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Optimal salmon lice treatment threshold and tragedy of the commons in salmon farm networks

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ABSTRACT

The ectoparasite *Lepeophtheirus salmonis* has for decades plagued salmon aquaculture by decreasing profits and impacting wild salmon stocks. To protect migrating wild salmon stocks and avoid excessive cross-farm infections, authorities require treatments when sea lice level reach a given threshold. The treatment threshold is set to protect wild salmonid stocks but also to avoid costly lice infections on neighboring farms. Here we make a bio-economic estimation of optimal treatment thresholds. We are particularly interested in identifying conflicts between the optimal threshold of for the entire system of farms and for the individual farmer. We show that isolated individual farms can maximize profit by operating with a high threshold, while the maximum profit for an entire network of farms occurs with a threshold about 0.1 gravid female lice/salmon. These findings substantiate the Norwegian policy of lowering the lice treatment threshold below 0.5 gravid lice/salmon. The results also demonstrate that too low a treatment threshold results in high treatment rates. The difference between the optimal treatment strategy of individual farmers and that for the total system demonstrates that management of salmon lice infections operates in a tragedy-of-the-commons environment, where individual farmers may have an incentive to disregard legislation at the expense of the others in the network. This means that strong enforcement is needed to achieve optimal management of salmon lice infections.

1. Introduction

Salmon aquaculture industry has grown over the last 3 decades from an annual production of 0.23 mio metric tonnes in 1990 to 2.36 mio metric tonnes salmon in 2017 and is now a major industry with an annual production representing a value of €15 billion (FAO, 2006–2019). Salmon aquaculture has nearly always been afflicted by sea lice which currently represents the main bottleneck for further expansion of the industry. Sea lice, a common name for a range of marine ectoparasitic copepods within the Caligidae family, feed on the fish's skin and mucus (Pike and Wadsworth, 1999) with *Lepeophtheirus salmonis*, also known as salmon louse, being particularly harmful to salmonid species in the northern hemisphere.

There are three main issues with elevated levels of sea lice in salmon farms. One issue is impaired salmon growth where in the worst case, salmon can die of infection either directly or indirectly by secondary infections (Pike and Wadsworth, 1999). Another issue is the treatment itself, which is both costly and can have a negative effect on the local environment. The third and perhaps the most studied issue is the artificially increased infection pressure on wild salmonids (Krkošek et al.,

2007; Kristoffersen et al., 2018) which has been shown to pose a serious risk to wild salmonid stocks (Krkošek et al., 2013).

To protect wild stocks, and to a lesser degree avoid excessive cross-farm infections, authorities in salmon farming countries have put up legislation or guidelines stipulating the maximum number of lice per salmon in a farm before treatment has to be conducted. In Norway regulations for allowed sea lice limits were introduced relatively early and in 2009 these limits were lowered to 0.5 gravid lice salmon⁻¹ allowed for the first 8 months in a year and 1 gravid lice salmon⁻¹ for the rest of the year. In 2017 these limits were further lowered to 0.5 gravid lice salmon⁻¹ in general and to 0.2 in the migrations periods (Anon, 2012).

Recently, Norway introduced a new national operational salmon lice monitoring system which essentially estimates the infection pressure on wild salmonids (Myksvoll et al., 2018) which is used to regulate production into zones that are allowed to grow, decrease or keep current production; the so-called “traffic light system” (Vollset et al., 2017).

In Scotland the “Code of Good Practice” recommends treatments above 0.5 gravid lice salmon⁻¹ in migrations periods and otherwise 1

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Table 1
List of parameters used in the population dynamic model.

Parameters	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 femal stage duration	37	D	Johnson and Albright (1991)
τ_{ji}	Larval duration	10	D	Amundrud and Murray (2009)
μ_1	Chalimus mortality rate	0.0255	d^{-1}	Revie et al. (2005)
μ_2	Pre-adult stage mortality rate	0	d^{-1}	Revie et al. (2005)
μ_3	Adult stage mortality rate	0	d^{-1}	Revie et al. (2005)
μ_4	Gravid female mortality rate	0.0269	d^{-1}	$1/t_4$
α	Number of eggs produced per gravid female	40	eggs d^{-1}	á Norði et al. (2015)
ϵ	Proportion of copepodids successfully attached	0.25	#	Gravil (1996); Samsing et al. (2016)
f	Number of viable larvae per gravid female	10	lice d^{-1}	$\alpha\beta$
$\alpha_i l$	External infection pressure	0.001 0.1	larvae d^{-1}	Own adjustment
α_f	Variable	10	#	Own adjustment
β_f	Variable	10	#	Own adjustment

gravid lice salmon⁻¹ (Anon, 2015), while it is regulated that weekly counts exceeding an average of 3 adult female sea lice/salmon be reported to the authorities, with an intervention limit of 8 adult female sea lice/salmon (Marine Scotland, 2017).

In the Faroe Islands the story is somewhat different. Apart from a small introduced stock maintained since the 1940's in four rivers, salmon are non-native in Faroese rivers (www.laks.fo, 2018). However, in order to reduce spread of sea lice and its impact on farmed and wild salmon, a monitoring system was introduced in 2009 with a limit of 2 gravid lice salmon⁻¹, which was lowered to 1.5 gravid lice salmon⁻¹ in a revision of the regulations in 2017 (Faroese Ministry of Foreign Affairs and Trade, 2016).

So far, there has been limited research on the optimal lice treatment threshold from a farm network perspective and how well such salmon lice management strategies operate in a environment where individual farmers can benefit from circumventing legislation at the expense of the whole farm network; that is, within the context of the tragedy of the commons (Hardin, 1968). This tragedy of the commons dynamic was showed in a study based on game theory where Scottish salmon farmers within a management area or network could on an area level benefit from testing for rare high-impact diseases even though all individual farms are better of not testing (Murray, 2014). Further, Milinski et al. (2002) showed how reputation can help solve the tragedy of the commons problem.

Two early mathematical descriptions of salmon lice population dynamics were proposed by Revie et al. (2005) and Stien et al. (2005), using delayed stage structured models to simulate population growth. Later Robbins et al. (2010) and Gettinby et al. (2011) adopted the Revie et al. (2005) model implemented in the SLiDESIm computer model (Sea Lice Difference Equation Simulation) and looked at the optimal timing of treatment's and how different treatments affect the salmon population dynamics in individual farms. Robbins et al. (2010) found the SLiDESIm model to be able to give valuable insight to lice management and that a small decrease in treatment efficiency highly impacts lice control. Gettinby et al. (2011) found that a more robust understanding of the underlying biological processes is needed to better predict the lice population dynamics. Murray (2011) constructed a simpler model and looked at development of resistance and the interaction between wild and farmed salmon and found that resistance is selected most heavily under moderate levels of treatment. Groner et al. (2013) developed an agent-based model to simulate the effect of cleaner fish in farmed cages and found cleaner fish to be able to effectively control sea lice. Groner et al. (2014) used stochastic matrix population models to understand the influence of temperature on the population growth, reproduction and demography of sea lice and found control measures that target preadult and chalimus stages are most effective. Murray and Salama (2016) constructed a simple presentation of Scottish farm

networks and found coordinated management was effected with-in management areas as long as boundaries between management areas was strong which is consistent with Guarracino et al. (2018) who found that coordinated fallowing is inefficient when external infection pressure from neighboring areas is high using real lice counts from Norway. Adams et al. (2015) coupled Revie et al. (2005) population dynamics model with his connectivity matrices (Adams et al., 2012) and found that control of sites with the highest magnitude of incoming connections is most effective in terms of reducing overall lice density.

Here we aim to identify the optimal treatment threshold from a profit point of view for an isolated system (single farm) and connected farm networks. We use and expand Adams et al. (2015) version of Revie et al. (2005) model by coupling it to a bioeconomic model. The optimal treatment threshold is measured as the highest profit per time. Further, we investigate and show that tragedy of the commons may appear in sea lice management in aquaculture farm networks with overlapping production cycles.

2. Methods

To estimate the optimal treatment threshold, a conceptual bioeconomic model was constructed. The model consists of three parts: a salmon lice population dynamic model, a model of salmon growth and survival, and a bioeconomic model of salmon production and salmon lice treatments. The optimal treatment threshold is identified by the treatment threshold that yields the highest profit per time.

2.1. Salmon lice population dynamics

The salmon lice population dynamics model is based on Revie et al. (2005), which is a series of delayed stage structured differential equations describing the dynamics on a single farm:

$$\frac{d\rho_{1,i}(t)}{dt} = \beta_i(t) - \beta_i(t - t_1)e^{-\mu_1 t_1} - \mu_1(t)\rho_{1,i}(t) \tag{1}$$

$$\frac{d\rho_{2,i}(t)}{dt} = \eta\beta_i(t - t_1)e^{-\mu_1 t_1} - \beta_i(t - t_1 - t_2)e^{-\mu_1 t_1 - \mu_2 t_2} - \mu_2(t)\rho_{2,i}(t) \tag{2}$$

$$\frac{d\rho_{3,i}(t)}{dt} = \eta\beta_i(t - t_1 - t_2)e^{-\mu_1 t_1 - \mu_2 t_2} - \beta_i(t - t_1 - t_2 - t_3)e^{-\mu_1 t_1 - \mu_2 t_2 - \mu_3 t_3} - \mu_3(t)\rho_{3,i}(t) \tag{3}$$

$$\frac{d\rho_{4,i}(t)}{dt} = \eta\beta_i(t - t_1 - t_2 - t_3)e^{-\mu_1 t_1 - \mu_2 t_2 - \mu_3 t_3} - \mu_4(t)\rho_{4,i}(t). \tag{4}$$

$\rho_{1,i}$, $\rho_{2,i}$, $\rho_{3,i}$ and $\rho_{4,i}$ are the chalimus, pre-adult female, adult female and egg/larvae producing gravid female, respectively, at time t and farm number is indicated by i . μ_{1-4} are the mortality rates at the 4 stages and t_1 , t_2 and t_3 are lengths of each stage. Revie et al. (2005)

values for μ_{1-4} and t_{1-3} were adopted (Table 1). η is the proportion of lice being female. $\beta_i(t)$ is the amount of viable larvae entering a farm from 3 sources: Self-infection, from other farms in the network and from the background or external infection pressure.

Adams et al. (2015) reformulated β to account for connectivity between farms:

$$\beta_i(t) = \frac{1}{N_i(t)} \sum_{j=1}^n C_{ij} F_{ij}(t - \tau_{ij}) + \alpha_1 l(t = t_{Ext}) \quad (5)$$

where N_i is the number of fish at farm i and C_{ij} defines the connectivity between the emitting farm j and receiving farm i . $F_{ij}(t - \tau_{ij})$ is the number of viable larvae that can potentially be transmitted from farm j to farm i and $\alpha_1 l(t = t_{Ext})$ is the external infection pressure, where t_{Ext} defines when external pressure starts.

$F_{ij}(t - \tau_{ij})$ is defined as:

$$F_{ij}(t) = \rho_{4,i}(t - \tau_{ij}) N_j(t) f s(\rho_{4,j}(t)) \quad (6)$$

$\rho_{4,j}(t - \tau_{ij})$ is the amount of gravid female lice/salmon (will be referred to as just gravid lice salmon⁻¹ in the following sections) at time $t - \tau_{ij}$, which is the time it takes larvae to travel from farm j to i . f is the amount of viable larvae produced per gravid female. Here we have extended the model with a fertilization parameter $s(\rho_{4,j}(t))$, which is the proportion of females fertilized as a function of the amount of gravid lice salmon⁻¹ at time t (Stormoen et al., 2013), essentially creating an Allee effect:

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

α_f and β_f are both set to 10 salmon/(gravid lice) to sufficiently fit to the proposed fertilization curve by Stormoen et al. (2013) where fertilization success is close to zero at near zero abundances and close to 100% at around 2 gravid lice salmon⁻¹. f was also redefined here as:

$$f = \alpha \varepsilon, \quad (8)$$

where α is the number of eggs produced per day per female lice and ε is the attachment success. Number of eggs can range from 26 to 68 female⁻¹ d⁻¹ and is generally temperature dependent (Heuch et al., 2000; á Norði et al., 2016). For simplicity, here we assume a uniform temperature. Egg production was set to be constant at 40 egg female⁻¹ d⁻¹ roughly corresponding to 10 °C. The attachment success ε , is also dependent on temperature and age of infective copepodids. A study showed a 22% infection success of 1 day old copepodids and 18% for 7 day old (Gravil, 1996). Samsing et al. (2016) found infection success to be around 2, 50 and 40% with temperatures of 5, 10 and 20 °C, respectively. Attachment success was set to 25%. The f parameter was sensitivity tested and simulations were robust to change (Appendix S1: Fig. S2). Note that the aim here is not to have highly precise parameters but to estimate parameters within a realistic range.

2.1.1. Connectivity

Estimating realistic connectivity is important to get meaningful model output. Adams et al. (2012) found self-infection to be up to 1.15% and connectivity between farms to be up to 2%. Kragestein et al. (2018) found the self-infection to be up to 53%, although this represents the connection of fjords as a whole rather than individual farms, and thus can not directly be compared. Other studies on connectivity (Johnsen et al., 2016; Samsing et al., 2017; Cantrell et al., 2018) represent results as larvae transported from one farm to another divided by the total number of released larvae, making it difficult to directly included these results in this study. Here a self-infection between 0 and 10% will be explored.

A way to overcome the problem in estimating connectivity is to look at the ratio between self-infection and infection from other farms. This infection ratio has been found on average to be 0.35 in summer and 0.18 in winter (Adams et al., 2012; Samsing et al., 2017), while Johnsen

et al. (2016) found the ratio to be 0.32 on average with maximum value of 0.57, meaning there can be 2–4 times as many lice coming from other farms than lice originating from the farm itself. Here we choose to work with a 5 farm network although real farm networks may contain more farms. Therefore, we can justify setting the connectivity in a small network artificially high e.g. a 5 farm network with a self-infection of 5% can have a (equal) connectivity of 5%.

2.1.2. External infection pressure

External infection pressure, i.e. that arising from natural sources, is poorly known. Given the high ratio between farmed and wild salmonid stocks (Anon, 2018), we can generally assume external infection pressure to be low compared to the infection pressure from the farmed salmon. We use a 0.005 lice/day (1 lice for every 200 days), which is sufficient to maintain a stable population of salmon lice, but a range of external infection pressures from 0.001 to 0.1 lice/day is also explored.

2.1.3. Connectivity matrix

The aim here is to illustrate the patterns of the explored connectivity networks. The range of self infection and connectivity is stated in the connectivity section. Five different connectivity matrices (Fig. 1) were investigated to represent different geometries of farm networks: a) an isolated matrix, where there is no connection between farms, i.e. essentially is a single farm, b) a well mixed matrix where there is equal connection between all farms, c) an diffusive matrix where the connection decreases with distance between sites, d) a cyclic directional matrix representing, for instance, an island with a persistent coastal circulation, and e) a closed directional matrix such as a long fjord with a unidirectional current out of the fjord. Self infection is the same in all matrices and the sum of out and in going connections is equal in all matrices except for a) & e) where a) has no connectivity and where farm 1 in network e) emits lice to all other farms and receives no lice from other farms whereas farm 5 receives lice from all other farms and emits no lice to other farms.

2.2. Bioeconomic model

The bioeconomic model quantifies the profit of the salmon production per unit time as a function of the treatment threshold. The profit, Π , is the difference between revenue from the sale of salmon and the production and treatment costs:

$$\Pi = \frac{1}{t_{tot}} \left(\sum_{j=1}^{n_H} (\pi - C) W(t_{H,j}) P(t_{H,j}) - \sum_{j=1}^{n_H} \sum_{i=1}^{n_{treat}(t_{H,j})} C_{treat} W(t_{T,i,j}) P(t_{T,i,j}) \right), \quad (9)$$

where π is price per kg salmon and C is production cost, excluding treatment costs. $(\pi - C)$ is estimated to be 3.1 €/kg salmon (Anon, 2017). n_{treat} is number of treatments and C_{treat} is the treatment cost which range from 0.05 to 0.15 €/kg treated fish depending on the treatment (Holan et al., 2017). For simplicity treatment cost was set to 0.1 €/kg salmon. W and P are the weight and survival of salmon through time and t_H and t_T represent time of harvest and time of treatment, respectively. t_{tot} is the total time from production start to last harvest.

Growth of salmon is expressed with a standard von Bertalanffy growth function (Von Bertalanffy, 1938) augmented with a reduction, k , due to salmon lice (ρ_4):

$$\frac{dW}{dt} = a_{salmon} W^{2/3} (1 - (W/w)^{1/3}) k(\rho_4(t)), \quad (10)$$

where W is weight of salmon and w is asymptotic (maximum) weight where growth stops (in our case = 6 kg). The starting weight $W(0)$ is 0.1 kg and a_{salmon} is the growth rate of salmon and set to 0.028 d⁻¹ so a production cycle with a starting weight of 0.1 kg and no lice is about 500 days.

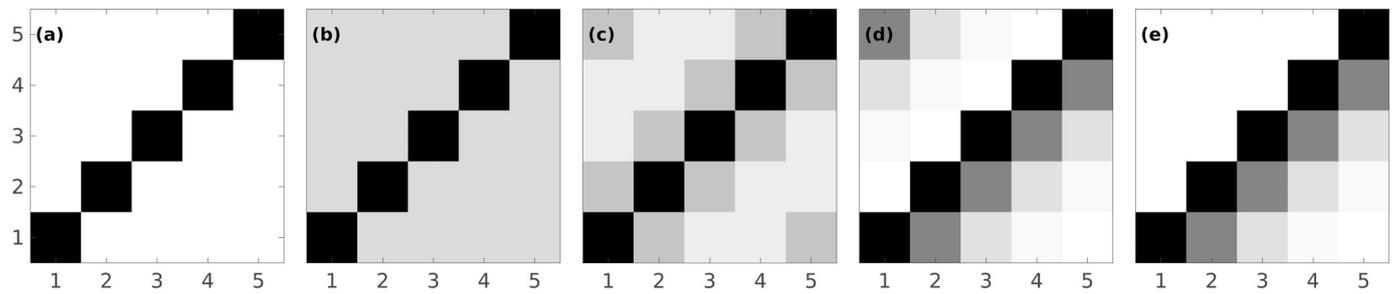


Fig. 1. The applied connectivity matrices: only self infection (a), self infection and equal connectivity between all farm sites (b), self infection and a decreasing connectivity with increasing distance in the matrix (c), self infection and a directional and cyclic connectivity (d), and self infection and directional non-cyclic connectivity (e).

The growth and survival of salmon is anticipated to decrease when they are infected by sea lice, depending largely on the lice density and size of the fish. For a 40 g smolt ≈ 30 chalimus larvae may be lethal when the lice reach the more pathogenic preadult and adult stages (Finstad et al., 2000), while in open sea large salmon seem unaffected with around 30 gravid females (Jacobsen and Gaard, 1997). Mustafa et al. (2000) investigated the levels of cortisol and glucose as indicators of stress responses due to sea lice infestation on post-smolts with infection intensities ranging from 15 to 285 lice per fish. They found that sea lice induce a stress response and immune suppression in their fish host, having greater effect during the later stages of their life cycle when they are mobile and able to cause the most damage. For smolts 37 g Wells et al. (2006) identified a consistent breakpoint of 12–13 lice fish⁻¹ across a range of physiological measures. Taranger et al. (2014) proposes that > 0.3 lice g⁻¹ salmon is lethal to < 150 g salmon and salmon larger than 150 g the lethal limit is > 0.15 lice g⁻¹ salmon.

Experience from the industry in the Faroe Islands indicates that caged salmon (> 1 kg) are virtually unaffected with 6–10 gravid lice, but with lice levels exceeding 10 gravid lice salmon⁻¹ there are visual effects with loss of appetite and/or open neck injuries (Pers. comm., Kirstin Eliassen, head of lice monitoring in Faroe Island, 2018). Here we approximate the effect of sea lice on the growth by a hyperbolic tangent function and for simplicity salmon size is excluded and only gravid lice

are considered:

$$k(p_4) = 0.5 - 0.5 \tanh\left(\frac{p_4 - 20 \text{ gravid lice salmon}^{-1}}{8 \text{ gravid lice salmon}^{-1}}\right), \quad (11)$$

which implies little affect of salmon lice until the level reaches around 10 gravid lice per fish, but hereafter the growth gradually drops and reaches 0 when the gravid lice levels reach 40 (Fig. 2). Note here that 0.1 kg salmon tolerate the same level of gravid lice as 5 kg salmon which is an oversimplification. (See fig. S7 to see how including salmon weight will effect profit as a function of treatment threshold).

Mortality tends to decline with fish size (Soares et al., 2011), but here a constant mortality μ_{salmon} of $2.5 \cdot 10^{-1} \text{ d}^{-1}$ is assumed in estimating the salmon survival probability in a farming unit:

$$\frac{dP}{dt} = -\mu_{\text{salmon}} P(t). \quad (12)$$

In summary the farm profit (Eq. 9) links salmon lice population dynamics (Eqs. (1–8)), salmon weight (Eqs. (10–11)) and survival (Eq. (12)). N_i is assumed to be equal in all farms and set to 1 to get profit per salmon.

2.2.1. Treatments

Treatments occur when lice levels reach a given threshold. There

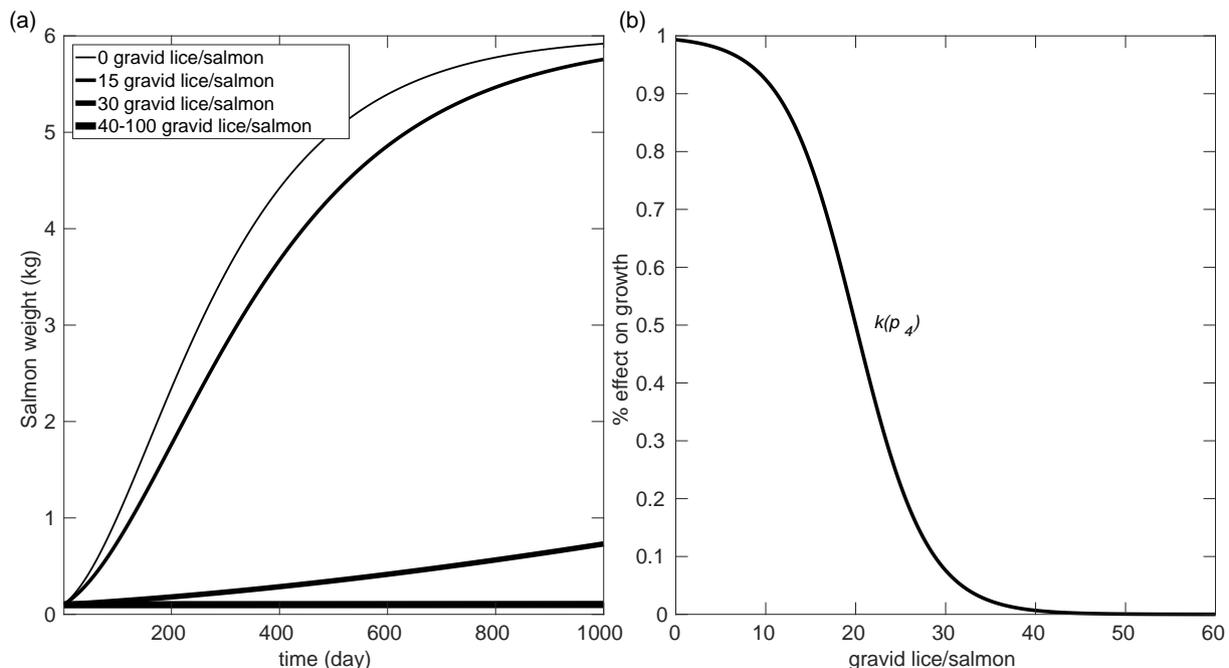


Fig. 2. (a) Salmon growth as function of time (day) with different levels of constant gravid lice/salmon based on Eq. (10). (b) Effect on salmon growth ($k(p_4)$) as a function of gravid lice/salmon based on Eq. (11).

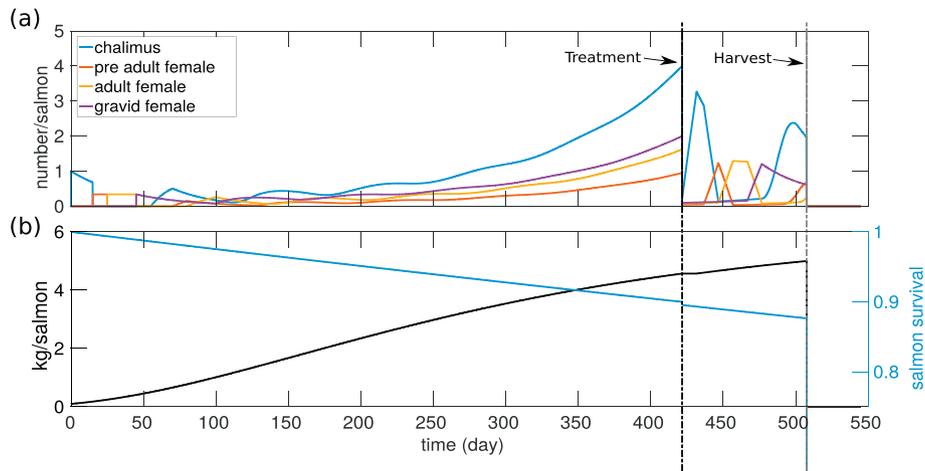


Fig. 3. Lice population growth (a) and salmon production and survival (b) as functions of time. Self-infection is 2%. Treatment when gravid lice salmon⁻¹ is > 2. Treatment efficiency is 95% reduction of all on fish lice stages. No constant external infection, however simulation starts with 1 chalmus.

are 3 costs associated with a treatment. First is the cost of the treatment, second there is an instant 0.5% fish mortality (Holan et al., 2017) and third a 10 days pause in fish growth due to fasting of fish before a treatment and/or general stress of handling the salmon associated with a treatment (Holan et al., 2017). The reduction of sea lice after a treatment is described by the treatment efficiency. For chemical treatments the efficiency has been shown to decrease over time as lice develop resistance (Aaen et al., 2015). Several studies use a 95% efficiency (Gettinby et al., 2011; Adams et al., 2015) while Gislason (2017) argued that treatments efficiency can be as low as 30–40%. Here a 95% treatment efficiency is adopted which must be considered a best case scenario, however other values are explored. The development of resistance is not taken into account.

2.2.2. Harvest

We assume that salmon are harvested at 5 kg (Anon, 2017). A lice-free production cycle with a starting weight of 0.1 kg takes about 500 days. However, high lice levels and treatments will increase the time salmon spend in growing to 5 kg. We impose harvest to occur at 5 kg or 1000 day, whichever ever comes first. The following period between harvest cycles is set to 60 days, which is the minimum allowed under Faroese legislation, however the following period differs between salmon farming countries.

2.2.3. Identifying optimal treatment threshold

The optimal treatment threshold is identified from a simulation with

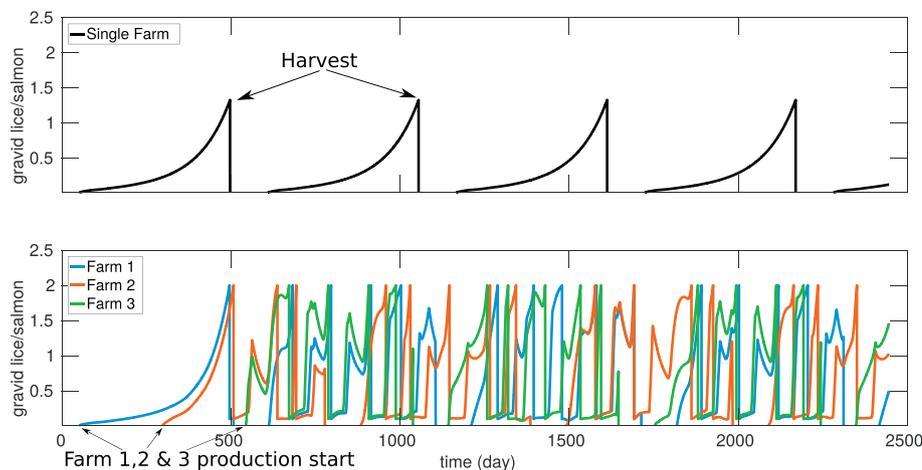


Fig. 4. Population growth for gravid lice for single farm system (a) and a 3 farm network with equal connectivity (b). Self infection is 2%, connectivity is 1% and with a 0.005 lice/day constant external infection pressure. When lines are not visible indicate following periods. Treatment occurs when gravid lice reach 2 gravid lice/salmon.

Table 2

List of parameters used in the bio-economic model.

Parameters	Description	Value	Unit	Source
w	Salmon max size	6	kg	
W_0	stocking size	0.1	kg	
α_{salmon}	Salmon growth rate	0.028	d ⁻¹	Own adjustment
μ_{salmon}	Salmon mortality	0.25×10^{-3}	d ⁻¹	Own adjustment

10 production cycles ranging between 497 and 1000 days. A 5 farm network was investigated as this included enough farms to resolve the desired dynamics. Production was set to overlap as synchronized production essentially behaves the same way as isolated farms. Production cycles are initiated with a 125 days interval, roughly evenly spread inside the 500 day production cycle.

2.2.4. Tragedy of the commons

Tragedy of the commons in aquaculture farm network lice management is investigated by looking at a 5 farm network that was equally connected (Fig. 1) and with overlapping production. Non-cheating farms use a 0.1 gravid lice salmon⁻¹ threshold and cheating farms use a 10 gravid lice salmon⁻¹ threshold. The profit of non-cheating and cheating farms and the farm network was investigated if 1, 2, 3, 4 or 5 farmers decided to circumvent official legislation.

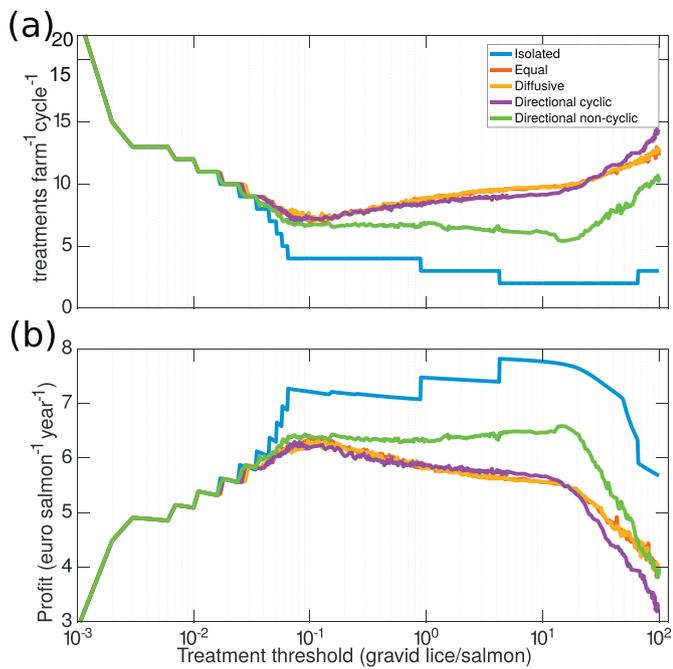


Fig. 5. Number of treatments (a) and profit (b) as function of treatment threshold of 5 different connectivity matrices. External infection is $0.005 \text{ lice d}^{-1}$ and self-infection is 5% in all simulations. Treatment efficiency is 95% for on fish lice stages. The sum of connectivity in equal, diffusive and directional cyclic matrix is the same and corresponds to 2.5% in the equal connectivity matrix. The added connectivity in the directional non-cyclic and isolated matrices is less compared to the other matrices (Fig. 1).

3. Results

3.1. Lice population dynamics

Examples to illustrate lice population dynamics are shown in Figs. 3 and 4. The first example is of a farm with no connection to other farms and a single production cycle (Fig. 3). To illustrate more clearly the population dynamics at the different stages this simulation has no external infection pressure but production starts with 1 chalmus. The initial 1 chalmus moults to a pre-adult female and later to a adult female and finally to a gravid female. With current model settings (Tables 1 and 2), a lice larvae spends 45 days from initial attachment until it starts producing eggs and a further 10 days until larvae start re-attaching to their host. After around 425 days, the infection load reaches the treatment threshold of 2 gravid lice salmon⁻¹, and a treatment was preformed. The treatment kills off 95% on all stages. Note the 10 days pause in salmon growth and the 0.5% decrease in salmon survival when a treatment is performed (Fig. 3). The treatment does not kill planktonic larvae and therefore the number of attached chalmus larvae increases directly after treatment. This results in a rapid increase in gravid lice around 55 days after treatment. When salmon reach a weight of 5 kg the fish are harvested and the production cycle is completed.

Fig. 4 shows a simulation of a single farm and 3 connected farms with overlapping production. Only the number of gravid lice salmon⁻¹ is shown. In the 3 farm network the number of treatments increase the first 2–3 cycles after which they stabilize at 3–4 treatments per cycle. The isolated farm has symmetric cycles and never reaches the 2 gravid lice salmon⁻¹ threshold with the applied settings.

3.2. Optimal treatment threshold

Fig. 5 shows the number of treatments and the profit as a function of the treatment threshold for different types of farm networks. Treatment rates are high for both really low or high thresholds. For low threshold,

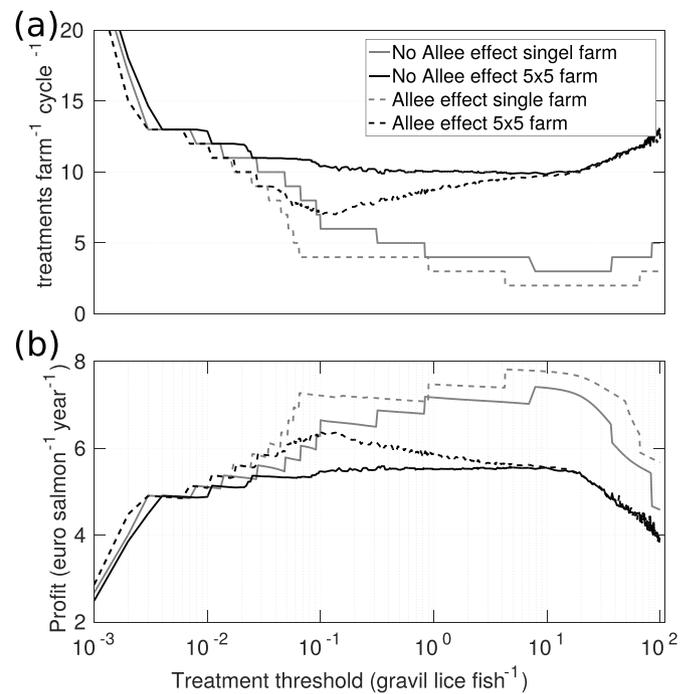


Fig. 6. Number of treatments (a) and profit (b) as function of treatment threshold. The plots shows Allee effect (dashed line) and no Allee effect (solid line) for a single farm (gray line) and a 5 farm network (black line). External infection is $0.005 \text{ lice d}^{-1}$ and self-infection is 5% in all simulations. Treatment efficiency is 95% for on fish lice stages. In the 5 farm networks the connectivity is equal with a 2.5% connection.

the high treatment rate is due to excessive treatments whenever even the smallest sign of infection is observed. These rigorous treatments will hinder the spread of infection and build up of younger stages of salmon lice in the water, however, since there is always a background infection load the infections will never be completely eradicated. At high thresholds, treatments fail to hinder the spread of infection, and consequently the number of salmon lice in the water runs out of control and infections become uncontrollable. The costs of treatments shape the profit in situations with different infection loads. An additional factor is the economic losses due to lower growth and survival of salmon at high infection loads. Overall, the profit shows a fairly flat plateau for thresholds in the range 0.1–10 lice per salmon. There are, however, important differences between the scenarios.

The equal, diffusive and directional cyclic connectivity matrices show very similar results, and in the following the results from these three experiments is represented by the results with the equal connectivity matrix.

In the case of an isolated farm, there is a weakly defined maximum profit at high treatment thresholds. A single farmer is therefore inclined to postpone the hassle and risk of treatments until the infection load is around 10 gravid lice per salmon. However, for the connected farms the overall profit suffers when the treatment threshold is high and the optimal overall profit occurs with a treatment threshold around 0.1 lice per salmon. Note that the connected farms have a lower profit per farm, even when salmon lice are optimally managed. This result indicates that there is a critical threshold as to the density of farms in a production area also showed by Frazer et al. (2012).

The effect of including the Allee effect (Eq. (5)) is shown in Fig. 6. Isolated farms have a optimal treatment threshold at around 10 gravid lice salmon⁻¹ with and without the Allee effect. Five farm networks have an optimal threshold at lower thresholds level when including the Allee effect. Not including the Allee effect results in profits for 5 farms networks plateauing between 0.1 and 10 gravid lice salmon⁻¹.

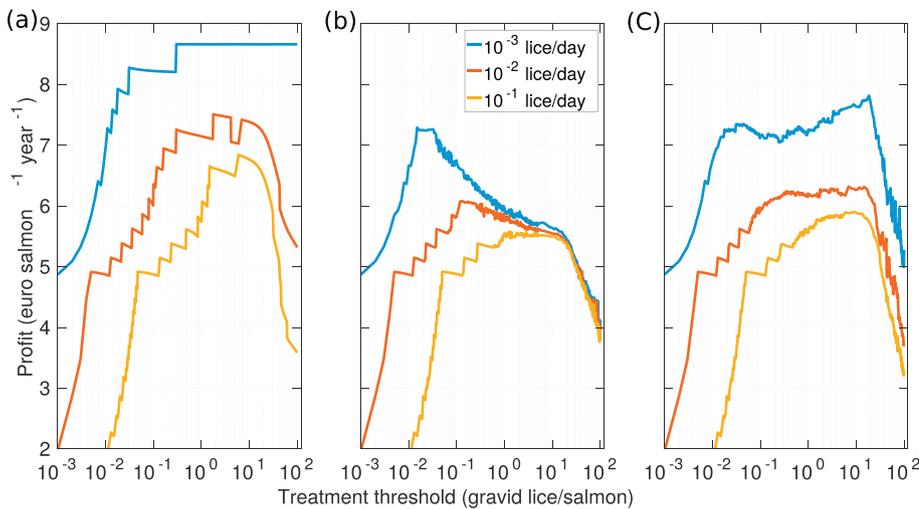


Fig. 7. Farm profit as function of treatment threshold with different external infection pressures for a single farm (a) and a 5 farm network with equal connectivity (b) and directional non-cyclic connectivity (c). Self-infection is 5% and connectivity between farms of 2.5%. Treatment efficiency is 95% on all stages. Legend shows external infection pressure in lice/day.

3.2.1. Effects of population dynamical parameters

Depending on the level of naturally occurring external infection pressure, high profits appear in some instances at high thresholds (Fig. 7a), in others at low thresholds (Fig. 7b) and sometimes at both (bimodal, Fig. 7c, blue line). The lower of these, high-profit treatment threshold disappears with sufficiently high external pressure. Isolated farms have again an optimal threshold around 10 gravid lice salmon⁻¹. Farms in a directional non-cyclic network have two optimal treatment thresholds that yield a higher profit when external infection pressure is 0.001 lice/day (Fig. 7c). The lower optimal threshold is where the external infection pressure becomes dominating and the higher optimal threshold appears where the cost of having lice significantly decreases profit (approx. Above 5–20 gravid lice salmon⁻¹).

Farm networks with equal connectivity, overlapping production and external pressure between 0.001 and 0.01 lice d⁻¹ have a profit optimum at thresholds between 0.01 and 0.5 gravid lice salmon⁻¹. With 0.01 lice d⁻¹ external infection pressure, farms have a profit optimum at thresholds of 0.2 gravid lice salmon⁻¹. In summary increasing external infection pressure increases the threshold where farms have optimal profits.

For isolated farms (0% connectivity) with low self-infection (Fig. 8a) all thresholds above 0.2 gravid lice salmon⁻¹ actually yield optimal profit as lice abundance does not exceed this level and therefore no treatments will be performed. When self-infection is increased to 5% for isolated farms (Fig. 8b–c) the optimal threshold is around 10

gravid lice salmon⁻¹ and when self-infection is increased to 10% the profit optimum plateaus between 0.1 and 10 gravid lice salmon⁻¹. Farm networks have a optimal threshold peak of around 10 gravid lice salmon⁻¹ with low self-infection and low connectivity between farms (0.1%). With higher self-infection the optimal threshold peak is around 0.1 gravid lice salmon⁻¹. However when connectivity between farms is 2.5 and 5% the optimal thresholds peak is around 0.1 gravid lice salmon⁻¹, regardless of the level of self-infection (Fig. 8).

Treatment efficiency has an interesting effect on profitability and optimal treatment threshold peaks (Fig. 9). Low treatment efficiency (30%) results in a low or negative profit (Fig. 9a). Further, the two optimal thresholds become very clear with no or low connectivity. With higher treatment efficiency there is a clear profit optimum threshold (around 0.1 gravid lice salmon⁻¹), except when there is no connectivity and a higher profit optimum threshold is clear (around 5–10 gravid lice salmon⁻¹). With high treatment efficiency, the lower profit optimum flattens out. However with no connectivity, there is a profit optimum threshold between 0.1 and 10 gravid lice salmon⁻¹.

In this study all farmers apply the same treatment threshold and the farm connectivity networks are symmetric. Formulating the cost of having lice is not straight forward. Eq. 11 assumes salmon weight has no effect on how many lice a salmon can tolerate and only includes gravid lice. This is an simplification and should be interpreted with care. As fig. S2 illustrates, including weight dependency in the number of lice tolerance essentially move the higher optimal treatment

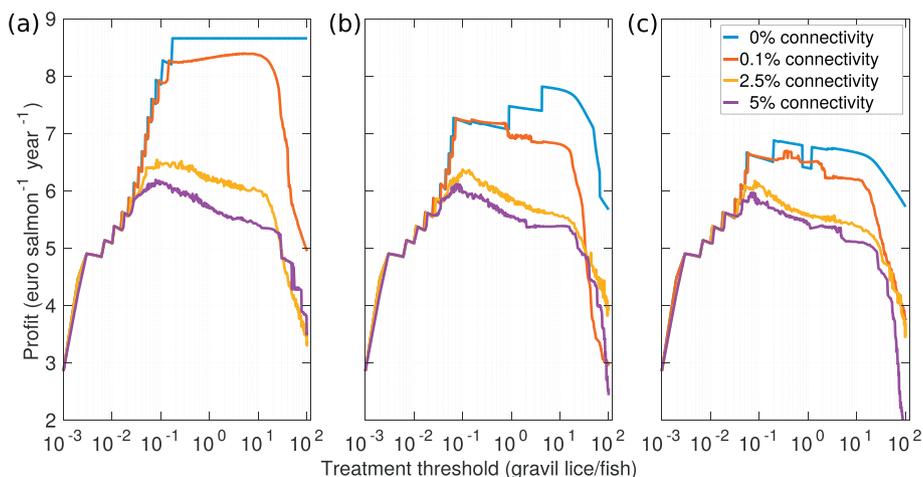


Fig. 8. Profit per time as function of treatment threshold with a 5 farm network with equal connectivity. Self-infection is 1% (a), 5% (b) and 10% (c). External infection pressure is 0.005 lice/day. Treatment efficiency is 95% on all stages.

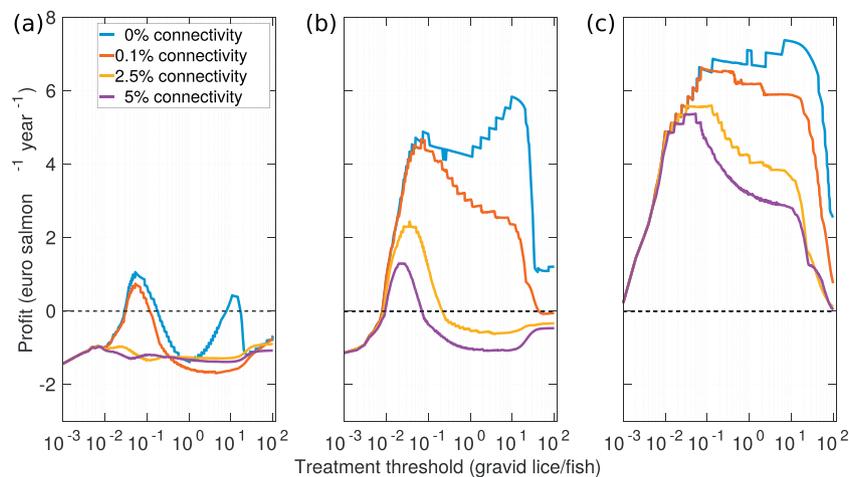


Fig. 9. Profit as function of treatment thresholds with treatment efficiency 30% (a), 60% (b) and 80% (c). External infection pressure is 0.005 lice/day and self-infection is 5%.

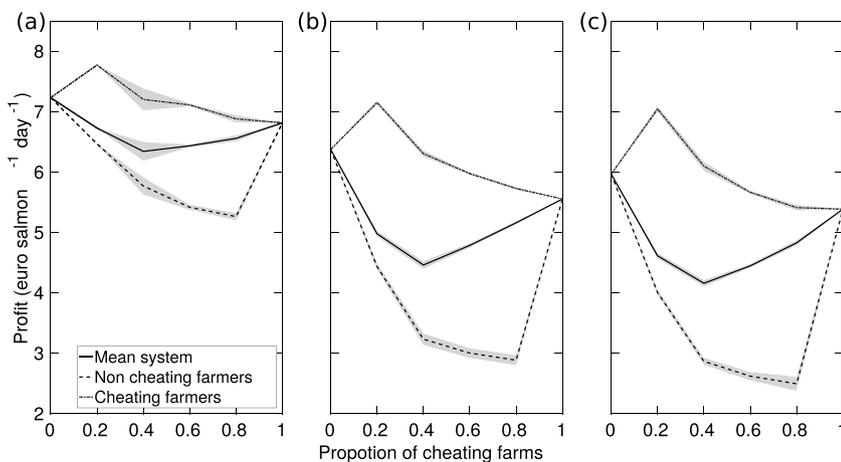


Fig. 10. Farm profit as function of proportion of cheating farmers. Non-cheaters and cheaters use a 0.1 and 10 gravid lice salmon⁻¹ treatment threshold, respectively. Connectivity is 0.1% (a), 2.5% (b) and 5% (c). Self-infection is 5%, external infection is 0.005 lice/day. Average farm profit for the whole system (black solid line), of the non-cheating farmers (dashed black line) and of cheating farmers (dashed gray line).

thresholds point to a higher or lower threshold level, and is considered to be included in a revised model.

In summary: Isolated farms have a optimal threshold around 5–10 gravid lice salmon⁻¹ although with higher self-infection this optimum flattens out. Connected farms with overlapping production have a low optimal threshold except when external infection pressure is sufficiently high as the benefit obtained by the Allee effect is bypassed. See Appendix S1 for sensitivity analysis.

3.3. A case of tragedy of the commons

Here, the tragedy of the commons is illustrated by showing the effect of mixing salmon farmers who obey regulation applying a treatment threshold of 0.1 gravid lice salmon⁻¹ with farmers who circumvent legislation and apply a higher treatment threshold (10 gravid lice salmon⁻¹). Having cheating farmers in the network decreases the overall profitability of the system (Fig. 10). However, the cheating farmers themselves obtain a substantial economic benefit compared to the farms who abide to the regulation. There are two interesting aspects in the tragedy of common. First, there is a clear benefit from a single farm perspective to apply a higher treatment threshold than the rest of the system. This benefit decreases as the number of cheating farms increases. Second, the profitability for the whole farm network is lowest when less than half of the farms circumvent legislation compared to when all or no farms obey legislation.

4. Discussion

We have identified two optimal treatment thresholds: a high threshold which optimizes the profit of an isolated farmer and a low threshold which optimizes the average profit of a connected farm network with overlapping production. Further, we show how non-compliance to a low threshold by just a single farmer compromises the profit of the entire system to the degree that it would have a higher profitability without management. In the following we discuss these two results, the uncertainties in the model, and finally explore the management implications of the results.

Individual or isolated farms maximize profit by accepting a high threshold of around 5–10 gravid lice salmon⁻¹. This high optimal threshold is where the cost of having lice becomes greater than the benefit of postponing a treatment. The intensity of this optimal threshold is sensitive to the level of the self-infection (Fig. 8). If the self-infection increases to above 10% the profit optimum plateaus between a 0.1–10 gravid lice salmon⁻¹ threshold.

Farm networks with equal connectivity and overlapping production maximize the total profit by enforcing a low threshold, typically around 0.1 gravid lice salmon⁻¹. We refer to this threshold as “the low optimal threshold”, in contrast to the “high optimal threshold” for the isolated farmer. This lower threshold is in line with tendency for reducing the treatment threshold limit e.g. in Norway (Mykssvoll et al., 2018), however, this reduction has been driven by the desire to protect wild salmonid stocks and not the profitability of the salmon farms. The profitability and position of the low optimal threshold depends on the

external background infection pressure, where low external infection pressure decreases the low optimal treatment threshold and visa versa. The low optimal threshold peak depends on existence of the Allee effect where infections disappear when the lice are too few to fertilize one another (Fig. 6). Guarracino et al. (2018) showed that synchronized fallowing in regions which are connected to other farming regions may be inefficient and even could result in “explosive” salmon lice growth at the end of the farming cycle. Our results support this finding as farms which are connected to other farms will start with a higher infection pressure than the natural background infection pressure present in most farming areas. Abolofia et al. (2017) found that the cost of lice in Norway was between 2.3 and 13% of revenue depending on when and which region farms are stocked. Our model estimates that if a farm has relatively high connectivity (Fig. 8b, 2.5%) the average cost of lice is 13% and 18% when managed with a 0.1 and 10 gravid lice salmon⁻¹ treatment thresholds, respectively. This indicates that our model may over-estimate the cost of lice, however it does remain within a realistic range.

4.1. Management implications

A tragedy of the commons situation (Hardin, 1968) occurs when farms are connected and are managed with a low treatment threshold. In this case, the individual farmer has an incentive to operate with a higher treatment threshold because the farmer only suffers a small cost of having the elevated sea lice infection, but does not pay for the additional infection pressure on the neighboring farms. This is a common situation, similar to the management of invasive species or insect pests between terrestrial farms (Fenichel et al., 2014) and when managing rare high-impact diseases in aquaculture farms within a management area (Murray, 2014). Such cases are often externally managed through legislation. A particular feature of the salmon lice case is the strong effect of non-compliance of just a single actor on the profit of the entire system. A single non-compliant farmer will create a haven of disease that spreads freely to all connected farms, which need to apply costly delousing at an increased rate. To illustrate this effect we have used an extreme example where the cheating farms have a 100 fold higher treatment threshold than compliant farms. In reality, cheating farms would probably apply only a little higher threshold, however, the effect will be similar (Appendix S1: Fig.S6). The effect of just a single non-compliant farmer is so strong that the profit is significantly lower than in the non-managed case. Therefore, successful management for optimal profit requires 100% compliance.

The economic incentive for the individual farmer to apply a high treatment threshold presents a challenge to management. Besides single ownership of a connected farm network or management area there exist several ways to deal with the externality of a disease threat to production: State intervention, e.g., a “Pigouvian” tax, legislation and punishment, or allowance for local area management agreements, e.g., Coase-like exchanges, or targeting reputation damage (Milinski et al., 2002), e.g., by supermarkets requiring public salmon lice counts. A Pigouvian tax is a tax on any market activity that generates negative externalities. This would address the externality generation, in this case by taxing the salmon production itself. Such a scheme is not an optimal regulation because it reduces the value of the production, which then also reduces the incentive to deal with the infection (Fenichel et al., 2014). Further, taxing raises the question of how the tax should be distributed. The alternative, a Coase-like exchange – based on the Coase theorem where two parties can come to an agreement without a governmental third party if transaction costs are low – instead operates only among the farmers. Farms benefitting from their neighbour's delousing efforts will chip in to help pay their neighbours' effort (Fenichel et al., 2014). While this seems immediately logical, it requires that it is possible to accurately identify infection connections between farms and construct an appropriate system for the exchange of costs. While there have been improvements in the simulation of exchanges of infections

between farms from advanced hydrodynamic models (Adams et al., 2012; Johnsen et al., 2014; Kragestein et al., 2018; Myksvoll et al., 2018; Cantrell et al., 2018), they are not yet accurate enough to act as widely trusted assessments of infection risk. Further, since all farmers are delousing anyway, setting up an elaborate cost exchange system may well be perceived as an overly bureaucratic and complex exchange of cost with little net benefit. Nevertheless, if a clear transmission pathway between farms can be identified, potential legal disputes could be settled or avoided by setting up Coase exchanges of delousing costs bi-laterally between farms. Farmer can also set up local area management agreements for treatment thresholds which requires a degree of trust among farmers in order to work. Trust or confidence between farmers can be established by regular sharing of information between farmers. Such a system is most likely to succeed in smaller networks, as the trust required increases with number of farms in a management area (Murray, 2014). Structuring salmon lice management strategies for farm networks where individual farms may benefit from disregarding legislation is difficult. However, management strategies must be structured in such a way that individual farms see the long term benefit of keeping to legislation rather than seek the short term benefit of disregarding legislation.

Given the above problems with traditional economic schemes to internalize the costs of disease management the most likely future regulation is to maintain national legislation. An important implication of our simulations was to show that efficient management requires compliance by all actors and that an imperfect management leads to a worse economic outcome than no management. In this situation it is important to know the individual farmers' economic rationale for their actions and design repercussions for non-compliance that will clearly deter non-compliance. The cost of non-compliance is the foregone production and costs of delousing of all the other farmers, and non-compliance should at least amount to these costs. In addition to economic sanctions, the social incentives should not be underestimated. If it is publicly known whether a farmer obeys the legal treatment threshold – as is the case in Norway, Faroe Island and Chile – the farmer will be required to justify (non)action, and will be open for claims of private compensation from neighboring farms (the Coase-like exchange). Efficient social regulation requires transparency and publicly known louse-counts of each farm. Legislation should therefore not only punish but also mandate transparency.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aquaculture.2019.734329>.

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