



Evaluation of aquaculture management zones as a control measure for salmon lice in Norway

Mario Guarracino, Lars Qviller*, Atle Lillehaug

Norwegian Veterinary Institute, PO Box 750 Sentrum, 0106 Oslo, Norway

ABSTRACT: We evaluated the use of coordinated fallowing as a means to control salmon lice *Lepeophtheirus salmonis* infestation in farmed Atlantic salmon *Salmo salar*. In discrete management zones, aquaculture operations such as stocking, fallowing, treatments and harvesting are synchronized at all sites in coordinated areas within the zones. The expected benefit of synchronized generations is to reduce the presence of salmon lice larvae after a period of fallowing, as well as to minimize external infestation pressure from surrounding aquaculture sites. A regression analysis was used to evaluate the effectiveness of coordinated fallowing on the progression of external salmon lice infestation pressure and abundance in Atlantic salmon farming sites in 2 areas (zones) in Norway. The overall results show that external infestation pressure was higher inside than outside the management zones, and the external infestation pressure increased with increasing biomass throughout the production cycle. However, within the zones, the external infestation pressure at the beginning of a production cycle was high and in many cases even higher than the general external infestation pressure in the non-coordinated areas. This suggests that external infestation pressure from the neighboring areas has a considerable effect on the fallowed area. Higher numbers of salmon lice were recorded within the zones than outside and, as the production cycle progressed, this phenomenon became more evident. We conclude that the high infestation pressure from salmon lice at the beginning of the grow-out period after fallowing raises severe doubts about the effectiveness of coordinated fallowing practices.

KEY WORDS: Aquaculture · Fish diseases · Parasites · Salmon lice · Atlantic salmon · Epidemiology · Management

INTRODUCTION

Farming of Atlantic salmon *Salmo salar* L. in Norway has developed as an industry since the 1970s, with a production of approx. 1.2 million t in 2016 (Hjeltnes et al. 2017). The increase in fish density in areas suitable for Atlantic salmon aquaculture has affected the interactions between the salmon and its natural endemic pathogens. The increased population of salmon lice *Lepeophtheirus salmonis* that follows a growing host biomass has become an especially important factor regarding mortality in wild salmonids, animal welfare and the costs of control measures (Heuch & Mo 2001, Torrissen et al. 2013, Kristoffersen et al. 2018).

The salmon louse is a parasitic copepod which occurs naturally on wild salmonids in the marine environment (Pike & Wadsworth 1999). It feeds on host mucous, skin and blood and may cause lesions ranging from scale loss to deep ulcerations. Infected fish may be subjected to stress, osmoregulatory problems, anemia and secondary bacterial pathogens (Jones et al. 1990, Jónsdóttir et al. 1992, Grimnes & Jakobsen 1996). The most important concern caused by increased salmon lice populations in Norway is the possible consequences this might have for infestation pressure and subsequent mortality in wild salmonids (Torrissen et al. 2013, Thorstad et al. 2015, Kristoffersen et al. 2018, Vollset et al. 2018).

*Corresponding author: lars.qviller@vetinst.no

The Norwegian Food Safety Authority (FSA), the governmental body responsible for fish health in Norway, has established a registration system for reporting lice infestation and has set maximum levels of *L. salmonis* burdens in farmed salmonids, which, when these are reached, require the implementation of control measures. During the study period from 2012 to 2017, treatments were compulsory with lice loads >0.2 lice fish⁻¹ prior to salmon runs in the spring, and with 0.5 lice fish⁻¹ during the rest of the year (Norwegian Ministry of Fisheries and Coastal Affairs 2012). Salmon lice infestations have traditionally been controlled with pharmaceutical treatments, but the development of resistance to pharmaceuticals has become an increasing problem, with reduced sensitivity reported for all commonly used substances (Sevatdal et al. 2005, Aaen et al. 2015, Helgesen et al. 2015, 2017).

In general, it is mandatory to segregate generations as a measure to mitigate problems with pathogens. The positive effect of a such an 'all in/all out' strategy is well documented for salmon lice, with low numbers of salmon lice several months after stocking and less need for pharmaceutical treatments (Bron et al. 1993). Re-infestation with salmon lice from surrounding farming sites may limit the duration of the effects of treatments and fallowing. The impact of external infestation pressure on salmon lice population dynamics on both wild and farmed fish is thoroughly described in the literature (Jansen et al. 2012, Aldrin et al. 2013, 2017, Asplin et al. 2014, Kristoffersen et al. 2014, 2018, Adams et al. 2016, Sandvik et al. 2016).

A strategy to reduce the abundance of pelagic salmon lice larvae to as low as possible at a site when a marine production cycle of salmonids starts, as well as to cope with the infestation pressure from nearby sites, is the implementation of an integrated pest management (IPM) approach, which entails management, biological and pharmaceutical measures (Sommerville 1998). In the context of FSA regulations for salmon lice control, this has developed into the imposition of discrete zones and the subdivision of the zones into management areas where fish stocking and harvesting, fallowing of sites, as well as anti-lice control measures, are coordinated. Coordinated fallowing will reduce the functional host population for salmon lice inside a fallowed area to only wild fish, thus aiming to reduce the external parasitic infestation pressure from the previous generation of fish, as well as from surrounding sites when restocking. The theory behind this is well defined for emerging infectious diseases (Werkman et al. 2011), and coordi-

nated fallowing has been successful in coping with diseases like furunculosis (Rae 2002) and infectious salmon anemia (Thorud & Håstein 2003). There is also some evidence suggesting that coordinated treatments reduce overall salmon lice numbers (Arriagada et al. 2017). Adams et al. (2016) used a simulation based on particle tracking in a hydrodynamic model to establish that salmon lice larvae spread over large distances. The abundance, however, was reduced when entering neighboring management areas, and the authors argue that this indicate a benefit of coordinated fallowing. On the other hand, they did not consider population dynamics of the salmon lice nor the biomass fluctuations that follow coordinated fallowing and synchronized generations. Another simulation study applied a design where the sites were organized evenly spaced around a circle, where transmission occurred between the closest neighbors (Murray & Salama 2016). This study allowed for more realistic population dynamics in salmon lice, and they found positive effects of coordinating fallowing in most scenarios. One should keep in mind however that this simulation study assumed that farms evenly spaced in a circle exhibit the same transmission dynamics as farms in the real world. There is, to our knowledge, no justification in the literature for coordinated fallowing in reducing problems with salmon lice based on empirical evidence nor have we been able to find any discussion on the differences between such actions regarding rare diseases and endemic pathogens.

In the present paper, we evaluated the effects of coordinated fallowing on the external infestation pressure of salmon lice. We modelled the progression of external infestation pressure through the production cycle and evaluated the spread of salmon lice over the boundaries into fallowed neighboring areas based on real salmon lice counts. We also discussed whether such actions have beneficial effects on the development of salmon lice loads in Atlantic salmon aquaculture.

MATERIALS AND METHODS

Management zones and fallowing areas

The zoning system investigated in this study was introduced in Norway in 2010, with official regulations called 'Regulations on zoning to prevent and combat salmon lice in aquaculture installations', in 2 areas in Norway (Norwegian Ministry of Fisheries and Coastal Affairs 2010a,b). The regulations de-

defined the 2 zones, delineated with the purpose of preventing and limiting salmon lice infestation in both farmed and wild fish. The zones were divided into several management areas. Each management area held a variable number of sites, locations where Atlantic salmon were farmed in one or more cages. Within each area, companies were obliged to coordinate management actions, i.e. smolt stocking, harvesting and fallowing, together with fish health-related activities, like counting of salmon lice and treatments with pharmaceuticals or other delousing methods. Our focus is on areas designed to coordinate fallowing, and we refer to these management units as 'fallowing areas'.

The Hardanger management zone (the Hardanger Zone), situated in Hordaland and Rogaland counties, included 137 sites in 7 fallowing areas, covering an area of approximately 3200 km². The Vikna management zone (the Vikna Zone), was situated in the county of Nord-Trøndelag, and included 60 sites in 13 fallowing areas, covering an area of approximately 2300 km² (Fig. 1). Data from 393 sites outside of the management zones, designated No Zone, was also used in the study for comparison. In the No Zone data set, we only included sites from south of the town of Brønnøysund (65° 28' 30" N, 12° 12' 43" E, WGS84). The reasoning behind this choice is that climatic differences and lower farm densities make data from the areas farther north less comparable to the management zone data. We used data from every site in the study area that was active at least at some point during the study period, which was from 2012 through 2016. Note that some coordinated fallowing was also performed in the No Zone areas, but these were not compulsory, and coordinated fallowing was less common than in the Hardanger and Vikna zones.

All sites in each fallowing area had to be fallowed simultaneously for at least 30 d every other year after harvesting of fish in the Hardanger Zone, and for at least 180 degree days + 7 days every other year in the Vikna Zone. The Vikna Zone was decommissioned in 2014, and the Hardanger Zone was functional until summer 2017.

Parameters and data set

Since 2002, all active Norwegian aquaculture sites have been obliged to report key statistics on salmon production to the government on a monthly basis. These statistics include number of fish, current biomass at the site, fish health statistics including salmon lice counts, and other parameters relevant to the production. From 1 January 2012, and during the entire study period, the procedure for reporting salmon lice numbers was in weekly reports when the water temperature was above 4°C. Each farming site had to report lice counts from at least 10 fish from each of at least half of the cages. Lice counting was performed in an alternating pattern, so that all cages were sampled during a 2-week period. The reported lice number from this sampling was the mean of all cage means (Norwegian Ministry of Fisheries and Coastal Affairs 2012, Kristoffersen et al. 2014).

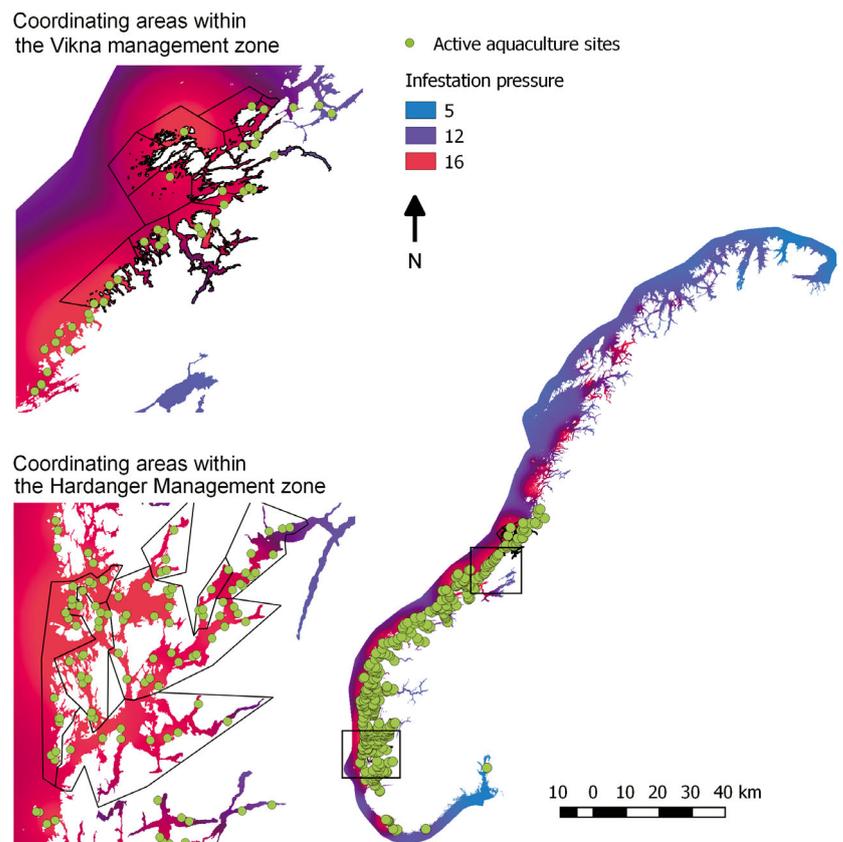


Fig. 1. Study area and the spatial distribution of sites south of Brønnøysund that were active in week 41 of 2016 (green dots). The northern Vikna and southern Hardanger management zones for salmon lice are expanded in the 2 maps on the left. The background color illustrates the salmon lice infestation pressure in Week 41 of 2016 expressed as a log-transformed (natural logarithm), distance-penalized number of salmon lice that have survived until the pre-adult stage, ranging from low (blue) to high (red)

The reported average salmon lice counts were categorized into 3 groups according to the developmental stages of the louse: chalimus stages (attached salmon lice), pre-adult lice and adult males (PAAM) and adult females. The small chalimus larvae may be difficult to see; we therefore suspected lower reliability for reported numbers from this group. In addition, high adult female lice abundances often lead to costly interventions and could have been underreported in some cases. Based on initial analyses, previous experiences with this specific data set (Kristoffersen et al. 2014) and similar data (Aldrin et al. 2017), we found the reported averages from the PAAM stages to be the most reliable. Whenever salmon lice counts or abundance is given in the present paper, we are reporting the PAAM lice counts. Note, however, that we used the adult female lice counts to calculate infestation pressure (see below).

A data set of weekly reported lice numbers for every active site from 1 January 2012 to 31 December 2016 was constructed using linear interpolation between the monthly registrations of production data to estimate production data comparable to weekly salmon lice counts. To avoid the effect of salmon lice treatments with anti-parasitic pharmaceuticals, we removed all the weeks when treatments were employed and the first week after.

External infestation pressure

In addition, the external infestation pressure for each site was calculated according to Kristoffersen et al. (2014) and added to the weekly data. The external infestation pressure in a given site at a given time is an estimate based on the production of salmon lice larvae in all the surrounding sites, a reduction of larval concentration with distance according to the relative risk function in Kristoffersen et al. (2014) and an expected mortality until the pre-adult stage. For the purpose of this paper, it can be understood as a measure of the influx of pelagic salmon lice larvae from the surrounding aquaculture sites. The model uses adult female lice counts, estimated louse larvae survival, which is temperature dependent, and the distances between aquaculture sites to calculate the infestation pressure.

The final dataset is comprised of information about salmon lice counts, external infestation pressure, year, which zone the site belonged to and the age of the fish, measured as number of weeks since stocking in the seawater phase of the production cycle.

Analyses

In order to understand any possible effect of coordinated fallowing, we calculated the general increase in external infestation pressure over the course of the production cycle in each zone and outside the zones. We used a log-linear regression model with external infestation pressure as a response, predicted by the age of the fish in all sites included over 5 yr. Included variables and interactions were explored with a forward model selection, using the Bayesian information criterion (BIC) to evaluate the model fit.

Comparisons of average (averages of averages) salmon lice counts between the zones and outside the zones were done using Tukey's HSD test, following the log-normal distribution, and a special Tukey's HSD test designed for the negative binomial (negbin) distribution from the multcomp package in the data program package R (Hothorn et al. 2008). We handled the time series autocorrelation by taking the average over all registrations in each site. In order to obtain the discrete count values required by the negative binomial test, we multiplied the mean by 30, with the result being rounded off to the closest integer number. This approach, similar to the methods used by Kristoffersen et al. (2014), results in standardized count values, comparable to registrations in the field with salmon lice counts on 30 fish or more, which is a reasonable number of fish included in the reported averages.

Data management and analyses were performed using R version 3.4.1 (R Core Team 2017).

RESULTS

A simple comparison with box plots shows that the external infestation pressure in farming sites outside the zones with compulsory synchronized fallowing (No Zone) was generally lower than inside the zones. The Hardanger Zone showed the highest external infestation pressure (Fig. 2). The registered reported salmon lice counts were also higher, on a general basis, inside the zones than elsewhere (Fig. 3), with a similar pattern to that of external infestation pressure. Tukey's HSD test revealed significant differences in salmon lice abundance between the Hardanger Zone and Vikna Zone (log-normal approach: $p < 0.0001$, negbin approach: $p < 0.0001$) and between the Hardanger Zone and the areas outside the zones (log-normal approach: $p < 0.0001$, negbin approach: $p < 0.0001$). There were no significant differences between the Vikna Zone and the areas outside the zones (No Zone).

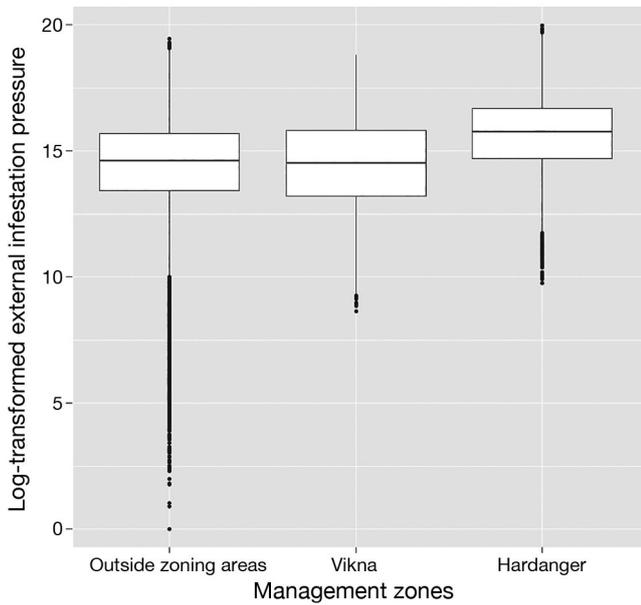


Fig. 2. Comparison of the external infestation pressure within the coordinated areas in the Hardanger Zone, in the Vikna Zone and outside the zones. The centerline in the box is the median infestation pressure, the upper and lower 95 percentiles are outlined by the box, and the dots show extreme values. The unit for infestation pressure is a log-transformed, distance-penalized number of salmon lice *Lepeophtheirus salmonis* that have survived until the pre-adult stage

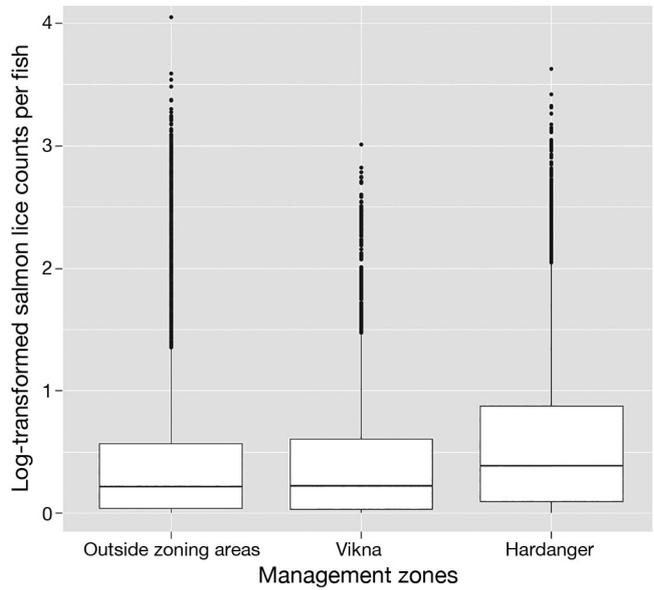


Fig. 3. Comparison of average salmon lice *Lepeophtheirus salmonis* counts within coordinated areas in the Hardanger Zone, in the Vikna Zone and outside the zones. The calculated averaged salmon lice count values are log-transformed (natural logarithm). The centerline in the box is the median lice counts, the upper and lower 95 percentiles are outlined by the box, the dots show extreme values

External infestation pressure in the log-linear regression model was best explained using year, whether the site was in the Hardanger Zone, the Vikna Zone or the No Zone, the age of the fish, and the interaction between year and age as explanatory variables (Table 1). We found that the initial external infestation pressure (the intercept values of the model; Figs. 4 & 5) was higher in the areas with coordinated practices than in the other areas, although this tendency was not that clear in the Vikna Zone. This result means that the following period between generations did not lead to an elimination of external infestation pressure.

The external infestation pressure increased with the age of the fish at a constant log-linear rate with no interactions, but it varied on the back-transformed scale (Fig. 5). The variation in the rate of increase, presented in Fig. 5, is therefore an effect of the starting point of the curve, e.g. the initial external infestation pressure. The initial external infestation pressure was always higher in the Hardanger Zone, while the uncoordinated areas and the Vikna Zone shifted between years. The external infestation pressure in Vikna was lower than areas without coordi-

Table 1. Results from the stepwise forward model selection. The Bayesian information criterion (BIC) is used as a measurement of fit, where lower values indicate a model that better fits the data. X means that the variable is included in the model as an independent variable. Columns with more than one variable indicate an interaction effect between these variables. The best, chosen model is highlighted in **bold**. Year: the year when external infestation pressure was recorded; zone: a factor variable that denotes whether the recorded external infestation pressure was in the Hordaland Zone, the Vikna Zone or outside the regulated areas; age: the age of the fish, recorded as number of weeks since stocking in seawater

Year	Zone	Age	Year:Zone	Age:Year	Zone:Age	Age:Year:Zone	BIC
X							306761
X	X						305223
X		X					302478
X	X	X					306257
X	X						301984
X	X	X					300928
X	X	X	X				300410
X	X	X		X			300314
X	X	X			X		300415
X	X	X				X	302004
X	X	X	X	X			300317
X	X	X	X		X		300334
X	X	X				X	300398

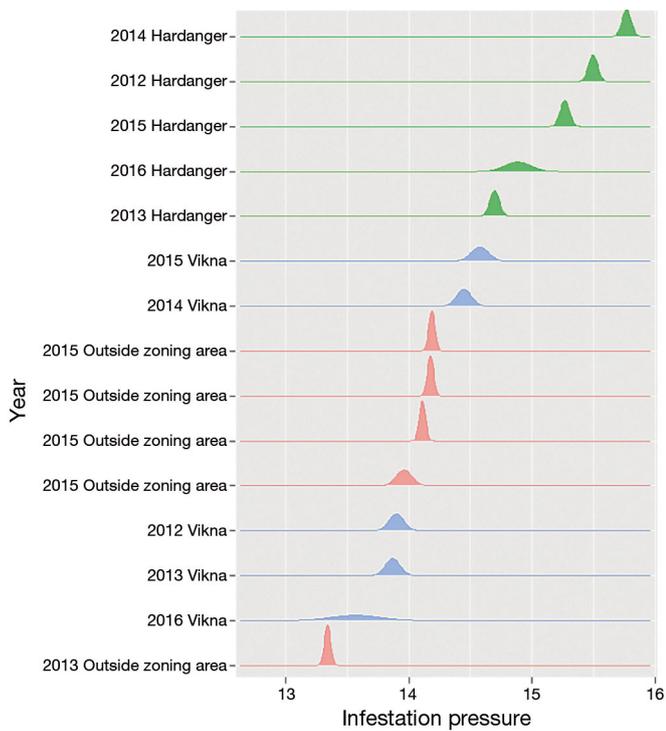


Fig. 4. Estimates for all levels of factor variables in the best model explaining external infestation pressure of salmon lice *Lepeophtheirus salmonis* outside and within the coordinated areas in the Hardanger Zone and in the Vikna Zone, presented as complete Gaussian distributions. The zonal division is illustrated with colors. The unit for infestation pressure is a log-transformed, distance-penalized number of salmon lice that have survived until the pre-adult stage

nated practices in 2012, higher in 2013 and 2014, and lower again in 2015 and 2016.

DISCUSSION

The goal of the present study was to evaluate the effectiveness of synchronized fallowing of marine salmon farming sites in controlling salmon louse *Lepeophtheirus salmonis* infestations and to discuss the theories behind this disease control strategy. Our results indicate that the external infestation pressure is generally higher inside the zones throughout the production cycle, with high external infestation pressure also at the beginning of the production cycle. This is especially evident in the Hardanger Zone. The salmon biomass at all the sites within the same fallowing area prior to a production cycle should amount to zero, and consequently, the external infestation pressure and salmon lice counts should be low. High external infestation pressures at the beginning of the grow-out period inside the zones suggest that

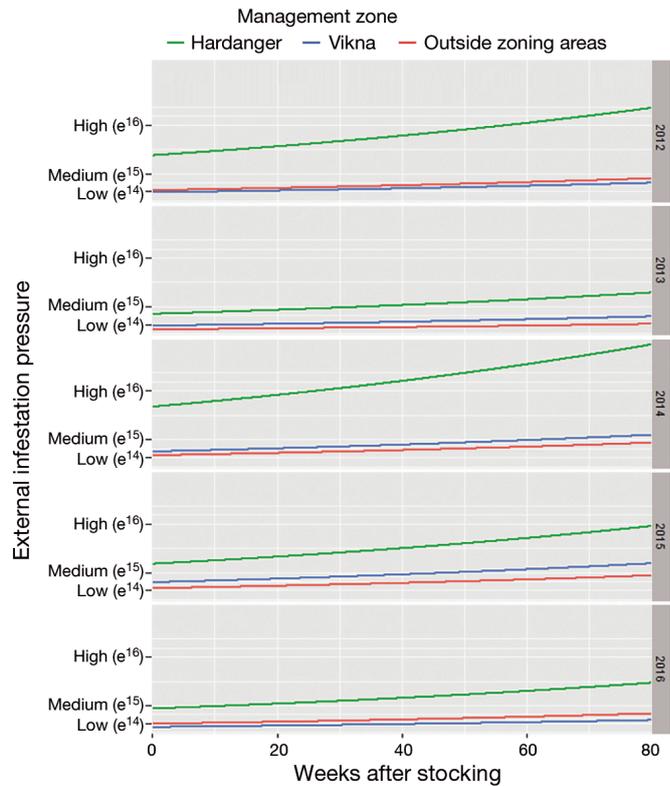


Fig. 5. Trends of weekly salmon lice *Lepeophtheirus salmonis* infestation pressure after stocking of fish in seawater, during different years within salmon lice management zones in Hardanger (green), in Vikna (blue), and outside the zones (red). The unit for infestation pressure is a log-transformed, distance-penalized number of salmon lice that have survived until the pre-adult stage

the following practices do not work, at least not fully as intended. A substantial influx of salmon louse larvae from the surrounding fallowing areas reduces the effect of coordinated fallowing.

As shown in Fig. 5, the external infestation pressure in the Vikna Zone in 2016, after the national regulation defining the zone was terminated in 2014, was reduced to levels below the No Zone group. Hence, there were no trends in the data to indicate that the regulated fallowing practices reduced the external infestation pressure on a general basis.

The external infestation pressure increased with the age of fish inside the fallowing areas, probably due to an increase in overall biomass. This is as expected, since all parasite populations depend on their host's density and biomass (May & Anderson 1979). This has also been proven specifically for the salmon louse parasite host system in aquaculture (Jansen et al. 2012, Kristoffersen et al. 2014). Areas with high biomass at the end of a production cycle may also increase external infestation pressure levels beyond that of areas with mixed generations, thus

having a massive effect on fallowed areas. A similar increase in infestation pressure with increasing age was also apparent in areas not included in the regulations (Fig. 5). Increasing external infestation pressure with age may not only contribute to the substantial initial infestation pressure that we demonstrate herein, but could also produce a potential problem when controlling salmon lice numbers in the later stages of the production cycle.

The model by Kristoffersen et al. (2014) performs well in predicting the salmon lice burdens in aquaculture sites, and it is reported to outperform the best contemporary model that uses hydrodynamics to predict salmon lice burdens on wild salmon smolt placed in sentinel cages for surveillance (Aldrin 2016). The model is therefore adequate to illustrate how infestation pressure can breach the boundaries of the fallowing areas.

Our model did not include larval production in wild salmonids, nor did we include larval production at the site. The calculated infestation pressures are therefore independent from both lice on wild salmonids and internal infestation pressure. Furthermore, the mortality of the pelagic stages of salmon lice larvae, as presented in Stien et al. (2005), suggest a very low survival through a period of coordinated fallowing. High external infestation pressure in the beginning of the grow-out period in the zones was therefore almost exclusively produced in the neighboring fallowing areas. In other words, the initial external infestation pressure can only be that high due to the proximity to fish farms with high salmon biomass and a large population of reproducing salmon lice females, even when coordinated fallowing is mandatory. Hence, the newly stocked fish may quickly build up heavy salmon lice burdens. This is visualized with a map of the calculated external infestation pressure in Week 43 of 2016 (Fig. 1), showing the extent of lice spreading into neighboring areas during periods with high salmon lice activity, regardless of host biomass and fish age.

On the other hand, both wild salmonids and larval production on the sites may contribute markedly to the salmon lice loads on the fish. These mechanisms will become more important when salmon lice at the farm start to reproduce and the internal, on-site infestation pressure drives the growth of salmon lice populations as the host biomass increases.

We have demonstrated that the sites in fallowed areas are not sufficiently isolated to mitigate infestation pressure from the active sites in the surrounding areas, and evidence from hydrodynamic modelling supports this finding. Asplin et al. (2014) show that

salmon lice larvae may be transported as far as 100 km in the Hardangerfjord, in the center of the Hardanger management zone. Samsing et al. (2017) found similar dispersal potential on the Norwegian coast in both winter and spring (winter 36.5 km, spring 17.8 km), Johnsen et al. (2016) found 20–45 km average dispersal in the Folda fjord system, and a study from Altafjorden in northern Norway shows how lice dispersal from 6 salmon farms covers the entire fjord system (Skarðhamar et al. 2018). Some simulation models use boundaries between fallowing areas and suggest that larger coordinated areas may improve the effect of coordinated fallowing (Adams et al. 2016, Murray & Salama 2016). This may very well be the case because fallowed sites that are close to active neighbors constitute a smaller proportion of a larger fallowed area. On the other hand, a large area with coordinated generations produce more biomass at the end of the production cycle than a smaller one, with possible negative effects on lice numbers as the coordinated biomass increases. It is not known whether the benefits from coordinated fallowing in areas with sufficient isolation outweigh the negative prospects of increased biomass at the end of the production cycle. Further simulation studies based on empirical evidence on population dynamics and dispersal potential of salmon lice may indicate whether it is possible to attain an optimal structure of areal fallowing that is beneficial (possibly using parameters from Aldrin et al. 2017).

When interpreting the results that both the Vikna and Hardanger Zones have higher median lice counts than areas where no coordination occurred (not significant for the Vikna Zone, Fig. 3), one should keep in mind that the zones were established in these areas because of high production density and extensive salmon lice problems in the first place. There has also been an increase in production density prior to and during the study period, and differences in coordinated treatment efforts and geographic distribution of pharmaceutical resistance may have affected both salmon lice numbers and overall infestation pressure. Furthermore, we know that some sites outside the regulated zones (the No Zone group) also practice coordinated fallowing. Hence, the structure of our data does not provide any reliable control group, and all comparisons between our 3 groups should be interpreted with care. Nevertheless, the observed lack of effect, i.e. the unexpected high infestation pressure in the beginning of the production cycle also inside the zones, is indisputable.

There is a fundamental difference between specific pathogenic disease agents with limited or sporadic

distribution and endemic pathogens. The eradication of a specific sporadic infection using coordinated fallowing makes re-infection unlikely, while the re-infestation of salmon lice is unavoidable, and possibly even enhanced, by the coordination in the adjacent areas. A successful coordinated fallowing requires sufficient isolation from high lice-producing neighbors, and that the benefits of isolation from other areas outperform the negative prospects of increased overall biomass in the fallowing area at the end of the production cycle.

CONCLUSIONS

In conclusion, we argue that the relatively high external infestation pressure of salmon lice found at the beginning of the grow-out period for Atlantic salmon after fallowing of a coordinated area for Atlantic salmon calls into question the effectiveness of this practice in controlling infestation. High salmon biomass and high salmon louse reproduction in neighboring areas are likely the main contributors to this finding. Furthermore, the explosive growth in salmon lice populations at the end of the salmon production cycle as the host biomass increases may be a negative result of coordinated fallowing.

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Editorial responsibility: Stephen Feist,
Weymouth, UK

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