus, not all farms are active and simultaneously in production. The locations are distributed in 13 PZs (Figure 1), defined based on an analysis of the dispersion of lice between the aquaculture sites, and 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 PZ are less likely to infest farms in another PZ, making it beneficial to consider each zone as independent management units.

### The salmon lice model

The density of infective salmon lice was computed with a bio-hydrodynamic lice dispersion model system (Johnsen *et al.*, 2014, 2016; Sandvik *et al.*, 2016, 2020b; Myksvoll *et al.*, 2018; Ådlandsvik, 2019), where an individual-based model with known behaviour and life development for salmon louse is implemented in the Norwegian Coastal Current model (NorKyst800, Albretsen *et al.*, 2011, Asplin *et al.*, 2020; Dalsøren *et al.*, 2020). The results from the lice dispersion model are publicly available weekly ([www.lakselus.no](http://www.lakselus.no)) and as an archive from 2012 to 2020, on the 800 × 800 m horizontally resolved NorKyst800 grid (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, 2016,

2018; Kough *et al.*, 2015; Samsing *et al.*, 2017; Cantrell *et al.*, 2018; Kragesteen *et al.*, 2018; Kristoffersen *et al.*, 2018).

### 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 indicator 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  $2 \times 2$  contingency table 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  $F = 0$ . Based on the recorded mean number of lice on hatchery-reared Atlantic salmon smolts held in sentinel cages for the years 2012–2017, a ROC was developed to predict salmon lice infestation pressure (Sandvik *et al.*, 2016, 2020b). The ROC-method uses three categorical events (high, medium, and low) for a potential lice infestation pressure, and is at present in use as one of the proxies for the sustainability indicator in the Norwegian traffic light system.

### ROC-index and subjective assessment

The results from the ROC-method can most easily be interpreted as the predicted infestation pressure from numerous “virtual” smolt cages in a high-density mesh (here on the  $800 \times 800$  m NorKyst800 grid) along the Norwegian coastline and fjords. The ROC-products constitute 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) showing the relative size of the affected area (within PZs), where the fish would most likely be infected by a salmon

lice dose above the given threshold. The deployment time for the virtual cages can be any period of interest. Here we have used 30 days during spring in accordance with how it is used in the traffic light assessment.

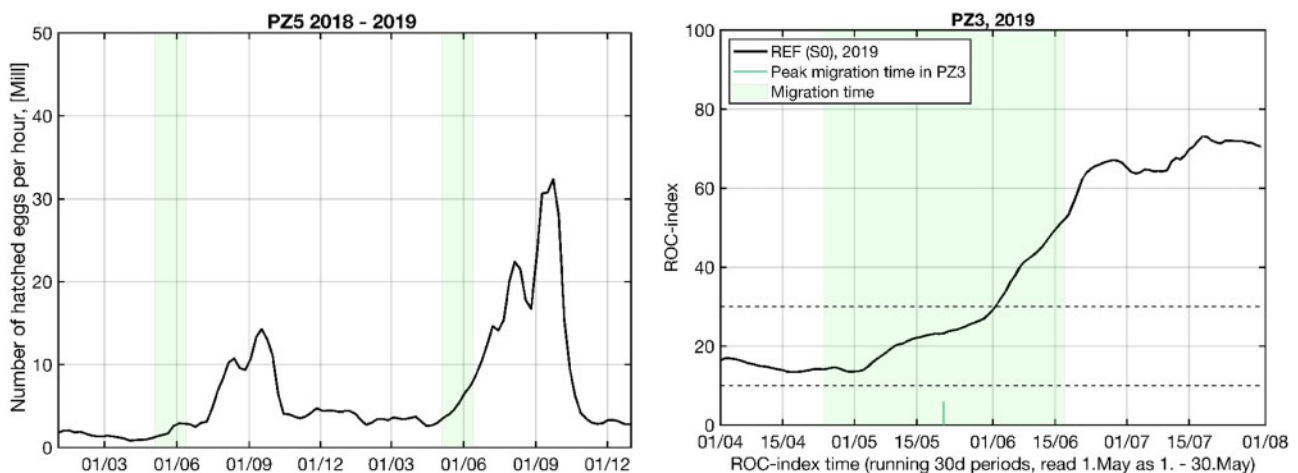
The tolerance of the wild post-smolts to infection is dependent on the size of the fish, where 100% mortality is assumed if there are  $>0.3$  lice/g fish and no mortality is assumed when there are  $<0.1$  lice/g fish (Taranger *et al.*, 2015). In the traffic light assessment, it is assumed that a wild Atlantic salmon post-smolt is 20 g, thus 2 and 6 lice per fish becomes the class limits for low, moderate and high infestation pressure, and these levels of salmon lice on the smolts in the sentinel cages were further used to develop the present ROC-method. As such, the colours in the ROC-maps should be interpreted as: wild fish staying in red areas for 30 days will likely be infected with more than 6 lice (i.e. 100% mortality expected), while those staying in green areas most likely will be infected with less than 2 lice (0% mortality expected) and in yellow areas with between 2 and 6 lice (50% mortality expected).

To have an objective measure of the salmon lice impact on wild salmonids within each of the 13 PZs, the ROC-index (infestation indicator) is defined as:

$$I = \frac{R + 0.5 Y}{(R + Y + G)} \cdot 100,$$

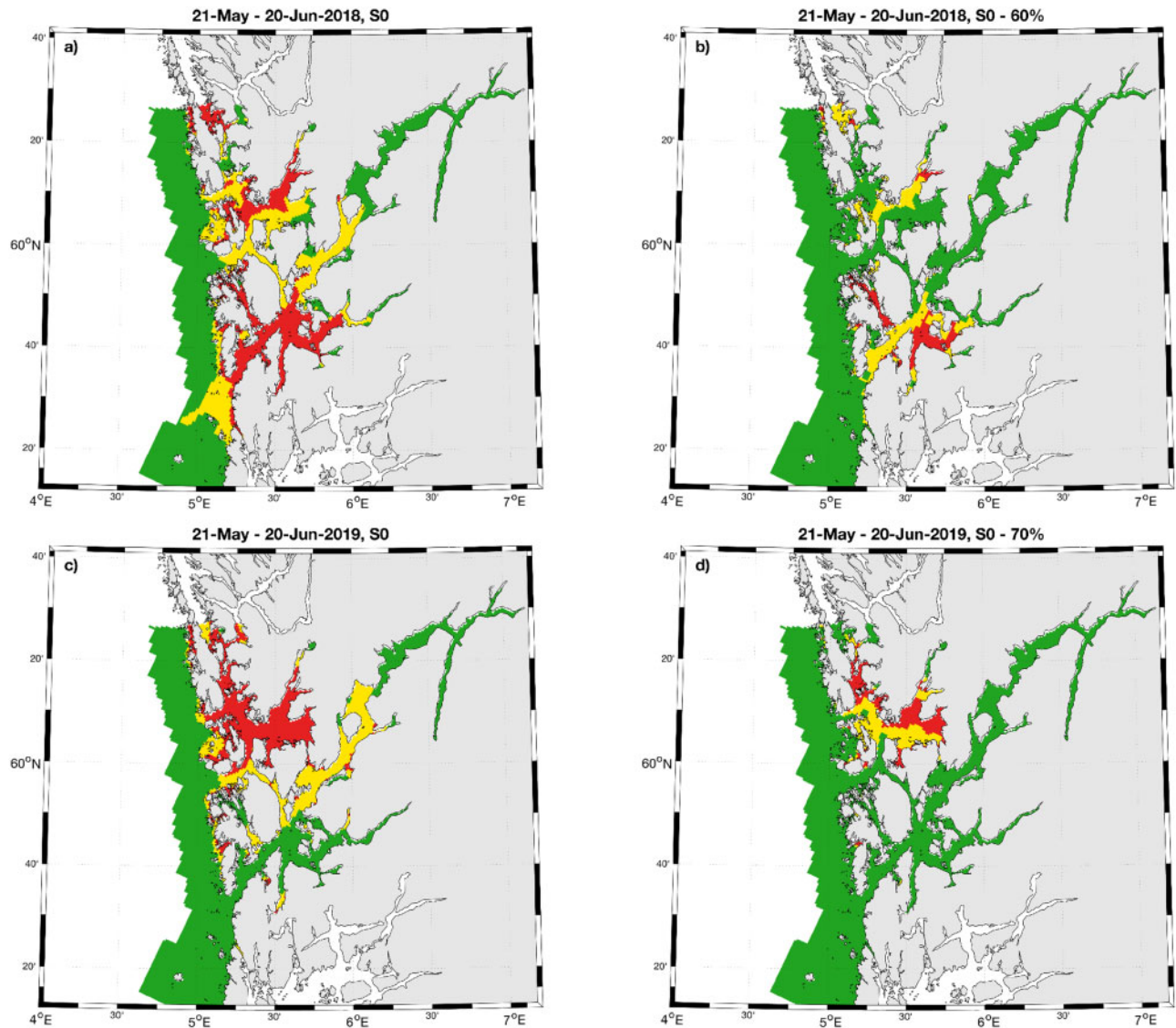
where  $R$ ,  $Y$ , and  $G$  is the size of the red, yellow, and green areas inside the respective PZ, when the number of infective copepods in the virtual smolt cages have been summed over a 30-day period. The whole potential habitat for wild fish is defined as the area within a PZ extending out 9.6 km ( $12 \times 800$  m) from land, as seen in Figures 3 and 6.

In the present work, the greatest emphasis has been placed on the value of the index from the estimated date that 50% of salmon post-smolts would have started their migration (PZ2: 18/5, PZ3: 21/5, PZ4: 23/5, PZ5: 24/5, and PZ10: 22/6), and 30 days thereafter (Figure 2, right panel). This period is termed the *ROC-index period*, covering a large part of the smolt migration period and the early feeding period for trout and char.



**Figure 2.** Left: Hourly number of nauplii released from salmon farms in PZ5 during 2018 and 2019. The green-shaded areas indicate the post-smolt migration period. Right: Time series of ROC-indexes during 2019 in PZ3. The green-shaded areas indicate the post-smolt migration period from rivers in PZ3 and the green vertical line indicates the date when it is assumed that 50% of the Atlantic salmon post-smolt has started their migration from rivers in PZ3.





**Figure 3.** ROC-maps for PZ3 that display areas where wild salmonids, occupying the area for the given time period, are expected to be infected by  $>6$  lice (red colour), between 2 and 6 lice (yellow colour), and  $< 2$  lice (green colour). Shown are outcomes for S0 in 2018 and 2019 (upper and lower left panels), and S1 in 2018 and 2019 (upper and lower right panels).

The index is generally lower before this period and higher later (Figure 2). At the PZ level, the ROC-index is defined to be low ( $I < 10$ ), moderate ( $10 < I < 30$ ) and high ( $I > 30$ ). Thus, if only a small area within the PZ has elevated salmon lice pressure (i.e.  $I < 10$ ), this method will suggest that the PZ 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/increased salmon lice pressure (i.e.  $I > 30\%$ ) the indicator will suggest that the PZ should be categorized as having a high risk of mortality in the wild fish population (red colour). However, the distribution of salmon lice is uneven within each PZ, thus a full assessment also has to include ROC-maps to consider where in the PZs the elevated lice pressure is located, and if it is likely that there will be an overlap with wild fish populations. In the traffic light

assessments, the geographic location of the red areas and variation in the ROC-index around the selected date is used to assess the uncertainties in the estimates.

### Release of salmon lice from fish farms

In the period from 1 April to 1 August 2018 and 2019, there were 648 and 688 active salmon farms in Norwegian waters respectively, with a total of 400–500 million Atlantic salmon in open net-pens. By legislation, all active farm sites must submit weekly reports on the average number of adult female lice on their fish and the temperature in 3-m depth, and the total number of fish on the site every month, to the management authorities.

Mature adult female lice extrude a pair of egg-strings, which hatch directly into the water column as planktonic nauplii. Based

on the reported numbers of adult female lice per fish (APF), the number of fish and the water temperature, the number of nauplii released into the water masses from each farm was calculated using a published formula (Stien *et al.*, 2005). More details on this calculation can be found in Myksovoll *et al.* (2018).

### Regulations of salmon lice in fish farms

Currently, the aquaculture industry in Norway is strictly regulated and must maintain low lice levels on the farmed fish in open cages. Legislation limits up to 0.5 APF on farmed salmon before triggering delousing action, but to protect the salmon, sea trout and Arctic charr post-smolts when they migrate from the rivers, more stringent regulations have been applied to minimize the number of lice on farmed fish during this spring migration (Norwegian Ministry of Fisheries and Coastal Affairs, 2017). Since 2017, this has been achieved by reducing the permitted number of lice per fish from 0.5 to 0.2 over a 6-week period from spring to early summer. With the present regulation the limit is 0.2 APF in PZ1–PZ7 from weeks 16 to 21, while in northern Norway, including PZ10, the limit is 0.2 APF from weeks 21 to 26. These region-dependent periods are expected to continue to apply in future years, being independent of the traffic light system.

Due to a combination of seasonality in water temperature and the low permitted lice levels during spring, the number of nauplii hatched into the water masses thus also exhibit strong seasonality. Minimum numbers are estimated in spring (before the peak salmon smolt migration) and maximum numbers in early autumn (when the water temperature is at its yearly maximum); however, the interannual variability can be large, e.g. as seen PZ5 in 2019 (Figure 2, left panel).

### Testing of release scenarios of salmon lice from fish farms

The environmental impact of aquaculture was assessed for seven different nauplii release scenarios (S1–S7) and discussed relative to a reference scenario where weekly reported lice levels were used under the concurrent management regime (S0). Three of the tested scenarios (S1–S3) were generated by modifying the reported levels of APF in the fish farms in 2018 and 2019. In S1, the reported APF were uniformly reduced by a percentage in all farms, whereas in S2 and S3 the APF was reduced to meet the legal limit in farms reporting higher values. Scenarios S4–S7 were generated independently of the reported lice levels, using uniform lice levels throughout the season at all farm locations. The tested scenarios were:

- S0—Reference simulation using reported lice levels.
- S1—Stepwise (10%) reduction of reported APF in all farms until ROC-Index < 10.
- S2—Extending the low-limit period (of 0.2 APF) to match the end of the ROC-index period.
- S3—As S2, but in addition the lowered statutory lice limit is reduced to 0.1 APF.
- S4—Lice level fixed at 0.2 APF for all fish in all farm sites.
- S5—Lice level fixed at 0.1 APF for all fish in all farm sites.
- S6—Lice level fixed at 0.05 APF for all fish in all farm sites.
- S7—Lice level fixed at 0.03 APF for all fish in all farm sites.

**Table 1.** ROC-index values used in the traffic light management system ( $I_{S0}$ , 2018/2019), estimated required reduction in infective copepods (in steps of 10%) until  $I_{S1} < 10$ , and ROC-index after the reduction ( $I_{S1}$ , 2018/2019), for the tested PZs.

	$I_{S0}$ 2018	S1 %	$I_{S1}$ 2018	$I_{S0}$ 2019	S1, %	$I_{S1}$ 2019
PZ2	32	–50%	9	24	–60%	9
PZ3	27	–60%	7	23	–70%	8
PZ4	17	–40%	9	24	–60%	8
PZ5				31	–70%	5
PZ10				15	–30%	7

Bold text was selected to make it easier to read.

In S2 and S3, PZ10 was not considered, as the regulation in northern Norway is in another period (from weeks 21 to 26) than the other considered PZs.

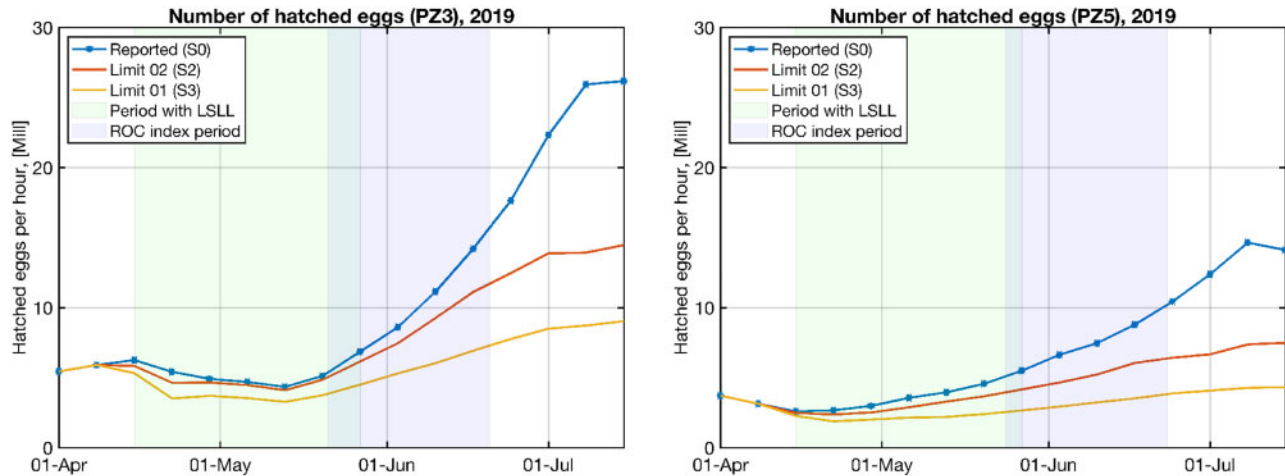
### Results

The results from the reference run are taken from the traffic light system report 2018–2019 (Vollset *et al.*, 2019), which showed a highly variable ROC-index among the 13 PZs. In the five targeted PZs (2, 3, 4, 5, and 10) the ROC-index was high in PZ2 and moderate in PZ3 and PZ4 in 2018, whereas in 2019 the estimated environmental impact was higher, with a high value in PZ5 and moderate values in PZ2, 3, 4, and 10 (Table 1,  $I_{S0}$ ). In the remaining PZs, the index was low ( $I < 10$ ).

### Scenario 1: flat percentage reduction

In S1, a flat reduction of the APF level was applied to determine how much the lice pressure would have to be reduced before the red and yellow PZs ( $I_{S0} > 10$ ) became green (using the ROC-index). The reduction was applied in 10% step reductions across all farms, and thus the relative contributions from the different farms were not changed. To obtain a ROC-index below 10 (low impact, green), the number of released nauplii had to be reduced by 30–70%. The required reduction varied between the PZs and years (detail provided in Table 1 under  $I_{S1}$ ).

When taking into consideration ROC-map results, the scenarios became slightly more complex. In PZ3 e.g. the ROC-index did not fall below 10 until the APF was reduced by 60% in 2018. Even with this reduction, the outer part of the main fjord (Hardangerfjord) in the PZ was yellow and red (Figure 3, upper right panel). This is an area where the salmon post-smolt from all the rivers in the fjord system must migrate through on their route towards open ocean (Halttunen *et al.*, 2018). Taking this into consideration, the reduction in APF would have to be even higher to acquire low impact status through the ROC-method. In 2019, the spatial distribution of salmon lice in the PZ was different to 2018, and the Hardangerfjord became completely green after a 70% flat reduction (Figure 3, lower right panel). In this year, the area with elevated lice pressure was found north of the Hardangerfjord, where far fewer wild salmon smolt would be exposed during their migration route.



**Figure 4.** Number of hatched eggs in PZ3 (left) and PZ5 (right) if the limit is set to 0.2 (S2) and 0.1 (S3) APF, and the period with lowered APF limit is extended. The shaded area shows the period when the lower statutory lice limit (LSSL) is set to 0.2 in 2019 (15 April as the first day in week 16 and 27 May). The blue-shaded area shows the ROC-index period (from the estimated date of 50% salmon post-smolt migration completed, and 30 days ahead).

### Scenarios 2 and 3: extending and lowering the spring statutory lice limit

In S2 and S3, first evaluated was the direct effect on the number of hatched eggs by extending the period of lower statutory lice limit (S2) and in addition lowering the limit to 0.1 APF (S3). Both scenarios were further analysed by evaluating the extent of the influenced area in the PZs, using the ROC-maps and ROC-index.

Reported number of APF per PZ in 2018 and 2019 showed that nearly all farms in these zones were able to keep the APF below the legal limit of 0.2 APF (data not shown). The number of farms with more than 0.2 APF began to increase in most PZs from week 21 (when the period of lower statutory lice limit ended) both in 2018 and 2019; however, most farms remained well below 0.2 APF (data not shown). Thus, an extension of the 0.2 APF threshold only influenced the release abundance of lice from a small number of farms. Further, the delay in the steep gradient, which normally occurs just after the middle of the estimated post-smolt migration period (green-shaded areas in Figure 2), was not as pronounced as expected (Figure 4). The reduction in number of hatched eggs was highly variable between weeks, years, and PZs; Figure 4 exhibits the weekly effects of S2 and S3 for PZ3 and PZ5, in 2019.

In S3, where the statutory lice limit was reduced to 0.1 APF from week 16, the impact was more pronounced than in S2. However, as many farms reported continual lice levels well below 0.1 during this period, the reduction in number of hatched eggs for this scenario was also a result of modifications from only a proportion of the farms. When compared with S0, releases of hatched eggs were reduced by 20–30% in week 16 and 50–60% at the end of the ROC-index period (Figure 4). In S2 the estimated salmon lice pressure was reduced in PZ2–PZ5, but not sufficiently to bring the ROC-index below 10. In PZ2, the ROC-index was reduced from > 30 to between 10 and 30 in 2018, while the classification was not altered for any PZ in 2019 (Table 2). The effect was more pronounced in S3 where the ROC-index was estimated to below 10 for PZ2 and PZ4 in 2018, but not for PZ3. In 2019, S3 did not lower the ROC-index below 10 for any of the

**Table 2.** ROC-indexes for 2018 and 2019, estimated with adult female per fish as reported by farmers ( $I_{S0}$ ), when the applied lice limit is kept below 0.2 for Scenario 2 ( $I_{S2}$ ), and when the limit is kept below 0.1 for Scenario 3 ( $I_{S3}$ ) from week 16 to end of ROC-period (blue-shaded areas in Figure 4)

	2018			2019		
	$I_{S0}$	$I_{S2}$	$I_{S3}$	$I_{S0}$	$I_{S2}$	$I_{S3}$
PZ2	32	20	9	24	19	15
PZ3	27	23	15	23	22	17
PZ4	17	12	7	24	20	13
PZ5				31	21	12

Bold text was selected to make it easier to read.

PZs 2–5. The largest effect of applying such a reduction was observed in PZ2 in 2018 and PZ5 in 2019, whereas the effect was lowest in PZ3 in 2019. The ROC-maps showed smaller red and yellow areas in both S2 and S3 compared with S0, but the effect was rather local, owing to the location of the modified farms and the hydrodynamic circulation patterns in the area.

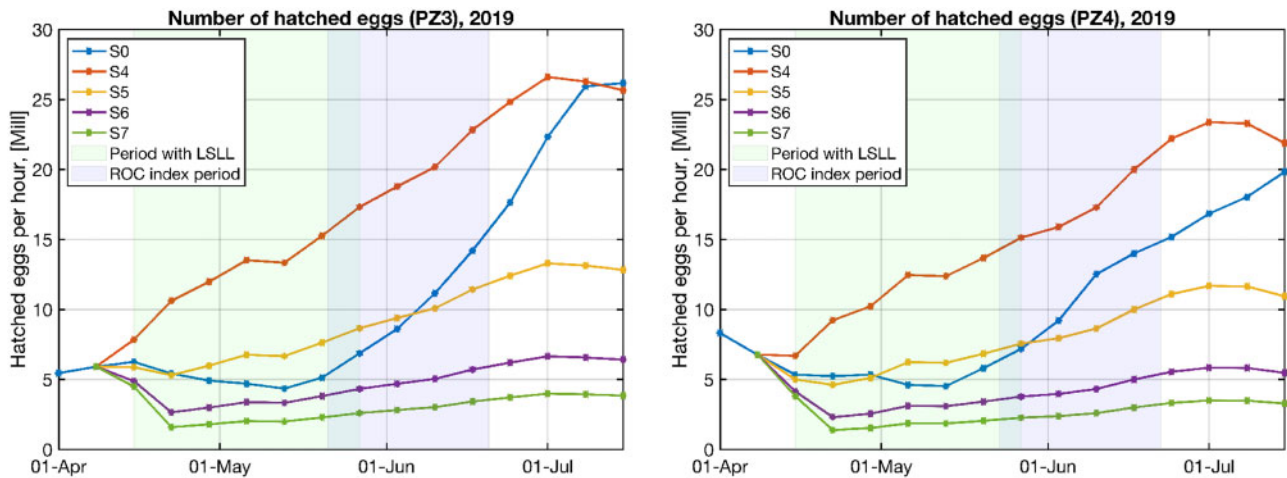
### Scenarios 4–7: theoretical uniform lice levels on all farmed fish

Although S1–S3 investigated the effect of different management strategies based on the reported lice levels from the salmon farms, S4–S7 evaluated the effect of uniform theoretical levels of lice, set to 0.2, 0.1, 0.05, and 0.03 APF, respectively.

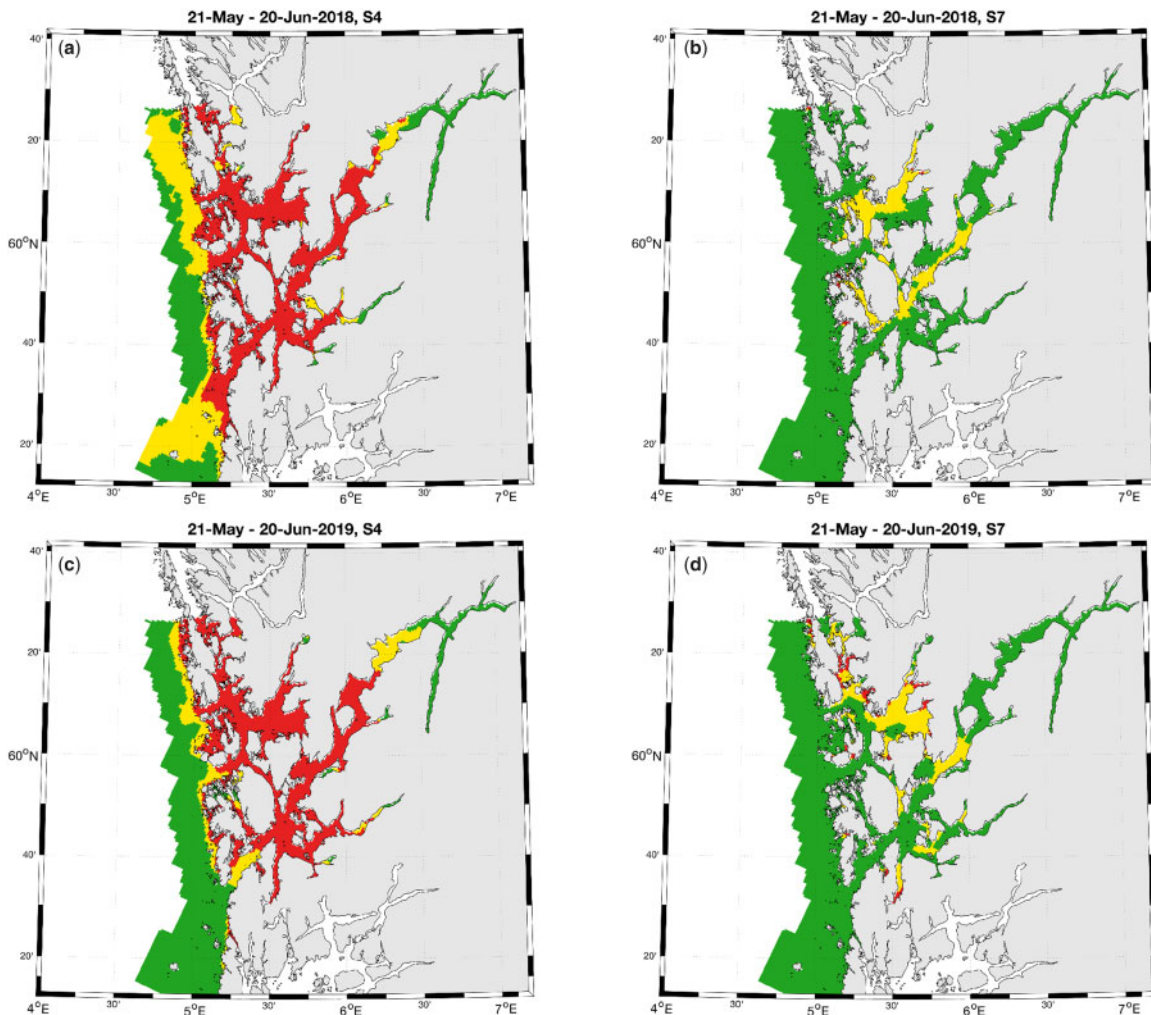
The time series of hatched eggs for S4–S7 in 2019 are shown in Figure 5 for PZ3 and PZ4, together with the number of hatched eggs from S0 (blue line).

A theoretical fixed number of 0.2 APF (S4) in all farms over the year gave a substantial increase in the number of hatched eggs in all PZs in 2018 and 2019, whereas the theoretical fixed number of 0.1 APF (S5) subtly increased the number of released eggs in some PZs, except for some weeks (Figure 5). A further decreased level of 0.05 APF (S6) generally reduced the number of released eggs, whereas the lowest tested fixed number of 0.03 APF (S7)





**Figure 5.** Number of hatched eggs in PZ3 (left) and PZ4 (right) in 2019. Blue lines show the egg releases estimated from reported values from the farms (S0). Red, yellow, purple, and green lines show number of released eggs in S4–S7, respectively. The green-shaded area shows the period when the LSSL is set to 0.2 in 2019. The shaded blue area shows the ROC-index period (from the estimated date for 50% salmon post-smolt migration completed, and 30 days ahead).



**Figure 6.** ROC-maps for PZ3 that display areas where wild salmonids, occupying the area for the given time period, are expected to be infected by >6 lice (red colour), between 2 and 6 lice (yellow colour), and <2 lice (green colour). Shown are outcomes for S4 in 2018 and 2019 (upper and lower left panels), and S7 in 2018 and 2019 (upper and lower right panels).

**Table 3.** ROC-indexes for 2018 and 2019, estimated from an overall uniform lice limit of 0.2, 0.10, 0.05, or 0.03 APF (Scenarios 4–7) for all

	2018					2019				
	I <sub>S0</sub>	I <sub>S4</sub>	I <sub>S5</sub>	I <sub>S6</sub>	I <sub>S7</sub>	I <sub>S0</sub>	I <sub>S4</sub>	I <sub>S5</sub>	I <sub>S6</sub>	I <sub>S7</sub>
PZ2	<b>32</b>	45	21	3	0	<b>24</b>	38	26	14	7
PZ3	<b>27</b>	57	36	17	6	<b>23</b>	45	34	19	8
PZ4	<b>17</b>	29	13	4	1	<b>24</b>	39	23	10	4
PZ5	<b>7</b>	18	4	1	0	<b>31</b>	37	16	4	2
PZ10	<b>3</b>	43	23	8	3	<b>15</b>	50	26	9	2

Bold text was selected to make it easier to read.

gave the lowest number in all PZs except PZ10 in 2018, and in all PZs in 2019.

A fixed lice level of 0.2 APF (S4) at all farms gave a ROC-index between 18 and 57 in 2018, and between 37 and 50 in 2019 (Table 3). Even though the ROC-index was lowered in S5–S7, only S7 produced a ROC-index < 10 for all PZs in both 2018 and 2019 (Figure 6 and Table 3). The increase from S0 to S4 was substantial in all areas, with a maximum in PZ10 and a minimum in PZ5. The lice infestation pressure was generally lower in 2018 than in 2019, as only PZ3 was still elevated for S6 in 2018, while three PZs (2–4) were high in 2019. ROC-maps from S4 showed substantial areas with elevated salmon lice pressure in PZ3, 2018 and 2019, and low salmon lice pressure in S7 (Figure 6).

## Discussion

In this study, we defined a sustainability index and used it to assess how various management strategies could contribute to improve the environmental sustainability in the Norwegian aquaculture industry. The analyses revealed that for the reference run (S0) the level remained well below the statutory lice limit in the majority of the salmon farms both in 2018 and 2019. Nevertheless, the environment was still classified as highly and moderately affected by salmon lice in some PZs, demonstrating that even though many individual farms keep their lice level below the legal limit, this is not necessarily sufficient to reach the sustainability goal on a regional scale.

A flat percentage reduction of the number of hatched eggs (S1) was shown to improve environmental sustainability status through a gradually decreasing ROC-index. However, a substantial reduction (30–70%) had to take place before all PZs were classified as having a low environmental impact from salmon lice. A similar approach was recently used in PZ7, to evaluate a possible increase in lice releases in a PZ that was categorized as green in 2017 and 2019 (Myksvoll *et al.*, 2020). Their study found that in years when the estimated mortality was well below 10%, a substantial flat increase in released lice was tolerated before the PZ turned into yellow, but they also concluded that the effect of this increase was of the same order as the impact from the inter annual variability in the ocean physics.

An extension of the lowered statutory lice limit period (S2) appeared to have a relatively small effect compared with the reference scenario (S0), though local effect was apparent. This was likely because only a small proportion of the salmon farms had reported more than 0.2 APF. Further, a lowering of the lice limit to 0.1 APF throughout the weeks 16–26 (S3) resulted in a stronger reduction in the releases, but similarly, as many farms already had very low lice levels during the period of interest, this

management strategy had less significance than expected. In fact, applying a new fixed APF level to all farms (S4–S7) indicated that a level of only 0.03 APF was required to make all PZs classified as green (low environmental impact).

Even so, an extension of the lower-limit period (from 6 to 11 weeks) would have a beneficial effect on the environmental assessment for the area. In addition to the results presented herein, a lower lice limit will also lead to more and/or earlier delousing in a larger proportion of the farms, which will give a positive retroactive effect of lower emissions and less infection between farms. Therefore, any reduction of lice pressure will influence the farm lice levels in general, leading to a positive feedback loop with an even lower number of lice on farmed and wild fish as the infection pressure decreases.

The effect of delousing events has not been implemented in the bio-hydrodynamic model system and would require an additional model branch with interplay between copepodids in the water masses and a salmon lice population dynamics model. If S2 (or S3) is introduced as the new regulation (management plan), a delousing event will be the consequence of exceeding the limit. Thus, depending on the efficacy of the delousing, the lice levels will most likely become well below the legal limit afterwards. The efficacy of delousing is typically not 100% and will depend on the type treatment used; the variability in reducing lice levels can however be large, unpredictable, and vary between louse stages (Gismervik *et al.*, 2017). Thus, more knowledge about the efficacy of delousing is needed before it can be realistically incorporated in our model tool. Nevertheless, it is worth noting that when the water temperature is 6–9°C (typical values during the smolt migration period), the time it takes a louse to develop, from first attachment to a host salmon to an adult female, is 40–60 days (Brooks 2005; Hamre *et al.*, 2019). It takes a further few days to develop egg strings and hatch nauplii into the water masses. Thus, if delousing-efficiency is 100% on all lice stages in week 16, the first adult female should not appear on farmed fish before weeks 23–24 (beginning of June) at the earliest, which would have reduced the infestation risk on out-migrating smolt, and sea trout and Arctic char residing in the area.

The different proxies used to assess the environmental impact of salmon lice represent comprehensive and complementary information. Due to limited knowledge about crucial variables (e.g. temporal-spatial representativity), each of the proxy methods used to calculate the salmon lice-induced mortality in wild salmonids have one or more assumptions. These assumptions are carefully considered and based on the best available knowledge, but the uncertainty will affect the results. For the ROC-method, these will be:

- (i) The assumed limit value for high/medium/low infestation pressure on smolt in the sentinel cages (Bjørn *et al.*, 2011; Pert *et al.*, 2014), with subsequent threshold values that come from the ROC-method.
- (ii) The duration and time defined as the ROC-index period.
- (iii) The seaward extent of the area considered.
- (iv) Definition of threshold values to define when the ROC-index is high, medium or low.

A higher threshold value for what is assumed to be high infestation pressure in the sentinel cages (i), and a shorter or earlier ROC-index period (ii) will generally give a lower index, while an



assumed habitat that does not extend as far seaward (iii) will give a higher index. Finally, it is (iv) the limit value for what is considered a high, medium or low ROC-index that determines the outcome of this method. We have used parameters equal to those used in the traffic light assessments 2019. High and low ROC-index is mainly in accordance with high and low lice loads on observed fish (Myksvoll *et al.*, 2018). However, by adhering to a fixed set of parameters, we have an objective method that remains consistent between years and between the different PZs, which in addition is very well suited to easily conduct sensitivity experiments. It should also be noted that for most PZs and years, the assessments made with the ROC-method agree well with the other proxies in the traffic light system, as well as the final science-based advice delivered by the expert group (Vollset *et al.*, 2019). Time series of the ROC-index for all PZs might be found in Sandvik and Myksvoll (2020).

Similar to the indirect observations of salmon lice on hatchery-reared Atlantic post-smolt in sentinel cages (Bjørn *et al.*, 2011; Pert *et al.*, 2014), the ROC-maps and index are not directly related to mortality of wild fish. Although there exists some information on the behavior of wild salmonids, information on fish density within the PZ it is still a knowledge gap and thus not included in the ROC-method. However, the model exhibited high skill in predicting areas with elevated salmon lice infestation in the Hardangerfjord 2012–2017 (Sandvik *et al.*, 2020b). Thus, it is likely that the wild fish remaining in red areas during the defined time period will be infected with a dose, which is deadly for a 20 g fish. As the water temperature, salinity and current conditions can vary considerably between years, the ROC-index will accordingly have an interannual variability due to varying environmental conditions (Myksvoll *et al.*, 2020), in addition it will naturally change if the number of fish in the PZs changes.

A complementary method to model infection pressure (which is also another proxy in the traffic light system) is the virtual smolt model where the whole migration from river to ocean is simulated (Johnsen *et al.*, 2021). Salmon usually enter the sea in spring and need to swim from their river of origin through the fjords toward the open ocean. The distance and route they swim will affect their risk of being infected, particularly with the patchiness in density of salmon lice larvae along the route. As the release of salmon lice usually increases during spring and summer due to temperature and farming practices (Figure 2), a later migratory departure from the fjords results in a higher risk of exposure to a higher infestation pressure.

Information from entire PZs (as the ROC-method) is a valuable and necessary assessment tool, particularly as there is large and inconsistent uncertainty in knowledge of the habitat of the wild fish between the PZs (Thorstad *et al.*, 2012, 2015; Ounsley *et al.*, 2019). Although it is likely that the other proxies for the traffic light system's key sustainability indicator will change in a similar way, the results from this study should be used as an indication, rather than a robust conclusion, on how environmental sustainability regarding salmon lice could be attained in Norwegian aquaculture.

Aquaculture management strategies implemented to combat water-borne pathogens (Groner *et al.*, 2016; Kragesteen *et al.*, 2018; Nekouei *et al.*, 2018; Gallardo-Escárate *et al.*, 2019) can often be informative and transferred between countries. In particular, model-based management tools, similar to the one described in this article, can easily be exchanged among countries running bio-hydrodynamic model (Adams *et al.*, 2016; Cantrell *et al.*,

2020; Toorians and Adams 2020; Rabe *et al.*, 2020), and further be used to test mitigation strategies before management plans are implemented.

## Concluding remarks

A good management plan is necessary to ensure environmental sustainability and further growth in the Norwegian aquaculture industry. However, there are many approaches to how this management plan could be defined. Despite the records that the lice level on most farmed fish is well below the legal level of 0.2 lice in weeks 16–21, high lice levels are still found on wild salmonids in some areas. And several of the proxy sustainability indicators in the traffic light system, like the ROC-index, indicate that the lice infection pressure is unacceptably high in the PZs that were classified as yellow or red.

Although a substantial flat reduction can give a ROC-index below 10, areas of elevated salmon lice pressure can still be found in the critical smolt migration routes, indicating that a flat reduction is not an optimal strategy. A lowering and extension of the legal lice limit will potentially dampen the largest outputs, but since the regulation is on adult females per fish and not adult females per farm, this might not necessarily be the case. Nor might this strategy ensure that the reduction is occurring in the areas critical for migrating wild salmonids. Scenarios that assessed the theoretical impact if all farming sites had identical lice levels year-round (S4–S7) exemplified the severity of the case, whereby lice levels would have to be all the way down at 0.03 APF before a ROC-index <10 is ensured with the current farming intensity. Scenarios that involve all farms having the same lice level on the fish are a purely theoretical scenario, but it illustrates the difference between a legal lice level at each farm and a lice level that can be considered environmentally sustainable on a regional scale.

The scenarios presented here use an universal legislation, where all farms are restricted by the same rules. A study with another approach for PZ3 is presented by Huserbråten *et al.* (2020), where the biomass was removed from locations contributing most to the export of salmon lice to the other locations and redistributing this biomass to the remaining locations. Thus, decreasing the number of locations while the production in the area was maintained. This reduced the total infestation pressure among the farms and in turn could ease operations at the farms with lower lice abundances. The effect on wild salmonids has not been investigated, but we argue that relocating farms away from areas where the expected transmission to migrating post-smolts is high will significantly reduce mortality on wild salmonid populations on their way to the ocean. Future studies should also look at the combined effect of universal legislation and stronger actions for selected locations.

To mitigate the increasing aquaculture production there is a need to minimize the release of salmon lice from farmed fish. A regulation with legal total number of adult females per farm could be a fair practice to control the salmon lice pressure. A shorter production cycle at sea and reducing the number of fish in the sea during the out-migration of salmon post-smolts and during the sea-feeding period for trout and Arctic char could also be an efficient approach to protect wild salmonid populations. Further, closed cages, lice skirts and submerged cages are among the innovative solutions, which are tested to reduce the encounter rates between fish and the parasitic salmon lice (Barrett *et al.*, 2020).

## Data availability

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

## Funding

This work was financed by the Norwegian Department of Trade, Industry and Fisheries in its funding to the Institute of Marine Research (internal project no. 14650). The simulations were performed on resources provided by UNINETT Sigma2—the National Infrastructure for High Performance Computing and Data Storage in Norway. The authors thank people from the industry for constructive comments.

## References

- Adams, T., Black, K., MacIntyre, C., MacIntyre, I., and Dean, R. 2012. Connectivity modelling and network analysis of sea lice infection in Loch Fyne, west coast of Scotland. *Aquaculture Environment Interactions*, 3: 51–63.
- Adams, T., Proud, R., and Black, K. 2015. Connected networks of sea lice populations: dynamics and implications for control. *Aquaculture Environment Interactions*, 6: 273–284.
- Adams, T. P., Aleynik, D., and Black, K. D. 2016. Temporal variability in sea lice population connectivity and implications for regional management protocols. *Aquaculture Environment Interactions*, 8: 585–596.
- Ådlandsvik, B. 2015. Forslag til produksjonsområder i norsk lakse- og ørretoppdrett. Rapport Fra Havforskningsinstituttet 20-2015. Institute of Marine Research, Bergen.
- Ådlandsvik, B. 2019. LADiM documentation. <https://ladim.readthedocs.io> (latest accessed 8 April 2021).
- 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 Fiske og Havet 2/2011. Institute of Marine Research, Bergen.
- Anon. 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, In: government TN (ed). Ministry of Trade, Industry, and Fisheries, Oslo.
- Anon. 2020. Regjeringen skrur på trafikkliset i havbruksnæringen. <https://www.regjeringen.no/no/aktuelt/regjeringen-skrur-pa-trafikkliset-i-havbruksnaringen/id2688939/> (last accessed April 2021).
- Asplin, L., Albretsen, J., Johnsen, I. A., and Sandvik, A. D. 2020. The hydrodynamic foundation for salmon lice dispersion modeling along the Norwegian coast. *Ocean Dynamics*, 70: 1151–1167.
- Barrett, L. T., Oppedal, F., Robinson, N., and Dempster, T. 2020. Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. *Reviews in Aquaculture*, 12: 2527–2543.
- 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.
- 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.
- Cantrell, D.L., Groner, M., Ben-Horin, T., Grant, J., and Revie, C. 2020. Modeling pathogen dispersal in marine fish and shellfish. *Trends in Parasitology*, 36: 239–249. doi:10.1016/j.pt.2019.12.013.
- Cantrell, D.L., Rees, E. E., Vanderstichel, R., Grant, J., Filgueira, R., and Revie, C. W. 2018. The use of kernel density estimation with a bio-physical model provides a method to quantify connectivity among salmon farms: spatial planning and management with epidemiological relevance. *Frontiers in Veterinary Science*, 5: 269.
- Dalsøren, S. B., Albretsen, J., and Asplin, L. 2020. New validation method for hydrodynamic fjord models applied in the Hardangerfjord, Norway. *Estuarine, Coastal and Shelf Science*, 246: 107028.
- Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjosæter, H., Falkegård, M., Hindar, A. *et al.* 2017. The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, 74: 1496–1513.
- Forseth, T., Thorstad, E. B., Barlaup, B.T., Einum, S., Finstad, B., Fiske, P., Falkegård, M. *et al.* 2019. Status for Norske Laksebestander I 2019 [Status for Norwegian Salmon Stocks in 2019]. Vitenskapelig Råd for Lakseforvaltning. <https://brage.nina.no/nina-xmlui/handle/11250/2619889> (latest accessed 8 April 2021).
- Fjørtoft, H. B., Besnier, F., Stene, A., Nilsen, F., Bjørn, P. A., Tveten, A. K., Finstad, B. *et al.* 2017. The Phe362Tyr mutation conveying resistance to organophosphates occurs in high frequencies in salmon lice collected from wild salmon and trout. *Scientific Reports*, 7: 14258.
- Fjørtoft, H. B., Nilsen, F., Besnier, F., Stene, A., Bjørn, P. A., Tveten, A. K., Aspehaug, V. T. *et al.* 2019. Salmon lice sampled from wild Atlantic salmon and sea trout throughout Norway display high frequencies of the genotype associated with pyrethroid resistance. *Aquaculture Environment Interactions*, 11: 459–468.
- Gallardo-Escárate, C., Arriagada, G., Carrera, C., Gonçalves, A. T., Nuñez-Acuña, G., Valenzuela-Miranda, D., and Valenzuela-Muñoz, V. 2019. The race between host and sea lice in the Chilean salmon farming: a genomic approach. *Reviews in Aquaculture*, 11: 325–339.
- Gismervik, K., Nielsen, K. V., Lind, M. B., and Vijugrein, H. 2017. Norwegian Veterinary Institute's Report Series: 6-2017. Mekanisk Avulsing Med FLS-Avusersystem - Dokumentasjon av Fiskevelferd og Effekt Mot Lus. Norwegian Veterinary Institute.
- Groner, M. L., Rogers, L. A., Bateman, A. W., Connors, B. M., Frazer, L. N., Godwin, S. C., Krkošek, M., Lewis, M. A. *et al.* 2016. Lessons from sea louse and salmon epidemiology. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 371: 20150203. PMID: 26880836; PMCID: PMC4760134.
- Halttunen, E., Gjelland, K. Ø., Glover, K. A., Johnsen, I. A., Serra-Llinares, R. M., Skaala, Ø., Nilsen, R. *et al.* 2018. Migration of Atlantic salmon post-smolts in a fjord with high infestation pressure of salmon lice. *Marine Ecology Progress Series*, 592: 243–256.
- Hamre, L. A., Bui, S., Oppedal, F., Skern-Mauritzen, R., and Dalvin, S. 2019. Development of the salmon louse *Lepeophtheirus salmonis* parasitic stages in temperatures ranging from 3 to 24°C. *Aquaculture Environment Interactions*, 11: 429–443.
- 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.
- Hindar, K., Hutchings, J. A., Diserud, O. H., and Fiske, P. 2010. Stock, recruitment and exploitation. In *Atlantic Salmon Ecology*. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Blackwell Publishing Ltd. 10.1002/9781444327755.ch12 (latest accessed 8 April 2021).
- Huserbråten M, Ådlandsvik B., Bergh Ø, Grove S, Karlsen Ø., Taranger G. L., Qviller L., Dean K. R., Jensen, B. B., and Johnsen, I. A. (2020). Endret lokalitetsstruktur i produksjonsområde 3 - vurdert virkning på spredning av lakselus, pankreassykdom og infektøslakseanemi. Rapport fra havforskningsen 2020–2. ISSN: 1893-4536.
- 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.
- Johnsen, I. A., Harvey, A., Sævik, P. N., Sandvik, A. D., Ugedal, O., Ådlandsvik, B., Wennevik, V. *et al.* 2021. Salmon lice induced mortality of Atlantic salmon during post-smolt migration in Norway. *ICES Journal of Marine Science*, 78: 142–154.
- Kough, A. S., Paris, C. B., Behringer, D. C., and Butler, M. J. 2015. Modelling the spread and connectivity of waterborne marine pathogens: the case of PaV1 in the Caribbean. *ICES Journal of Marine Science*, 72: i139–i146.
- Kragesteen, T. J., Simonsen, K., Visser, A. W., and Andersen, K. H. 2018. Identifying salmon lice transmission characteristics between Faroese salmon farms. *Aquaculture Environment Interactions*, 10: 49–60.
- Kristoffersen, A. B., Qviller, L., Helgesen, K. O., Vollset, K. W., Viljugrein, H., and Jansen, P. A. 2018. Quantitative risk assessment of salmon louse-induced mortality of seaward-migrating post-smolt Atlantic salmon. *Epidemics*, 23: 19–33.
- Liu, Y., Olaussen, J. O., and Skonhoft, A. 2011. Wild and farmed salmon in Norway - a review. *Marine Policy*, 35: 413–418.
- 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.
- Myksvoll, M. S., Sandvik, A. D., Johnsen, I. A., Skarðhamar, J., and Albretsen, J. 2020. Impact of variable physical conditions and future increased aquaculture production on lice infestation pressure and its sustainability in Norway. *Aquaculture Environment Interactions*, 12: 193–204.
- Nekouei, O., Vanderstichel, R., Ming, T., Kaukinen, K. H., Thakur, K., Tabata, A., Laurin, E. *et al.* 2018. Detection and assessment of the distribution of infectious agents in juvenile Fraser River Sockeye Salmon, Canada, in 2012 and 2013. *Frontiers in Microbiology*, 9: 3221–3216.
- Norwegian Ministry of Fisheries and Coastal Affairs. 2017. Forskrift om endring i forskrift om bekjempelse av lakselus i akvakulturanlegg. <https://lovdata.no/dokument/LTI/forskrift/2016-03-14-242> (latest accessed 8 April 2021).
- Ounsley, J. P., Gallego, A., Morris, D. J., and Armstrong, J. D. 2019. Regional variation in directed swimming by Atlantic salmon smolts leaving Scottish waters for their oceanic feeding grounds—a modelling study. *ICES Journal of Marine Science*, 77: 315–325.
- 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.
- 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.
- Rabe, B., Gallego, A., Wolf, J., Murray, R., Stuiver, C., Price, D., and Johnson, H. 2020. Applied connectivity modelling at local to regional scale: The potential for sea lice transmission between Scottish finfish aquaculture management areas. *Estuarine, Coastal and Shelf Science*, 238: 106716. doi:10.1016/j.ecss.2020.106716.
- Salama, N. K. G., Collins, C. M., Fraser, J. G., Dunn, J., Pert, C. C., Murray, A. G., and Rabe, B. 2013. Development and assessment of a biophysical dispersal model for sea lice. *Journal of Fish Diseases*, 36: 323–337.
- Salama, N., Dale, A., Ivanov, V., Cook, P., Pert, C., Collins, C., and Rabe, B. 2018. Using biological–physical modelling for informing sea lice dispersal in Loch Linnhe, Scotland. *Journal of Fish Diseases*, 41: 901–919.
- Salama, N., Murray, A., and Rabe, B. 2016. Simulated environmental transport distances of *Lepeophtheirus salmonis* in Loch Linnhe, Scotland, for informing aquaculture area management structures. *Journal of Fish Diseases*, 39: 419–428.
- Samsing, F., Johnsen, I., Dempster, T., Oppedal, F., and Trembl, E. A. 2017. Network analysis reveals strong seasonality in the dispersal of a marine parasite and identifies areas for coordinated management. *Landscape Ecology*, 32: 1953–1967.
- Samsing, F., Oppedal, F., Dalvin, S., Johnsen, I., Vågseth, T., and Dempster, T. 2016. Salmon lice (*Lepeophtheirus salmonis*) development times, body size, and reproductive outputs follow universal models of temperature dependence. *Canadian Journal of Fisheries and Aquatic Sciences*, 73: 1–11.
- 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., and Myksvoll, M. S. 2020c. Påvirkning fra lakselus på vill laksefisk. Rapport Fra Havforskningen, 2020–55. <https://www.hi.no/hi/nettrapper/rapport-fra-havforskningen-2020-55> (latest accessed 8 April 2021).
- Sandvik, A. D., Ådlandsvik, B., Asplin, L., Johnsen, I. A., Myksvoll, M. S., and Albretsen, J. 2020a. Lakselus LADiM V2, doi:10.21335/NMDC-410516615 (latest accessed 8 April 2021)
- 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.
- Sandvik, A. D., Johnsen, I. A., Myksvoll, M. S., Sævik, P. N., and Skogen, M. D. 2020b. Prediction of the salmon lice infestation pressure in a Norwegian fjord. *ICES Journal of Marine Science*, 77: 746–756.
- Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M., and Asplin, L. 2014. Salmon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. *Aquaculture Environment Interactions*, 5: 1–16.
- Serra-Llinares, R. M., Bøhn, T., Karlsen, Ø., Nilsen, R., Freitas, C., Albretsen, J., Haraldstad, T. *et al.* 2020. Impacts of salmon lice on mortality, marine migration distance and premature return in sea trout. *Marine Ecology Progress Series*, 635: 151–168.
- Serra-Llinares, R. M., Freitas, C., Nilsen, R., Elvik, K. M. S., Albretsen, J., Bøhn, T., Karlsen, Ø. *et al.* 2018. Towards direct evidence of the effects of salmon lice (*Lepeophtheirus salmonis* Krøyer) on sea trout (*Salmo trutta* L.) in their natural habitat: proof of concept for a new combination of methods. *Environmental Biology of Fishes*, 101: 1677–1692.
- Skarðhamar, J., Albretsen, J., Sandvik, A. D., Lien, V. S., Myksvoll, M. S., Johnsen, I. A., Asplin, L. *et al.* 2018. Modelled salmon lice dispersion and infestation patterns in a sub-arctic fjord. *ICES Journal of Marine Science*, 75: 1733–1747.
- 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.
- 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.
- Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., and Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behavior and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81: 500–542.
- Toorians, M. E. M., and Adams, T. P. 2020. Critical connectivity thresholds and the role of temperature in parasite metapopulations. *Ecological Modelling*, 435: 109258.
- 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., Nilsen, F., Ellingsen, I., Finstad, B., Helgesen, K. O., Karlsen, Ø., Sandvik, A. D., Sægrov, H., Ugedal, O., Qviller, L., and Dalvin, S. 2019. Vurdering av lakselusindusert villfiskdødelighet per produksjonsområde i 2019. Rapport fra ekspertgruppe for vurdering av lusepåvirkning.

*Handling editor: Carrie Byron*