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Geographic redistribution of farmed salmonids reduces salmon lice infestations and treatment frequency in a simulation study

Lars Qviller[1,*], Katharine Rose Dean[1], Mats Huserbråten[2], Ingrid Askeland Johnsen[2], Britt Bang Jensen[1,3]

[1]Norwegian Veterinary Institute, 1433 Ås, Norway
[2]Institute of Marine Research, 5817 Bergen, Norway
[3]Technical University of Denmark, 2800 Kongens Lyngby, Denmark

ABSTRACT: Host density is a key driver in parasite population dynamics, and often the number of parasites increases rapidly with host density. In the context of Norwegian salmonid farming, this mechanism has led to a disparity between the desire to increase cultured salmonid production, and to reduce the negative effects of parasite infestations. Salmon lice infestations are detrimental to animal welfare due to salmon lice treatments and spillover from farms to wild salmonids. Here, we examine how a redistribution of the salmonid farm biomass may hamper exchanges of lice larvae between farms, and consequently reduce the salmon lice burdens and treatment frequencies. More specifically, we use a stochastic simulation model, fitted to empirical data from Norwegian aquaculture, to examine how lice abundances and treatments responded when the biomass in the system was distributed onto fewer, larger farms situated farther apart. To maintain realistic fish growth, seasonality and cohort development, lice population dynamics were simulated on top of historic production data from Norway. We simulated several scenarios, where an increasing number of farms were closed, and their biomass was redistributed to other farms with matching cohorts. The results indicate that fewer and larger farms reduce lice numbers and treatment frequency, and that a strategic removal of farms, based on their importance for connectivity in an oceanographic lice dispersal network, improves this effect. Some core mechanisms are highlighted that should be considered in regional production planning, and in the allocation of production concessions in salmonid farming.

KEY WORDS: Salmon lice · Atlantic salmon · Aquaculture management · Simulation study · Spatial planning

1. INTRODUCTION

Host density is a key driver in parasite population dynamics, with studies showing a positive correlation between host population density and individual host parasite load (Arneberg et al. 1998). This relationship is especially pertinent in farming, where high host densities can elevate the risks of parasite infestations, impacting both plant and animal yields (Bondad-Reantaso et al. 2005, Mennerat et al. 2010). Specifically, farmed salmonid (Salmonidae spp.) densities influence the population growth of salmon lice *Lepeophtheirus salmonis* in marine farming systems in Norway (Grimnes & Jakobsen 1996, Jansen et al. 2012, Kristoffersen et al. 2014, Aldrin et al. 2019, Dean et al. 2021). Beyond mere density, the spatial distribution of hosts in dense farms adds complexities, affecting both between-farm dispersal and local infestation

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*Corresponding author: lars.qviller@vetinst.no

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dynamics. Consequently, Norway's salmonid farming industry grapples with the challenge of increasing production while mitigating the adverse impacts of salmon lice infestations on farmed and wild fish.

The monthly average standing stock in a Norwegian salmonid farm during our study period between 2014 and 2017 was 713 000 fish, but the numbers vary greatly (67 000–1 578 000, 5–95% percentile range). The entire Norwegian standing stock of Atlantic salmon currently varies annually between 350 and 450 million fish (Kristoffersen et al. 2018). Dempster et al. (2021) estimated that farmed salmonids in 2017 outnumbered wild salmonids by somewhere between 267:1 and 281:1, and that farmed salmonids produced about 98% of the mated (ovigerous) female salmon lice in Norwegian coastal waters. Therefore, when the salmon louse is established in farms situated in areas with intense salmonid farming, the contribution to infestation pressure from wild populations is regarded as insignificant (Heuch & Mo 2001, Heuch et al. 2005, Johansen et al. 2011, Samsing et al. 2019, Dempster et al. 2021).

Salmonids are usually farmed in open net-pens that allow for exchange of oxygenated water, but also planktonic organisms such as transmissible salmon lice larvae. Globally there is a trend of increasing size of salmon farms, where the size of the net-pens has grown over 200% in surface area from 2005 to 2020 in Norway (McIntosh et al. 2022). During the same period (2005–2020), the distance between sites increased in Norway (McIntosh et al. 2022). The marine phase of the production cycle of salmonids usually has a duration of between 14 and 19 mo (Bang Jensen et al. 2020b), and only 1 generation is allowed at the farm per production cycle. After the production cycle is ended, the farm must be fallowed for approximately 2 mo as a biosecurity measure (Ministry of Trade, Industry and Fisheries 2008).

Salmon lice are harmful to their hosts (Costello 2006), and have been a major problem in Norwegian fish farming since the beginning of industrial salmon aquaculture in the 1970s. Lice surveillance, prevention and control measures are mandatory, and include weekly reports of lice counts in 3 groups: adult females (AF), adult males and preadult lice (other motile, OM), and chalimus larvae (sessile lice). The current legislation stipulates that the parasite load cannot exceed 0.2 AF lice per salmonid on average during the wild salmon smolt outmigration in the spring, and 0.5 for the remainder of the year (Ministry of Trade, Industry and Fisheries 2012).

Salmon lice feed on host mucus, skin and blood (Pike & Wadsworth 1999, Costello 2006). The spillover of salmon lice from farmed to wild fish is regarded as one of the major threats to wild salmonids in Norway (Taranger et al. 2015, Forseth et al. 2017, Vollset et al. 2019, Sandvik et al. 2021). The lice level on farmed fish is therefore monitored and managed to a low level where the treatments rather than the lice infestations are harmful to the farmed salmonids per se. The indirect deleterious effects may still be considerable. Treatments to control salmon lice are costly and harmful to the fish and cause losses and mortality (Overton et al. 2019, Oliveira et al. 2021, Sviland Walde et al. 2021), and increased salmon lice proliferation is therefore a major sustainability concern, which negatively impacts the profitability of the industry, animal welfare, biodiversity, as well as the availability of farmed salmonids to the global food market. Salmonid farming intensity is now regulated according to the industry's environmental impact on wild salmonids in 13 discrete production areas that covers the entire Norwegian coastline (Ministry of Trade, Industry and Fisheries 2015, 2017, Kristoffersen et al. 2018, Myksvoll et al. 2018, Sandvik et al. 2020, Johnsen et al. 2021). The impact is currently assessed based on the mortality of out-migrating wild salmon smolts, caused by salmon lice spillover from farmed fish (Ministry of Trade, Industry and Fisheries 2015, 2017, Kristoffersen et al. 2018, Sandvik et al. 2020, Johnsen et al. 2021).

The salmon louse naturally inhabits an ocean with low host densities (Dempster et al. 2021). In areas with intensive salmonid farming, the ocean is scattered with dense clusters of suitable hosts in the farms, with varying degrees of contact between the clusters/farm (Samsing et al. 2017, Huserbråten & Johnsen 2022). This structure, a population of populations, is commonly referred to as a metapopulation (Levins 1969), illustrating the uneven distribution of a host population across distinct, yet interconnected subpopulations. Within this structure, a subpopulation can experience lice infestations through 2 primary pathways: (1) through 'self-infestations', where the lice population within a farm is sustained by local reproduction; and (2) via dispersal, where lice are introduced from neighboring farms and then proliferate within the new environment (Toorians & Adams 2020). Subpopulations face local extinctions or recolonizations, but if these are balanced, the metapopulation as a whole remains stable. In the case of salmon lice in salmonid farming, extinctions or significant drops in lice subpopulations occur at the end of the production cycle or with lice treatments, and farms are recolonized through the inter-farm network of lice dispersal

(Samsing et al. 2019). It is the size of the lice metapopulation, which is accelerated by connectivity between subpopulations, however, that limits the sustainability in salmonid farming within the production areas.

One suggestion to manage the salmon lice population has been to modify the structure of the farming system. For example, if the biomass is distributed on fewer farms, the distances between the subpopulations will increase, leading to increased network fragmentation. Moreover, if certain farms that are especially important for connectivity are removed, it is possible to create 'firebreaks', or barriers between parts of the network (Samsing et al. 2019).

Here, we use a simulation model (Aldrin et al. 2019) to analyze how sea lice abundances respond to a redistribution of the overall biomass in an area onto fewer and larger farms. We achieved this by closing some farms and redistributing the biomass onto other farms, with matching cohorts. We then compared the effects of removing a random selection of farms with a strategic selection, informed by a biophysical model (Huserbråten et al. 2020, Huserbråten & Johnsen 2022) that identified farms with the strongest influence on the other farm sites.

2. MATERIALS AND METHODS

2.1. Study area

The simulation study was conducted with data from production area PA3 (PO3 in Norwegian) on the western coast of Norway (Fig. 1). The area covers 2 main fjords, Bjørnafjorden in the north, and Hardangerfjorden in the south. The fjords are divided into several smaller fjord arms with deep basins, numerous small and large islands, sills, sounds and several openings to the outer ocean (Sandvik et al. 2020). PA3 covers an area of 3646 km^2, and includes 147 farms that were actively producing salmonids during the study period (January 2014–December 2017). The average standing stock in the farms in PA3 during the study period was 544 000 fish (64 000–1 084 000, 5–95% percentile range).

2.2. Data

The simulations were performed using data from 2 different datasets. Farm locations were collected from the Norwegian aquaculture register, hosted by the

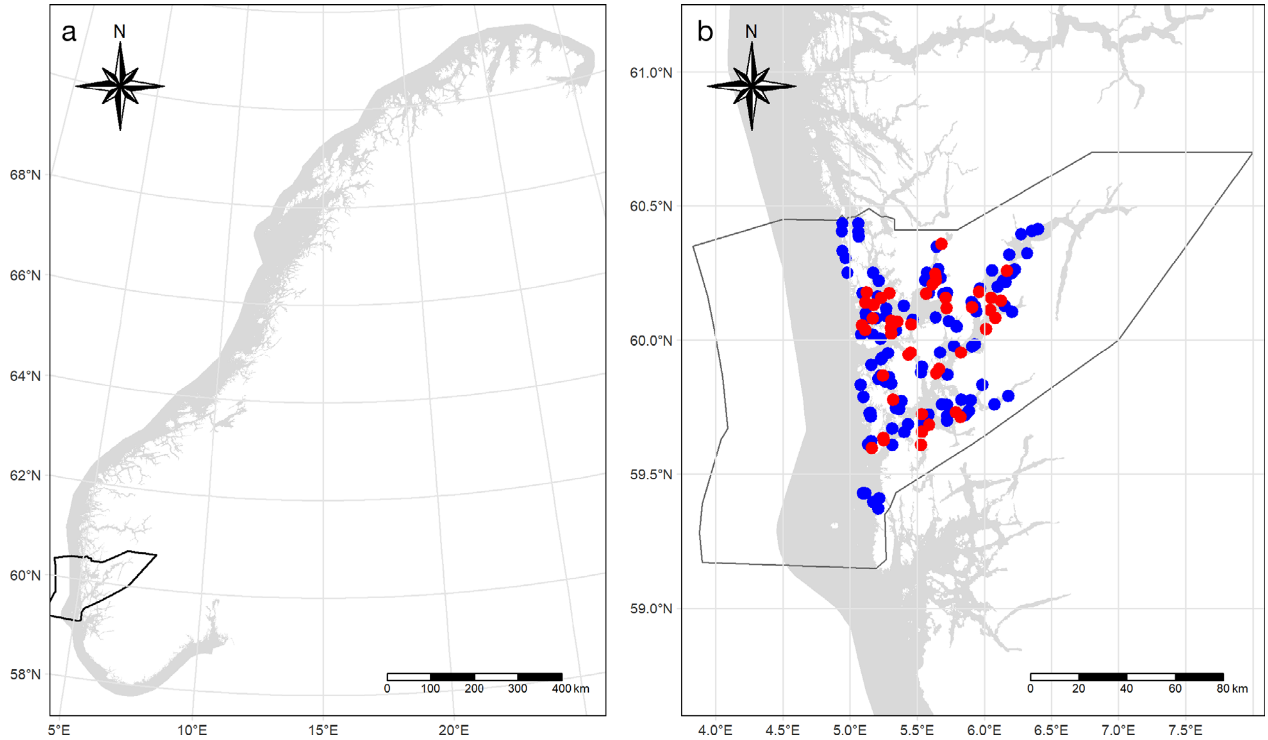

Fig. 1. (a) Study area in Norway. Black outline: production area PA3. (b) The sites in PA3, with the coloration of the farms illustrating an example of a scenario. Red dots: the farms being removed with a strategic removal of 30% of the most connected farms (Scenario 7 in Table 1); their biomass was distributed onto those of the remaining farms (blue dots) with cohorts that match in time. The connectivity network used for the strategic removal of farms is presented in Fig. 2 in Huserbråten & Johnsen (2022)

Norwegian Directorate of Fisheries (https://www.fiskeridir.no/Akvakultur/Registre-og-skjema/akvakulturregisteret) (in Norwegian, downloaded May 1, 2022), and data on number and weight of salmonids were retrieved from a national registry hosted by the Norwegian Directorate of Fisheries on a monthly basis. Seaway distances between farms were calculated as distances between farms in the water, around islands, peninsulas and hindrances in the water (see Dean et al. 2021 for a thorough description of the calculation of seaway distances).

2.3. Simulation model

The simulations performed in the present study are based on a previously published model for predicting sea lice abundances (Aldrin et al. 2019). The model describes the spatiotemporal development of salmon lice in the farms, and was fitted using production data from all Norwegian farms with a standing stock of either rainbow trout *Oncorhynchus mykiss* or Atlantic salmon *Salmo salar* in weekly time steps, from Week 1 in 2012, to Week 44 in 2016. The model consists of 2 sub-models, 1 for AF lice and 1 for OM lice. The number of AF in the current week depends on the number of AF the previous week and their survival, and the recruitment from the OM stages. The model calculates the number of OM in the current week based on the number of OM the previous week, their survival, recruitment from reproduction in the current farm, and recruitment from farms in the neighborhood. Development times, reproduction and mortality of the lice depend on temperature. Local recruitment is a function of the number of AF in the current farm, while the external recruitment is a function of AF in the surrounding farms, and the seaway distances between farms. The model also includes treatments against salmon lice based on average number of lice counted on fish in the farms, as required by Norwegian legislation (Ministry of Trade, Industry and Fisheries 2012). Manual counting of AF and OM abundances per fish in the farms were therefore simulated in the model, performed by random draws from the underlying distributions in the simulation model, and registered weekly from 40 fish. Treatments were initiated when the average number of salmon lice in the simulated counts was above 0.5, or below 0.2 during the period for wild smolt out-migrations (Weeks 16–21), as required by the legislation (Ministry of Trade, Industry and Fisheries 2012). Treatment in the model was set to reduce the lice counts by 75% for both AF and OM.

Here, we use the same model and parameters as described above for simulations, with the exception of treatment mortality, as discussed above, and we removed a downward trend in lice abundance over time (denoted β_k^{susc} in Aldrin et al. 2019). This parameter was included in the original model to account for a downward trend in the historical data, but it is not needed to compare between scenarios. This trend was therefore removed (β_k^{susc} was set to zero) in this effort. The first 16 wk in the simulations were considered a spin-up period used to calibrate the model and to construct the lagged variables, as described in Aldrin et al. (2019).

2.4. Scenario simulations

We simulated the AF and OM populations using historical data of fish abundances and farm locations from 2014 to 2017 to inform the simulations. We simulated 9 different scenarios (Table 1): the baseline scenario where we made no changes to farm structure (Scenario 1); 4 scenarios where we randomly removed

Table 1. The 9 scenarios, with description, total number of simulations and maximum cohort size. Cohort size defined as the maximum number of fish registered with that cohort in the dataset. Note that max cohort size for scenarios R20, R30, R40 and R50 gave 1 maximum cohort size for each randomization, and the values are given as an interval, from the lowest to highest recorded max cohort size in all 10 randomizations

Scenario	Name	Description	Simulations	Max cohort size
1	Baseline	Current farm structure	1000	2 066 561
2	R20	Random removal of 20% of the farms	10 000	4 324 984–7 195 871
3	R30	Random removal of 30% of the farms	10 000	6 038 964–10 014 704
4	R40	Random removal of 40% of the farms	10 000	6 057 988–15 296 941
5	R50	Random removal of 50% of the farms	10 000	7 953 479–18 185 020
6	S20	Strategic removal of 20% of the farms	1000	6 286 232
7	S30	Strategic removal of 30% of the farms	1000	9 797 388
8	S40	Strategic removal of 40% of the farms	1000	12 001 915
9	S50	Strategic removal of 50% of the farms	1000	14 586 857

an increasing percentage of farms (random removal) (Scenarios 2–5); and 4 scenarios where we removed an increasing percentage of the farms based on farm connectivity (strategic removal) (Scenarios 6–9).

We performed Scenarios 2–5 on 10 different random selections of farms from the dataset, to avoid drawing conclusions based on especially beneficial or harmful constellations appearing by chance. We moved the biomass from all cohorts in the closed farms to other farms with matching cohorts in time, to ensure that the biomass in the area did not change. The consequence of this redistribution scheme was that the farms grew, and in some cases the farms grew to become unrealistically large, with a few farms in the most radical scenarios exceeding 5 million fish, and a maximum of 18.2 million fish (Table 1).

In Scenarios 6–9, we removed the farms that were shown to contribute the most to the external infestation pressure on the other farm sites, based on results of a connectivity analysis performed by the Institute for Marine Research (Huserbråten et al. 2020, Huserbråten & Johnsen 2022). This connectivity analysis was based on a coupled biological–physical model that used realistic nauplii production on farms (based on industry-provided lice counts and temperature), and the pelagic lice stages were dispersed and tracked by a high-resolution hydrodynamic model until settlement. Here, total export to other farms (i.e. all outgoing connections) were quantified as the sum of salmon lice larvae produced/released at Farm A that was transmitted to Farm B, C, D; and from Farm B to Farm A, C, D, etc.; iterated over all farms in the model domain. Subsequently a ranked list of which farm exported the most to other farms was compiled, and in the strategic removal scenarios farms were removed sequentially according to this list. As with the random farms, we eliminated an increasing percentage of farms in each subsequent scenario, as presented in Table 1.

Fig. 1b illustrates one specific scenario geographically, as an example (Scenario 7). We simulated each scenario 1000 times using the procedure in Aldrin et al. (2019).

Each simulation returned the average number of AF salmon lice per fish and the average number of OM lice per fish. From the simulated treatments, we calculated the number of annual fish treatments by taking the sum of the number of fish in all treated farms every month.

All simulations were performed using R statistical software (R Development Core Team 2017). The map in Fig. 1 was made using the R package 'tmap' (Tennekes 2018). Seaway distances were calculated using the 'gdistance' library in R (van Etten 2017). The code for making Figs. 2–5 is available at GitHub (https://github.com/NorwegianVeterinaryInstitute/PO3_paper.git). The code includes a download of the results from the simulations (available at: https://zenodo.org/record/7308221/files/boxplot_df.RDS?download=1).

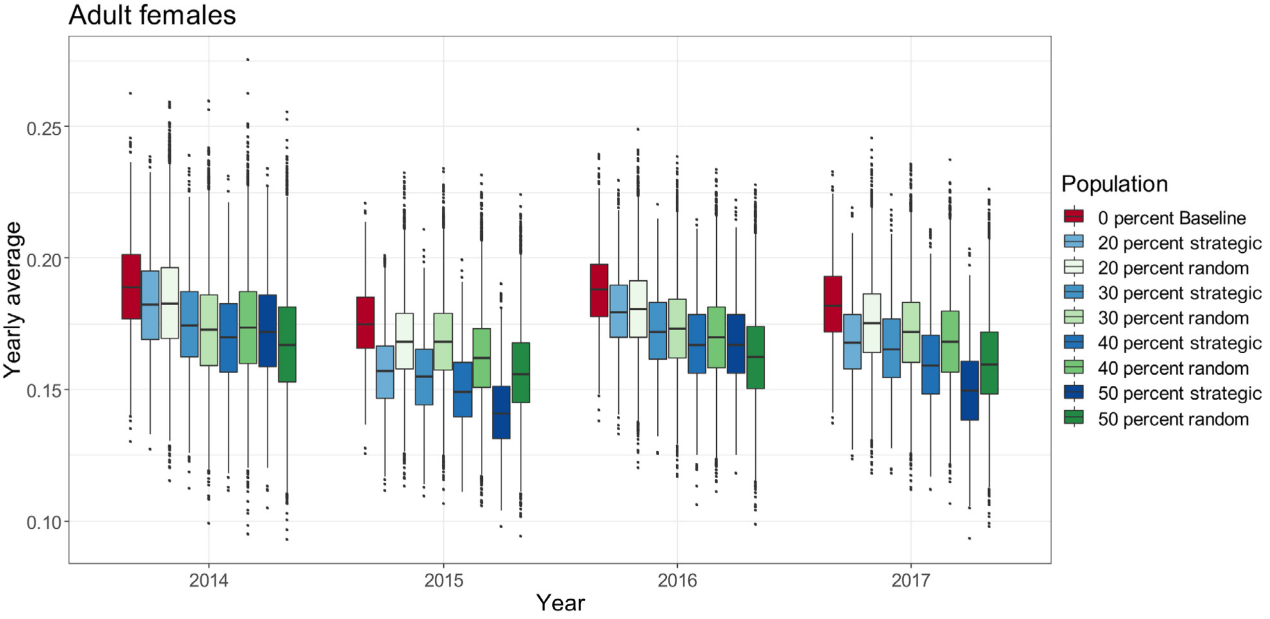

Fig. 2. Mean and variability of simulated yearly mean adult female sea lice per fish from all simulations. Box: interquartile range (IQR); line: median; whiskers: max./min. value ⩽ 1.5 × IQR; dots: outliers

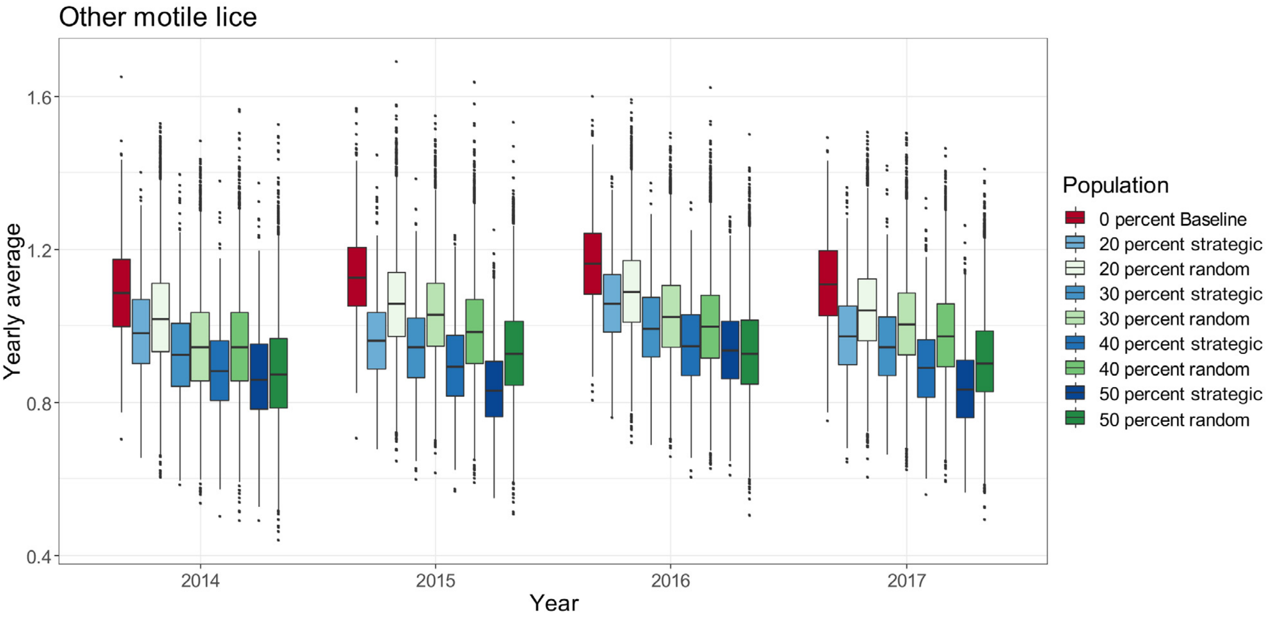

Fig. 3. Mean and variability of simulated yearly mean other motile lice per fish, from all simulations. Boxplot parameters as in Fig. 2

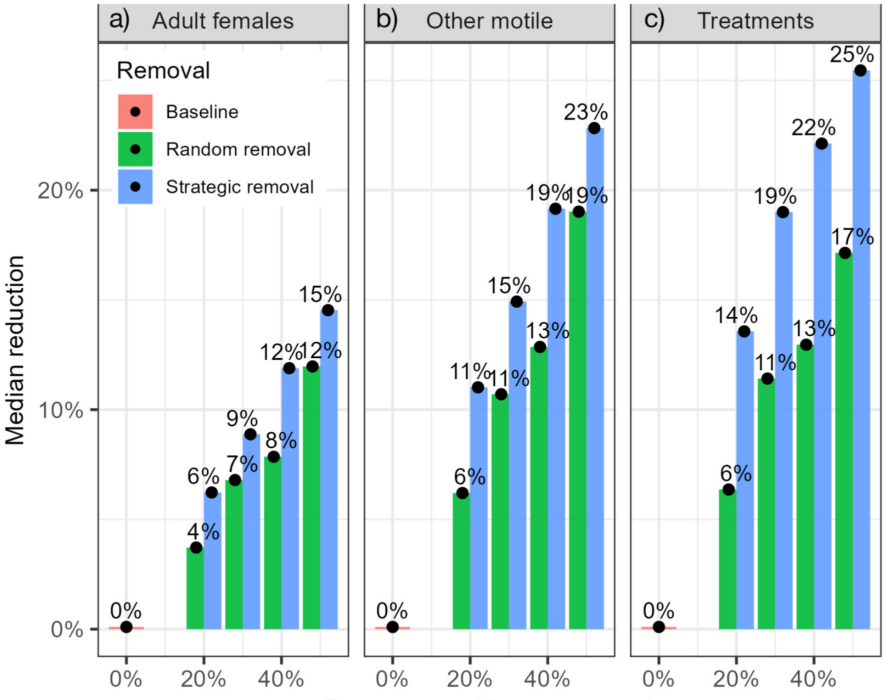

Fig. 4. Percent reduction of (a) adult female lice, (b) other motile lice and (c) treatment intensity, when comparing strategic removal scenarios and random removal scenarios with the baseline

3. RESULTS

The results are summarized from the 9 scenario simulations described in Section 2.4 (Table 1). The biomass from the closed farms was redistributed to other farms with matching cohorts to ensure that changes in treatment intensity or salmon lice numbers were not an effect of host population size, but rather the spatial distribution of the biomass.

The results from all 45 000 simulations are summarized as yearly averages for each of the 9 scenarios in Table 1. By closing farms and relocating the bio-

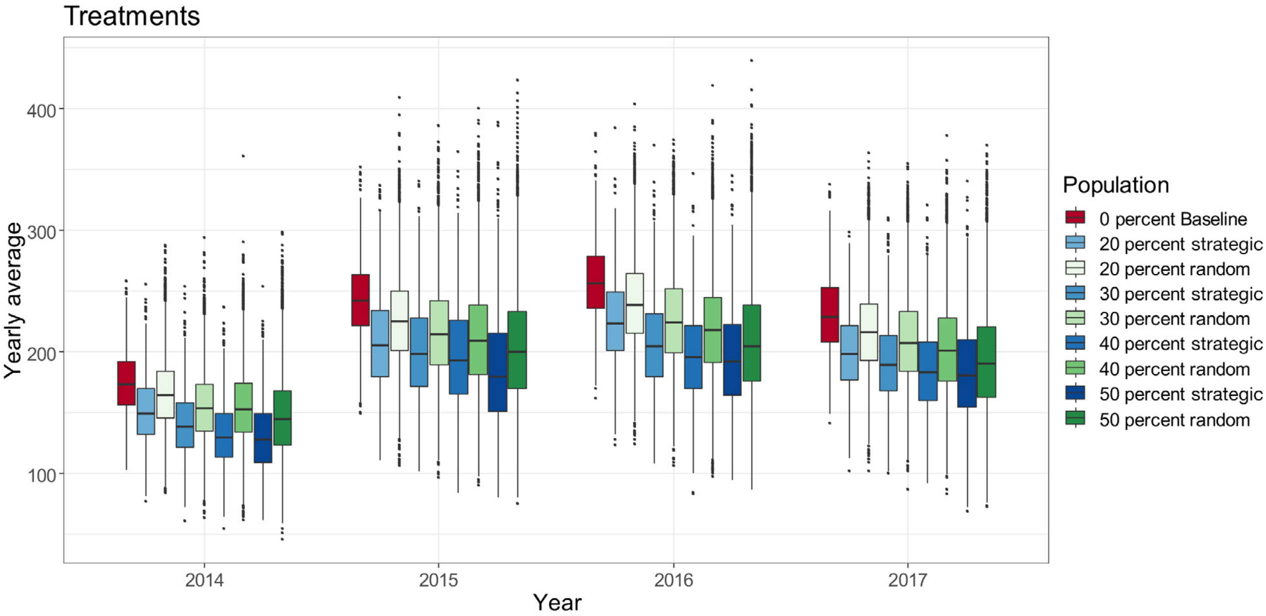

Fig. 5. Mean and variability of simulated annual fish treatments divided by 1 million. Note that each fish may be exposed to several treatments, and this number will therefore exceed the number of fish in the production area. The simulations use 16 wk to stabilize, and those weeks are left out of the data. This is the reason for the lower number of fish in treated farms in 2014. Boxplot parameters as in Fig. 2

mass to other farms, the average number of AF and OM salmon lice was reduced by 4–15 and 6–23%, respectively (Figs. 2–4). With the reduced number of lice, the annually averaged number of fish treatments per year was also reduced, by 6–25% (Figs. 4 & 5). Note that each fish may be exposed to several treatments, and the treatment number therefore exceeded the number of fish in the production area. The model used the first 16 wk of 2014 to construct the lagged variables, and these weeks are not included in the results. The treatments recorded for 2014 therefore included fewer weeks, which resulted in fewer treatments in 2014 (Fig. 5).

The model predicted considerable variation between scenarios, and some variation between years (Figs. 2, 3 & 5). There was a general tendency, however, that closing a greater number of farms led to a greater reduction in the number of lice and treatments. Moreover, the strategic removal of farms seemed to reduce the number of treatments and lice numbers more than removing farms randomly.

The percentage reduction of strategic removal and random removal compared with the baseline revealed that the most effective measure to mitigate the impact of salmon lice was Scenario 9, to remove 50% of the farms strategically. This measure led to a 15% median reduction of AF, as compared to the baseline value, 23% median reduction in OM lice and 25% median reduction in the number of fish treatments over the entire simulation period (Fig. 4).

4. DISCUSSION

Here, we demonstrate that distributing the biomass of salmonids (the hosts) onto fewer farms with greater distance between them may be an effective preventative measure against salmon lice infestations. Larger distances between farms reduces between-farm dispersal, disrupts transmission networks, and consequently reduces the average number of lice in the metapopulation. AF lice (Fig. 2) and OM lice (Fig. 3) are consequently less abundant in all redistribution scenarios with increasingly larger and fewer farms, despite increased farm sizes. The effect is least pronounced for AF in all scenarios. The latter result may be an effect of the treatment regime. Fish are treated based on AF counts, and the treatment regime will reduce the simulated numbers of female lice when the maximum allowed AF lice burden is exceeded, as long as the treatment efficacy is able to counteract the lice population growth. A reduced development of female lice when the salmonids are redistributed will therefore be partly manifested as a reduced treatment frequency. The results also indicate that each fish will experience fewer treatments when there are fewer and larger farms, as expected with a slower development of AF lice populations (Figs. 4 & 5).

Salmon lice dispersal has usually been modeled in 2 different paradigms. The simulation model (Aldrin et al. 2019) belongs to a group of lice models where the transmission contact between farms is an effect of seaway distances (Aldrin et al. 2013, Kristoffersen et al. 2014, 2018), effectively assuming that the large-scale distribution of water movement evens out over time, as well as geographically over several farm locations. By contrast, the model used to target important farms in the system models lice larvae transmission in a hydrodynamic model (Asplin et al. 2014, Sandvik et al. 2016, 2020, Myksvoll et al. 2018, Johnsen et al. 2021). Networks built with the 2 different approaches are not equal, and the farms that are removed based on the hydrodynamic model are not necessarily the best choice for a distance-based model. A model suitable to simulate the population dynamics of salmon lice that includes the hydrodynamic properties is not currently available. The hydrodynamic properties, however, are important for the dispersal of planktonic organisms like salmon lice larvae, and a model that includes the movement of the water is probably better suited to identify important nodes in the real-world network. Here, we demonstrate that simulated scenarios with a strategic removal of farms based on a hydrodynamic network model is a better mitigation measure than the random removal of farms. Therefore, the illustrated potential in removing farms strategically is valid across model specifications, which implies a robustness to this finding.

The system of salmonid farms in Norway can be thought of as a network composed of nodes. Although it is shown that this network has great temporal variability, spatial networks that are highly structured can be identified where there are farms that support high densities of salmon lice in subpopulations (Huserbråten & Johnsen 2022). These salmon lice subpopulations are connected through water exchange between the farms, the intensity of which is determined by distance, geographical features, water currents and temperature-controlled development of the salmon lice (Samsing et al. 2019). The distribution of the connections between nodes/farms is important for the resilience of the network. Real-world networks often display an extremely inhomogeneous connectivity between nodes, and some nodes may connect otherwise distinct or significantly less connected populations (Albert et al. 2000). The removal of a random farm in this case could be redundant, and is consequently not likely to alter the path structure of lice larvae exchange, or the overall network topology (Albert et al. 2000). The random removal of several farms may reduce connectivity, but the intervention becomes stronger than necessary, because the removed farms contribute to the desired effect to a varying degree.

An informed management strategy, on the other hand, can target key farms in the system for removal, thus exploiting the properties of the network for disease control (Albert et al. 2000, Chami et al. 2017), effectively producing 'firebreaks' that disconnect parts of the network, as suggested by Samsing et al. (2019). Recent research, however, argues that natural networks are more resilient than previously believed (Broido & Clauset 2019). It is also important to note that the salmon lice in the present simulation study are not restricted to farms, but are also naturally occurring in the absence of salmonid aquaculture. While the infestation pressure from wild sources is regarded as insignificant in calculations of infestation pressure in most cases (Heuch & Mo 2001, Heuch et al. 2005, Johansen et al. 2011, Samsing et al. 2019, Dempster et al. 2021), it makes a total isolation from salmon lice impossible in aquaculture with open cages that are exposed to the environment. Both the simulation model and the real world includes a background infestation rate from natural sources, which may reduce the effect of network fragmentation between farms to some degree. In addition, the wild host populations interact with the salmon lice densities produced in farms. A complete transformation into disconnected subnetworks may therefore not be feasible. Nevertheless, our results indicate that the benefits of removing farms becomes bigger when we remove them strategically, based on the connection network developed in Huserbråten & Johnsen (2022). For instance, the average fish experience between 6 and 17% less treatments in the random removal scenarios, and between 14 and 25% less treatments in the strategic removal scenarios.

Treatments in the model were set to reduce lice counts by 75% for both AF and OM lice. The effectiveness chosen in the present study was therefore somewhat higher than the estimated 44 to 47% in the development of the simulation model (Aldrin et al. 2019). The authors do, however, argue that this value was unexpectedly low, and it is unclear whether treatments cover the entire farm or some selected cages. A more detailed model with similar outlines that were fitted to cage-level data describes treatment effectiveness between 0 and 99% (Aldrin et al. 2017). We assumed that there is knowledge in the industry about treatment effectiveness, and chose an effectiveness closely resembling the estimated effect of azamethiphos in Aldrin et al. (2017). Moreover, synchronization of generations and salmon lice treatments were mandatory in the study area during the study period (Ministry of Trade, Industry and Fisheries 2010, Guarracino et al. 2018), and synchronized treatments are known to be an effective measure (Arriagada et al. 2017).

The modeling paper by Aldrin et al. (2019) did include an analysis where the authors looked at how the infestation pressure increased by doubling the farm sizes, and by doubling the number of farms. The results from this analysis indicated that larger and fewer farms reduce lice burdens, thus concurring with the results from the present study. The authors simultaneously suggest that causal effects should be interpreted with care, due to confounding factors related to regions where the farms are located and how farms are managed. Here, in the present study, we add realism to the simulations by redistributing the biomass between existing farms with matching cohorts, and we show that the location of the farms does matter in the strategic removal scenarios.

Time-series simulations have been effectively applied to study disease transmission of other agents, such as those that cause pancreas disease (PD) and infectious salmon anemia (ISA). These outbreak simulations typically factor in distances between farms, with their sizes and overlapping production history revealing that both farm size and increasing inter-farm distances are significant predictors of disease transmission in Norwegian salmonid aquaculture (Aldrin et al. 2019, 2021, Bang Jensen et al. 2020a, 2021, Stige et al. 2021). There is a prevailing trend showing a rapid decline in transmission probability as distance between farms increases. On the other hand, bigger farms constitute a larger transmitter and receiver of infectious agents, which may contradict the effect of increasing distances between farms. Modeling of viral and bacterial diseases does suggest, however, that distributing the biomass over larger farms situated farther apart may also reduce transmission of viruses and bacteria (Salama & Murray 2012).

It is important to note that the results of the present study are the product of a modeling and simulation exercise, and there are several caveats to generalizing the results to the real world. First, we did not consider whether the location of removed farms is suitable for the increased biomasses and fish abundances that were created in the scenarios. Second, we did not consider whether the increased fish abundance was within the numbers that can be managed in a salmonid farm, and some of the farms did become unrealistically large, especially in the 50% removal scenarios (Table 1). Large farms will cover more cages and a larger area, the handling of fish may become more difficult, and ordering wellboats for treatment etc. may be delayed in big farms. Third, the treatments in the model were carried out the week after the farm exceeded the threshold for mandatory treatments. This is probably not realistic in many cases, because lice treatments are big operations that include wellboats with proper equipment. The availability of wellboats and equipment may be limited, especially in periods with high lice burdens in many farms. Fourth, the farm sizes in the redistribution scenarios exceed the data used to fit the simulation model to a large degree (Table 1). Extrapolations outside the range of the data used to fit the model will introduce unknown uncertainty in the simulations.

The methods behind the present paper are therefore not a straightforward procedure to optimize farm structure in the study area. The qualitative results, however, point to some core mechanisms that could be considered in the planning of farm structure in salmonid aquaculture to ease the burden of salmon lice.

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