



Implications of Post-Smolt Salmon Production for Local Sea Lice Populations

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January 2023

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EXECUTIVE SUMMARY

A mathematical model of sea lice population dynamics has been applied to a small network of four finfish farms in Loch Etive, a Scottish west coast sea loch (fjord). The model was used to demonstrate that switching from a traditional two-year on-growing production cycle to production of post-smolt salmon with 6-month growing periods separated by full fallowing of sites results in substantially lower lice numbers on the farms throughout the year. This results in a reduced risk to local wild fish populations and also reduces (or obviates) the need for medicinal lice treatments.

Lice counts from 2021 and 2022 during traditional on-growing production cycles of rainbow trout revealed high lice numbers during late summer and autumn of both years, when water temperatures were highest and surface salinity levels also relatively high (both conducive to sea lice reproduction). The lice count data were used to estimate the external sea lice infection pressure on the farmed fish by fitting the model results, as best as possible, to the data.

Once an appropriate value for the external lice infection pressure was determined, the model was applied to a post-smolt production cycle. The production cycle assumes lice-free fish are put to sea every six months, so initial lice densities were set to zero. The model was run for two years, incorporating four post-smolt production cycles. The model was tested for sensitivity to parameter f , the success rate of released lice larvae reaching the chalimus stage, which was varied from 3.3% to 33.3%.

Results showed that under the post-smolt production plan, lice levels did not exceed 0.26 adult females per fish, which occurred for the highest value of f . For a moderate value of $f = 5$ (16.67%), maximum lice levels were in the range 0.1 – 0.2 adult females per farmed fish. This compared favourably to the traditional farming production methods, where lice numbers exceeded 10 adult females per fish on all sites in the late summer of 2021 and again on one site in 2022. The efficacy of medicinal treatments was included in the model, but was unable to accurately reproduce the effect of actual treatments on lice numbers; this aspect of the model needs further work. However, the model was still able to demonstrate that without full fallowing, increasing numbers of medicinal treatment events are required to keep lice numbers under control.

The substantial reduction in lice numbers on the farmed fish has two principal benefits: the risk to wild fish migrating through Loch Etive from infective lice larvae is substantially reduced, and second, the need for medicinal treatments is also substantially reduced, if not obviated. In conclusion, the modelling study suggests that switching production in Loch Etive from traditional farming of rainbow trout to production of post-smolt Atlantic salmon is likely to have significant benefits for both the farmed fish and the local wild fish populations.

1. INTRODUCTION

Sea lice infestations continue to pose challenges to salmon farmers, particularly in the second year of production during the late summer and autumn, when water temperatures are warmest. For farms in inshore waters, higher lice levels are not only problematic for farmed fish, but also pose a potential risk to migrating wild salmon and sea-trout post-smolts navigating coastal waters after leaving their natal rivers.

Traditional salmon farming typically involves about 22 months of on-growing production every two years, interspersed with a fallow period when farms are left empty. The fallow periods allow the seabed beneath the farm pens to recover, but also break the life cycles of local sea lice populations. When farms are restocked with lice-free smolts, it typically takes several months for local lice populations to regenerate to levels of concern. Ultimately, however, lice numbers during the second year of production and/or during the late summer and autumn remain problematic with traditional farming cycles. In Scotland, the salmon farming industry has been gradually seeking new sites further offshore, away from the inshore waters of Scottish sea lochs and the migrating wild fish populations, in order to reduce the potential risk to wild fish from sea lice.

Post-smolt production involves truncated production cycles, growing salmon from sizes of 70 – 100 g through to about 750 g over a period of about six months. The fish are then transferred to open water sea pens, when on-growing to harvest size take place. Post-smolt production may take place in land-based facilities or in closed or semi-closed facilities at sea.

Post-smolt production in inshore waters, even utilising traditional open pens, has the potential to reduce sea lice levels in local waters because of the truncated period of time that fish are at sea and the regular fallowing engendered by the short production cycles. The regular breaks in production and regular re-stocking with lice-free fish prevents lice populations building up to troublesome levels. In this report, we use a mathematical lice population model to demonstrate the implications and benefits of post-smolt production for sea lice populations in a Scottish sea loch system.

1.1 Site Details

Our study site is Loch Etive, in Argyll, Western Scotland (Figure 1). Four active sites in the loch are currently consented for fish farming: Sailean Ruafh, Aird Point, Inverawe and Port na Mine. The consented maximum biomasses at each site are listed in Table 1.

Loch Etive is one of the larger Scottish inlets, with a length of 30 km and a maximum depth of 140 m. It has six sills, the entrance sill being the shallowest with a maximum depth of 7 m. This sill, known locally as “The Falls of Lora”, has a strong choking effect on the tide, reducing the external spring tidal range from 3.6 m to 1.8 m inside the inlet. The deepest basin lies landward of the sixth sill, with the sill itself located at Bonawe. The sill depth is 13 m. Loch Etive has a large watershed of 1350 km², compared to its surface area of 29 km², with much of the

freshwater discharging via the River Awe; the water in the inlet is more brackish: deep water salinity values are typically 27 – 30 psu, with surface layer salinity values typically in the range 5 – 28 psu (Edwards and Edelsten, 1977), lower than is usual in Scottish inlets. Sea lice do not favour brackish water, which reduces their reproductive success and increases mortality.



Figure 1. Loch Etive in Argyll, western Scotland, and the locations of the four fish farms in the loch.

During the summers of 2021 and 2022, weather conditions were relatively dry. Unfortunately, flows in the River Awe, or in any other rivulet flowing into Loch Etive, are not gauged, so the extent of the dry conditions cannot be easily quantified. However, predictions of surface layer salinity in Loch Etive, taken from an operation hydrodynamic model WestCOMS (Aleynik et al., 2016), suggest that surface layer salinity in the loch was relatively high during the summers of 2021 and 2022, with values generally above 15 – 20 psu. (Figure 2). During these summers then, sea lice in Loch Etive were less likely to be affected by low salinity conditions.

Table 1. Locations and consented biomasses at the four farming sites in Loch Etive

Site	Easting	Northing	Consented Biomass (T)
Port na Mine	203310	733130	458.4
Inverawe	202510	733070	250
Aird Point	199160	733980	1545.3
Sailean Ruadh	198350	734160	1500

Until recently, the four farm sites in Loch Etive have been used to produce rainbow trout. In 2023, production is planned to switch to post-smolt Atlantic salmon. Sea lice affect both species, and the model described below has been applied equivalently to both trout and salmon.

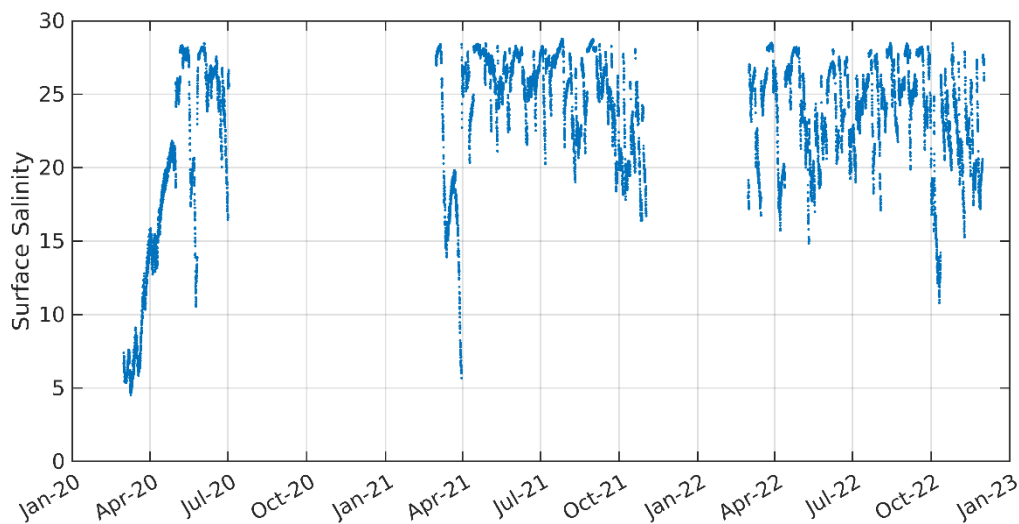


Figure 2. Predicted surface layer salinity at Sailean Ruadh, from the WestCOMS hydrodynamic model (Aleynik et al., 2016) for 2020 – 2022.

1.2 Recent History of Lice Levels, 2021 and 2022

Over the past two summers (2021 and 2022), lice levels in Loch Etive have been high (Figure 3). Dry summers have removed any salinity control on lice numbers and allowed populations to mushroom. Connectivity between sites is relatively high (see Annex B) and high numbers at one site have quickly transferred to the other sites (Figure 4).

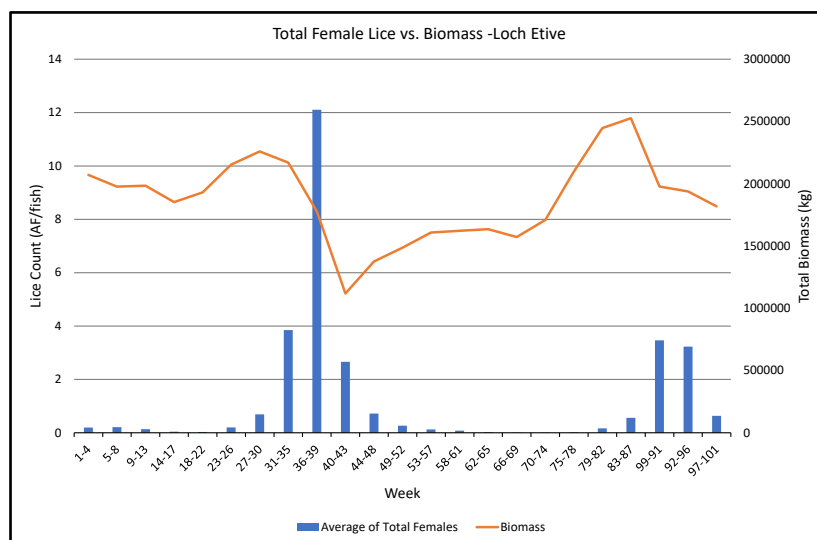


Figure 3. Total biomass (—) and average sea lice counts (■) across the four sites in Loch Etive during 2020 – 2022.

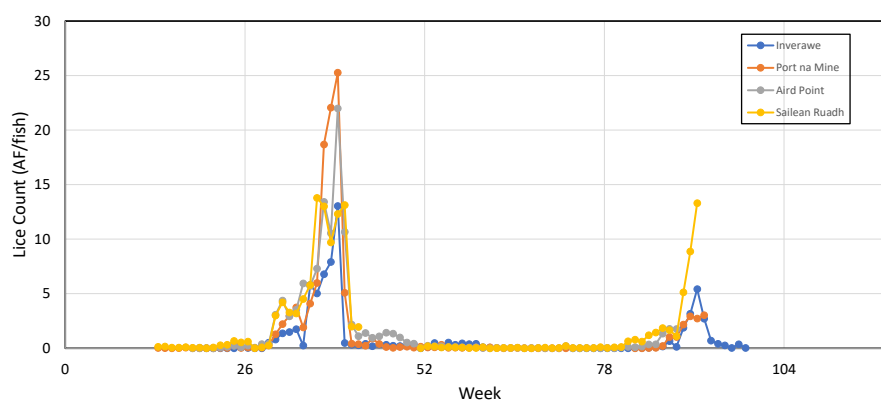


Figure 4. Adult female lice counts (AF/ fish) at each of the four Etive sites during 2021 – 2022.

The purpose of this report is not to explore the reasons for the high numbers of lice during 2021 and 2020, but to use these as a baseline, and to demonstrate that moving to post-smolt production will lead to much greater control of lice numbers with significant beneficial effects for local wild fish populations.

2. MODEL DETAILS

2.1 Sea Lice Population Model

The population model follows the method first described by Revie et al. (2005) and later developed further by Adams et al. (2015) and Kragasteen et al. (2019). The mathematical formulae are presented in Annex A, but here we give a brief description and outline the key parameters needed to drive the model.

The model predicts the evolution in numbers of four stage of attached sea lice on farmed fish: chalimus, pre-adult, adult and gravid (egg-bearing) adult female. Initial conditions for all stages can be specified. Over time, chalimus numbers on the fish at any particular site are influenced by two sources: (i) a constant background external infection pressure (perhaps arising from lice on wild fish populations or from other farms in the region); and (ii) internal infection pressure from lice arriving directly from sites within the local network, in this case the four sites in Loch Etive. The numbers of lice arriving at each site due to (ii) is dependent on the inter-farm connectivity, which is calculated using connectivity modelling (see Annex B) and includes site self-infection.

Once chalimus stages become established on a farm, individuals progress through each stage over time, until gravid female lice are present. These are then assumed to release eggs and larvae at a specified rate, which are subsequently available to infect all sites in the network according to the site connectivity.

The model is stepped forward in time, with a time step of 1 day, from a set of initial conditions for the density of each stage at each site. For the case of new smolts being put to sea, the initial density is zero, as fish are assumed to be lice-free. In that case, any subsequent infection is first driven by the external infection pressure only. As lice populations become established on individual sites, then the inter-farm connectivity adds to the infection pressure at each site.

Following at a site is simulated in the model by setting both the number of fish on the site and the densities of each lice stage to zero. The daily numbers of fish used in the simulations described here are described in §2.3.

Medicinal lice treatments, whether topical or in-feed, can be included in the model through specification of an additional mortality term. Treatments of either type are assumed to take seven days and reduce lice numbers by 95%. A treatment at a site is triggered when the adult female (AF) density exceeds a specified trigger density, for example 3 AF fish⁻¹. During treatment, the fish on site are still subject to infection pressure.

2.2 Input parameters

Two key parameter that are relatively poorly understood are the number of larval lice (per adult female louse per day) that reach chalimus stage (parameter f , Table A1) each day and the background external infection pressure. The former was estimated using data from Stien et al., (2005). Each adult female louse is assumed to release 30 eggs per day which hatch as nauplii. We are interested primarily in the late summer and autumn period, when water temperatures are highest, and conditions are most conducive to rapid lice development. With typical summer water temperatures of ~14 °C, nauplii are likely to moult to the infective copepodid stage after about 3 days (Stien et al., 2005). Given a larval mortality rate of 1% per hour (Salama et al., 2018), only 50% of nauplii survive to moult after 3 days. However, not all the resulting copepodids will find themselves immediately in the vicinity of a farmed salmon, and larval mortality will continue to reduce numbers. We assume that successful attachments

are likely to take place in the first 3 days after moulting, meaning that about 34% of released larvae may survive to attempt to attach to a host fish. Assuming an infection success rate of 50% (Adams et al., 2015; Kragestein et al., 2019), the number of released larvae that successfully attach to a host fish is estimated at 5 per adult female louse per day. The sensitivity of the model to this value of f will be tested.

Secondly, the external infection pressure is unknown, and must be specified through calibration. Background open-water concentrations of sea lice are typically of the order of 0.1 lice m^{-3} (e.g. Nelson et al., 2017), though clearly this is highly variable. Due to the brackish nature of Loch Etive, and the limited influence of external farms due to the constricted entrance, we might expect background lice levels to be lower within Loch Etive. Sea lice dispersal modelling for 2021 and 2022, incorporating all salmon farms in the Wider Loch Linnhe System, and using reported lice numbers from the farms, gave average concentrations of infective copepodids of about 0.01 – 0.04 lice m^{-3} in Loch Etive. Assuming a stocking density of farmed fish of the order 15 kg m^{-3} for traditional production methods, and assuming standard production weight of 3 kg, an estimated number of fish per cubic metre would be 5 fish m^{-3} . From the above, assuming a reduced background lice density in Loch Etive of 0.05 lice m^{-3} , the external infection pressure per fish, α , might be expected to be of the order of:

$$\alpha = \frac{0.05 \text{ lice } m^{-3}}{5 \text{ fish } m^{-3}} = 0.01 \text{ lice fish}^{-1}$$

If the background lice density was specified as 0.1 lice m^{-3} , then $\alpha = 0.02 \text{ lice fish}^{-1}$.

For post-smolt production, numbers of fish per cubic metre will be higher, since the fish are transferred from the sites at a much smaller size, perhaps 750 g. We assume therefore, that there will be **four times** the fish numbers compared to the traditional on-growing model i.e. 20 fish m^{-3} . The external infection pressure for post-smolt production, therefore, might be in the range $0.0025 < \alpha < 0.005 \text{ lice fish}^{-1}$.

Specification of the value of α is considered further in §3.1.

2.3 Numbers of Fish on Site

2.3.1 Traditional On-growing, 2021 – 2022

Exact numbers of fish on site during 2021 and 2022 are not known and consequently were estimated from the consented biomass at each site. The number of fish assumed an average fish weight of 3 kg. The number of fish at each site remained constant except during fallowing periods, when the number was set to zero. Times of fallowing were also uncertain, but were estimated from a combination of monthly reported biomass and sea lice count data. The resulting estimated time series of fish numbers during 2021 – 2022 are shown in Figure 5.

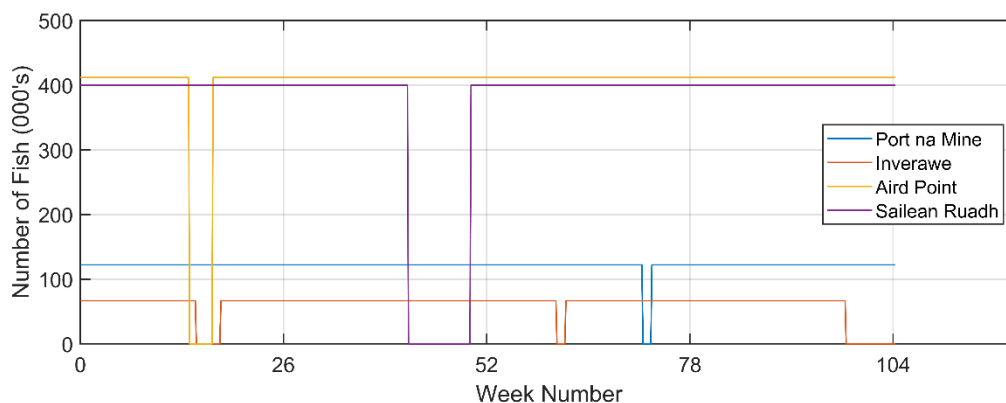


Figure 5. Estimated fish numbers at the four sites in Loch Etive for 2021 – 2022.

2.3.2 Post-smolt Production

Fish numbers for post-smolt stocking were based approximately on an average fish weight of 0.75 kg, one quarter of the size used for traditional farming. The stocking plan involved two production periods per year, lasting 24 and 22 weeks respectively, and separated by a 3-week fallow period (Figure 6). During fallowing, all four sites were emptied; however, the effects of not fallowing individual sites was explored (§2.4).

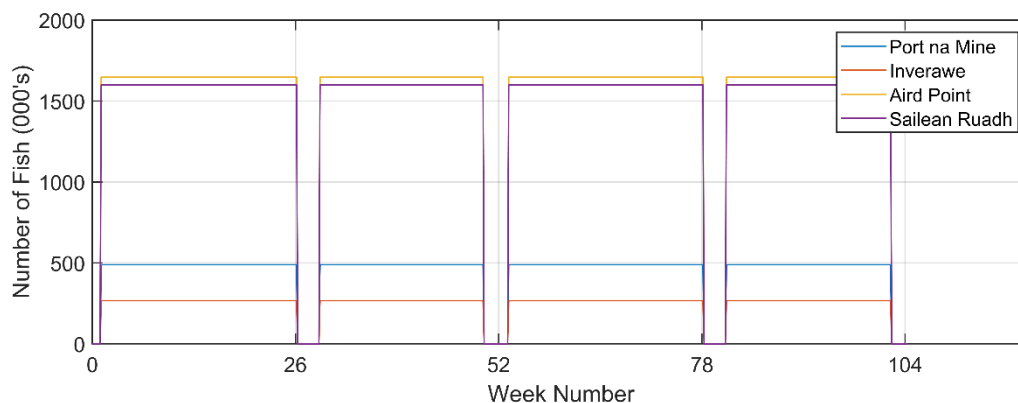


Figure 6. Post-smolt numbers at the four sites in Loch Etive used in the modelling.

2.4 Model Runs

A list of model simulations is presented in Table 2. The first set (Runs 1 – 4) tested the model against the lice data from 2021 and 2022 using the traditional on-growing farming methods. Run 1 was used to select an appropriate value of α . An exact fit between model and data was not expected, since many assumptions have been made in the modelling. However, the goal was to broadly reproduce the high lice numbers seen in summer 2021 and summer 2022 (Figure 3 and Figure 4). The simulations are performed without (Run 1) and with (Run 2)

medicinal sea lice treatments. The sensitivity of the model to the parameter, f , was be tested (Run 4).

Initial conditions for the 2021 – 2022 simulations (Runs 1 – 4) were 0.05 lice fish⁻¹ for all stages. For post-smolt runs, the initial value for all stages was zero.

For the sensitivity run 3, the value of f was varied over the range 1 – 10 (3.3% - 33.3%) in increments of 1.

The model was then run for post-smolt production, using the same model parameters, except for the background external infection pressure, α (lice fish⁻¹ d⁻¹), which was modified to account for the higher numbers of fish per cubic metre (Table 2).

The role of fallowing in the post-smolt production cycle was explored by allowing one site to contain fish all year round i.e. only three sites were fallowed. Keeping some fish within the loch system allows a population of lice to remain productive, ready to infect new fish more quickly when sites are re-stocked. Eight runs were performed, with and without treatments, with each site in turn being stocked continuously all year round (Runs 6 – 13, Table 2).

Table 2. Model runs performed. The value under Treatment Trigger indicates the density of adult female (AF) lice that triggers a treatment. Where the value is N/A, treatments are not simulated. The number of larval lice per adult female louse per day that successfully reach the chalimus stage, f , and the external infection pressure, α , are shown for each run.

Run No.	Description	Treatment Trigger (AF fish ⁻¹)	f (lice AF ⁻¹ d ⁻¹)	α (lice fish ⁻¹ d ⁻¹)
Traditional On-growing, 2021 – 2022				
1	Sensitivity/calibration	N/A	5	Variable
2	Baseline on-growing	N/A	5	0.020
3	With treatments	3	5	0.020
4	Sensitivity test	N/A	Variable	0.020
Post-smolt Production				
5	Baseline post-smolt	N/A	5	0.005
6	Sensitivity test	N/A	Variable	0.005
7	No fallowing at Port na Mine	N/A	5	0.005
8	No fallowing at Port na Mine	0.2	5	0.005
9	No fallowing at Inverawe	N/A	5	0.005
10	No fallowing at Inverawe	0.2	5	0.005
11	No fallowing at Aird Point	N/A	5	0.005
12	No fallowing at Aird Point	0.2	5	0.005
13	No fallowing at Sailean Ruadh	N/A	5	0.005
14	No fallowing at Sailean Ruadh	0.2	5	0.005

3. RESULTS

3.1 Traditional On-growing, 2021 – 2022

Results from Run 1 are shown in Figure 7. The figure shows the mean density of adult female lice across all four sites for a range of values of α , for comparison with Figure 3. Medicinal treatments were not included, and lice numbers increased to high values, particularly during the second year. In the observations, average lice counts reached about 12 AF fish⁻¹ in week 36 (Figure 3). From the model, average lice counts reached 12 AF fish⁻¹ by weeks 37 – 39 when the value of α was 0.02 lice fish⁻¹ or greater. We chose $\alpha = 0.02$ lice fish⁻¹ for subsequent model runs (e.g. Run 2, Figure 8). Whereas in the observations, treatments after Week 39 were successful in bring lice numbers down, the absence of treatments in this model run means that lice numbers were only reduced by fallowing, and rapidly increased when sites were re-stocked, exceeding 100 AF fish⁻¹ during the second year of production. The effect of medicinal treatments in constraining these high modelled values is explored in Run 3.

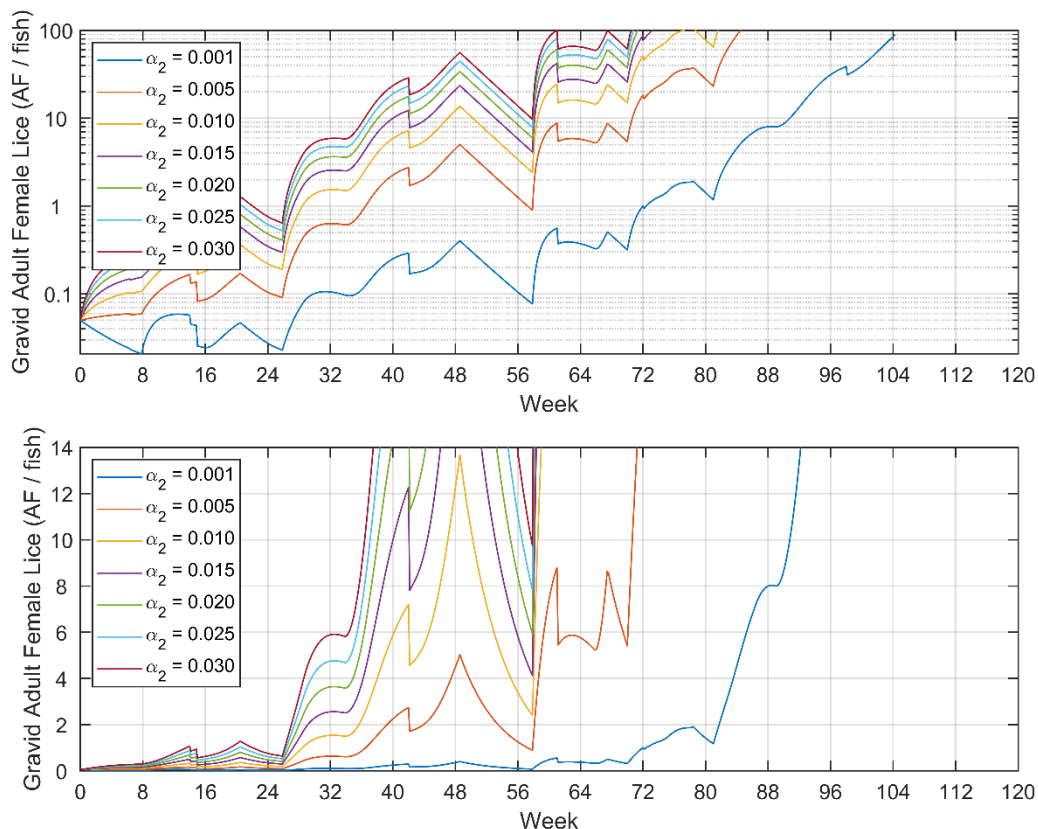


Figure 7. Predicted mean densities of gravid adult female lice across all four sites for a range of values of α (Run 1) for traditional on-growing farming. No treatments were simulated. The results are shown using a log scale on the y-axis (top) and also with a truncated linear scale (bottom) to highlight the lower numbers earlier in the cycle.

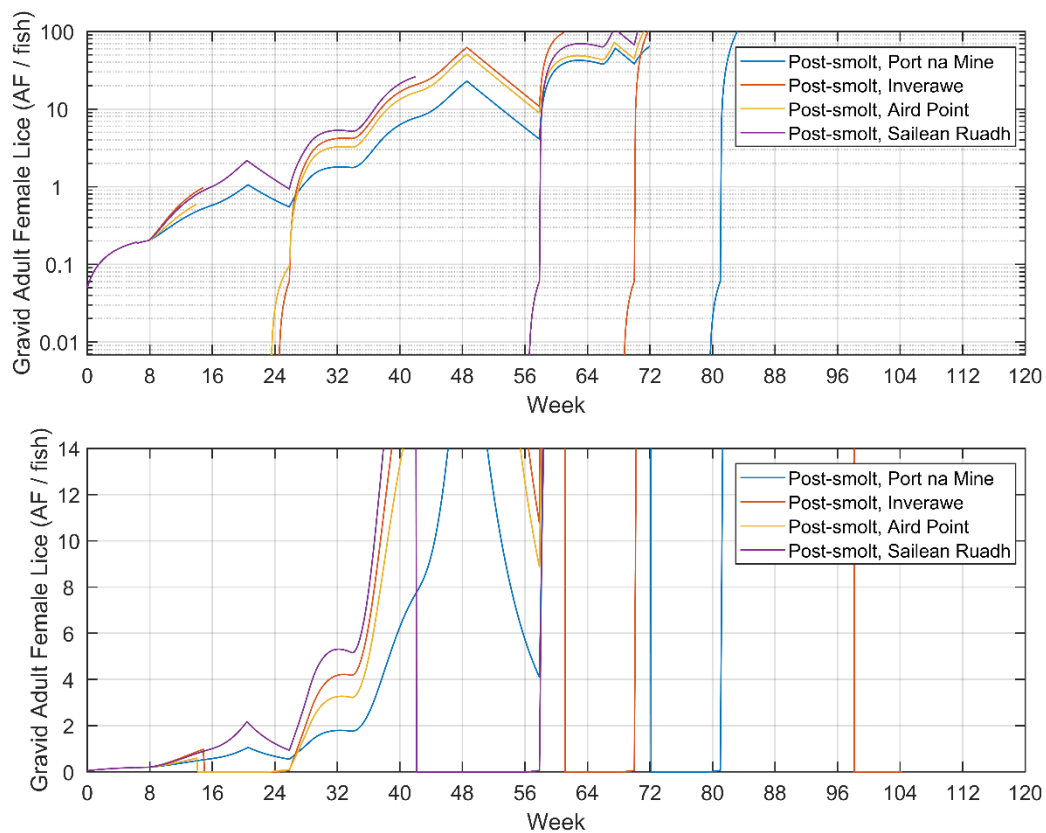


Figure 8. Predicted densities of gravid adult female lice at each site from Run 2 for traditional ongrowing farming with $\alpha = 0.02$ lice fish⁻¹. No treatments were simulated. The results are shown using a log scale on the y-axis (top) and also with a truncated linear scale (bottom) to highlight the lower numbers earlier in the cycle.

The model run with medicinal treatments (Run 3, Figure 9) reduced the lice numbers in the latter part of the cycle relative to Run 2, but the model results did not compare well with the observation. A high treatment threshold (20 AF fish⁻¹) was used to recognise the difficulties in controlling lice numbers experienced in 2021 and 2022. Actual treatments in 2021 and 2022 consisted of a mix of mechanical and topical medicinal treatments; the varying effectiveness of individual treatments within this ongoing treatment schedule was difficult to simulate. Further work on the model is required to more accurately reproduce the efficacy of treatments. However, the model does demonstrate that once control of lice numbers is lost, that control is difficult to regain without following.

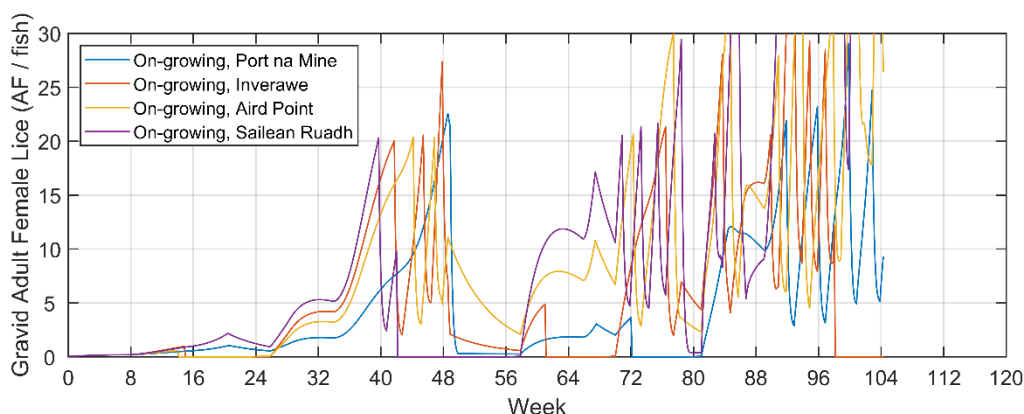


Figure 9. Predicted densities of gravid adult female lice at each site from the Run 3 for traditional on-growing farming. Treatments are simulated with a trigger density of 20 AF fish⁻¹. Only one site was permitted to be under treatment at any time.

The sensitivity to the parameter f (the number of eggs released per day per gravid female that reach the chalimus stage) increases as populations develop (Figure 10). Sensitivity was not high for the first 26 weeks or so, but as lice numbers increased rapidly thereafter, the rate of increase was strongly influenced by the value of f . The value of $f = 5$ derived from egg release and mortality rates (§2.2) lies in the middle of this range and seems a reasonable value to use for the present purposes, but the sensitivity of the model to the parameter, particularly during longer runs, should be noted.

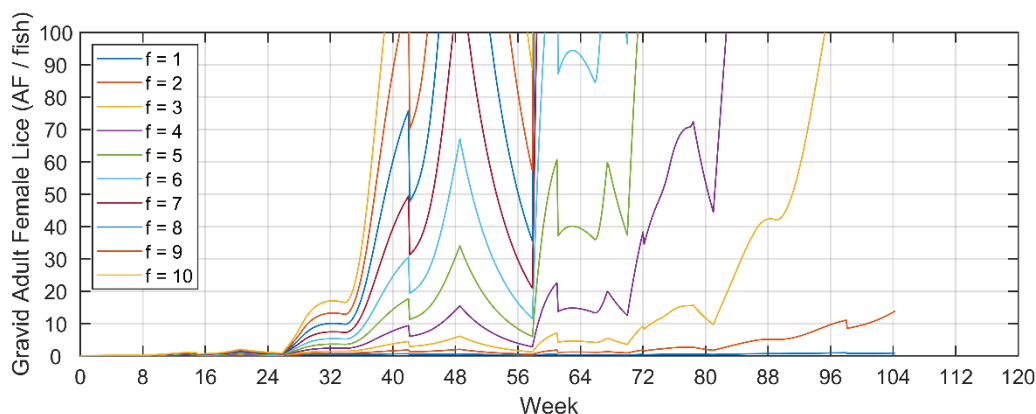


Figure 10. Predicted mean densities of gravid adult female lice across all four sites for a range of values of f (Run 4) for traditional on-growing farming. No treatments were simulated.

3.2 Post-smolt Production

For the post-smolt simulations, the value of α was set to $\alpha = 0.005$ lice fish⁻¹ to reflect the fourfold increase in numbers of (smaller) fish.

Results from Run 5 are shown in Figure 11. Lice levels build more slowly than the traditional on-growing, due to the reduced external infection pressure per fish. Critically, lice levels only reached 0.1 – 0.2 AF fish⁻¹ after 26 weeks, when all the fish were transferred out and all the sites followed. Medicinal treatments were not therefore required (we assume a treatment threshold greater than 0.2 AF fish⁻¹). The pattern of slowly increasing lice numbers dropping to zero on following was repeated, with the regular following cycle repeatedly breaking the build-up of lice population numbers.

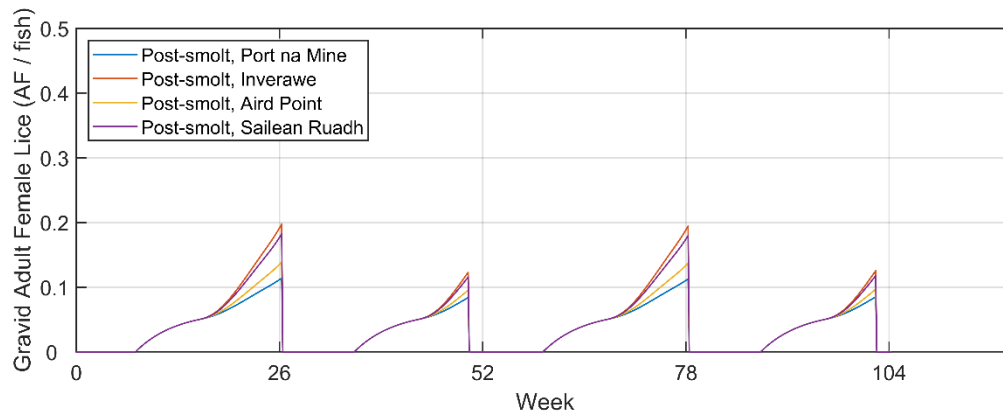


Figure 11. Predicted densities of gravid adult female lice at each site from the baseline run (Run 5) for post-smolt production. No treatments were simulated.

Comparison with the on-growing simulation (Figure 12) demonstrates the benefit of post-smolt production compared to traditional on-growing for controlling lice numbers. While the second year of production leads to high lice numbers (or high levels of treatment) for traditional farming, the repeated following of the loch system for post-smolt production keeps lice numbers low all year round.

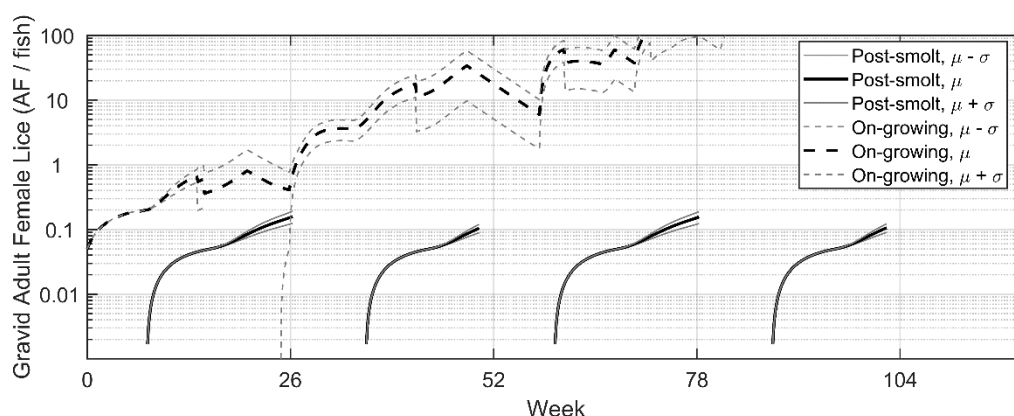


Figure 12. Predicted mean (μ) and standard deviation (σ) of gravid lice densities across all four sites for both the post-smolt and on-growing simulations (Runs 2 and 5). No treatments were simulated. The results are plotted on a log scale.

Sensitivity to the parameter f , the number of larvae released per adult female per day that successfully reach the chalimus stage, was tested for post-smolt production. Even with the highest value of $f = 10$, predicted gravid lice densities only reached ~ 0.26 AF fish⁻¹ (Figure 13). These results seem to confirm that post-smolt production with six-monthly fallowing should keep lice numbers well within the industry code of good practice level (0.5 AF fish⁻¹) at all times, and obviate the need for medicinal lice treatments.

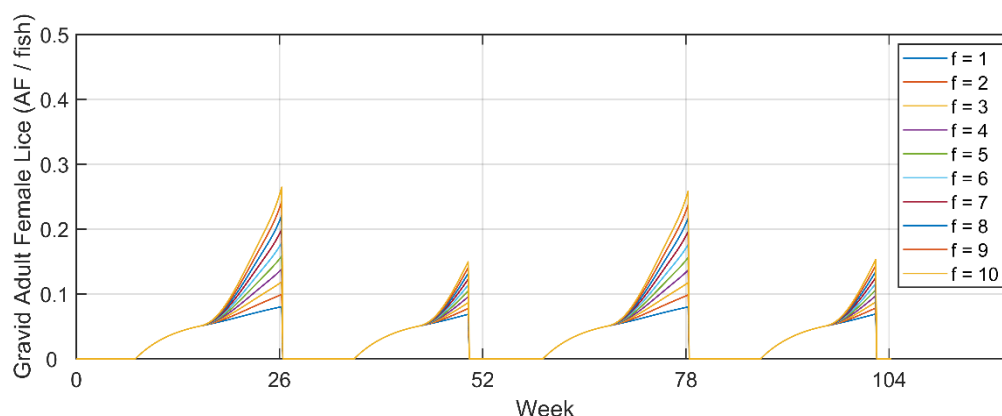


Figure 13. Predicted mean densities of gravid adult female lice across all four sites for a range of values of f (Run 6) for post-smolt production. No treatments were simulated.

3.3 The Role of Fallowing

The role of fallowing in controlling sea lice numbers has long been understood, and forms the basis for industry farm management areas (Salmon Scotland, 2015). The importance of complete fallowing during post-smolt production was explored by keeping each site in turn fully stocked with fish throughout the year. The other three sites were fallowed every six months as usual (Figure 6). The runs were performed with and without medicinal treatments; where treatments were included, the trigger for treatment was 0.2 AF fish⁻¹. Apart from the continuous stocking at individual sites, the parameter values were identical to Run 5 (§3.2).

The results for maintaining stocking at all four sites individually all showed similar features (Figure 14 – Figure 17). Without treatment, lice numbers at the continuously stocked site increased steadily throughout the simulation, with only small decreases in numbers when the other sites were fallowed. At the other sites, lice numbers after successive re-stocking events recovered more quickly each time and ultimately reached higher numbers each cycle.

The rate of increase varied, depending on which site was not fallowed, with fastest increases occurring when stocking was maintained at Port na Mine (Figure 14) and Sailean Ruadh (Figure 17). Conversely, lice numbers increased most slowly when Aird Point remained stocked (Figure 16).

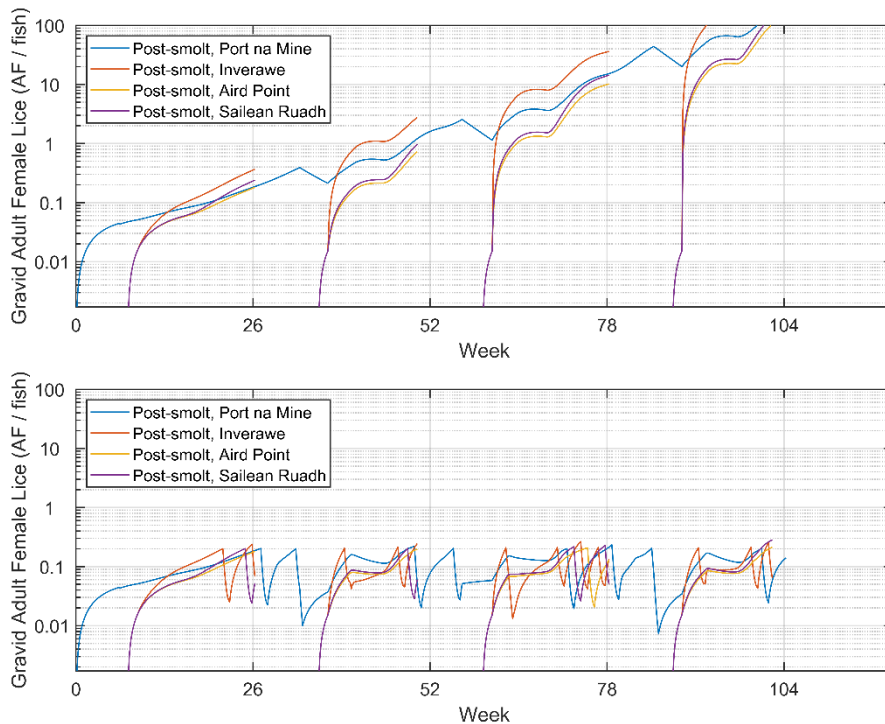


Figure 14. Predicted densities of gravid female lice at each site for post-smolt production from the run with no following at Port na Mine (Runs 7 and 8). The runs were performed without (top) and with (bottom) medicinal treatments. Where treatment was included, the trigger density was 0.2 AF fish^{-1} .

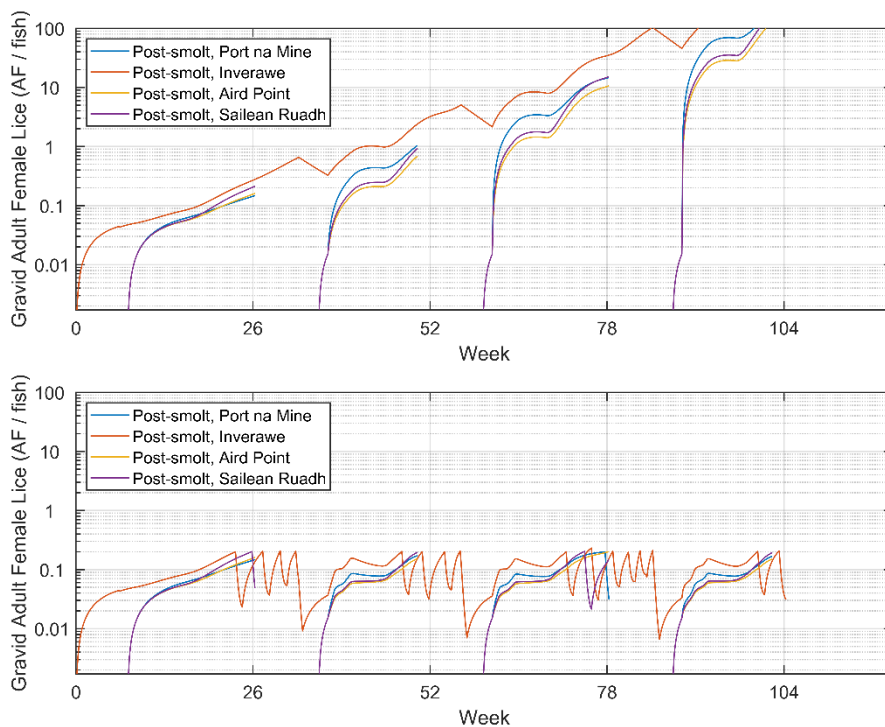


Figure 15. Predicted densities of gravid female lice at each site for post-smolt production from the run with no following at Inverawe (Runs 9 and 10). The runs were performed without (top) and with (bottom) medicinal treatments. Where treatment was included, the trigger density was 0.2 AF fish^{-1} .

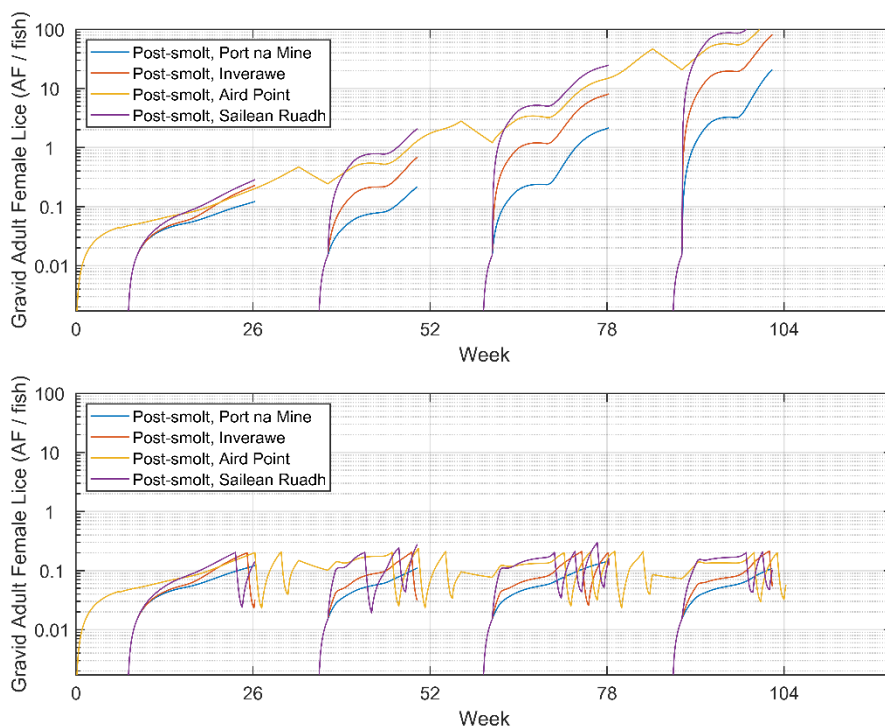


Figure 16. Predicted densities of gravid female lice at each site for post-smolt production from the run with no following at Aird Point (Runs 11 and 12). The runs were performed without (top) and with (bottom) medicinal treatments. Where treatment was included, the trigger density was 0.2 AF fish^{-1} .

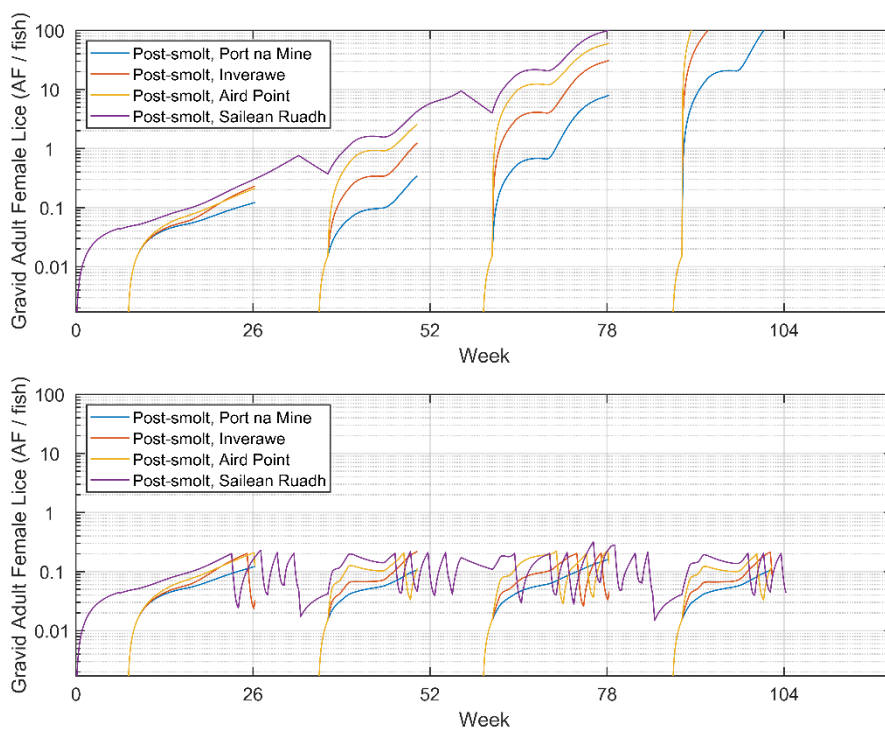


Figure 17. Predicted densities of gravid female lice at each site for post-smolt production from the run with no following at Sailean Ruadh (Runs 13 and 14). The runs were performed without (top) and with (bottom) medicinal treatments. Where treatment was included, the trigger density was 0.2 AF fish^{-1} .

When medicinal treatments were included in the simulations, lice numbers were kept below 0.2 AF fish^{-1} , but regular treatments were required to do so. The difference between these simulations and the baseline run where all sites were fallowed simultaneously is evident: simultaneous fallowing obviates the need for medicinal treatments entirely (with these model parameter values), where retaining fish on just a single site may lead to multiple treatments being necessary to keep lice numbers low.

4. DISCUSSION

Sea lice population models have become an established tool in understanding the dynamics of lice populations of finfish farms. The model first proposed by Revie et al. (2005), and modified by Adams et al. (2015) and Kragestein et al. (2019), was applied here to explore the implications for lice population numbers in a small network of four farms in Loch Etive, a Scottish sea loch, of moving from a traditional two-year on-growing production cycle to the production of post-smolts for subsequent transfer to open water sites.

A simple calibration process was used to fit the key external infection pressure parameter, α , using data from 2021 and 2022. Given incomplete knowledge of the numbers of stocked fish and the densities of the various attached lice stages, a more sophisticated fitting procedure for the external infection pressure (Kragestein et al., 2021) was not possible. Nevertheless, a value of $\alpha = 0.02 \text{ lice fish}^{-1} \text{ d}^{-1}$ for the traditional on-growing production fits well within the range of values used by other authors (Adams et al., 2015; Kragestein et al., 2019, 2021), and also corresponded well with an estimated value based on background infective lice densities and fish stocking density. With a fourfold increase in fish numbers estimated for post-smolt production, the external infection pressure value was reduced fourfold to an equivalent rate ($\alpha = 0.005 \text{ lice fish}^{-1} \text{ d}^{-1}$).

Results demonstrated that switching from a traditional on-growing form of finfish farming in Loch Etive to production of post-smolts with a truncated growing cycle would significantly reduce the potential lice burden on the farmed fish. Fallowing breaks the growth cycle of lice numbers, and re-stocking with lice-free smolts means that lice production has to start again. As a result of significantly fewer adult female lice, the consequent lice infection risk to wild salmonids should also be significantly reduced.

It is also evident that all sites within the local network, in this case the four sites in Loch Etive, must be fallowed simultaneously to obtain the maximum benefit. Leaving just a single site stocked allows lice populations to recover much quicker when the other sites are re-stocked.

Medicinal treatments not well simulated for 2021 and 2022, when a mix of mechanical and medicinal methods were used with varying success. But the model demonstrates that, with traditional production, keeping lice numbers down requires multiple treatments at all sites, and with post-smolt production, treatments may be necessary if not all sites are fallowed together.

The model could be further improved by accounting for the impacts of low salinity water and seasonal temperatures on sea lice reproduction and mortality. Neither of those effects have been included in the results presented here, and both are likely to inhibit lice reproduction and constrain population numbers below those shown here.

5. CONCLUSIONS

The modelling presented here suggests that switching from a traditional on-growing form of finfish farming in Loch Etive to production of post-smolts with a truncated growing cycle should significantly reduce the potential lice burden on the farmed fish (Figure 12) and consequently significantly reduce the potential lice infection risk to wild salmonids. Further, with simultaneous fallowing across all sites, the need for medicinal treatments may also be obviated, or at least substantially reduced.

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ANNEX A. MATHEMATICAL MODEL DESCRIPTION

The mathematical model largely follows Revie et al. (2005), but includes some of the modifications proposed by Adams et al. (2015) and Kragestein et al. (2019). A list of model parameters is given in Table A1.

Table A1. List of model parameters, default values, units and sources.

Param	Description	Value	Unit	Source
t_1	Chalimus stage duration	15	d	Revie et al. (2005)
t_2	Pre-adult stage duration	10	d	Revie et al. (2005)
t_3	Adult stage duration	20	d	Revie et al. (2005)
t_4	Gravid female stage duration	37	d	Adams et al. (2015)
τ_{ji}	Larval duration	10	d	Kragestein et al. (2005)
μ_1	Chalimus mortality rate	0.0255	d^{-1}	Revie et al. (2005)
μ_2	Pre-adult mortality rate	0	d^{-1}	Revie et al. (2005)
μ_3	Adult mortality rate	0	d^{-1}	Revie et al. (2005)
μ_4	Gravid female mortality rate	0.0269	d^{-1}	Adams et al. (2015)
η	Proportion of larvae that develop into females	0.5	-	Adams et al. (2015)
f	No. eggs per day per gravid female that reach chalimus stage	5	lice d^{-1}	Adams et al. (2015)
N_j	Number of fish each day on farm j	variable	fish	
n	Number of farms in local network	4	-	
C_{ij}	Connectivity from farm i to farm j	variable	-	
F_i	No. larvae released by site i	variable	lice d^{-1}	
t_{EXT}	Start of external infection pressure	0	d	
s	Fertilization parameter	variable	-	Kragestein et al. (2019)
α_f	Fertilization constant	10	-	Kragestein et al. (2019)
β_f	Fertilization constant	10	-	Kragestein et al. (2019)
β	Time-varying infection pressure	variable	lice fish $^{-1}$ d^{-1}	
α	External infection pressure	0.005*, 0.02#	lice fish $^{-1}$ d^{-1}	Adams et al. (2015) Kragestein et al. (2019)
H	Heaviside step function	0, 1	-	
λ_0	Treatment efficiency	0.43	d^{-1}	

* post-smolt production

traditional ongrowing

The model consists of a set of coupled delayed differential equations to describe to the evolution of density, p_j , of attached sea lice stages j , where $j = 1$ (chalimus), 2 (pre-adult), 3 (adult) or 4 (gravid female):

$$\frac{d\rho_1(t)}{dt} = \beta(t) - \beta(t - t_1)e^{-\mu_1 t_1} - (\mu_1 + \lambda)\rho_1(t) \quad (1)$$

$$\frac{d\rho_2(t)}{dt} = \eta\beta(t - t_1)e^{-\mu_1 t_1} - \eta\beta(t - t_1 - t_2)e^{-\mu_1 t_1 - \mu_2 t_2} - (\mu_2 + \lambda)\rho_2(t) \quad (2)$$

$$\frac{d\rho_3(t)}{dt} = \eta\beta(t - t_1 - t_2)e^{-\mu_1 t_1 - \mu_2 t_2} - \eta\beta(t - t_1 - t_2 - t_3)e^{-\mu_1 t_1 - \mu_2 t_2 - \mu_3 t_3} - (\mu_3 + \lambda)\rho_3(t) \quad (3)$$

$$\frac{d\rho_4(t)}{dt} = \eta\beta(t - t_1 - t_2 - t_3)e^{-\mu_1 t_1 - \mu_2 t_2 - \mu_3 t_3} - (\mu_4 + \lambda)\rho_4(t) \quad (4)$$

where ρ_j is the sea lice density per fish (lice fish⁻¹) for stage j , and t is time (days).

The external infection pressure, $\beta(t)$, was calculated daily (following Kragesteen et al., 2019):

$$\beta(t) = \alpha H(t - t_{EXT}) + \frac{1}{N_j(t)} \sum_{i=1}^n C_{ij} F_i(t - \tau_{ji}) \quad (5)$$

where $H(t - t_{EXT})$ is the Heaviside step function with $H = 0$ when $t < t_{EXT}$ and $H = 1$ when $t \geq t_{EXT}$. In the simulations described in this report, a constant infection pressure was applied, with $t_{EXT} = 0$.

The connectivity, C_{ij} , between sites in the Loch Eive network was established through sea lice connectivity modelling, described in Annex B. The connectivity matrix between sites in the local network describes the proportion of lice larvae released by site i (source) that reach site j (destination). The daily release of larvae from site i , F_i , multiplied by the connectivity between site i and j , C_{ij} , provides an estimate of the daily number of lice arriving at site j from site i . By summing over all the neighbouring sites, the total source of lice at site j from the local network was estimated.

The daily release of lice from site i , F_i , is given by:

$$F_i(t) = \rho_{4,i}(t)N(t)fs(t) \quad (6)$$

Here, $s(t)$ is a fertilization parameter, the proportion of females fertilized as a function of the number of gravid lice per salmon at time t (Kragesteen et al., 2019). Essentially, if numbers of lice are too low, females (or males) cannot find a mate and are unable to breed. As numbers increase, successful mating becomes more likely, becoming close to 100% likely at around 2 gravid lice per salmon. The fertilization parameter is calculated by:

$$s_i(t) = \frac{\alpha_f \rho_{4,i}(t)}{1 + \beta_f \rho_{4,i}(t)} \quad (7)$$

The model is stepped forward in time, with a time step of 1 day, from a set of initial conditions for ρ_j . If $\rho_j(0) = 0 \forall j$, as in the case of new smolts being put to sea, then any subsequent

infection is first driven by the external infection pressure α . As lice populations become established on individual sites, then the inter-farm connectivity adds to the infection pressure at each site.

When sites are fallowed, the number of fish on the site is set to zero, $N_j(t) = 0$, and the densities of each lice stage are also set to zero ($\rho_j(t) = 0 \forall j$).

Medicinal lice treatments, whether topical or in-feed, are effected by an additional mortality term, $\lambda = 0.43$, which reduces the lice population numbers by 95% over seven days of treatment. A treatment at a site is triggered when the adult female (AF) density, $\rho_{4,j}$, exceeds a specified trigger density, for example $\rho_{tr} = 3$ AF lice fish⁻¹; otherwise $\lambda = 0$ i.e.

$$\lambda(t) = \lambda_0 H(t = [t_0, t_7]) \quad (8)$$

where the Heaviside step function $H(t = [t_0, t_7])$ is 1 for $t_0 \leq t \leq t_0+7$, and is zero otherwise. When the trigger density is first exceeded, at time $t = t_0$, the value of λ is set to λ_0 for the next seven days. This is an approximate representation of a bath treatment procedure or an application of in-feed medicine, both of which take several days. In the absence of other influences, the value $\lambda = 0.43$ would reduce lice numbers by 95% over the seven days of treatment; in reality, fish are still affected by external infection pressures, particularly for bath treatment procedures which provide no lasting protection following treatment. The continuing external infection pressure is included in the model.

The number of larval lice (per adult female louse per day) that reach chalimus stage (parameter f , Table A1) was estimated using data from Stien et al., (2005). Each adult female louse is assumed to release 30 eggs per day which hatch as nauplii. We are interested primarily in late summer and autumn, when water temperatures are highest, and conditions are most conducive to rapid lice development. With typical summer water temperatures of 14 °C, nauplii are likely to moult to the infective copepodid stage after about 3 days (Stien et al., 2005). However, not all copepodids may immediately be in the vicinity of a farmed salmon, and larval mortality will continue to reduce numbers. We assume that successful attachments are likely to take place in the first 3 days after moulting, meaning that about 34% of released larvae may attempt attachment to a host fish. Assuming an infection success rate of 50% (Adams et al., 2015; Kragesteen et al., 2019), the number of release larvae that successfully attach to a host fish is estimated at 5 per adult female louse per day. The sensitivity of the model to this value of f was tested.

Finally, the external infection pressure, α , is unknown, and can be estimated only through calibration. Background open-water concentrations of sea lice are typically of the order of 0.1 lice m⁻³ (e.g. Nelson et al., 2017), though clearly this is highly variable. Due to the brackish nature of Loch Etive, and the limited influence of neighbouring farms due to the constricted entrance, we might expect background lice levels to be lower within Loch Etive. Sea lice dispersal modelling for 2021 and 2022, incorporating all salmon farms in the Wider Loch Linnhe System, and using reported lice numbers from the farms, gave average concentrations of infective copepodids of about 0.01 – 0.04 lice m⁻³ in Loch Etive. Assuming a stocking density of farmed fish of the order 15 kg m⁻³ for traditional production methods, and assuming standard production weight of 3 kg, an estimated number of fish per cubic metre would be 5 fish m⁻³. From the above, assuming a reduced background lice density in Loch Etive of 0.05 lice m⁻³, the external infection pressure per fish could be estimated as

$$\alpha = \frac{0.05 \text{ lice } m^{-3}}{5 \text{ fish } m^{-3}} = 0.01 \text{ lice fish}^{-1} \quad (9)$$

If the background lice density was specified as 0.1 lice m⁻³, then $\alpha = 0.02$ lice fish⁻¹.

For post-smolt production, numbers of fish per cubic metre may be higher, since the fish are transferred from the sites at a much smaller size. We assume a fourfold increase in fish numbers compared to the traditional ongrowing model, with the external infection pressure therefore 25% of the value selected during the calibration process.

The sensitivity of the results to both values of α will be tested.

ANNEX B. SEA LICE CONNECTIVITY MODELLING

Sea lice connectivity modelling is a well-established technique for understanding the potential transfer of these parasites between finfish farm sites (e.g. Adams et al., 2012; Rabe et al., 2020). The usual approach is to couple a particle tracking model, where the numerical particles represent clusters of sea lice larvae, to a three-dimensional hydrodynamic model. The hydrodynamic model typically provides hourly three-dimensional fields of current speed and direction, and water temperature and salinity. The particle tracking model uses the modelled temperature and salinity to inform the biological development and behaviour of the particles representing sea lice larvae. The water currents are used to advect the particle around the model domain. In this way, particles released as nauplii from fish farm sites evolve over time into infectious copepodids. The number of lice each particle represents reduces over time through natural mortality until after about 15 – 20 days (depending on temperature), the lice represented by the particle are effectively dead.

The locations of all particles, together with the particle characteristics (e.g. number of larvae currently active per particle) are recorded at specified intervals, typically hourly. From these particle locations, the distance between the particle and fish farm sites can be calculated every hour.

We modelled the transport of sea lice larvae from the four Loch Etive farms sites in summer and autumn of 2021 and 2022 using a coupled hydrodynamic-particle tracking modelling system. The hydrodynamic model was the operational coastal ocean model WestCOMS (Aleynik et al., 2016; Davidson et al., 2022). The particle tracking model was UnPTRACK (Gillibrand et al., 2022). The biological and behavioural characteristics of sea lice larvae represented in the model included:

- temperature-dependent planktonic stage development (nauplii and copepodid stages);
- phototactic vertical swimming behaviour;
- avoidance of low salinity water (< 20 psu) by downward swimming;
- natural mortality of 1% per hour (Salama et al., 2018)

As part of the SPILLS project (Marine Scotland, 2021, <https://marine.gov.scot/information/salmon-parasite-interactions-linnhe-lorn-and-shuna-spills>), this configuration of the UnPTRACK model has been found to be capable of predicting infestation levels on salmon held in sentinel cages in Loch Linnhe.

The numbers of lice, N_i , released from each site in Loch Etive were derived from the consented biomass, M , which was converted to fish numbers by assuming an average fish weight of 3.33 kg. An average adult female lice count of 0.5 AF/fish was assumed, with each adult female louse producing 30 larval lice per day. The model was run from 1st July – 1st November for both 2021 and 2022 using the appropriate WestCOMS predicted fields.

Particles were assumed to connect with a destination site if the particle was less than 500 m from the site centre. Using this criteria, total connections were build using the number of infective copepodids represented by the particle. The final connectivity between source and destination sites is the sum of all connections for all active particles over the course of the simulation, normalised by the number of particles released by each source i.e.

$$C_{ij} = \sum_{i=1}^{N_i} \frac{e^{-0.01t_{ijn}}}{N_i} \quad (10)$$

where t_{ijn} is the time taken for the n th particle to travel from source site i to destination site j .

The inter-farm connectivities for July – October 2021 and 2022 are shown in Figure B-1 and Figure B-2 respectively. Both years show that the two inner sites at Port na Mine and Inverawe acted as a source of lice to all four sites. The outer sites at Aird Point and Sailean Ruadh were also well connected to each other. However as expected, given the strong freshwater input to the loch from the River Awe, there were much weaker connection from the outer sites to the inner sites.

The connectivity values from July – October 2021 (Figure B-1) were used in the population modelling (C_{ij}).

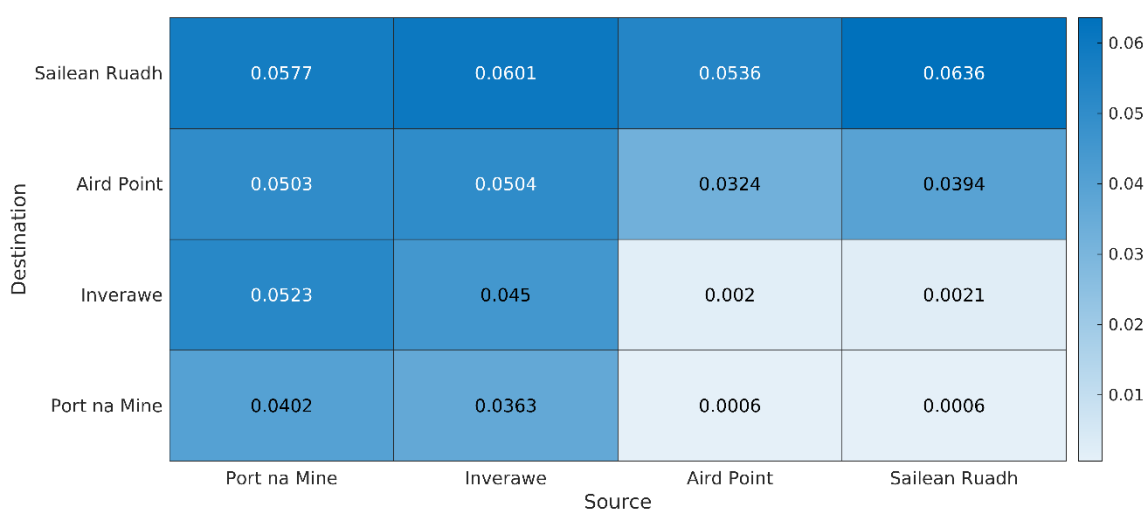


Figure B-1. Connectivity matrix for the Loch Etive sites for July – October 2021. The sites acting as sources are on the x-axis, destinations on the y-axis.

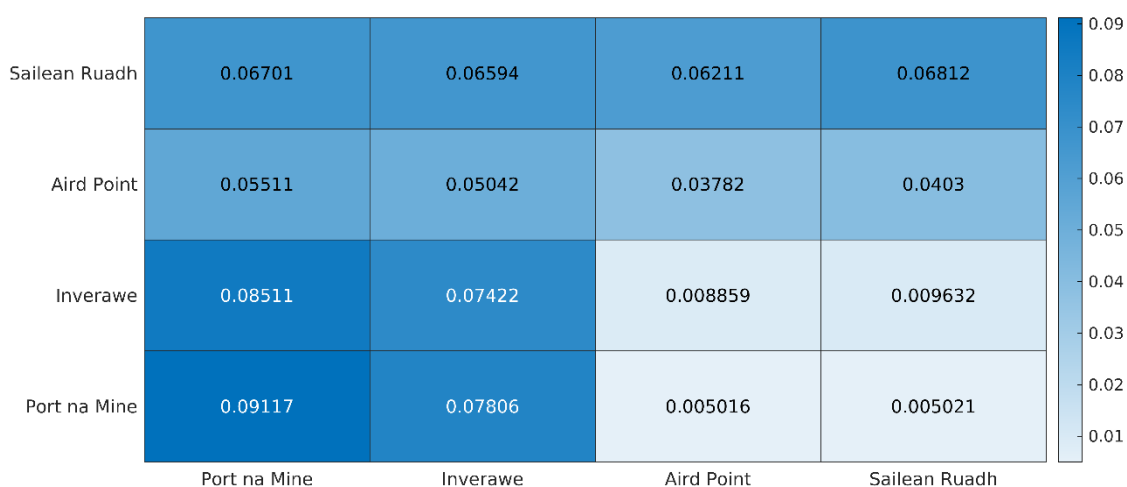


Figure B-2. Connectivity matrix for the Loch Etive sites for July – October 2022. The sites acting as sources are on the x-axis, destinations on the y-axis.