

Salmon lice should be managed before they attach to salmon: Exploring epidemiological factors affecting *Lepeophtheirus salmonis* abundance on salmon farms

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Abstract

The ectoparasite *Lepeophtheirus salmonis* has for decades been a serious challenge to the sustainability of salmonid aquaculture and has the potential to disrupt the ecosystem of wild salmonids. To tackle this challenge, efforts have been made to develop effective lice control strategies that deter ecto-parasitic infestations on salmon farms. Infestation control can be enhanced by understanding *L. salmonis* population dynamics that may reveal critical points at which to intervene. Here, we investigate the impact of key parameters affecting *L. salmonis* population dynamics on salmon farms with a view to informing *L. salmonis* management. We built a system dynamics model to simulate *L. salmonis* populations in a hypothetical Atlantic salmon (*Salmo salar* L.) farm. Our model focused on three key parameters in the life cycle of *L. salmonis*: external pressure (rate of introduction of planktonic *L. salmonis* from outside the farm), attachment proportion (proportion of *L. salmonis* that successfully infest salmon), and treatment efficacy (proportion of *L. salmonis* that are killed as a result of treatment). By applying various combinations of plausible values for these three parameters, their modelled impacts on *L. salmonis* management were evaluated in terms of the total number of required treatments and the total infestation burden during a typical production cycle. These two modelled outcomes represent the cost of treatment and a proxy for other likely costs, such as lost growth or mortality caused by the parasite. Our results indicated that overall *L. salmonis* infestation levels were more sensitive to changes in the proportion of successful attachment, followed by changes in external pressure, and were least affected by changes in treatment efficacy. While attachment proportion and external pressure are involved at the pre-infestation stages in the life cycle of *L. salmonis*, treatment efficacy is involved in the post-infestation stages. Therefore, these findings suggest that preventing infestation before lice attach to fish is a more effective *L. salmonis* control strategy than treating already infested salmon. Overall, the presented results provide numerical evidence for the efficiency of prevention and support the development and application of prevention measures that have been on the rise in recent years.

Keywords: Atlantic salmon; attachment proportion; external pressure; *Lepeophtheirus salmonis*; mathematical model

1. Introduction

Salmon aquaculture has been rapidly growing over the past decades (Asche et al., 2018). However, parasitic infestations have hindered the development of the salmon farming sector, as they have in other farming systems. In particular, *Lepeophtheirus salmonis* are ecto-parasites of the Caligidae family, commonly known as “salmon lice”, in the northern hemisphere, feed on the skin and mucus of fish and are one of the most detrimental problems, threatening the sustainability of salmon aquaculture and impairing further expansion of the sector. It has been

estimated that the damage due to typical sea lice infestation patterns on a Norwegian salmon farm could account for as much as 13% of their total revenues, indicating the economic seriousness of this ectoparasite (Abolofia et al., 2017).

Effective control of salmon lice infestation on salmon farms relies on understanding the salmon lice life cycle on these farms. The life cycle of salmon lice can be broadly divided into planktonic stages during which salmon lice have not yet attached to a host and freely move in the ocean and parasitic stages during which the sea lice are attached to a salmon host and reproduce (Costello, 2006) (Fig. 1). Parasitic salmon lice must maintain this attachment to be able to survive and reproduce. After harvesting salmon, farms observe a fallowing period to ensure that no planktonic salmon lice are present in the water. After stocking, planktonic salmon lice are first introduced from outside the salmon farm environment, initiating the reproduction cycle of salmon lice in the farm. Within this cycle, three important events can be observed (Fig. 1): the introduction of externally sourced planktonic salmon lice (“Immigration”), the “Attachment” of planktonic salmon lice to fish, and “Treatment” events that kill parasitic salmon lice. Although these three steps are critically important in understanding salmon lice population dynamics, their relative impacts on salmon lice infestation have not been thoroughly explored.

The level of immigration is incorporated using “external pressure”, which signifies the rate at which planktonic salmon lice enter the farm. External pressure has been demonstrated to be correlated with salmon lice population growth and has been noted as an important aspect of any integrated pest management programme that seeks to control salmon lice on farmed salmon (Brooks, 2009; Adams et al., 2015; Kragesteen et al., 2021). Without a well-coordinated salmon lice management plan, the level of salmon lice infestation cannot be kept low due to the migration of planktonic salmon lice between farms (Kragesteen et al., 2019). Fallowing has been found to be effective in removing planktonic salmon lice in certain situations and in extending the period from stocking to first treatment (Werkman et al., 2011; Toorians and Adams, 2020). Although fallowing can effectively remove salmon lice from the location of a farm site, salmon lice can be introduced to a farm from the external environment soon after stocking (Guarracino et al., 2018). Also, background sources from surrounding farms and the environment constitute the external infestation pressure (Eisenhauer et al., 2020). Internal infestation pressure can be estimated based on locally acquired monitoring data, whereas external infestation pressure is more difficult to assess (Kristoffersen et al., 2014). Although several modelling studies have assumed values of external pressure, the values in each study have varied considerably (Gettinby et al., 2011; Groner et al., 2013; McEwan et al., 2015; Kragesteen et al., 2019).

In addition to external pressure, the parameterisation of attachment proportion, the proportion at which planktonic salmon lice succeed in attaching to their host fish before they die, plays an important role in modelling salmon lice population dynamics, as an attachment is essential to complete the transition from the planktonic stages to the parasite stages. Studies have shown that the attachment depends on salinity (Bricknell et al., 2006; Connors et al., 2008; Groner et al., 2016), but the proportions reported in observational studies (Tucker et al., 2000;

Samsing et al., 2016) and assumed in modelling studies (Groner et al., 2013; McEwan et al., 2015; Kragestein et al., 2019) have varied considerably among studies. Finally, although several modelling studies have assumed treatment efficacies, the proportion of salmon lice that are detached from their host due to treatments, of around 95% (Saksida et al., 2010; Gettinby et al., 2011; Adams et al., 2015; McEwan et al., 2015), it has been suggested that in some circumstances treatment efficacy may be as low as 35% (Lees et al., 2008; Jones et al., 2012; Gislason, 2018). Also, the development of resistance of salmon lice to chemotherapeutics has highlighted the need to apply a wider range of treatment efficacy parameter values when modelling salmon lice (Aaen et al., 2015).

The costs of salmon lice to salmon aquaculture vary and include impacts such as reduced growth, reduced feed conversion rates, a downgrading of fish at harvest, secondary diseases, mortality, and treatments (Mustafa et al., 2001). In this study, we divide these into two categories: the direct cost of salmon lice treatments and additional costs of salmon damage due to salmon lice infestation. The relative weight of the two categories to some extent depends on the treatment threshold of acceptable salmon lice abundance before treatment (“treatment threshold”). For example, if we set a low treatment threshold, the cost of salmon damage will decrease but the cost of salmon lice treatment will increase. Therefore, it is important to find an appropriate balance between these two opposing factors to maximize the productivity of salmon aquaculture (Janssen et al., 2018). In our study, we explore the key parameters in light of their impact on these two cost categories.

By using a deterministic system dynamics model, we simulate salmon lice population dynamics in a salmon farm and track the number of salmon lice per salmon during a production cycle. Wide plausible ranges of the three key parameter values are applied in the simulation to assess their relative impact on salmon lice infestation levels. We then discuss the implications of the modelled results for effective management strategies of salmon lice on salmon farms.

2. Materials and Methods

We built a system dynamics model using the *AnyLogic* modelling software platform (www.anylogic.com). The model tracked salmon lice over all development stages from egg to adult on an Atlantic salmon farm over a production cycle. The production cycle was 550 days from smolt stocking to harvesting. The unit of time used within the model was one day.

2.1. *Salmon lice life cycle*

Salmon louse (*Lepeophtheirus salmonis*) developmental stages are largely divided into the planktonic stages, in which salmon lice are freely floating in the water, and the parasitic stages, in which salmon lice are attached to fish hosts (Byrne et al., 2018). The planktonic stages consist

of two nauplius stages and the infective copepodid stage, while the parasitic stages are two chalimus stages, two pre-adult stages, and the adult stage (Hamre et al., 2013). Female adults produce a pair of egg strings, and the first strings have a smaller number of eggs than successive strings (Heuch et al., 2000). Eggs hatch into nauplii that are free-living in the water column and do not take up any nutrients, solely depending on the energy supply gained from the egg stage. Nauplii then develop into copepodids. The copepodid stage is infective, in which salmon lice must attach to a host fish, otherwise they cannot survive. After attachment, copepodid moult into the chalimus stage where they sexually differentiate. Chalimus then moult into the pre-adult stage. In the pre-adult stage, parasitic salmon lice are motile and may move around on the fish. Lastly, the final stages of adult females and males develop, and reproduction occurs in these dioecious adult stages.

While we simplified the stages of nauplius, chalimus, and pre-adult, we subdivided the adult stage based on their reproductive state (Fig. 2). Adult males are not explicitly described in the model but are assumed to have an equal abundance to adult females (Hurford et al., 2019). Thus, we modelled eight life stages of salmon lice: ‘Eggs’, ‘Nauplius’, ‘Copepodid’, ‘Chalimus’, ‘Female pre-adult’, ‘Female adult’, ‘First gravid’, and ‘Subsequent gravid’ (Table 1 and 2).

2.2. Seawater temperature and salinity

The finding that developmental time in each sea louse stage is highly dependent on temperature made it vital to incorporate temperature into our model (Stien et al., 2005). To incorporate the effects of seasonal temperature variation, we modelled temperature as a function of time by fitting water temperature data to an oscillatory sinusoidal curve, as in (Groner et al., 2013):

$$\text{temperature} = a + b \times \sin\left(\pi \times \frac{\text{time} + c}{365}\right)^2$$

where “time” refers to the day of a year (i.e., number of days into the cycle), a is the minimum temperature, b is the difference between the maximum and minimum temperatures (amplitude), and c is the day of the year that stocking occurred. Minimum and maximum temperatures were assumed to be 5 and 13 °C, which is the typical temperature range in Sognefjorden area, Norway (Aldrin et al., 2013). The variable c takes on the value 105 or 185, to represent a typical day for spring or fall stocking, respectively.

Groner et al. (2016) quantified the effect of salinity on salmon lice mortality at each life stage by using observational data and demonstrated the consequence of salinity on modelling salmon lice population dynamics. As such salinity should be included within mathematical models, particularly where variations in salinity will be an important part of the environmental context. However, including salinity within modelling frameworks is not straightforward for at least three reasons: first, depending on region, salinity has been observed to vary between salmon

farms (Brooks, 2005; Arriagada et al., 2016; Groner et al., 2016; Rittenhouse et al., 2016); second, salmon lice mortality is very sensitive to short term variations in salinity (Groner et al 2016); and third, many farms tend to be outside the influence of substantive freshwater flows and thus experience relatively stable salinity conditions. For these reasons, and because the impact of salinity was not a focus of our study, we chose to assume a constant salinity of 30 PSU. This constant level of salinity is favourable to salmon lice and hence will not contribute to reductions in sea louse numbers in the model results or cause interactions that could obscure the effects of other key parameters.

We modelled sea louse mortality at each life stage using equations that depend on salinity (Table 1). Development rates of salmon lice were modelled by using the equations depending on temperature (Stien et al., 2005; Rittenhouse et al., 2016). The one exception is the copepodid stage, which has not been found to depend on temperature (Johnson and Albright, 1991), and therefore we used the recommended constant value of 4.6 days (Stien et al., 2005). In addition, we modelled the mortality of subsequent gravid females, using the life span of reproductively mature salmon lice (Heuch et al., 2000).

2.3. Reproduction

When the abundance of salmon lice is low, reproduction in salmon lice is limited by mate availability, rather than being proportional to abundance (Krkosek et al., 2012). To incorporate the density-dependent effect, we used an equation to calculate the fertility rate using the negative binomial distribution (Groner et al., 2014), which has been found to be appropriate to describe the statistical distribution of the salmon lice count per fish (Treasurer and Pope, 2000; Heuch et al., 2011; Jeong and Revie, 2020). In our model, we used an equation from Groner et al. (2014) to calculate the probability that a female louse will mate:

$$\phi(m, k) = 1 - \left(1 - \frac{m}{m + k}\right)^{1+k} \left(1 - \frac{m}{2(m + k)}\right)^{-1-k}$$

where m is the mean number of adult lice on a host (i.e., female adult abundance) in each time step, and k is the dispersion parameter in the negative binomial distribution. We used $k=2.19$ as previously estimated across salmon farms in various locations in (Jeong and Revie, 2020). Additionally, female adult lice were assumed to generate an average of five pairs of egg clutches during their lifetime (Heuch et al., 2000). The number of eggs in the first and subsequent clutches were 273 and 513, respectively (Heuch et al., 2000). No evidence of gender imbalance has been found (Eichner et al., 2015), and therefore we assumed 50% of copepodids would develop into female chalimus.

2.4. Assumptions around key model parameters

In our study, we varied four key parameters – external pressure, attachment proportion, treatment efficacy, and to a lesser extent treatment threshold. In the system of open-cage salmon farms, salmon lice continuously immigrate to and emigrate from farms. Instead of modelling both immigration and emigration of planktonic salmon lice, we modelled only net increase in the number of planktonic salmon lice within a farm, and the net increase occurred in addition to the reproduction of salmon lice within the farm. Thus, ‘external pressure’ was defined as the number of nauplii per host fish that were introduced into the farm from outside the farm and stayed in the farm. We varied external pressure between 0.002 and 0.5 (Kragesteen et al., 2019; Kragesteen et al., 2021).

Each farm cycle starts with zero lice in the system, on the assumption that there was a fallow period before the start of the new production cycle to ensure the complete removal of salmon lice from the salmon farm. As such, the initial infestation of planktonic lice must be from an external source. We defined attachment proportion as the proportion of copepodids that successfully attached to their host fish before they died. Although McEwan et al. (2015) and Kragesteen et al. (2019) assumed attachment proportions of 0.3 and 0.25 respectively in their models, there is little evidence to reliably support a given attachment proportion. It is also likely that values for this parameter will be strongly influenced by the type of modelling framework adopted. In our model, it seemed highly unlikely that as many as ~25% of all planktonic salmon lice would attach to a host. However, we did explore a relatively wide range of attachment proportions from 0.002 to 0.02, and both internally and externally sourced salmon lice were treated equally.

We defined ‘treatment efficacy’ as the proportion of parasitic salmon lice that detach as a result of treatment. We varied treatment efficacy from 0.50 to 0.95 in 0.05 increments. Salmon lice that detached from their host fish due to treatment were assumed to have no opportunity to re-attach and died. We defined ‘treatment threshold’ as the abundance of adult female salmon lice that triggered treatment. We varied the treatment threshold from 0.2 to 3.0 adult female lice per host.

2.5. Model output

Our model outcomes were the number of treatments (NT) and the infestation burden (IB). We determined NT by counting treatments applied, with treatment being initiated each time that the treatment threshold for adult females was reached during the production cycle. We determined IB by summing the daily abundance over the production cycle, as in (Robbins et al., 2010). This calculation is equivalent to summing the area shown under the line of adult female salmon lice abundance over a full production cycle (e.g., abundance lines in Fig. 3 and Fig. 4).

We used our model to explore the relationship between these two outcomes and different combinations of values for the key parameters.

3. Results

3.1. Spring stocking and fall stocking

The choice of stocking season led to differences in the number of treatments (NT) and infestation burden (IB) (Fig. 3). Spring stocking led to a slight increase in NT (8 treatments) when compared to fall stocking (6 treatments). Because the production cycle ran for around 1.5 years (550 days), the mean temperature during a production cycle was higher in the case of spring stocking than the case for fall stocking. In addition, the temperature was more critical in the later phase of the production cycle than in the earlier phase because abundance reached the treatment threshold more frequently in the later phase. Spring stocking resulted in higher temperature towards the later phase of a production cycle, which caused more treatments than fall stocking that had a lower temperature in its later phase of the production cycle. Like NT, spring stocking had a higher value of IB than fall stocking, as the value of IB for spring stocking was 260 but only 207 for fall stocking. The higher IB of spring stocking was mainly due to the gradual increase in abundance until the first treatment because of the low temperature in the middle phase of the production cycle. Depending on circumstances such as temperature range, salinity, and treatment threshold, it has been shown that IB values could be higher with spring stocking or could be higher with fall stocking. However, spring stocking always generated NT values that were higher or equal to fall stocking. In the following sections, all simulations were based on spring stocking as these represent the more challenging scenarios.

3.2. Impact of key model parameters

External pressure, attachment proportion, and treatment efficacy were shown to influence salmon lice population dynamics at different periods of the production cycle (Fig. 4). As might be expected, external pressure affected the period from stocking to the first treatment. Once abundance reached the treatment threshold, the influence of external pressure on abundance was negligible. This result suggested that internally sourced infestation dominated the overall infestation pressure compared to externally sourced infestation subsequent to the first treatment. In contrast, attachment proportion influenced the salmon lice population dynamics for the whole period of the production cycle. With higher attachment proportions, the period until the first treatment was shorter, and so were the temporal gaps between each successive pair of treatments. Fairly intuitively, changes in treatment efficacy only affect salmon lice population dynamics after the first treatment has taken place.

Fig. 5 shows the relative impact of changes in two of the three key parameters on NT (left-hand plots) and IB (right-hand plots) while keeping the value of the remaining parameter constant. None of the three parameters were found to be overwhelmingly powerful to the other two, but the parameters certainly did affect the model outcomes. It was noteworthy that the effect of treatment efficacy on NT and particularly on IB was weaker compared to the effect of changes in external pressure and attachment proportion. On the other hand, differences between the impact of changes in external pressure and attachment proportion were difficult to identify, although attachment proportion appeared to be slightly more influential than external pressure (Fig. 5A and A'). Also, the IB profiles in Fig. 5A', B', and C' show a similar pattern of variation to those seen for NT, but the difference of their relative impact was more prominent when considering IB than was the case for NT.

3.3. Effect of treatment threshold on the factors, NT and IB

Fig. 6 shows the relationship between NT and IB with different values of the three key parameters and levels of treatment threshold. As expected, a lower treatment threshold will tend to reduce the IB but at the expense of incurring a higher NT; conversely, higher treatment thresholds reduce the number of treatments but lead to higher IB values. The ideal scenarios look to reduce both NT and IB while acknowledging the trade-off between these two outcomes. Selecting a low treatment threshold led to slopes that were relatively flat across the range of values for the parameter of interest, whereas selecting a high treatment threshold led to much steeper slopes. This result indicates that for a high treatment threshold, changes in the parameter values can have a large effect on both NT and IB, but at a low treatment threshold changes in the parameter values can still affect NT but have little impact on IB. Both attachment proportion and external pressure had great potential to reduce IB. While various values of attachment proportion showed obvious differences on NT, external pressure showed a limited impact on NT. For the case of treatment efficacy, its ability to reduce both NT and IB was shown to be limited; even the highest treatment efficacy still resulted in points far from the zero points of NT and IB in Fig. 6C, unlike the external pressure and the attachment proportion.

4. Discussion

Previous modelling studies of salmon lice population dynamics have addressed the parameters of external pressure, attachment proportion, and treatment efficacy in generating the results of their models (Groner et al., 2013; McEwan et al., 2015; Kragesteen et al., 2019). However, the studies chose a point value of the parameters or used wide ranges of parameter values, and they lacked in-depth exploration of the effects of these parameters on the salmon lice population dynamics. Here, we rather wanted to investigate the effect of three key parameters by

using a system dynamics model in which various combinations of different values of the parameters were used.

It is obvious that higher treatment efficacy is more desirable, but it has not been well investigated how much benefit can be expected from a degree of improvement in treatment efficacy, compared to a degree of improvement in other factors such as reduced infection pressure or attachment proportion. The modelling results shown in Fig. 6 emphasise that improvement in treatment efficacy has a limited effect on salmon lice management; in contrast, reductions in attachment proportion or external pressure have the potential to massively reduce salmon lice infestation. These results indicate that preventing salmon lice infestation is a more effective control measure than treating already salmon lice-infested salmon because external pressure and attachment proportion are involved in managing salmon lice before they infest, while treatment efficacy is involved in managing salmon lice after they infest. Due to the high degree of resistance to medicinal treatments (Aaen et al. 2015), the salmon farming industry is forced to use non-medicinal delousing methods that induce increased mortality (Overton et al., 2019) and potentially reduces fish welfare (Gismervik, 2019). Hence treatments are costly concerning fish welfare, mortality, and economics, as well as being less effective than the farmers taking preventative measures (Barrett et al., 2020; Gentry et al., 2020).

Recently increasing interest and research into various preventative measures appear to be desirable for efficiently reducing the cost inflicted by salmon lice on salmon farms. For example, skirts (Frank et al., 2015; Stien et al., 2018) and snorkels (Stien et al., 2016; Oppedal et al., 2017) are physical barriers that may block salmon lice from attaching to salmon. More novel is the attempt to influence salmon behaviour by using deep feeding and deep lights to encourage the salmon to maintain a swimming depth below the lice-infested surface waters (Trengeid et al., 2021). In addition, prevention can be facilitated by making salmon more resistant to attachment. Functional feeds that deter the attachment of salmon lice to salmon have been developed (Martin & Krol 2017) and are already commercially available (Barrett et al., 2020). Selective breeding of salmon has the potential to increase the proportion of salmon that is more resistant to salmon lice (Gharbi et al., 2015). Despite these developments of measures to prevent attachment, the efficiency of preventive methods has not been supported by numerical evidence. Thereby, this study provides the mathematical analyses of key parameters of planktonic and parasitic stages of salmon lice and contributes to motivating the application of preventive measures.

Varying the values of external pressure and attachment proportion resulted in similar patterns in terms of IB, but these variations generate different patterns when looking at NT. With the exception of the case when the external pressure is kept very low, the effect of external pressure on the number of treatments is relatively minor (Fig. 6A). It is important to extend the period from salmon stocking to the first treatment as long as possible by suppressing external pressure to low levels. Therefore, spatially coordinated salmon lice intervention measures among neighbouring farms that aimed at reducing external pressure should be stringent, reducing salmon lice exchange (Kristoffersen et al., 2013).

Economic models have been used to assess the costs of salmon lice for salmon aquaculture (Mustafa et al., 2001; Liu and Bjelland, 2014; Abolofia et al., 2017; Dresdner et al., 2019). The studies relied on the empirical estimates of abundance controlled by the enforced treatment thresholds and estimated the economic cost incurred by salmon lice. Instead of using the current states, using hypothetical abundance controlled by an arbitrarily set treatment threshold can be expected to provide guidelines in finding an appropriate treatment threshold for minimising cost. Thus, the studies did not come to the point of presenting an effective treatment threshold for minimising the cost due to salmon lice. Janssen et al. (2018) estimated the economic cost of salmon lice for salmon aquaculture in terms of the basic economic principle of the loss-expenditure frontier, in which the economic optimum is reached when the sum of loss and expenditure is minimal. In our study, loss and expenditure correspond to IB and NT, respectively. Low treatment threshold reduces IB, but increases NT, while a high treatment threshold reduces NT, but increases IB. Overall, low treatment thresholds appear to generate more economic optimum, because IB is sensitively affected by treatment threshold, whereas NT is not. Nevertheless, defining the most desirable treatment threshold is not straightforward because the two elements of IB and NT use different units and thereby cannot be compared directly. Besides, estimation of the elements importantly depends on a farm's environmental and spatial conditions, which makes it difficult to find an economic optimum point that can be applied to all salmon farms. Also, due to the importance of immigration of planktonic salmon lice between farms, the impact of the IB should be considered through relationships with neighbouring farms. Thus, trials to find treatment thresholds for the economic optimum should be focused on detailed environmental and spatial conditions, in which factors can be well addressed. For example, Kragesteen et al. (2019) concentrated on connectivity with other farms in a region to investigate the desirable treatment threshold for maximising salmon aquaculture profit and showed that optimal management of salmon lice infestations needs strict regulation that does not allow even a few violations of the treatment thresholds.

In this study, the key parameters were varied over a range of values and the results were evaluated based on various combinations. That is because the parameters do not independently affect the simulation outcomes. We mapped results over the parameter space, as the difference in our measures when changing multiple parameters was not the same as the sum of the differences from changing them independently. By doing so, we were able to capture many different settings. Numerous factors – such as the marine environment, salmon farm networks, and salmon lice management protocols – are involved in determining the actual values of the parameters (Revie et al., 2003). Adoption of a range of values made it possible to explore various situations that might exist in practice. In addition, this allows us to offer guidance on effective means by which to reduce salmon lice numbers. Because we have evaluated the parameter space around a particular setting, we can identify those parameters most likely to lead to an overall reduction in lice load.

Conflict of interest statement

No conflict of interest to declare.

None of the authors have a financial or personal relationship with other people or organizations that could inappropriately influence (bias) our work.

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References

- Aaen, S.M., Helgesen, K.O., Bakke, M.J., Kaur, K. and Horsberg, T.E., 2015. Drug resistance in sea lice: a threat to salmonid aquaculture. *Trends Parasitol.* 31(2), pp.72-81.
- Abolofia, J., Asche, F., Wilen, J.E., 2017. The cost of lice: quantifying the impacts of parasitic sea lice on farmed salmon. *Mar. Resour. Econ.* 32, 329-349.
- Adams, T.P., Proud, R., Black, K.D., 2015. Connected networks of sea lice populations: dynamics and implications for control. *Aquac. Environ. Interact.* 6, 273-284.
- Aldrin, M., Storvik, B., Kristoffersen, A.B. and Jansen, P.A., 2013. Space-time modelling of the spread of salmon lice between and within Norwegian marine salmon farms. *PLoS One.* 8(5), p.e64039.
- Arriagada, G., Vanderstichel, R., Stryhn, H., Milligan, B., Revie, C., 2016. Evaluation of water salinity effects on the sea lice *Lepeophtheirus salmonis* found on farmed Atlantic salmon in Muchalat Inlet, British Columbia, Canada. *Aquaculture* 464, 554-563.
- Asche, F., Cojocar, A.L., Roth, B., 2018. The development of large scale aquaculture production: A comparison of the supply chains for chicken and salmon. *Aquaculture* 493, 446-455.
- Barrett, L.T., Oppedal, F., Robinson, N., Dempster, T., 2020. Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. *Rev. Aquac.* 12(4), pp.2527-2543.
- Bricknell, I.R., Dalesman, S.J., O'Shea, B., Pert, C.C., Luntz, A.J.M., 2006. Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. *Dis. Aquat. Org.* 71, 201-212.
- Brooks, K.M., 2005. The effects of water temperature, salinity, and currents on the survival and distribution of the infective copepodid stage of sea lice (*Lepeophtheirus salmonis*) originating on Atlantic salmon farms in the Broughton Archipelago of British Columbia, Canada. *Rev. Fish. Sci. Aquac.* 13, 177-204.
- Brooks, K.M., 2009. Considerations in developing an integrated pest management programme for control of sea lice on farmed salmon in Pacific Canada. *J Fish Dis.* 32, 59-73.
- Byrne, A.A., Pearce, C.M., Cross, S.F., Jones, S.R., Robinson, S.M., Hutchinson, M.J., Miller, M.R., Haddad, C.A., Johnson, D.L., 2018. Planktonic and parasitic stages of sea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*) at a commercial Atlantic salmon (*Salmo salar*) farm in British Columbia, Canada. *Aquaculture* 486, 130-138.
- Connors, B., Juarez-Colunga, E., Dill, L., 2008. Effects of varying salinities on *Lepeophtheirus salmonis* survival on juvenile pink and chum salmon. *J. Fish Biol.* 72, 1825-1830.
- Costello, M.J., 2006. Ecology of sea lice parasitic on farmed and wild fish. *Trends Parasitol.* 22, 475-483.

- Dresdner, J., Chávez, C., Quiroga, M., Jiménez, D., Artacho, P., Tello, A., 2019. Impact of *Caligus* treatments on unit costs of heterogeneous salmon farms in Chile. *Aquaculture Economics & Management*. 23, 1-27.
- Eichner, C., Hamre, L.A., Nilsen, F., 2015. Instar growth and molt increments in *Lepeophtheirus salmonis* (Copepoda: Caligidae) chalimus larvae. *Parasitol. Int.* 64, 86-96.
- Eisenhauer, L., Solvang, T., Alver, M., Franklin Krause, D. and Hagemann, A., 2020. Dispersal of salmon lice (*Lepeophtheirus salmonis* Krøyer, 1837) egg strings from open-cage salmon farming: A neglected source for infestation dynamics. *Aquac. Res*, 51(11), pp.4595-4601.
- Frank, K., Gansel, L., Lien, A., Birkevold, J., 2015. Effects of a shielding skirt for prevention of sea lice on the flow past stocked salmon fish cages. *J. Offshore Mech. Arct. Eng.* 137.
- Gentry, K., Bui, S., Oppedal, F., Dempster, T., 2020. Sea lice prevention strategies affect cleaner fish delousing efficacy in commercial Atlantic salmon sea cages. *Aquac Environ Interact.* 12, 67-80.
- Gettinby, G., Robbins, C., Lees, F., Heuch, P.A., Finstad, B., Malkenes, R., Revie, C.W., 2011. Use of a mathematical model to describe the epidemiology of *Lepeophtheirus salmonis* on farmed Atlantic salmon *Salmo salar* in the Hardangerfjord, Norway. *Aquaculture* 320, 164-170.
- Gharbi, K., Matthews, L., Bron, J., Roberts, R., Tinch, A. and Stear, M., 2015. The control of sea lice in Atlantic salmon by selective breeding. *J. R. Soc. Interface.* 12(110), p.20150574.
- Gislason, H., 2018. Statistical modelling of sea lice count data from salmon farms in the Faroe Islands. *J. Fish Dis.* 41(6), pp.973-993.
- Gismervik, K., Gåsnes, S.K., Gu, J., Stien, L.H., Madaro, A. and Nilsson, J., 2019. Thermal injuries in Atlantic salmon in a pilot laboratory trial. *Vet. Anim. Sci.* 8, p.100081.
- Groner, M.L., Cox, R., Gettinby, G., Revie, C.W., 2013. Use of agent-based modelling to predict benefits of cleaner fish in controlling sea lice, *Lepeophtheirus salmonis*, infestations on farmed Atlantic salmon, *Salmo salar* L. *J. Fish Dis.* 36, 195-208.
- Groner, M.L., Gettinby, G., Stormoen, M., Revie, C.W., Cox, R., 2014. Modelling the impact of temperature-induced life history plasticity and mate limitation on the epidemic potential of a marine ectoparasite. *PLoS One* 9, e88465.
- Groner, M.L., McEwan, G.F., Rees, E.E., Gettinby, G., Revie, C.W., 2016. Quantifying the influence of salinity and temperature on the population dynamics of a marine ectoparasite. *Can. J. Fish. Aquat. Sci.* 73, 1281-1291.
- Guarracino, M., Qviller, L. and Lillehaug, A., 2018. Evaluation of aquaculture management zones as a control measure for salmon lice in Norway. *Dis. Aquat. Org.* 130(1), pp.1-9.

- Hamre, L.A., Eichner, C., Caipang, C.M.A., Dalvin, S.T., Bron, J.E., Nilsen, F., et al. 2013. The Salmon Louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) Life Cycle Has Only Two Chalimus Stages. PLoS ONE 8(9): e73539. <https://doi.org/10.1371/journal.pone.0073539>
- Heuch, P., Nordhagen, J., Schram, T., 2000. Egg production in the salmon louse [*Lepeophtheirus salmonis* (Krøyer)] in relation to origin and water temperature. Aquac. Res. 31, 805-814.
- Heuch, P.A., Gettinby, G., Revie, C.W., 2011. Counting sea lice on Atlantic salmon farms—empirical and theoretical observations. Aquaculture 320, 149-153.
- Hurford, A., Wang, X. and Zhao, X.Q., 2019. Regional climate affects salmon lice dynamics, stage structure and management. Proc. R. Soc. B. 286(1904), p.20190428.
- Janssen, K., Komen, H., Saatkamp, H.W., de Jong, M.C., Bijma, P., 2018. Derivation of the economic value of R_0 for macroparasitic diseases and application to sea lice in salmon. Genet. Sel. Evol. 50, 47.
- Jeong, J., Revie, C.W., 2020. Appropriate sampling strategies to estimate sea lice prevalence on salmon farms with low infestation levels. Aquaculture 518, 734858.
- Johnson, S., Albright, L., 1991. Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. J. Mar. Biol. Assoc. U. K. 71, 425-436.
- Jones, P., Hammell, K., Dohoo, I., Revie, C.W., 2012. Effectiveness of emamectin benzoate for treatment of *Lepeophtheirus salmonis* on farmed Atlantic salmon *Salmo salar* in the Bay of Fundy, Canada. Dis. Aquat. Org. 102(1), 53–64.
- Kragesteen, T.J., Simonsen, K., Visser, A.W., Andersen, K.H., 2019. Optimal salmon lice treatment threshold and tragedy of the commons in salmon farm networks. Aquaculture 512, 734329.
- Kragesteen, T.J., Simonsen, K., Visser, A.W. and Andersen, K.H., 2021. Estimation of external infection pressure and salmon-lice population growth rate in Faroese salmon farms. Aquac. Environ. Interact. 13, pp.21-32.
- Kristoffersen, A., Rees, E., Stryhn, H., Ibarra, R., Campisto, J.-L., Revie, C., St-Hilaire, S., 2013. Understanding sources of sea lice for salmon farms in Chile. Prev. Vet. Med. 111, 165-175.
- Kristoffersen, A.B., Jimenez, D., Viljugrein, H., Grontvedt, R., Stien, A., Jansen, P.A., 2014. Large scale modelling of salmon lice (*Lepeophtheirus salmonis*) infection pressure based on lice monitoring data from Norwegian salmonid farms. Epidemics 9, 31-39.
- Krkosek, M., Connors, B.M., Lewis, M.A., Poulin, R., 2012. Allee effects may slow the spread of parasites in a coastal marine ecosystem. Am. Nat. 179, 401-412.

- Lees, F., Baillie, M., Gettinby, G., Revie, C.W., 2008. Factors associated with changing efficacy of emamectin benzoate against infestations of *Lepeophtheirus salmonis* on Scottish salmon farms. *Jo J. Fish Dis.* 31(12), 947–51.
- Liu, Y. and Bjelland, H. V., 2014. Estimating costs of sea lice control strategy in Norway. *Prev. Vet. Med.* 117, 469-477.
- Martin, S.A. and Król, E., 2017. Nutrigenomics and immune function in fish: new insights from omics technologies. *Dev. Comp. Immunol.* 75, pp.86-98.
- McEwan, G.F., Groner, M.L., Fast, M.D., Gettinby, G., Revie, C.W., 2015. Using Agent-Based Modelling to Predict the Role of Wild Refugia in the Evolution of Resistance of Sea Lice to Chemotherapeutants. *PLoS One.* 10, e0139128.
- Mustafa, A., Rankaduwa, W., Campbell, P., 2001. Estimating the cost of sea lice to salmon aquaculture in eastern Canada. *Can Vet J.* 42, 54-56.
- Oppedal, F., Samsing, F., Dempster, T., Wright, D.W., Bui, S., Stien, L.H., 2017. Sea lice infestation levels decrease with deeper 'snorkel' barriers in Atlantic salmon sea-cages. *Pest Manag Sci.* 73, 1935-1943.
- Overton, K., Dempster, T., Oppedal, F., Kristiansen, T.S., Gismervik, K. and Stien, L.H., 2019. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. *Rev Aquac.* 11(4), pp.1398-1417.
- Revie, C.W., Gettinby, G., Wallace, C and others, 2003. Identifying Epidemiological Factors Affecting Sea Lice *Lepeophtheirus Salmonis* Abundance on Scottish Salmon Farms Using General Linear Models. *Dis. Aquat. Org.* 57, no. 1–2: 85–95.
- Revie, C.W., Robbins, C., Gettinby, G., Kelly, L., Treasurer, J., 2005. A mathematical model of the growth of sea lice, *Lepeophtheirus salmonis*, populations on farmed Atlantic salmon, *Salmo salar* L., in Scotland and its use in the assessment of treatment strategies. *J. Fish Dis.* 28, 603-613.
- Rittenhouse, M.A., Revie, C.W., Hurford, A., 2016. A model for sea lice (*Lepeophtheirus salmonis*) dynamics in a seasonally changing environment. *Epidemics.* 16, 8-16.
- Robbins, C., Gettinby, G., Lees, F., Baillie, M., Wallace, C., Revie, C.W., 2010. Assessing topical treatment interventions on Scottish salmon farms using a sea lice (*Lepeophtheirus salmonis*) population model. *Aquaculture.* 306, 191-197.
- Saksida, S.M., Morrison, D., Revie, C.W., 2010. The efficacy of emamectin benzoate against infestations of sea lice, *Lepeophtheirus salmonis*, on farmed Atlantic salmon, *Salmo salar* L., in British Columbia. *J. Fish Dis.* 33(11), 913–917.
- Samsing, F., Oppedal, F., Dalvin, S., Johnsen, I., Vågseth, T., Dempster, T., 2016. Salmon lice (*L. salmonis*) development times, body size, and reproductive outputs follow universal models of temperature dependence. *Can. J. Fish. Aquat. Sci.* 73, 1841-1851.

- Stien, A., Bjørn, P.A., Heuch, P.A., Elston, D.A., 2005. Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. Mar. Ecol. Prog. Ser. 290, 263-275.
- Stien, L.H., Dempster, T., Bui, S., Glaropoulos, A., Fosseidengen, J.E., Wright, D.W., Oppedal, F., 2016. 'Snorkel' sea lice barrier technology reduces sea lice loads on harvest-sized Atlantic salmon with minimal welfare impacts. Aquaculture. 458, 29-37.
- Stien, L.H., Lind, M.B., Oppedal, F., Wright, D.W., Seternes, T., 2018. Skirts on salmon production cages reduced salmon lice infestations without affecting fish welfare. Aquaculture. 490, 281-287.
- Stormoen, M., Skjerve, E. and Aunsmo, A., 2013. Modelling salmon lice, *Lepeophtheirus salmonis*, reproduction on farmed Atlantic salmon, *Salmo salar* L. J. Fish Dis. 36(1), pp.25-33.
- Treasurer, J.W., Pope, J.A., 2000. Selection of host sample number and design of a monitoring programme for ectoparasitic sea lice (Copepoda: Caligidae) on farmed Atlantic salmon, *Salmo salar*. Aquaculture. 187, 247-260.
- Trengereid, H., Simensen, B., Ritchie, G., 2021, January 19-20. Dynamic use of preventive measures in Mowi. Presented at the Lusekonferansen. Online Event.
<https://www.fhf.no/arrangementer/arrangementer/lusekonferansen-2021-digital/>
- Toorians, M.E. and Adams, T.P., 2020. Critical connectivity thresholds and the role of temperature in parasite metapopulations. Ecol. Model. 435, p.109258.
- Tucker, C., Sommerville, C., Wootten, R., 2000. The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon, *Salmo salar* L. J. Fish Dis. 23, 309-320.
- Werkman, M., Green, D.M., Murray, A.G., Turnbull, J.F., 2011. The effectiveness of fallowing strategies in disease control in salmon aquaculture assessed with an SIS model. Prev. Vet. Med. 98, 64-73.
- Wootten, R., Smith, J.W., Needham, E., 1982. Aspects of the biology of the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongatus* on farmed salmonids, and their treatment. P. Roy. S. Edinb. B. 81, 185-197.

Table 1. Parameter values used in the model.

Stage	Symbol	Description	Value	Reference
Egg	T_e	Time in days for eggs to hatch	$\frac{41.98}{(\text{Temperature} - 10 + 41.98 * 0.338)^2}$	(Stien et al., 2005)
	S_e	The proportion of hatching success	$1 - \frac{1}{1 + \left(\frac{\text{Salinity}}{20.82}\right)^{13.98}}$	(Groner et al., 2016)
	ρ	Number of eggs per clutch	400	(Wootten et al., 1982)
Nauplius	T_n	Time in days for nauplius to develop into copepodid	$\frac{24.79}{(\text{Temperature} - 10 + 24.79 * 0.525)^2}$	(Stien et al., 2005)
	S_n	The proportion of the development success	$1 - \frac{1}{1 + \left(\frac{\text{Salinity}}{19.09}\right)^{7.11}}$	(Groner et al., 2016)
	ε	Daily number of introduced planktonic salmon lice per salmon	External Pressure (0.002 ~ 0.5)	
Copepodid	T_c	Time in days for copepodids to attach on their host fish	4.6	(Stien et al., 2005)
	α	The proportion of copepodids to succeed in	Attachment Proportion (0.002 ~ 0.15)	

		attaching on fish		
Chalimus	T _{ch}	Time in days for chalimus to develop into pre-adult	$\left(\frac{74.7}{\text{Temperature} - 10 + .7 * 0.246}\right)^2$	(Stien et al., 2005)
	S _{ch}	Daily Proportion of the development success	$(1 - e^{(-0.229 * \text{Salinity})})^{24}$	(Groner et al., 2016)
Female Pre-adult	T _{pa}	Time in days for pre-adult to develop into adult	$\left(\frac{67.47}{\text{Temperature} - 10 + 67.47 * 0.0177}\right)^2$	(Stien et al., 2005)
	S _{pa}	Daily Proportion of the development success	$(1 - e^{(-0.229 * \text{Salinity})})^{24}$	(Groner et al., 2016)
Female Adult	ζ	The proportion of female adults that mate	$1 - \left(1 - \frac{m}{m+k}\right)^{1+k} \left(1 - \frac{m}{2(m+k)}\right)^{-1-k}$	(Groner et al., 2014)
	β	Number of Reproduction during the whole life of female adults	5	(Heuch et al., 2000)
	κ	the time between the hatching of one clutch and the release of the next egg string	-1.2*Temperature+19.64	(Groner et al., 2016)

Table 2. Equations in the model. Abbreviated terms can be found in Table 1.

Stage	Equation
Egg	$Gravid * 2 * \frac{\rho}{T_e} - \frac{Egg * (1 - S_e)}{T_e} - Egg/T_e$
Nauplius	$\frac{Egg}{T_e} + \varepsilon - \frac{Nauplius * (1 - S_n)}{T_n} - Nauplius/T_n$
Copepodid	$\frac{Nauplius}{T_n} - Copepodid * \frac{1 - \alpha}{T_c} - Copepodid * \alpha/T_c$
Chalimus	$Copepodid * \alpha/T_c - Chalimus * (1 - S_{ch}) - Chalimus * \frac{1}{2} * \frac{1}{T_{ch}}$
Preadult	$Chalimus * \frac{1}{2} * \frac{1}{T_{ch}} - Preadult * (1 - S_{pa}) - Preadult/T_{pa}$
Adult	$\frac{Preadult}{T_{pa}} - \zeta * Adult$
Gravid	$\zeta * Adult - Gravid / ((\frac{1}{T_e}) * \beta + \kappa * (\beta - 1))$

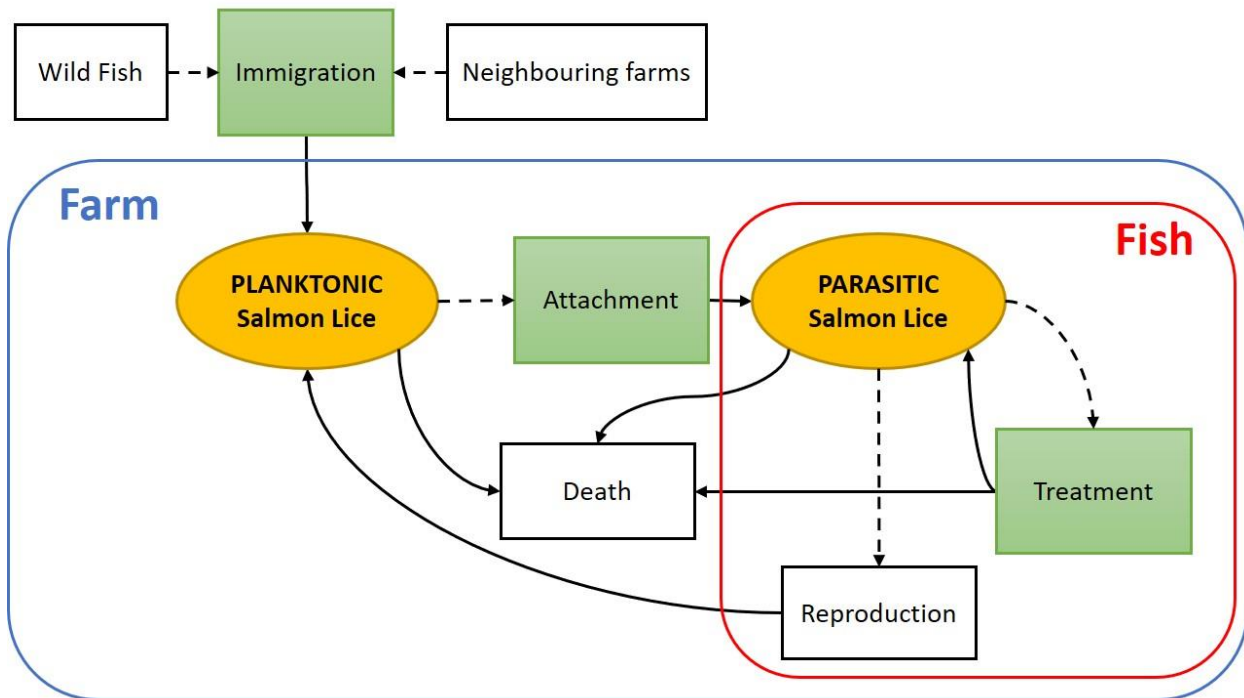


Fig. 1. Important events in the salmon lice life cycle on a salmon farm. The life cycle of salmon lice consists of planktonic and parasitic stages. Planktonic salmon lice are either introduced to the farm externally from neighbouring farms and/or wild fish or internally by the reproduction of parasitic adult salmon lice. Then, planktonic salmon lice become parasitic salmon lice by attaching to a host. Parasitic salmon lice can die through natural mortality, or from externally applied treatments. However, treatments will fail to kill all parasitic salmon lice. Dashed arrows indicate procedures that may lead to a change of state. The important events of immigration, attachment, and treatment (shown in green rectangles) are included as key parameters in the model, as external pressure, attachment proportion, and treatment efficacy, respectively.

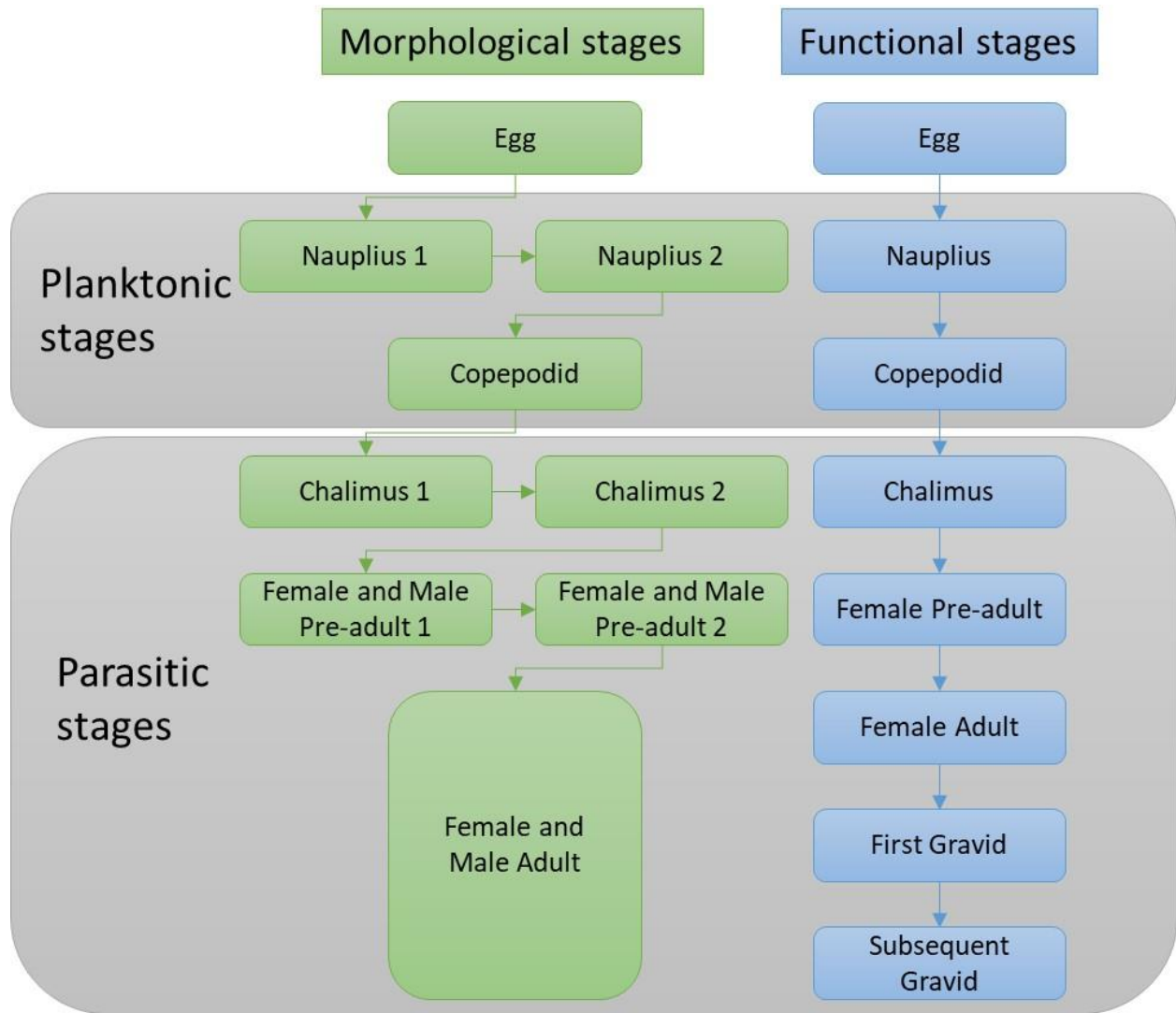


Fig. 2. Life cycle of salmon lice *Lepeophtheirus salmonis*. The nine morphological life cycle stages (left green column) grouped into the eight functional stages (right blue column) used within the model.

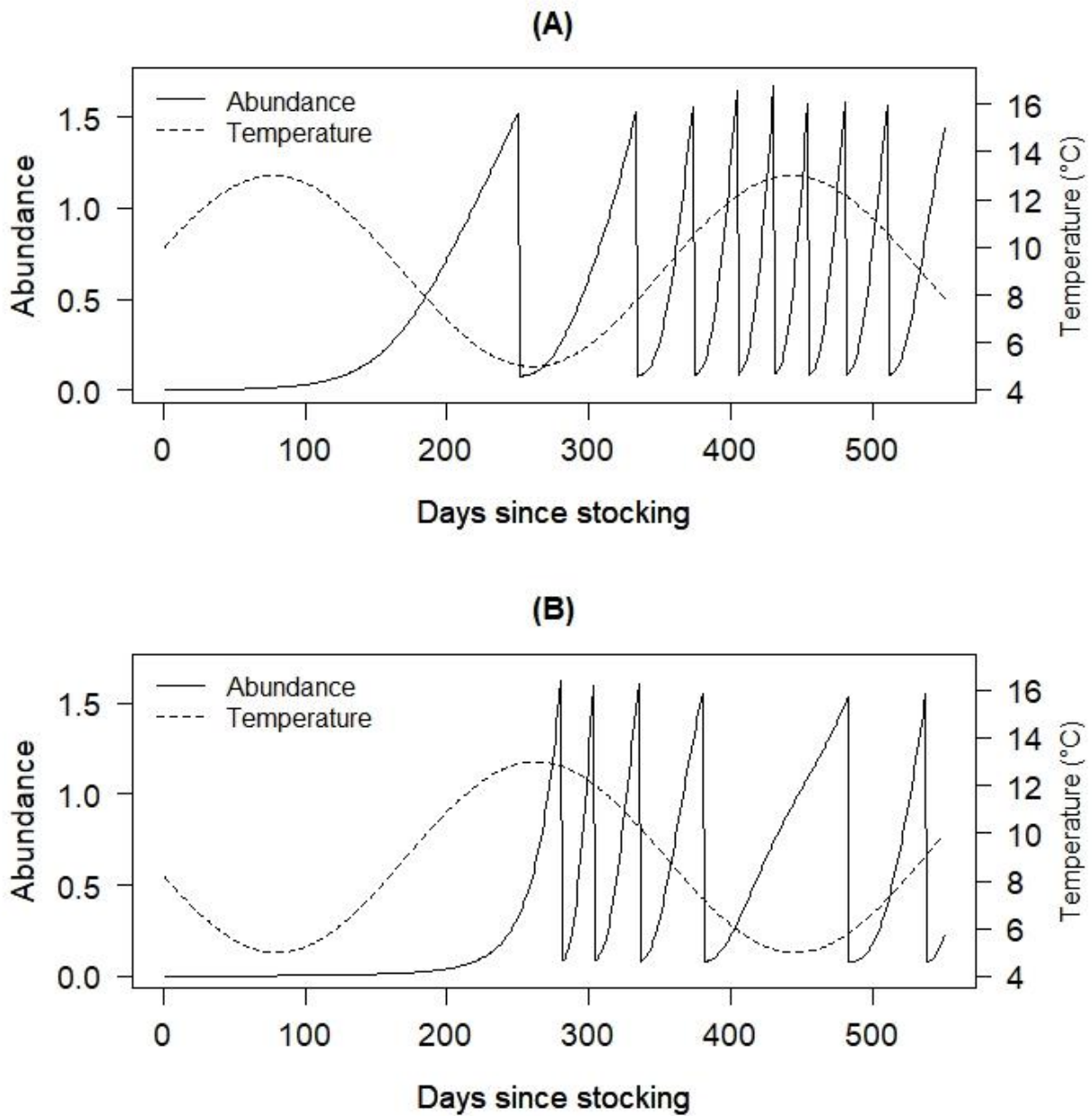


Fig. 3. Female adult salmon lice abundance and temperature during a production cycle stocked at two common times of year - (A) spring and (B) fall. Stocking at different times can generate substantially different patterns of salmon lice abundance. The temporal gaps between successive treatments differ depending on temperature. The external pressure, attachment proportion, and treatment efficacy parameters were set to 0.1, 0.01, and 0.95, respectively.

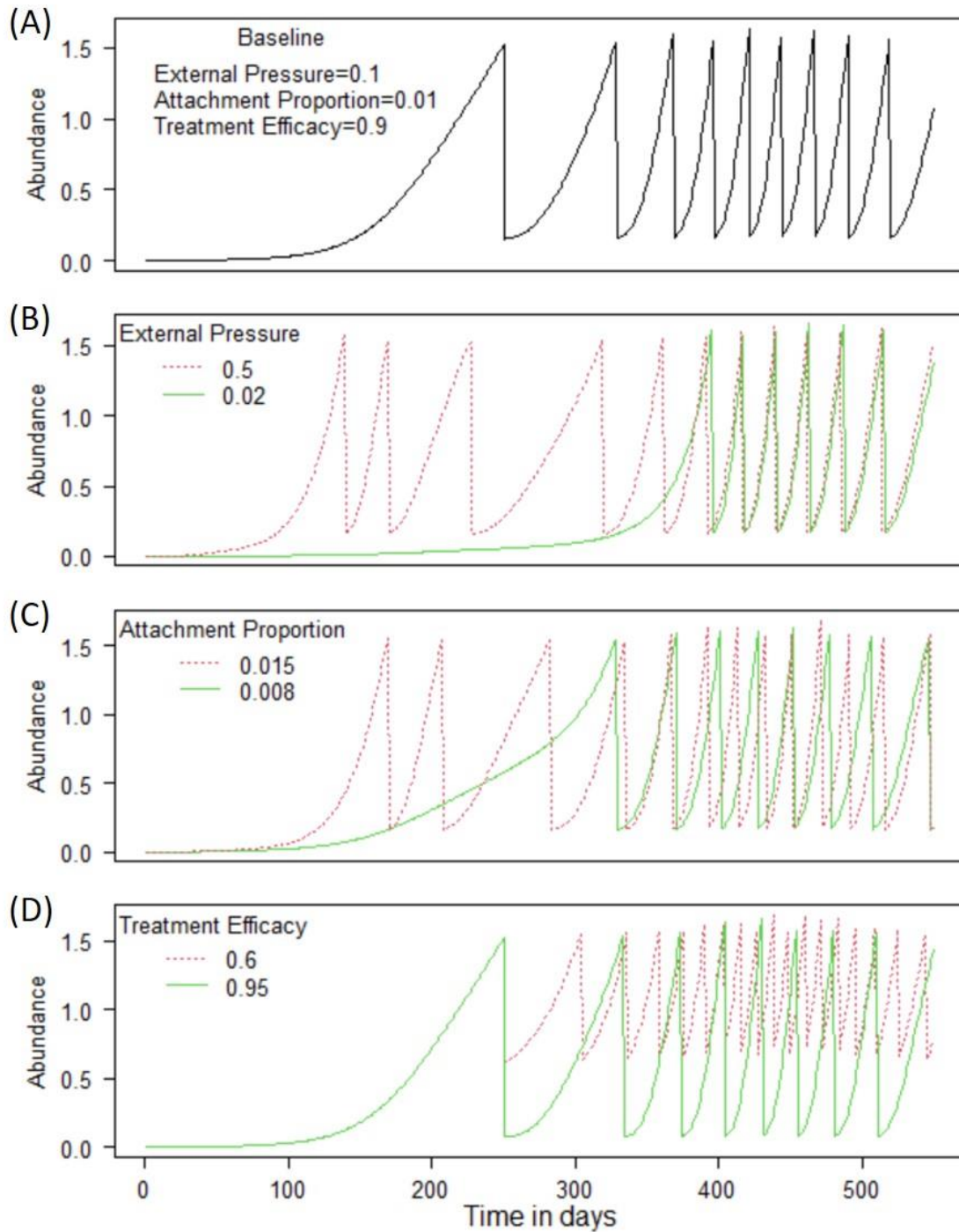


Fig. 4. Impact of changes to key parameter values. Adult female salmon lice abundance during a typical spring-stocked production cycle is illustrated with the different values of key parameters. (A) In the baseline simulation the values of external pressure, attachment proportion, and treatment efficacy were set to 0.1, 0.01, and 0.9, respectively. In the three remaining panels, one higher and one lower value for (B) External pressure, (C) Attachment proportion, and (D) Treatment efficacy, were selected for comparison to the baseline simulation.

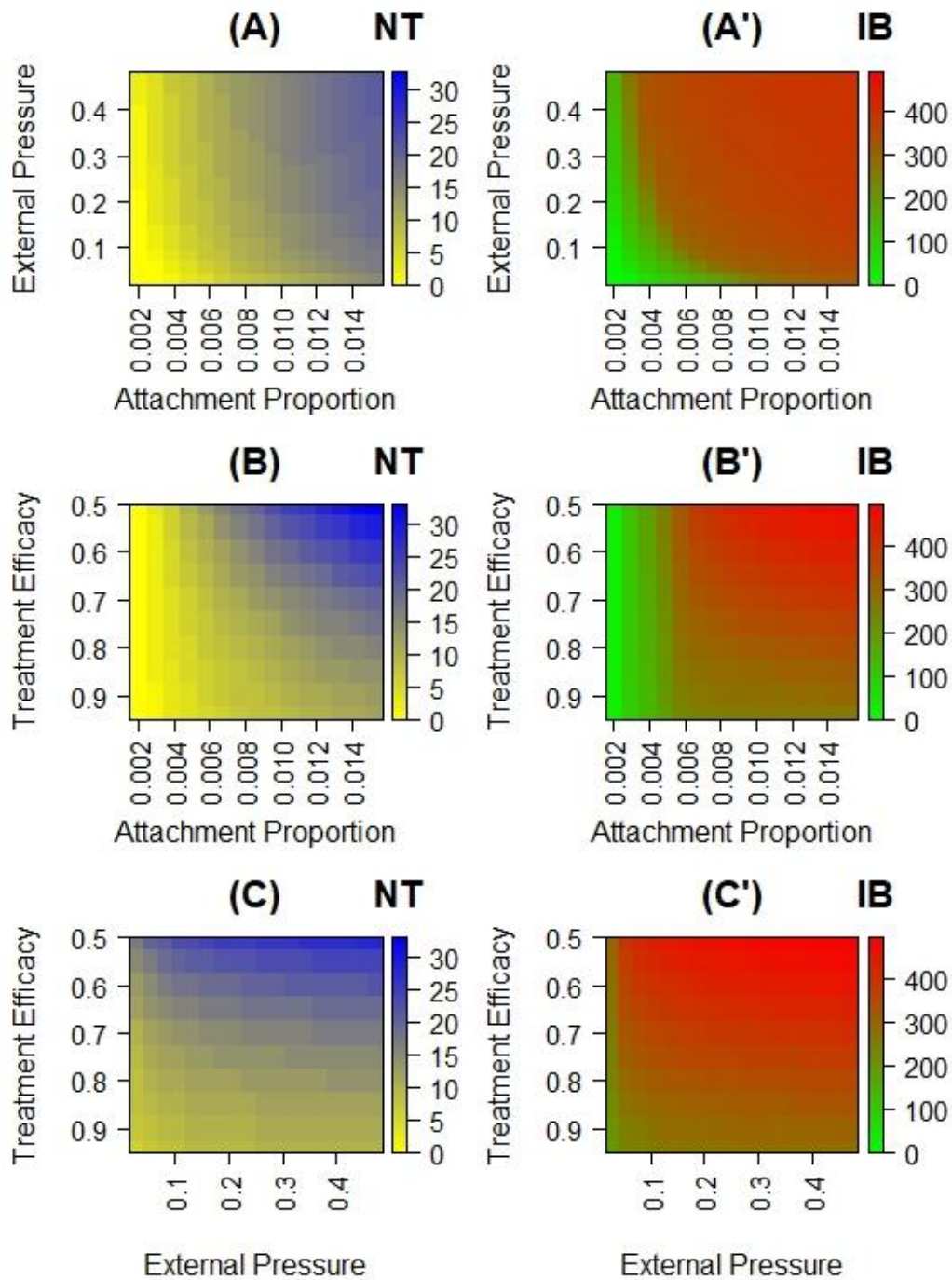


Fig. 5. The relative effect of the three key parameters. Two out of three parameters of external pressure, attachment proportion, and treatment efficacy are shown in each plot to show how the two parameters affect the number of treatments (NT – left-hand panels) and the infestation burden (IB – right-hand panels). When a parameter did not vary, external pressure, attachment proportion, and treatment efficacy were 0.1, 0.01, and 0.7, respectively. The treatment threshold was set at 1.5 adult females per salmon throughout.

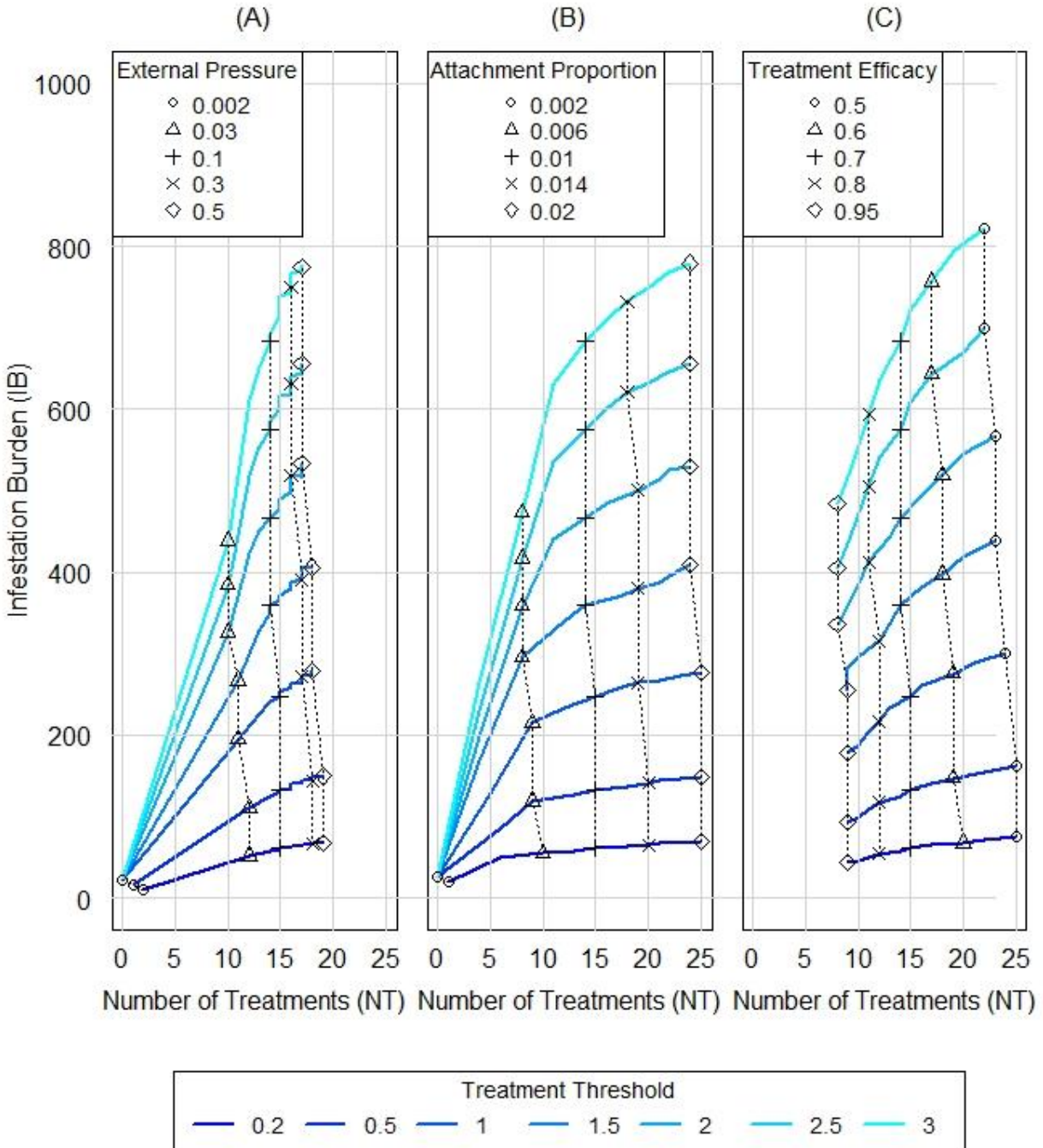


Fig. 6. The relation between the number of treatments (NT) and infestation burden (IB). Various values of (A) external pressure (B) attachment proportion and (C) treatment efficacy with multiple values of treatment threshold was used to simulate NT and IB in each scenario. The different levels of treatment threshold are shown as colored lines, while the different levels of parameters are shown as symbols. When the values of external pressure, attachment proportion, and treatment efficacy were not being varied, these were set to 0.1, 0.01, and 0.7, respectively.