Effects of Seasonally Varying Temperature and Salinity on the Dynamics of Sea Lice (*Lepeophtheirus salmonis*)

By

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A thesis submitted to the School of Graduate Studies in partial fulfillment of the requirements for the degree of

Master of Science

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St. John's, Newfoundland & Labrador

December 2015

Abstract

Sea lice (*Lepeophtheirus salmonis*) are an economically significant parasite in salmonid aquaculture. They exhibit temperature-dependent development rates and salinity-dependent mortality, which can greatly impact sea lice population dynamics, but no deterministic models have incorporated these seasonal variables. To understand how seasonality affects sea lice population dynamics, I derive a delay differential equation model with temperature and salinity dependence. I find that peak reproductive output in Newfoundland and British Columbia differs by four months. A sensitivity analysis shows sea lice abundance is most sensitive to variation in mean annual water temperature and salinity, whereas it is least sensitive to infection rate. Additionally, I investigate the effects of production cycle timing on sea lice management and find that optimal production cycle start times are between the 281st and 337th days of the year in Newfoundland. I also demonstrate that adjusting follow-up treatment timing in response to temperature can improve treatment regimes. My results suggest that effective sea lice management requires consideration of local temperature and salinity patterns.

Acknowledgements

Thank you to my supervisor, Amy Hurford, for her patient guidance. Thank you to my committee members, Crawford Revie and David Schneider, for sharing their advice and knowledge with me. Thank you to Jeffrey Bonazza, Sovit Chalise, Jonathan Ebel, Nichola Ellis, Abdou Fofana, Fábio Frazaõ, Shawn Leroux, Lucie Šmejdová, Amy Tanner, and Semra Yalcin for critiquing my writing. Finally, thank you to Bobbie Warren and her family for making me feel at home in Newfoundland.

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Chapter 1

Introduction and Overview

Sea lice (*Lepeophtheirus salmonis* and *Caligus spp.*) cost worldwide salmonid farmers over 305 million euros each year (Costello 2009). The largest cost of sea lice is the expenses involved in using pesticides to control them, with reduced fish growth also contributing to profit losses (Costello 2009). In addition to being an economic concern, sea lice have also been implicated in the decline of wild salmon populations (Marty et al. 2010, Krkošek et al. 2013). A recent task force of aquaculture practitioners and research scientists in the United Kingdom identified sea lice management as the fifth most important scientific advance needed to expand sustainable aquaculture, (Jones et al. 2014). This was considered the most important knowledge need in the diseases category.

Lepeophtheirus salmonis are marine ectoparasitic copepods within the order Siphonostomatoida, family Caligidae. They are specialists on salmonid hosts, while the closely related *Caligus spp.* are generalist parasites, which affect a number of fish species (Boxaspen 2006). Sea lice cause damage to their hosts by feeding on blood, mucus, and epidermal tissue, which leads to reduced growth in their host and increased susceptibility to secondary infections (Boxaspen 2006).

Lepeophtheirus salmonis hatch from double strands of eggs and develop through eight life stages: nauplius I, nauplius II, copepodid, chalimus I, chalimus II, pre-adult I, pre-adult II, and adult (Hamre et al. 2013). Sea lice mature faster through these stages when water temperatures are warmer. The relationship between temperature and development time is summarized and described by Stien et al. (2005). The nauplius and copepodid stages are planktonic. The copepodid stage seeks out a salmonid host and attaches itself to the host via a stylus. The chalimus stage is parasitic and non-motile. Male and female lice at this stage are still indistinguishable. When the chalimus stage molts into the pre-adult and adult stage, the sea louse becomes motile and the two sexes become distinguishable.

Sea lice do not readily tolerate fresh water and examples exist of heavily infested salmonids prematurely returning to freshwater, in order to rid themselves of their parasite burden (Thorstad et al. 2015). The most thorough treatment of the mortality-inducing effects of salinity was conducted by Johnson & Albright (1991). They examined and reported the viability of eggs and the survival of nauplii in salinities ranging from completely fresh water (0 psu) to salt water (32 psu). A simple linear model was fit to their nauplius survival data by Brooks & Stucchi (2005), who argued that salinity differences in the Broughton Archipelago of British Columbia could affect the accuracy of model predictions. Connors et al. (2008) report data on the relationship between mortality and salinity in adult sea lice, and found that a log-linear model fit their data. Bricknell et al. (2006) reported survival data on copepodids in relation to salinity. Data on the relationship between salinity and mortality for the chalimus and pre-adult stages was not found, although general mortality rates are comparable between pre-adults and adults, and mortality rates are slightly lower in chalimi (Stien et al. 2005).

Delay differential equations (DDEs) were first introduced to the field of mathe-

matical epidemiology by Sharpe & Lotka (1923), in order to account for incubation periods in malaria (*Plasmodium spp.*). A DDE model is similar to an ordinary differential equation (ODE) model, except a DDE model assumes there is a feedback lag in one or more biological processes. Often, this lag takes the form of a delay between birth and reaching reproductive maturity. Delay differential equations with state-based delays were first derived by Nisbet & Gurney (1983). These state-based models originally were used to describe insect populations where development from one instar to the next depended on mass. In recent years, the methods of Nisbet & Gurney (1983) have increasingly been used to model species with temperature dependent development, such as the bordered plant bug (*Largus californicus*; Johnson et al. 2015), or incubation, such as koi herpes virus (Omori & Adams 2011) and malaria (Beck-Johnson et al. 2013).

The first mathematical models of sea lice were DDEs with constant delays, developed by Tucker et al. (2002). Tucker et al. (2002) noted that their DDE model accurately described the population dynamics of a single laboratory cohort through multiple life history stages and that it could be used to plan chemotherapeutant treatment regimes. DDE models of sea lice with constant delays have been expanded upon through the SLiDESim model, derived in Revie et al. (2005) and utilized in Robbins et al. (2010) and Gettinby et al. (2011). Stien et al. (2005) proposed the use of state-based DDE models, such as those of Nisbet & Gurney (1983), in sea lice research and provided temperature-development curves that could be used in such a model. Several modellers have begun utilizing these temperature-development curves in stochastic models (Groner et al. 2014; Kristoffersen et al. 2014).

In this thesis, I derive a DDE model for farm-level sea lice population dynamics with temperature-dependent development and salinity-dependent mortality, which I utilize to examine several aspects of sea lice control. In the chapter two, I use the

model to explore some general trends in sea lice dynamics, with regards to temperature and salinity, to explore the intra-annual differences in reproductive output between case study sites in Newfoundland and British Columbia. Additionally, I conduct a sensitivity analysis of the model. In chapter three, I focus my attention on a pair of applied questions. First, I use the model to examine optimal timing of salmon farm production cycles, with regards to expected necessary sea lice treatments. Then, I address how optimal follow-up treatment timing depends on local temperature patterns.

1.1 Co-authorship Statement

The first manuscript in this thesis (chapter two) was co-authored with Amy Hurford and Crawford Revie, and was submitted for publication in *Epidemics*. I am the principle author for both chapters of this thesis, and was the principle contributor to project design, model derivation, model analysis, and manuscript preparation.

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Chapter 2

A Model For Sea Lice (*Lepeophtheirus salmonis*) Dynamics In A Seasonally Changing Environment

Abstract

Sea lice (*Lepeophtheirus salmonis*) are a significant source of monetary losses on salmon farms. Sea lice exhibit temperature-dependent development rates and salinity-dependent mortality, but to date no deterministic models have incorporated these seasonally varying factors. To understand how environmental variation and life history characteristics affect sea lice abundance, we derive a delay differential equation model and parameterize the model with environmental data from British Columbia and southern Newfoundland. We calculate the lifetime reproductive output for female sea lice maturing to adulthood at different times of the year and find differences in

the timing of peak reproduction between the two regions. Using a sensitivity analysis, we find that sea lice abundance is more sensitive to variation in mean annual water temperature and mean annual salinity than to variation in life history parameters. Our results suggest that effective sea lice management requires consideration of site-specific temperature and salinity patterns.

2.1 Introduction

The control of parasitic organisms is a major concern in marine aquaculture. In particular, sea lice (*Lepeophtheirus salmonis* and *Caligus spp.*) cause substantial economic losses on salmon farms (Costello 2009). Due to their economic importance, control of sea lice on salmon farms has been named one of the top priorities in aquaculture research by both scientists and aquaculture practitioners (Jones et al. 2014). Adequate control of sea lice is predicated on the ability to predict future lice levels from current population and environmental trends, as well as predicting the effectiveness of different treatment regimes. These two needs can be accomplished through mathematical modelling and it is imperative that tractable and biologically sound models are developed to aid practitioners in decisions regarding sea lice dynamics.

Seasonal environmental variability plays a major role in the dynamics of many disease systems (Altizer et al. 2006). Temperature and salinity affect several characteristics of sea lice life history (summarized in Table 2.1), thus models of sea lice dynamics must be able to incorporate the effects of seasonally varying temperature and salinity on the sea louse lifecycle.

A variety of deterministic (Revie et al 2005, Stien et al. 2005, Robbins et al. 2010, Gettinby et al. 2011, Aldrin et al. 2013, Groner et al. 2014, Kristoffersen et al. 2014) and stochastic (Aldrin et al. 2013, Groner et al. 2014) models have been derived

to predict sea lice dynamics. Revie et al. (2005) derived a life stage model with fixed delays and constant mortality rates that formed the basis for the simulation tool, SLiDESim. Robbins et al. (2010) utilized SLiDESim to search for optimal treatment strategies in Scottish farms. Gettinby et al. (2011) tested the SLiDESim model on sea lice collection data from the Hardangerfjord in south-west Norway. These authors concluded that for the model to be utilized in evaluating treatment strategies, a better understanding of the underlying biological and environmental factors, including temperature-dependent maturation and salinity-dependent survival, was necessary. Kristoffersen et al. (2014) used Bělehrádek functions derived in Stien et al. (2005) to estimate degree-days needed for sea lice to mature from one stage to the next and derived a life stage model with temperature-based delays and constant mortality rates. Aldrin et al. (2013) used a stochastic spatio-temporal model to show how seawater temperatures, fish stock population, and distance between farms contributed to predicted sea lice counts. Groner et al. (2014) created a stochastic matrix population model to examine the effects of seasonally varying temperature on treatment schemes and louse mate limitation.

A deterministic model capable of accounting for both the effects of seasonally varying temperature on sea lice maturation, and the effects of seasonally varying salinity on sea lice mortality has not yet been developed (Kristoffersen et al. 2014). Stien et al. (2005) suggest that the delay differential equation models described in Nisbet & Gurney (1983) as a method to address this need. Delay differential equations models of this type have been successfully used in epidemiological models of koi herpes virus (Omori & Adams 2010) and malaria (Beck-Johnson et al. 2014).

We present a delay differential equation model of the *Lepeophtheirus salmonis* life-cycle with temperature-dependent stage durations, salinity-dependent mortality, and time-dependent temperature/salinity. Where possible, model parameters are fitted to

values from the literature for the species, *Lepeophtheirus salmonis*. The time dependent basic reproductive ratio, $R_0(t)$, is calculated numerically to quantify seasonal differences in sea lice replenishment at sites in British Columbia and southern Newfoundland, Canada. Additionally, a sensitivity analysis is conducted to identify the parameters that most substantially affect the model predictions.

2.2 The Model

We developed a model for sea lice population dynamics on salmon farms that includes temperature-dependent maturation delays and salinity-dependent mortality. *Lepeophtheirus salmonis* exhibit 8 distinct life stages, consisting of nauplius I/II, copepodid, chalimus I/II, pre-adult I/II, and adult (Hamre et al. 2013). For the purpose of modelling, we assume that sea lice may be in 1 of 4 possible functional states: planktonic non-infectious nauplii (P), infectious copepodids (I), non-reproductive chalimus and pre-adults (C), or adult females, (A). Each individual matures through the states in order from nauplius (P), to copepodid, (I), to chalimus (C), and finally to adult, of which we only model females (A) (Fig. 2.1).

The length of time that a nauplius or chalimus requires to mature to their respective next life stages depends on water temperature (Table 2.1). Let $\gamma_x(T(t))$ be a function that describes the rate of change in the level of development for a given stage x, where x is equal to P or C, as it depends on temperature (T), which changes over time (t). For notational simplicity, we write simply $\gamma_x(t)$, because given functions that describe how temperature changes with respect to time ($T(t)$), and how the development rate changes with respect to temperature ($\gamma_x(T)$), we can then determine how the development rate changes with respect to time ($\gamma_x(t)$) without needing to explicitly reference the dependence on temperature.

The waiting times associated with maturation are such that a cohort exiting a state x at time t, will all have entered that stage at $t-\tau_x(t)$. The waiting time, $\tau_x(t)$, depends on the development rate, $\gamma_x(t)$, and is defined as the length of time that it takes sea lice to reach a threshold development level, q'_x, given that they entered the stage x with a development level $q_x = 0$. As such, $\tau_x(t)$ is implicitly defined as,

$$q'_x = \int_{t-\tau_x(t)}^{t} \gamma_x(t)\,\mathrm{d}t \tag{2.1}$$

(Nisbet & Gurney, 1983).

Natural mortality occurs in all stages at a per capita rate $\mu_y(S(t))$, where y is P, I, C, or A. Natural mortality is a function of salinity $S(t)$, which is a function of time (t). For notational simplicity, we write simply $\mu_y(t)$, because given functions that describe how salinity changes with respect to time $(S(t))$, and how the mortality rate changes with respect to salinity $(\mu_y(S))$, we can then determine how the mortality rate changes with respect to time $(\mu_y(t))$ without needing to explicitly reference the dependence on salinity. Not all members of a cohort who enter a stage x at time $t-\tau_x(t)$ survive to mature at time t. The proportion of the cohort that survive the maturation period is,

$$\phi_x = \mathrm{e}^{-\int_{t-\tau_x(t)}^{t} \mu_x(t)dt}.$$

The proportion of eggs that produce viable nauplii is a function of salinity, $v(t)$. All other events in the sea lice life history are assumed to not depend on temporally varying quantities and are assumed to occur at constant per capita rates. The complete model is a system of delay differential equations,

$$\frac{dP}{dt} = \eta\epsilon v(t)A(t) - \eta\epsilon v(t-\tau_P)A(t-\tau_P)\frac{\gamma_P(t)}{\gamma_P(t-\tau_P)}\phi_P(t) - \mu_P(t)P(t), \tag{2.2}$$

$$\frac{dI}{dt} = \eta\epsilon v(t-\tau_P)A(t-\tau_P)\frac{\gamma_P(t)}{\gamma_P(t-\tau_P)}\phi_P(t) - \iota N_f I(t) - \mu_I(t)I(t), \tag{2.3}$$

$$\frac{dC}{dt} = \iota N_f I(t) - \iota N_f I(t-\tau_C)\frac{\gamma_C(t)}{\gamma_C(t-\tau_C)}\phi_C(t) - \mu_C(t)C(t), \tag{2.4}$$

$$\frac{dA}{dt} = \frac{1}{2}\iota N_f I(t-\tau_C)\frac{\gamma_C(t)}{\gamma_C(t-\tau_C)}\phi_C(t) - \mu_A(t)A(t), \tag{2.5}$$

$$\frac{d\tau_P}{dt} = 1 - \frac{\gamma_P(t)}{\gamma_P(t-\tau_P)}, \tag{2.6}$$

$$\frac{d\tau_C}{dt} = 1 - \frac{\gamma_C(t)}{\gamma_C(t-\tau_C)}, \tag{2.7}$$

where η is the number of eggs per egg string, ϵ is the rate of egg string production, ι is the rate of infection per fish, N_f is the number of fish on the farm, and all model parameters are summarized in Table 2.2. Equations (2.6) and (2.7) arise from differentiating equation (2.1) with respect to time (Nisbet & Gurney 1983). The $\gamma_x(t)/\gamma_x(t-\tau_x)$ terms arise because we wanted to ensure a correspondence between our model (which lumps all individuals with a development level $q_x < q'_x$ together into one state) and a model that treats the development level as a continuous quantity (Nisbet & Gurney 1983; see Appendix A for further details).

It should be noted that our model lacks a mechanism for density dependence in the sea lice population. Sea lice could exhibit density dependence due to an Allee effect caused by difficulties in mate finding at low densities (Krkošek et al. 2012, Groner et al. 2014). They may also exhibit density dependence due to host mortality or decreased reproduction at high intensities. In an aquaculture setting, managers will typically intervene with chemotherapeutics before any natural density-dependent regulation of the sea louse population can occur.

2.3 Model Parameterization

For our model, the maturation rate is the reparameterized inverse of the Bělehrádek functions describing minimum development time, in days, as a function of temperature

(Stien et al. 2005),

$$\gamma_x(T) = \frac{1}{\hat{d}_x}\left(\frac{(T - T_{ref} +_x T_{min})}{{}_xT_{min}}\right)^2. \tag{2.8}$$

The shape of the function is described by the duration of the life stage ($\hat{d}_x$) at the reference temperature (T_{ref}) and by the location of an asymptote at $T_{ref} -_x T_{min}$. The terms $\hat{d}_P$ and $\hat{d}_C$ are equal to the ${\beta_2}^{-2}$ terms for time from hatching to copepodid and time from infection to adult females in Stien et al. (2005). The ${}_PT_{min}$ and ${}_CT_{min}$ terms are the product of β_1 and β_2 from Stien et al. (2005). The reference temperature is 10°C.

Water temperature ($T(t)$) and salinity ($S(t)$) on salmon farms varies over time. We use sinusoidal functions to describe the general annual patterns,

$$T(t) = \bar{T} - \tilde{T}\cos\left(\frac{2\pi t}{365}\right), \tag{2.9}$$

$$S(t) = \bar{S} - \tilde{S}\cos\left(\frac{2\pi t}{365}\right), \tag{2.10}$$

where $\bar{T}$ is the average annual temperature, $\bar{S}$ is the average annual salinity, and $\tilde{T}$ and $\tilde{S}$ are the respective amplitudes of the cosine functions. Sinusoidal functions of the form,

$$T(t) = \bar{T} + \tilde{T}_1\sin\left(\frac{2\pi t}{365}\right) + \tilde{T}_2\cos\left(\frac{2\pi t}{365}\right), \tag{2.11}$$

$$S(t) = \bar{S} + \tilde{S}_1\sin\left(\frac{2\pi t}{365}\right) + \tilde{S}_2\cos\left(\frac{2\pi t}{365}\right), \tag{2.12}$$

were fit, using the lm() function in R, to monthly temperature and salinity data from a salmon farm in the Broughton Archipelago of British Columbia (Marty et al., 2010; Fig. 2.2D and E) and to quarter-hourly temperature and salinity data from a salmon farm on the southern coast of Newfoundland (data provided by the Aquaculture Real-

Time Integrated Environmental System; Fig. 2.2D and E).

Mortality is related to salinity via linear and log-linear relationships from the literature. The salinity-mortality relationship ($\mu_A(S)$) is log-linear for adult sea lice (Connors et al. 2008). We assume that the mortality rate for adults and chalimi ($\mu_C(S)$) is similar. The salinity-mortality relationship for nauplii ($\mu_P(S)$) is a linear model from Brooks & Stucchi (2006), which is fit to data from Johnson & Albright (1991). We assume that the mortality rate for nauplii and copepodids ($\mu_I(S)$) is similar.

The number of eggs per egg string (η) was parameterized using data from Heuch et al. (2000). The lower bound on the egg string production rate (ϵ) is taken from Mustafa et al. (2000) and is used as the default egg string production rate. The upper bound for the egg string production rate, used in the uniform distribution for the sensitivity analysis, was taken from Heuch et al. (2000). Egg viability ($v(S)$) consists of a linear model fit to salinity-survivorship data from Johnson & Albright (1991).

The infection success rate (ι) is dependent on a number of variables and is not well understood at the farm level. As such, a wide range of values, from 0.001 to 0.9, were used in the sensitivity analysis and a value of 0.01 was chosen as the default value.

2.4 Model Dynamics

We numerically solved the system of equations (2.2)-(2.7) using the PBSddesolve package in R. Due to the lack of density dependence our model produces either unbounded growth or extinction (Figs. 2.3 and 2.4). The abrupt changes in the trajectory slope shown in Fig. 2.3 indicate the beginning of successive generations. When the initial infection occurs on the coldest day of the year, the second cohort will take less days to

mature to adulthood than the first, due to warming temperatures. Sites with higher average annual temperatures will take less time for cohorts to reach adulthood than sites with lower average annual temperatures (Fig. 2.3).

We ran the model with average annual temperatures of 6, 7, 8, or 9°C and average annual salinities of 14, 16, 18, or 20 psu. After simulating four years, environmental conditions that resulted in > 1 adult female per fish were considered to be favourable to sea lice, while environmental conditions with < 1 adult female per fish were considered unfavourable. Sea lice in low temperature/low salinity environments will die out. As either temperature or salinity increases, conditions for the sea lice population improve. Given the parameter values we used (Table 2.2), sea lice populations are viable at ≥ 18 psu at all temperatures investigated and sea lice populations can persist at lower salinities in warmer climates (Fig. 2.4).

2.5 Time Dependent Reproductive Ratio $(R_0(t))$

The basic reproductive ratio, R_0, is commonly used as a measure of reproductive success in populations. The basic reproductive ratio can be defined as the "expected number of secondary individuals produced by an individual in its lifetime" (Heffernen et al. 2005) and acts as a threshold condition that indicates either population persistence or extinction (Caswell 2009). When $R_0 \geq 1$ the population will grow with each subsequent generation and persist, whereas when $R_0 \leq 1$ the population will shrink with each subsequent generation until extinction. In seasonal systems, R_0 will depend on the time that the infection is introduced to the system. We define $R_0(t)$ such that it is the number of second generation adult females produced by a single adult female, who enters the system at time, t. As such, $R_0(t)$ depends on the probability that the nauplius survives each successive life stage and the timing and duration of egg string

hatching during the adult female stage (see Appendix B). We determined $R_0(t)$ numerically by augmenting the system of equations (2.2)-(2.7) with a delay differential equation describing the number of adult females in the second generation, where this second generation does not reproduce (see Appendix B for details).

In the Broughton Archipelago, temperatures are favourable year round (5th percentile = 6.61, median = 8.90, 95th percentile = 11.75), while salinity levels are very favourable to sea lice survival in the winter and very unfavourable during the summer (5th percentile = 16.11, median = 27.30, 95th percentile = 32.15). The environmental conditions most favourable to sea lice growth are asynchronous because high sea surface temperatures coincide with low salinities and visa versa. We find $R_0(t)$ to be highest in December, when salinity is high, but temperatures are low (Fig. 2.2A). As such, sea lice that enter the farm in December will go on to produce the most offspring despite having longer generation times than sea lice that hatch in the summer months (Fig. 2.2B). The value of $R_0(t)$ is not < 1 at any point during the year, so an adult female that enters at any given time can reasonably be expected to replace itself over the course of its lifetime. $R_0(t)$ reaches a peak of 475.13 in December and a low of 23.68 in June and has a mean value of 220.98.

In southern Newfoundland, temperatures are colder (5th percentile = 2.48, median = 6.00, 95th percentile = 13.20) than the Broughton Archipelago site and sea lice maturation can take a long time during the winter months. Salinity is mostly constant year round (5th percentile = 19.92, median = 22.77, 95th percentile = 26.06), with a low in the spring months. In southern Newfoundland, the environmental conditions that are most favourable to sea lice growth are synchronous: both high temperatures and high salinities occur towards the end of the summer. We find that $R_0(t)$ is highest in August (Fig. 2.2A), after maturation times plummet during the summer months (Fig. 2.2B) and when time to maturity is shortest (Fig. 2.2B). The value of $R_0(t)$

is not < 1 at any point during the year, so an adult female that enters at any given time can reasonably be expected to replace itself over the course of its lifetime. $R_0(t)$ reaches a peak of 125.41 in August, a low of 3.27 in December and has a mean of 46.72.

2.6 Sensitivity Analysis

We conducted a sensitivity analysis on seven model parameters to analyze the effects of their variation on the abundance of female adult sea lice (A). Parameter distributions were estimated from the literature (Table 2.3). A Latin Hypercube Sampling (LHS) scheme was used to sample the parameter space and partial rank correlation coefficients (PRCC) were used as a test statistic for the sensitivity analysis (Blower & Dowlatabadi 1994).

The simulation begins with only adult females and the only parameter that affects adult mortality is mean salinity ($\bar{S}$, Fig. 2.5A). After the cohorts start maturing the size of the adult female population is also affected by parameters relating to maturation, infection, and reproduction (Fig. 2.5A and B). The three most sensitive parameters at 180 days were mean temperature ($\bar{T}$), mean salinity ($\bar{S}$), and the number of eggs per egg clutch (η; Fig. 2.5A and B). Female sea lice abundance is more sensitive to the development time of the chalimus and pre-adult stages at 10°C ($\hat{d}_C$) than it is to the development time of the nauplius stage at 10°C ($\hat{d}_P$; Fig. 2.5A). Despite a large level of uncertainty about the value of the infection rate (ι), the model is least sensitive to infection rate, out of the seven parameters examined (Fig. 2.5B).

2.7 Discussion

Sea lice control is one of the top priorities in aquaculture research (Jones et al. 2014). Temperature and salinity affect maturation rates, mortality, and egg viability; so control of sea lice relies on understanding their population dynamics in relation to their environment. We derived a deterministic model of the sea louse lifecycle, with temperature-dependent maturation and salinity-dependent mortality. We conducted numerical analyses to: characterize sea lice population dynamics for different environmental conditions, determine the time-dependent basic reproductive number, R0(t), for BC and southern Newfoundland, and perform a sensitivity analysis.

Quantitative predictions we make using this model depend on the parameter values, notably the combination of the infection rate (ι) and the number of farmed fish (N_f). Our sensitivity analysis shows that, out of the seven parameters examined, the model is least sensitive to ι, even though we varied it over three orders of magnitude. However, estimates of this parameter value at the farm level do not exist to our knowledge and it is possible that the infection rate is much lower than we anticipate. The number of fish at a farm site is well known for any given farm site, but can vary over several orders of magnitude between farm sites. Therefore, it should be understood by aquaculture practitioners that the quantitative predictions we make are dependent on the assumptions that that the number of fish (N_f) and the infection rate (ι) are near the values specified in Table 2.2.

There is a substantial difference between the timing of the peak in $R_0(t)$ for British Columbia and Newfoundland. We found that the peak value of $R_0(t)$ for both the British Columbia and the Newfoundland sites occurred during peak salinity levels, although in Newfoundland the salinity levels were fairly constant and the highest salinity levels also coincided with the highest sea surface temperatures. As such, optimal treatment schemes will also differ between these two sites. In both the Broughton

Archipelago in British Columbia and southern Newfoundland, fecund sea lice are able to replace themselves at all times of the year, however, well-timed treatments may result in slower population growth, ultimately leading to fewer required treatments over a production cycle.

We also found that the mean $R_0(t)$ was much higher at the British Columbia site than at the Newfoundland site. In considering just the environmental data, it is not clear that this would necessarily be the case. On the one hand, British Columbia has higher mean temperatures, higher mean salinity, and higher maximum salinity: all conditions that are conducive to sea lice growth, while on the other hand, British Columbia also has lower minimum salinity and favourable environmental conditions for sea lice growth are not synchronous as they are in Newfoundland. Contrary to our results, it is generally acknowledged that control of sea lice is typically more straightforward in British Columbia than in Newfoundland. Our model suggests that something other than temperature and salinity's effects on louse life history may be responsible for the more successful management of sea lice in British Columbia. This may be the result of farm-level and regional-level management decisions, population size of wild hosts, potential genotype differences in sea lice populations (Yazawa et al. 2008, Skern-Mauritzen et al. 2014), or hydrodynamical differences.

The comparison of the British Columbia and the Newfoundland sites suggest no general patterns. To understand the dynamics of sea louse fecundity at other sites, environmental data would need to be provided for analysis using our model. This is especially pertinent as salinity patterns may vary substantially over small spatial scales due to their proximity to rivers, and even two sites within the same broad geographic region potentially could have very different salinity patterns.

It is important to note that the $R_0(t)$ we calculate is not a threshold condition for sea lice epidemics, since subsequent generations will hatch throughout the year and

experience their own $R_0(t)$ values. $R_0(t)$ also does not show the size of, or even the instantaneous growth rate of, the population. Rather, our $R_0(t)$ provides a means of comparing reproductive output at different times of the year. The methods outlined in Zhao (2015) provide a framework to analytically determine how environmental conditions affect the threshold for sea lice outbreaks. One of the advantages to using a deterministic delay differential equation approach is that the theoretical approaches outlined in Zhao (2015) can be utilized.

Our sensitivity analysis found that adult female sea lice abundance is most sensitive to average annual temperature and salinity. This is likely because a large number of parameters depend on temperature ($\tau_P(t)$ and $\tau_C(t)$), salinity ($\mu_P(t)$, $\mu_I(t)$, $\mu_C(t)$, and $\mu_A(t)$) or both ($\phi_P(t)$, $\phi_C(t)$). Our findings that lice abundance is more sensitive to the development rate of the combined chalimus/pre-adult stage than to the development rate of the nauplius stage is in line with sensitivity analyses conducted by Revie et al. (2005) and Groner et al. (2014), who found that sea lice numbers were most sensitive to the survival through the pre-adult stage, of which development time plays a major role.

In addition to the need for more empirical studies into the temperature-maturation relationship of chalimus/pre-adult stages that has already been highlighted, a number of avenues exist to improve model accuracy and usability. Because eggs per clutch (η) and egg clutch production rate (ϵ) are two parts of the same product, the difference in PRCC values between them is solely due to the distribution we sampled from for each parameter. Egg clutch size is highly variable and the number of eggs per egg string has been suggested to be dependent on the temperature history of the female louse during development (Ritchie et al. 1993, Heuch et al. 2000). Sea lice that develop in colder temperatures are suggested to produce more eggs per egg string as a compensatory strategy for slower development, although the exact mechanism linking

temperature history and egg string length is unknown (Ritchie et al. 1993). As such, a better understanding of the relationship between temperature and egg production is needed before it can be incorporated into mechanistic models of sea lice development. Difficulties in mate finding at low densities has also been indicated as a major facet of reproductive success (Stormoen et al. 2013, Groner et al. 2014). Future models may wish to explore the impacts of these biological complexities.

Salmon farms regularly treat for sea lice, which impacts population numbers at a level greater than environmental factors. The timing of treatment, in regards to the typical salmon farming cycle has been shown to have a large impact on sea lice numbers (Revie et al. 2005). Because salmon can be introduced to saltwater pens at most times of the year, our model is well suited to examining the effects of treatment timing on sea lice numbers. We conclude by recommending that future modelling studies incorporate detailed seasonal characteristics of their chosen study site into models of sea lice population dynamics.

2.8 Figures & Tables

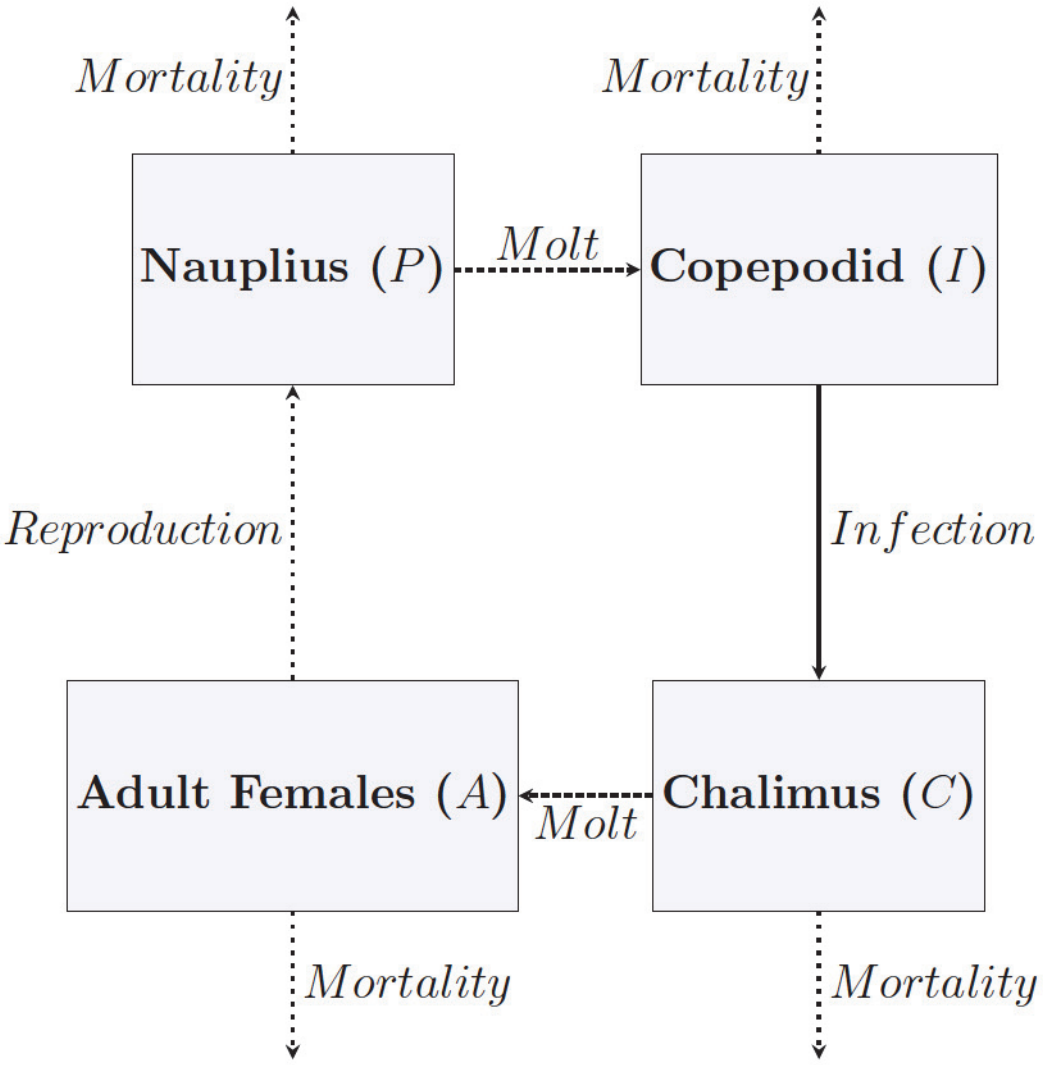

Figure 2.1: Modelled life cycle of the sea louse. Dashed arrows indicate aspects of the life history affected by temperature. Dotted arrows indicated aspects of the life history affected by salinity.

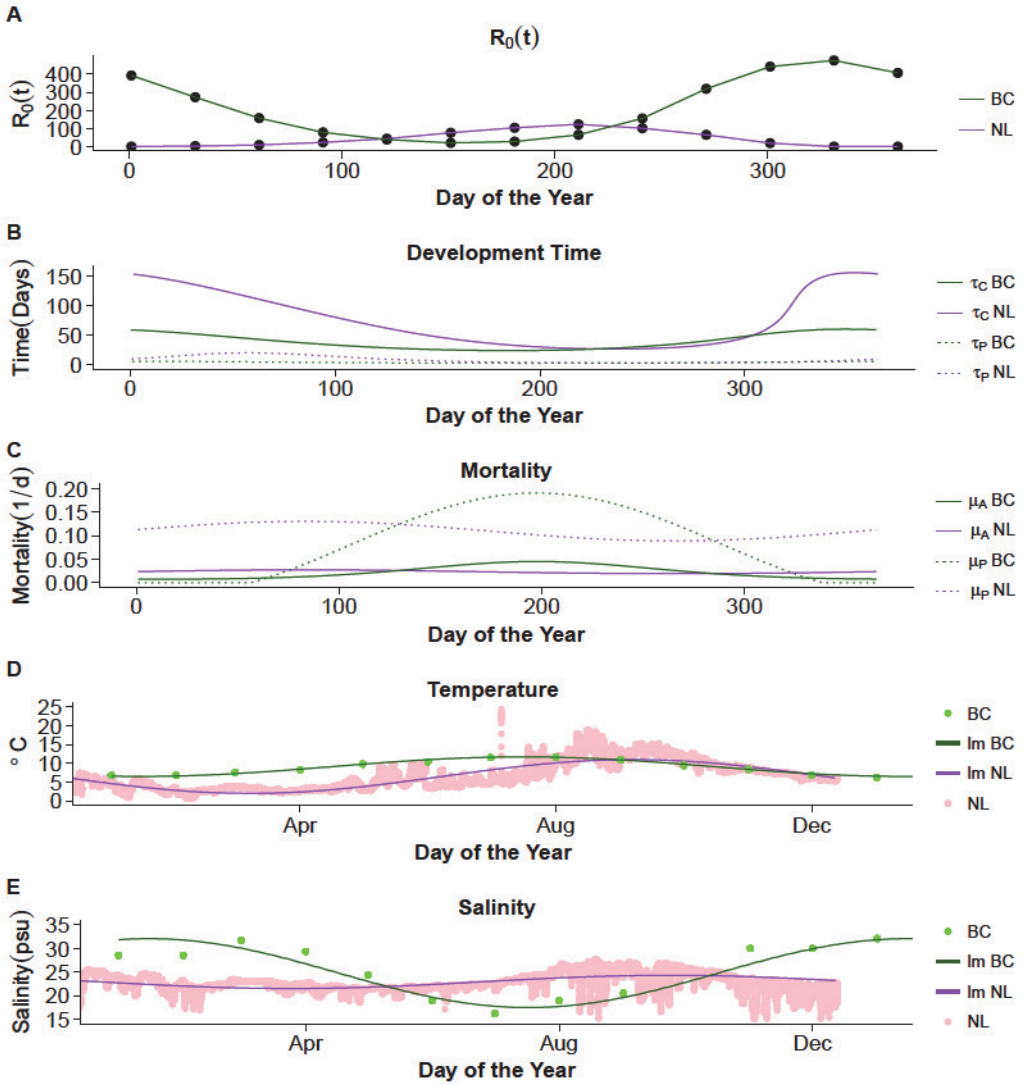

Figure 2.2: $R_0(t)$ is presented for sites in Newfoundland and British Columbia (A). $R_0(t)$ is affected by maturation time (B) and the mortality rates of parasitic stages $\mu_A(t)$ and free-living stages $\mu_P(t)$ (C). Temperature (D) and salinity (E) for the two sites affect development time (B) and mortality (C), respectively.

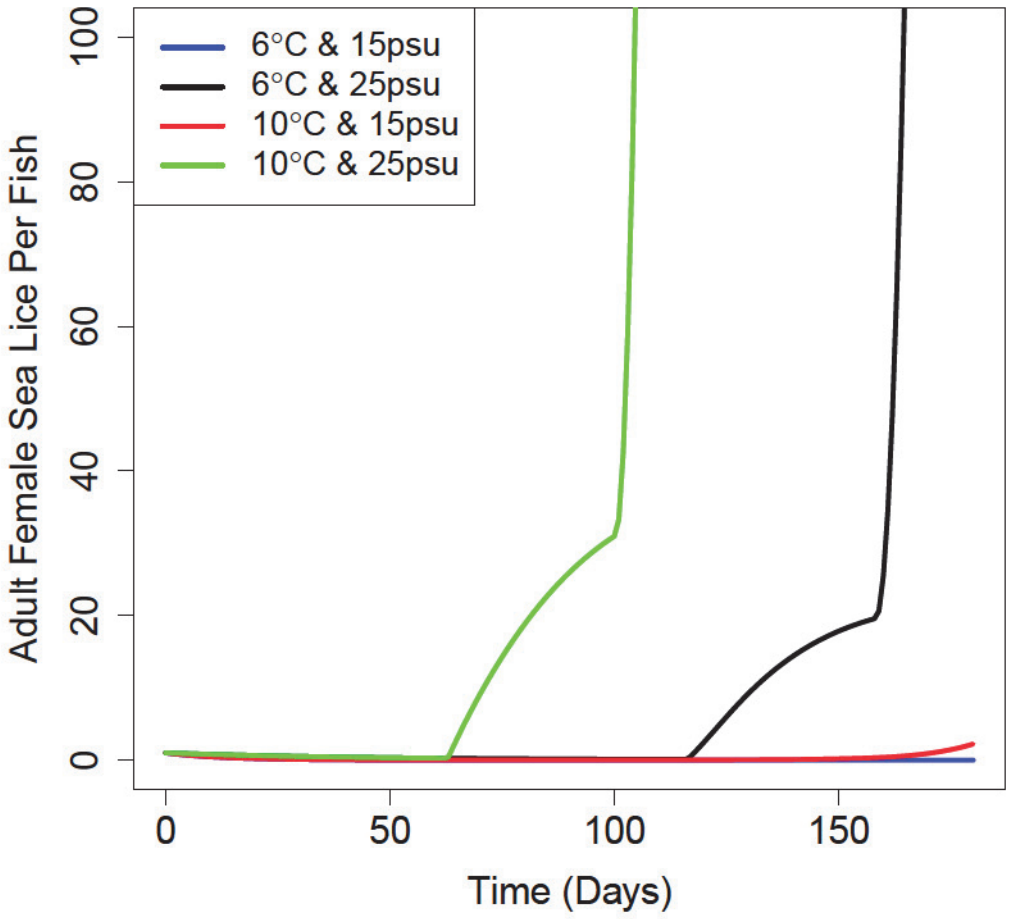

Figure 2.3: Four model simulations under high/high, high/low, low/high, low/low average annual temperature and salinity values. Amplitudes were 4 °C and 2 ppt for all simulations. All simulations began on the coldest, least saline day of the year. Note that increasing temperature increases parasite numbers and decreases generation time. Note also that generation time decreases as the simulation progresses, due to warming temperatures. The sea lice population dies off under the low/low temperature/salinity condition.

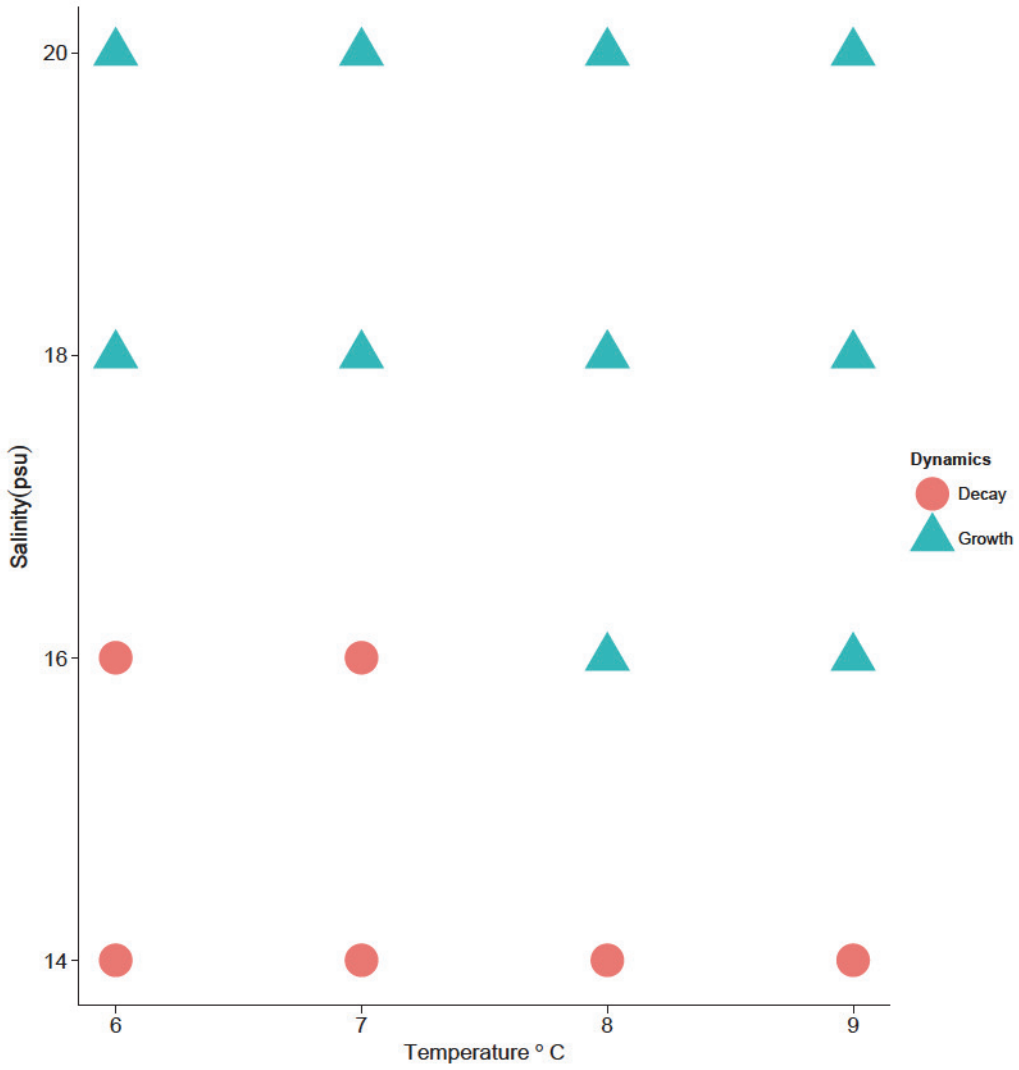

Figure 2.4: Long term persistence/extinction dynamics at sixteen temperature and salinity combinations. Amplitudes were 4 °C and 2 psu for all simulations. Environmental conditions that result in > 1 adult female sea louse per fish after four years are shown as triangles. Environmental conditions that result in < 1 are shown as circles.

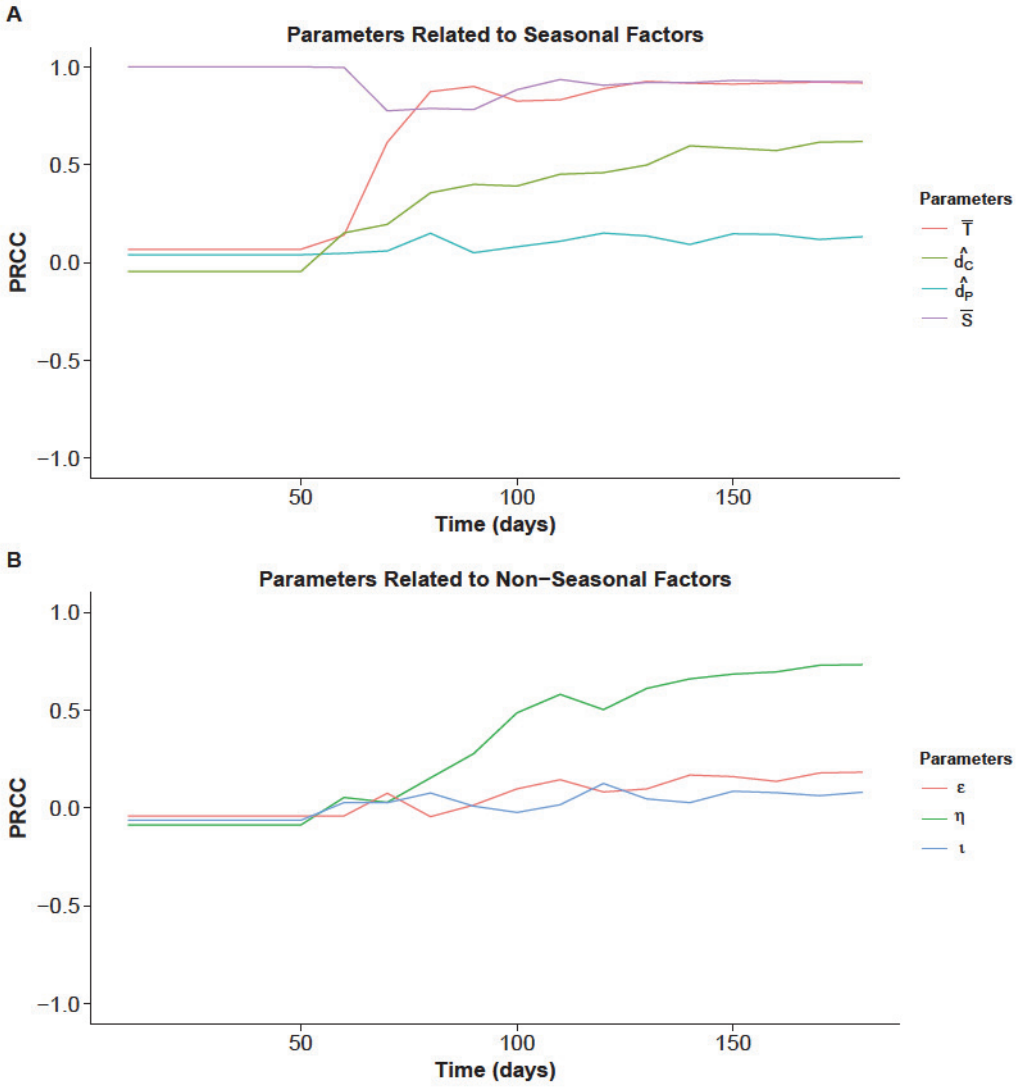

Figure 2.5: Sensitivity to 7 parameters. The PRCC values at 180 days (from highest PRCC to lowest) are average annual salinity, $\bar{S}$ (0.92), average annual temperature, $\bar{T}$ (0.92), number of eggs per egg string, η (0.73), chalimus development time at 10°C, $\hat{d}_C$ (0.62), the egg string production rate, ϵ (0.18), nauplius development time at 10°C $\hat{d}_P$ (0.13), and the infection rate, ι (0.08).

Table 2.1: The effect of water temperature and salinity on characteristics of sea lice life history.

Characteristic	Increasing Temp.	Increasing Salinity	Ref.
Nauplius maturation rate	Increase (2-19°C)	No effect	Stien et al. 2005
Chalimus maturation rate	Increase (7-15°C)	No effect	Stien et al. 2005
Egg viability	No effect	Increase (10-30 psu)	Johnson & Albright 1991
Nauplius mortality rate	No effect	Decrease (10-30 psu)	Johnson & Albright 1991
Copepodid mortality rate	No effect	Decrease (5-36 psu)	Bricknell et al. 2006
Chalimus mortality rate	No effect	Decrease (0-28 psu)	Connors et al 2008
Adult mortality rate	No effect	Decrease (0-28 psu)	Connors et al 2008

Table 2.2: Model Parameters

Parameter	Description	Units	Value	Ref.
η	eggs per clutch	eggs	592	Heuch et al. 2000
ϵ	egg string production rate	$\frac{1}{day}$	0.0476	Heuch et al. 2000
ι	infection rate	$\frac{1}{day}$	0.01	NA
N_f	number of fish	fish	1000	NA
$\bar{T}$	average annual temperature	°C	9	NA
$\tilde{T}$	temperature amplitude	°C	4	NA
$\bar{S}$	average annual salinity	psu	25	NA
$\tilde{S}$	salinity amplitude	psu	2	NA
$\hat{d}_P$	nauplius development time at T_{ref}	$days$	3.63	Stien et al. 2005
$\hat{d}_C$	chalimus development time at T_{ref}	$days$	31.92	Stien et al. 2005
T_{ref}	reference temperature for $\hat{d}_x$	°C	10	Stien et al. 2005
${}_PT_{min}$	nauplius development $= 0$ $(T_{ref} -_P T_{min})$	°C	13.01	Stien et al. 2005
${}_CT_{min}$	chalimus development $=$ 0 $(T_{ref} -_C T_{min})$	°C	11.94	Stien et al. 2005
β_{0E}	egg viability-salinity intercept	NA	-0.458	Johnson & Albright 1991
β_{1E}	egg viability-salinity slope	$\frac{1}{psu}$	0.037	Johnson & Albright 1991
β_{0P}	nauplius mortality-salinity intercept	$\frac{1}{day}$	0.4492	Brooks & Stucchi 2006
β_{1P}	nauplius mortality-salinity slope	$\frac{1}{day \cdot psu}$	-0.01484	Brooks & Stucchi 2006
β_{0I}	copepodid mortality-salinity intercept	$\frac{1}{day}$	0.4492	Brooks & Stucchi 2006
β_{1I}	copepodid mortality-salinity slope	$\frac{1}{day \cdot psu}$	-0.01484	Brooks & Stucchi 2006
β_{0C}	chalimus mortality-salinity intercept	$\ln hours$	4.12	Connors et al. 2008
β_{1C}	chalimus mortality-salinity slope	$\ln \frac{hours}{psu}$	0.124	Connors et al. 2008
β_{0A}	adult mortality-salinity intercept	$\ln hours$	4.12	Connors et al. 2008
β_{1A}	adult mortality-salinity slope	$\ln \frac{hours}{psu}$	0.124	Connors et al. 2008

Table 2.3: Parameter values for sensitivity analysis

Parameter	Units	Min	Max	Median	STD	PDF	Ref.
η	eggs	NA	NA	492	200	Normal	Heuch et al. 2000
ϵ	$\frac{1}{day}$	0.0476	0.0576	NA	NA	Uniform	Boxaspen 2006
ι	$\frac{1}{day}$	0.001	0.9	0.01	NA	Triangle	Groner et al. 2014
$\bar{T}$	°C	7	10	NA	NA	Uniform	Beamish & Jones 2011
$\bar{S}$	psu	20	30	NA	NA	Uniform	Beamish & Jones 2011
$\hat{d}_P$	days	NA	NA	3.63	0.22	Normal	Stien et al. 2005
$\hat{d}_C$	days	NA	NA	31.92	2.06	Normal	Stien et al. 2005

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Chapter 3

Treatment And Production Cycle Timing In Newfoundland: The Use Of An Environmentally Informed DDE Model

Abstract

Sea lice (*Lepeophtheirus salmonis*) development and mortality rates are dependent on seasonal environmental variables. As such, coordinating timing of production cycles and follow-up treatments on salmon farms with local environmental information can be important to control of sea lice epidemics. We investigate the effects of different production cycle start times on sea lice treatment in Newfoundland, Canada. We find that the optimal production cycle start times, with regards to sea lice management, are between the 281st and 337th days of the year. We recommend that production cycles beginning in the spring should begin as early as possible. We also demonstrate

that adjusting follow-up treatment timing in response to expected temperature can improve treatment regimes. Specifically we show that a follow-up treatment six weeks (42 days) after an initial treatment is not optimal in Newfoundland, Canada.

3.1 Introduction

Since the moratorium on the cod fishery in 1992, finfish aquaculture has played an increasingly important role in the economy of Newfoundland & Labrador. The large majority of finfish aquaculture in the province consists of Atlantic salmon (*Salmo salar*) and steelhead trout (*Oncorhynchus mykiss*). As of 2013, salmonid aquaculture produced 22,196 tonnes of salmon and contributed $182 million CAD to the provincial economy, the vast majority of it residing on the southern coast of Newfoundland (Newfoundland & Labrador Department of Fisheries & Aquaculture 2013). As the density of aquaculture increases in a region, so too does the risk of epidemics (Frazer et al. 2012, Jansen et al. 2012). In particular to salmonid aquaculture, sea lice (*Lepeophtheirus salmonis* and *Caligus spp.*) cause substantial economic losses in sites around the globe (Costello 2009).

Mathematical models have often been used by sea lice researchers to help understand sea lice epidemics and management. However, there has been a lack of deterministic models that account for the effects of seasonality on the sea louse life cycle. The usefulness of such a model has been stated on several occasions (Revie et al. 2005, Stien et al. 2005, Groner et al. 2014, Kristoffersen et al. 2014). Sea lice exhibit both temperature-dependent development rates (Stien et al. 2005) and salinity-dependent mortality rates (Johnson & Albright 1991, Bricknell et al. 2006, Connors et al. 2008). Temperature and salinity vary throughout the year. Therefore, the inclusion of seasonally-dependent maturation and mortality rates allows for

investigations into the intra-annual timing of certain production decisions, such as beginning salmon production cycles and chemical treatments.

Post-harvest fallowing (leaving pens empty of salmon) of production sites is a common sea lice management strategy. Aquaculture sites are left fallow for several months following harvest. The duration of the fallow period is longer than the duration of the sea louse life cycle, in order to prevent infection from the previous salmon cohort. However, beyond that minimal time requirement, fallowing decisions vary widely between sites. An aspect of sea lice management that has not been explored is how the timing of production cycles influences the risk of sea louse outbreaks for a salmon cohort. Aligning production cycles with certain times of the year can potentially increase the effectiveness of sea lice control, by influencing the environmental conditions sea lice are exposed to.

Chemical bath treatments (hydrogen peroxide, deltamethrin, etc.) are another popular tool for controlling sea lice outbreaks. However, continuous use of hydrogen peroxide can lead to resistance in the sea lice population (Treasurer et al. 2000, Helgesen et al. 2015), so it is important that treatments are not over-used. An initial treatment event typically occurs when observed sea lice densities on sampled salmon exceed a predefined level, which in Newfoundland and Labrador is determined by individual companies. In other regions treatment requirements are set by the government. In Ireland treatment is required when sea lice densities surpass 2.0 adult females per fish (Revie et al. 2009). In Scotland, treatment is required when sea lice densities surpass 1.0 adult females per fish (Revie et al. 2009). In Norway, requirements are even more strict, and treatment is initiated when sea lice densities surpass 0.5 adult female lice per fish (Revie et al. 2009). British Columbia uses a treatment threshold of 3.0 motile (male and female adults and pre-adults) sea lice per fish (Revie et al. 2009).

Treatment regimes of hydrogen peroxide and other chemical bath treatments have been found to be more effective when paired with a follow-up treatment of either three to four weeks (J. Treasurer personal communication reported in Robbins et al. 2010) or six weeks (42 days; results of model in Robbins et al. 2010). Robbins et al. (2010) suggest that this is because six weeks is longer than the amount of time it takes for a newly hatched nauplius to reach the parasitic chalimus stage, but shorter than the amount of time needed to reach reproductive maturity. However, this window of acceptable treatment timing may change with the temperature conditions that sea lice experience, due to temperature's influence on the sea louse development rate.

We use a delay differential equation (DDE) model to assess two aspects of sea lice control: 1) the best time of the year to begin production cycles on salmon farms, with regards to the number of chemical treatments necessary to maintain sea lice below a density of less than two fecund sea lice per fish; 2) how the optimal timing of follow-up treatments changes in response to seasonal temperature patterns.

3.2 Methods

3.2.1 Production Cycle Timing

The model we use to examine production cycle timing is the model outlined in the previous chapter of this thesis, with the following modifications. We assume that harvesting of salmon begins h days before the end of the production cycle (t_{fin}), which is held constant at 730 days after t_0. As such, the number of fish (N_f) is no longer a fixed parameter, but is now a function,

$$N_f(t) = \begin{cases} N_f(t_0)\left(1 - \frac{t - t_{start}}{h}\right) & \text{if } t \geq t_{start} \\ N_f(t_0) & \text{otherwise,} \end{cases} \tag{3.1}$$

where $t_{start} = 730 - h$.

Additionally, we introduce simple density dependence into the model to prevent the unrealistic exponential population growth of the louse population. Density dependence could come in the form of reduced reproductive output (Heuch et al. 2000), increased sea lice mortality, or increased host mortality (Krkošek et al. 2012). Host mortality in infected adult salmon is relatively rare (Revie et al. 2009), and organisms typically down-regulate reproductive energy usage prior to down-regulating somatic maintenance (Sousa et al. 2010). Studies of sea lice density dependence on adult salmon hosts are limited but markers of physiological stress are first noted above a density of 20 motiles per fish in large smolts (Revie et al. 2009) and densities up to 150 motiles per fish have been observed on wild adult salmon (Revie et al. 2009). We assume that a salmon host can only nutritionally support 100 infective stages, including chalimi, adult females, and adult males. Above this threshold, we assume that sea lice cease reproductive effort, so that reproductive effort ($E(t)$) is now a function,

$$E(t) = \begin{cases} \eta\epsilon & \text{if } \frac{C(t)+2A(t)}{N_f(t)} \leq 100 \\ 0 & \text{if } \frac{C(t)+2A(t)}{N_f(t)} > 100. \end{cases} \tag{3.2}$$

We assume that no sea lice are present at t_0, but that copepodids enter the system from outside sources at a constant rate (l) of copepodids per day. We implement treatment in the model by assuming that sea lice densities are checked at 28 day increments. When the density of adult female sea lice A/f is ≥ 2, the adult female sea louse population is reduced by 70%. This is consistent with field usage of hydrogen peroxide, where it is applied over a 20 minute period and results in 70% detachment of motile stages from fish (Revie et al. 2005). In our analysis of production cycle timing, we assume that a treatment does not initiate a follow-up treatment.

We run the model 53 times, with the initial time (t_0) increasing by 7 days every

simulation.

3.2.2 Follow-Up Treatment Timing

The delays ($\tau_x(t)$) have so far been presented in terms of a cohort exiting a state (x) at the same time, t, having all entered that state at the same time, $t - \tau_x(t)$. The delays can be expressed in a forward looking manner, where all sea lice that enter a state (x) at the same time, t, will all exit that state at the same time, $t + \vec{\tau}_x(t)$. The forward delays ($\vec{\tau}_x(t)$) can be inferred from $\tau_x(t)$ in the following manner,

$$\vec{\tau}_x(t) = \tau_x(t + \vec{\tau}_x(t)). \tag{3.3}$$

Because many chemical treatments do not affect the planktonic stages, treating before sea lice reach the chalimus stage is ineffective. Therefore, if we assume that the time spent in the copepodid class before infecting a salmonid host is negligible, the earliest desired follow-up treatment date is

$$\vec{\tau}_P(t), \tag{3.4}$$

and the latest desired treatment date is,

$$\vec{\tau}_P(t) + \vec{\tau}_C(t + \vec{\tau}_P(t)), \tag{3.5}$$

because after this time female lice will have reached reproductive maturity and begin producing eggs.

Additionally, some treatments, such as hydrogen peroxide, only affect the motile stages of sea lice. To account for this, we include an additional differential equation,

$$\frac{d\tau_{Pa}}{dt} = 1 - \frac{\gamma_{Pa}(t)}{\gamma_{Pa}(t - \tau_{Pa}(t))}, \tag{3.6}$$

where the Pa subscript indicates the pre-adult stage. The function, $\gamma_{Pa}(t)$, takes the same form as $\gamma_P(t)$ and $\gamma_C(t)$, with parameter values of ${}_{Pa}T_{min} = 18.38$ and $\hat{d}_{Pa} = 16.52$ (Stien et al. 2005). The earliest treatment date for chemicals that only affect the motile stages will be,

$$\vec{\tau}_P(t) + \vec{\tau}_{Pa}(t + \vec{\tau}_P(t)), \tag{3.7}$$

while the latest treatment date will still be the same as equation (3.5).

We test whether our follow-up treatment recommendations impact sea lice densities by simulating a salmon production cycle with no external copepodid source (l=0) and no harvesting ($h = 0$). No external copepodid source is included in the simulation because our follow-up treatment model assumes that the source of sea lice is entirely within the farm. The production cycle is started on the 100th day of the year, April 10th, and the initial treatment occurs on the 515th day of the production cycle, September 7th. These dates were chosen because production cycles often begin in April and because September 7th is within the range of dates where our model suggests follow-up treatment should occur prior to six weeks. We run simulations with follow up treatments earlier than the suggested treatment window, within the treatment window and consistent with the recommendation of Treasurer, and after the suggested treatment window but consistent with the suggestion of Robbins et al. (2010).

3.2.3 Description of Numerical Methods

All numerical simulations are conducted with the PBSddesolve (version 1.10.25) package in R (version 3.0.2). All figures are made using either the default R graphics package or ggplot2 (version 1.0.1) with cowplot (version 0.3.1.9000). We use the lm() function in R to fit sinusoidal models to temperature and salinity, utilizing quarter-hourly data from from an aquaculture site in Newfoundland, provided by the Aquaculture Real-time Integrated Environmental System (ARIES).

We can calculate the forward delays for a set of times ($t_1 \leq t \leq t_2$), provided we know $\tau_x(t)$ for all times, t, between $t_1 + \vec{\tau}_x(t_1)$ and $t_2 + \vec{\tau}_x(t_2)$. While it is not possible to know the values of $t_1 + \vec{\tau}_x(t_1)$ and $t_2 + \vec{\tau}_x(t_2)$ in advance, simply extending the simulation for a large, but arbitrarily long time after t_2 can accomplish this.

The initial number of fish ($N_f(t_0)$) is $1 \cdot 10^5$ and the infection rate (ι) is $8 \cdot 10^{-7}$. All other parameter values are as shown in table 2.2 of the previous chapter.

3.3 Results

3.3.1 Production Cycle Timing

Our model predicts that treatments primarily occur during the second year of the production cycle, because sea lice densities are too low in the first year to initiate treatments (Fig. 3.1). Fewer treatments are necessary when harvesting begins earlier in the production cycle (Fig. 3.2). The number of hydrogen peroxide treatments necessary to control sea lice outbreaks is lowest when the production cycle begins between the 281st and 337th day of the year, when 0 treatments are necessary (Fig. 3.2). The number of hydrogen peroxide treatments necessary to control sea lice outbreaks is highest when the production cycle begins between the 148th and 218th day of the

year, when 6 treatments are expected to be necessary. Within the the time of year that is typical of beginning production cycles (April-June), the number of hydrogen peroxide treatments necessary to control sea lice outbreaks is lowest between the 92nd and 141st day of the year. Within the time of year that is typical of saltwater entry, the number of hydrogen peroxide treatments necessary to control sea lice outbreaks is highest between the 148th and 190th days of the year.

3.3.2 Follow-Up Treatment Timing

For treatments that affect all parasitic stages of the lifecycle, earliest suggested follow-up treatments are 3 days after the initial treatment, when the initial treatment is between late summer and early autumn (between the 255th and the 297th day of the year; Fig. 3.3). Latest suggested follow-up treatments are 176 days after the initial treatment, when the initial treatment is in winter (between the 363rd day and the 7th day of the year; Fig. 3.3). The largest follow-up treatment window (the length of time between the earliest and latest suggested treatments) is 169 days, when the initial treatment occurs in winter (between the 364th and the 6th day of the year; Fig.3.3). The smallest follow-up treatment window is 29 days, when the initial treatment occurs in late summer (between the 252nd and the 253rd day of the year; Fig. 3.3).

For treatments that affect only the motile (pre-adult and adult) parasitic stages of the lifecycle, the earliest suggested follow-up treatments are 18 days after the initial treatment, when the initial treatment is between late summer and early autumn (between the 252nd and 280th day of the year; Fig. 3.3). The latest suggested follow-up treatment is the same as in the case where all parasitic stages are affected. The largest follow-up treatment window is 137 days, when the initial treatment occurs in early winter (between the 356th and 362nd day of the year; Fig. 3.3). The smallest follow-up treatment window is 14 days, when the initial treatment occurs in summer

(between the 240th and the 244th day of the year; Fig. 3.3).

The follow-up treatment window suggested by our calculations, for September 7th, is between 4 and 34 days after the initial treatment. Adult female sea lice abundance is lowest when follow-up treatment is applied during the follow-up treatment window (Fig. 3.4). Over the course of the production cycle, maximum adult female sea lice densities are 22.71 per fish when follow-up treatment is before the suggested window, 21.66 per fish when follow-up treatment is during the suggested window, and 21.91 when follow up treatment is after the suggested window. Over the course of the production cycle, mean adult female sea lice densities are 2.50 per fish when follow-up treatment is before the suggested window, 2.42 per fish when follow-up treatment is during the suggested window, and 2.43 per fish when follow-up treatment is after the suggested window.

3.4 Discussion

Sea lice life history depends on temperature and salinity and we examined how this impacted the timing of salmon production cycles and follow-up treatments. We find that ideal production start dates, in terms of sea lice control, are in late autumn, while the worst production start dates are in late summer (Fig. 3.2). Unfortunately, in Newfoundland, ideal production cycle start times for controlling sea lice are poor production cycle start times for salmon, due to low temperature's effects on salmon survival and growth. We also find that treatment regimes should consider temperature patterns when planning follow-up treatments, especially when preferred chemicals that only affect motile stages are used.

While there are official sea lice threshold levels in British Columbia, Ireland, Scotland, and Norway that will prompt treatment, no official threshold level exists for

either Newfoundland or New Brunswick salmon farming at this time. As such, individual farms are free to set their own metrics for initiating treatments, and their criteria may differ markedly from the threshold treatment criteria we use in our simulations. Additionally, treatments other than hydrogen peroxide are frequently used. These include other bath treatments, which will behave similarly to how we modelled hydrogen peroxide, in-feed treatments that, which have a slower but longer mortality effect on sea lice, and cleaner fish predation, which can be represented as a constant mortality rate. The effective co-usage of different treatment strategies can prevent an increase in chemical resistance among sea lice (Murray 2015).

Our results show that follow-up treatment timing decisions should account for the expected temperature in the weeks following the initial treatment. A follow-up treatment that occurs six weeks after an initial treatment, as suggested in Robbins et al. (2010), is within the treatment window predicted by our model for most of the year (Fig. 3.3). However, for some days of the year, sea lice will have already reached reproductive maturity before treatment occurs at six weeks. For treatments that only affect motile classes, such as hydrogen peroxide, the six week suggestion is even less appropriate in Newfoundland, since not only do sea lice sometimes reach reproductive maturity before treatment, but sea lice will often not reach the motile pre-adult stage before treatment occurs. The six week follow-up treatment suggested by Robbins et al. (2010) is likely more successful in Scottish salmon farms, where temperatures vary less drastically throughout the year. However, our simulations suggest that differences in average sea lice densities between early, on-time, and late follow-up treatments are small, and that treating late may not impact average sea lice densities at a biologically relevant level (Fig. 3.4). Additionally, our methods assume that temperatures following the initial treatment will be similar to historical patterns at the site, and our methods may not be as accurate if temperatures following the

initial treatment are unseasonably warm or cold.

We find that both maximum and mean sea lice densities are lowest when treating within our suggested follow-up treatment window. However, the difference between follow-up treatments of 24 days and follow-up treatments of 42 days is minimal. This may be due to the 42 day follow-up treatment killing a larger number of chalimi and adults, which would somewhat offset the disadvantage of more lice reaching reproductive maturity before the follow-up treatment.

Sea lice can exhibit a number of density dependent effects. While few other models of sea lice dynamics have considered density dependence, we find that our model predicts unreasonably high densities of sea lice, when sea lice densities are only assessed at 28 day intervals. Other models have usually avoided the issue of density dependence by either focusing on a single generation of sea lice (Tucker et al. 2002) or by fitting their models to data sets with high levels of treatment (Revie et al. 2005). One additional way that density dependence may limit sea lice populations is by causing host mortality at high densities. Krkošek et al. (2012) modelled host mortality by using the methods outlined in Anderson & May (1978) for overdisperspersed populations. However, there are arguments against combining the probabilistic model of over-dispersion in Anderson & May (1978) with deterministic ODE and DDE models (Yakob et al. 2014). An additional way that density may impact sea lice, which we chose for our model, is through decreased egg production in high-density environments. However, the underlying mechanisms affecting this are largely speculative (Heuch et al. 2000). Since the structural form of density dependence can impact the time it takes a population to return to pre-treatment levels (Churcher et al. 2006), further examination of the density dependence mechanisms is needed. In the absence of further experimental data, an uncertainty and sensitivity analysis on several functional forms of density dependence could be conducted to determine the degree that

the choice of the density dependence function impacts treatment estimates.

The development rates we use are average minimum development times. Actual development times are stochastically distributed after the average minimum development time (Stien et al. 2005). Furthermore, the data that Stien et al. (2005) use to fit a temperature-dependent relationship lack information below 7°C and above 15°C. Additional studies at these temperatures, as well as an updated model fit can substantially increase accuracy in Atlantic Canada, because water temperatures are often below 7°C in this region.

The future of sea lice modelling will increasingly depend on the inclusion of local environmental factors. These factors include both temperature and salinity, as presented in this work, as well as hydrodynamics (Aldrin et al. 2013, Kristoffersen et al. 2014). Our research suggests two recommendations. First, Newfoundland aquaculturists should begin production cycles earlier in the spring when possible. Secondly, aquaculturists should adapt follow-up treatment timing to degree day monitoring.

3.5 Figures

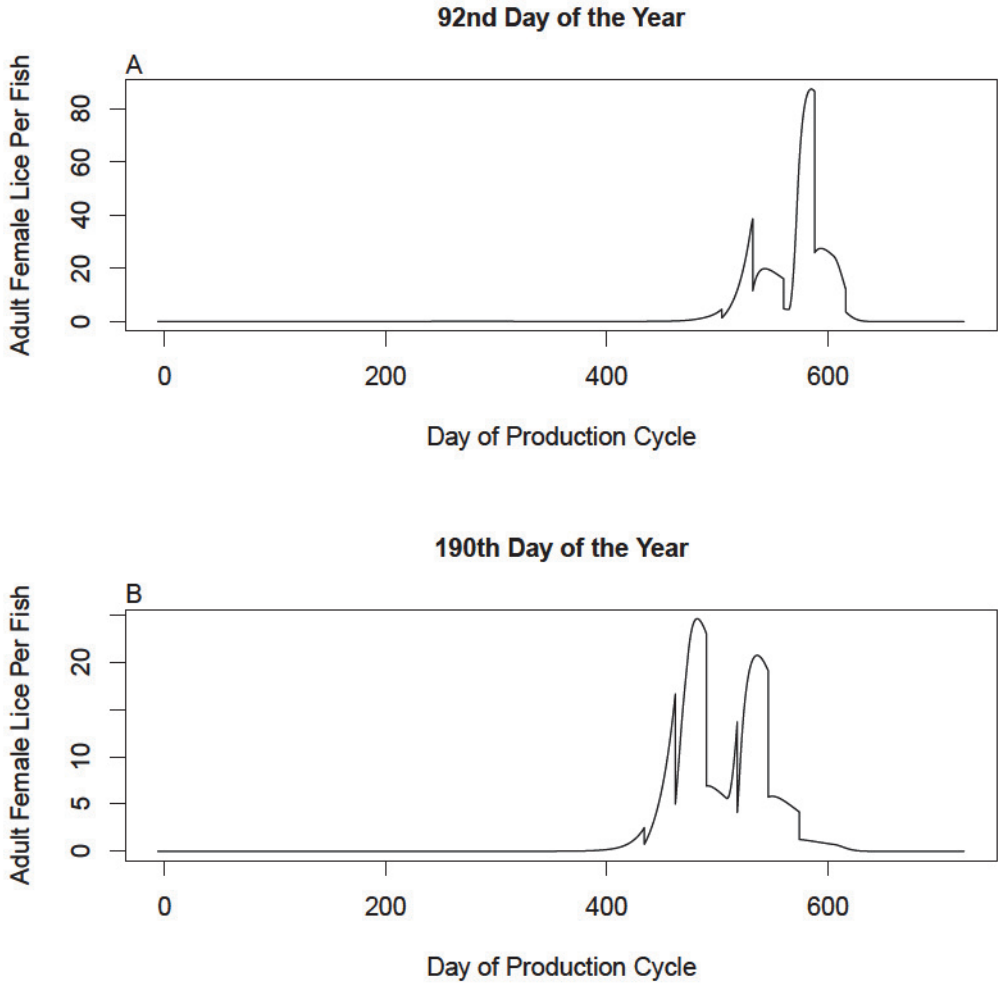

Figure 3.1: The number of adult female sea lice per fish, over the course of production cycles that start on the 92nd day of the year (A) and the 190th day of the year (B), and that begin harvesting 120 days before the production cycle ends.

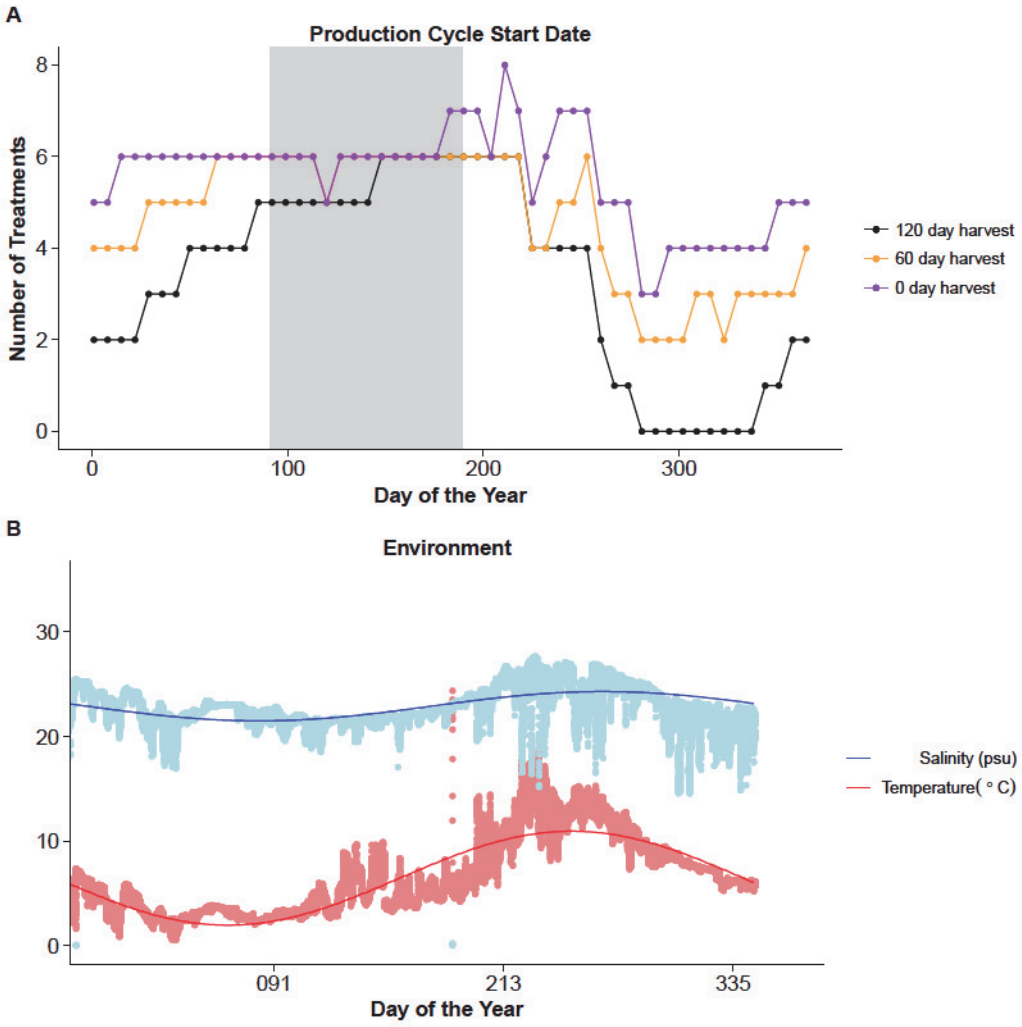

Figure 3.2: (A) The number of treatments necessary, over the course of a production cycle, to maintain sea lice abundance of less than two adult female lice per fish. The three scenarios shown assume that salmon harvest occurs over either the last 120 days of the production cycle, the last 60 days of the production cycle, or entirely on the final day of the production cycle. Abundance is checked every 28 days, so the maximum possible number of treatments in a 2 year production cycle is 26 treatments. Typical dates for starting production cycles (April-June) are highlighted in grey. (B) Annual temperature and salinity profile of a site in the Coast of Bays region of Newfoundland and Labrador. Dots represent data points and lines represent the linear model we fit to the data. Details of the environmental model fitting can be found in chapter two.

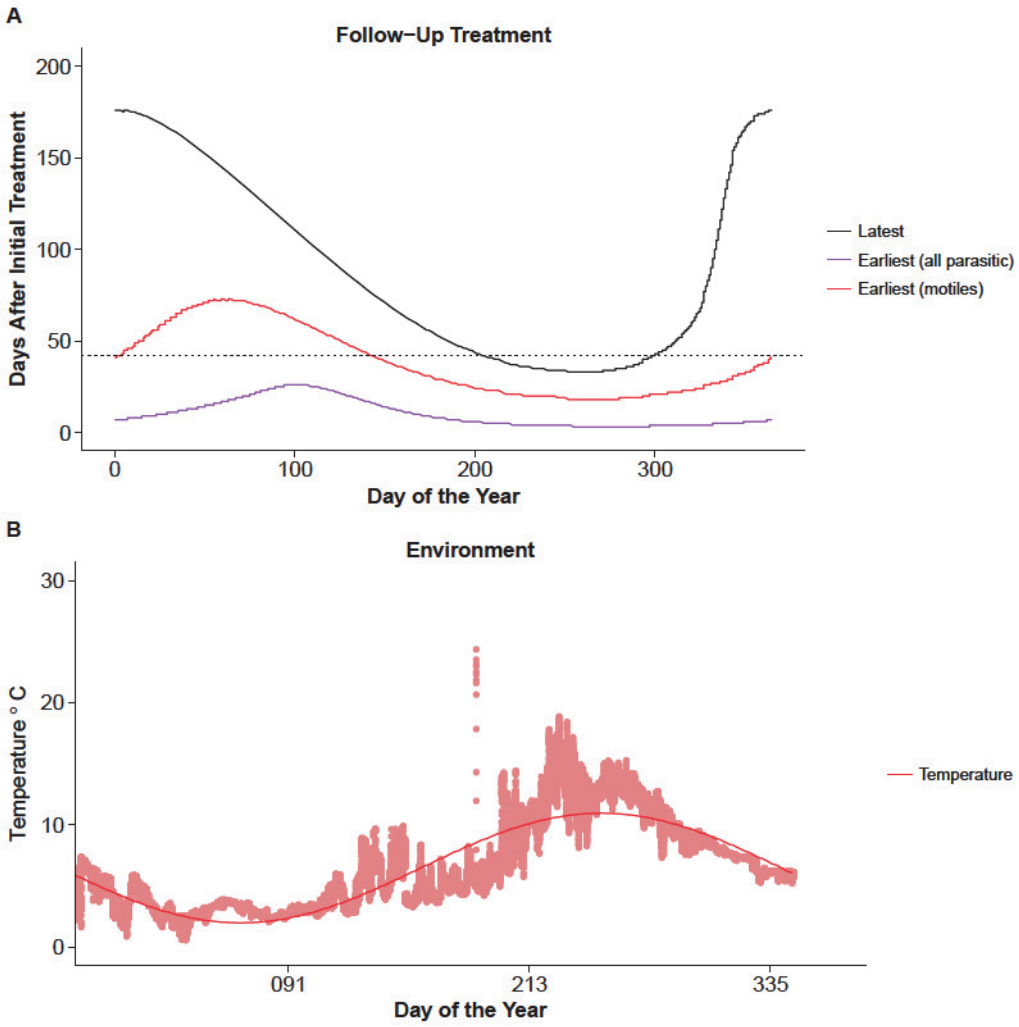

Figure 3.3: (A) Number of days needed to mature to the adult female, pre-adult, and copepodid stages, for a nauplius that hatches on a given day. The horizontal dotted line represents the six week (42 day) recommended follow-up treatment from Robbins et al. (2010). Maturation times are based off of (B) an annual temperature profile of a site in the Coast of Bays region of Newfoundland and Labrador. Details of temperature model fitting can be found in the previous chapter

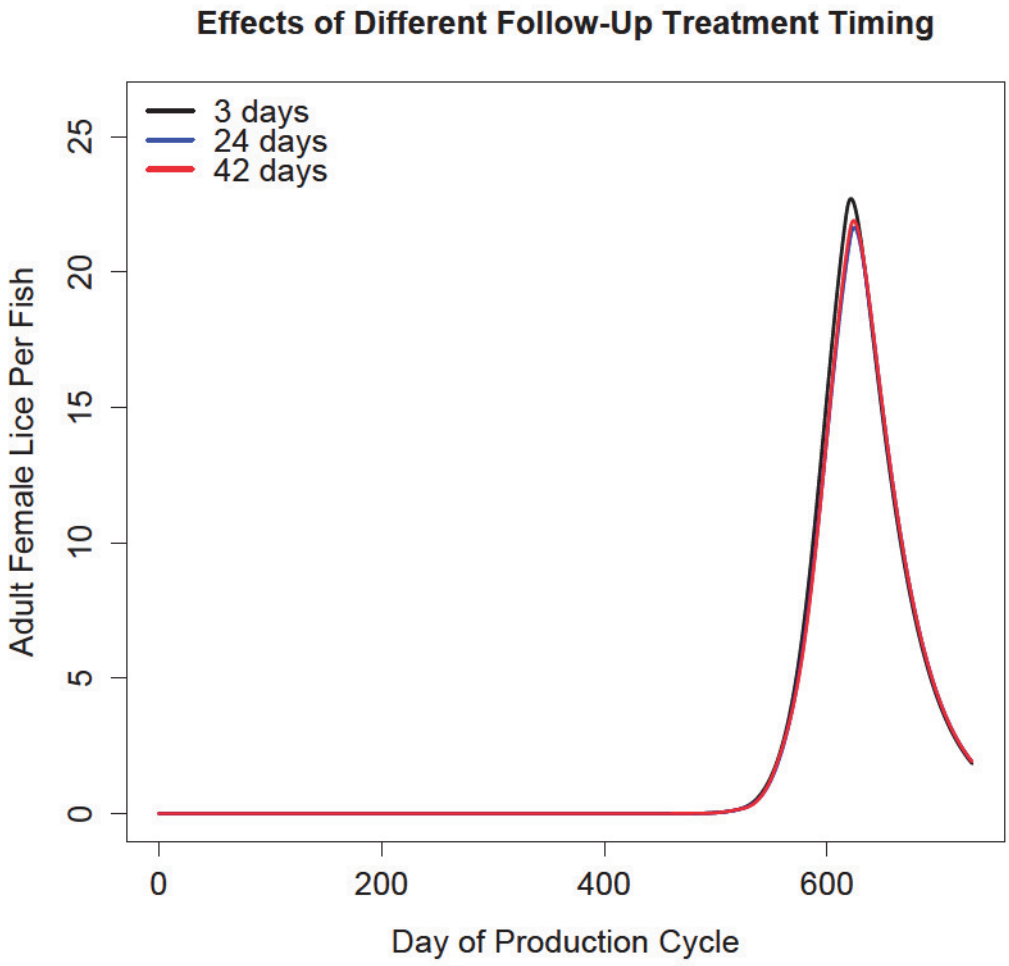

Figure 3.4: The follow-up treatment window suggested by our calculations was between 4 and 34 days after the initial treatment. Follow-up treatments are at 3 days (A), 24 days (B), or 42 days (C). Maximum adult female sea lice densities under these conditions are 22.71 (A), 21.66 (B), and 21.90 (C). Mean adult female sea lice densities under these conditions are 2.50 (A), 2.42 (B), and 2.43 (C).

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Chapter 4

Summary

Variations in local environments have increasingly informed sea lice modelling efforts (Stien et al. 2005, Aldrin et al. 2013, Groner et al. 2014, Kristoffersen et al. 2014). My work incorporated temperature-dependant and salinity-dependent mortality in a way that accounts for seasonal changes in these variables, within a deterministic model framework. These adaptations to the DDE model with constant delays and mortality allowed me to explore a number of attributes of sea lice dynamics relevant to their management.

In chapter two, I derived a DDE with temperature-based delays and salinity-based mortality. I then used the model to demonstrate three key findings. First, sea lice population dynamics shift from persistence to extinction as average annual temperature and average annual salinity decreases (Fig. 2.4). Second, sea lice reproductive potential ($R_0(t)$) peaks at different times of the year in Newfoundland and British Columbia (Fig. 2.2). Third, I demonstrate the importance of temperature and salinity on the model outputs through a sensitivity analysis (Fig. 2.5).

In chapter three, I used the model to examine the timing of production cycles and chemical treatments in Newfoundland. I demonstrated that production cycles begin-

ning in the late fall will require fewer treatments than production cycles beginning in late summer and that production cycles beginning in the early spring will require less treatments than production cycles beginning in late spring (Fig. 3.2). Additionally, I demonstrated that, in Newfoundland, there will be times of the year when fixed follow-up treatments will either treat before sea lice reach the parasitic stage or after they reach reproductive maturity (Fig. 3.3). Thus treatment plans should be flexible and based on seasonal temperature patterns.

Recent sea lice models have begun incorporating temperature-dependent development in their models (Groner et al. 2014, Kristoffersen et al. 2014). So far, these models have relied heavily on the temperature-development model fit in Stien et al. (2005). The model in Stien et al. (2005) was fit to data that was lacking at low and high temperatures. This limits the effectiveness of the established temperature-development relationship in environments that regularly drop below 7°C or rise above 15°C. Additional empirical work at low and high water temperatures needs to be conducted in order to account for the large variety of temperature profiles at salmon aquaculture sites. I further recommend that temperature-development relationship be expressed in the reparameterized form that we presented (Eqn. 2.8), in order to make the relationship between measured values and parameter units more explicit.

In addition to improvements in the empirical information, there are multiple paths forward in incorporating environmental factors into sea lice models. Several publications have examined the effects of hydrodynamics, both between farms (Aldrin et al. 2013, Kristoffersen et al. 2014) and within farms (Samsing et al. 2015). Hydrodynamics can impact infection success and spread of sea lice nauplii from farm to farm. Because of this, the correct spatial scale to model sea lice is likely at the regional level, rather than at the farm level.

The modelling approaches used in this thesis can be applied to a number of other

macroparasite systems. Notably, a number of nematode species exhibit environmentally dependent development and mortality, as well as having and both free living and parasitic life history stages. (Molnár et al. 2013). DDE models could be combined with metabolic models (Sousa et al. 2010, Molnár et al. 2013) offer an additional way to examine the effects of temperature and salinity on macroparasite life history traits.

In closing, DDE models with temperature-dependent maturation and salinity-dependent mortality are useful tools in analyzing sea lice dynamics. They can be used to assess an aquaculture site's vulnerability to sea lice epidemics, as well as to compare seasonal differences between sites. Temperature and salinity-dependent DDE models can also be used to plan management decisions, such as the timing of production cycles and the timing of follow-up treatments. As such, I hope that the framework of my model is improved and expanded upon by fellow researchers.

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Appendix A

Model Derivation

A.1 The Basic System

The following derivation is based on a model for stage-structured insect populations with varying instar duration (Nisbet & Gurney 1983) and a model for koi herpes virus with temperature-dependent latent period (Omori & Adams 2011).

Sea lice may be in 1 of 4 possible states: planktonic non-infectious nauplii ($P(t)$), infectious copepodids ($I(t)$), chalimus ($C(t)$), or adult females ($A(t)$). The processes by which the number of sea lice in each of these states changes are mortality, reproduction, infection, and maturation. The system can be written generally as influx due to reproduction, infection, or maturation ($Q_y(t)$), outflux due to maturation or infection ($M_y(t)$), and outflux due to mortality ($Z_y(t)$), where $y \in \{P, I, C, A\}$. So,

$$\frac{dP}{dt} = Q_P(t) - M_P(t) - Z_P(t), \tag{A.1}$$

$$\frac{dI}{dt} = Q_I(t) - M_I(t) - Z_I(t), \tag{A.2}$$

$$\frac{dC}{dt} = Q_C(t) - M_C(t) - Z_C(t), \tag{A.3}$$

$$\frac{dA}{dt} = Q_Z(t) - Z_A(t). \tag{A.4}$$

Each individual matures through the states in order from nauplius ($P(t)$), to copepodid ($I(t)$), to chalimus ($C(t)$), and finally to an adult female ($A(t)$). Let y denote the current state, y^- denote the previous state, and y^+ denote the next state. In all states except for the nauplius state, influx is due only to maturation or infection from the preceding state, so that $Q_y = M_{y^-}$. As such, equations 1.1-1.4 can be rewritten as,

$$\frac{dP}{dt} = Q_P(t) - M_P(t) - Z_P(t), \tag{A.5}$$

$$\frac{dI}{dt} = M_P(t) - M_I(t) - Z_I(t), \tag{A.6}$$

$$\frac{dC}{dt} = M_I(t) - M_C(t) - Z_C(t), \tag{A.7}$$

$$\frac{dA}{dt} = M_C(t) - Z_A(t). \tag{A.8}$$

The details of the model derivation, with regards to mortality, reproduction, infection, and maturation, are hereafter described.

A.1.1 Mortality

Natural mortality occurs in all stages at a per capita rate $\mu_y(S(t))$. The mortality rate is a function of salinity (S), which changes as a function of time (t). For notational simplicity, we write $\mu_y(t)$, because given a function that describes salinity (S) at time (t), we can use this function to determine μ_y without explicitly needing to reference the dependence on salinity. Mortality for the nauplius and copepodid stages is related to salinity via a linear relationship described in Brooks & Stucchi (2006), while mortality for the chalimus and adult stages is described as a log-linear relationship described in Connors et al. (2008). Hence,

$$Z_P(t) = \mu_P(t)P(t), \tag{A.9}$$

$$Z_I(t) = \mu_I(t)I(t), \tag{A.10}$$

$$Z_C(t) = \mu_C(t)C(t), \tag{A.11}$$

$$Z_A(t) = \mu_A(t)A(t). \tag{A.12}$$

A.1.2 Reproduction

Each adult female produces nauplii with a development level of 0 at a constant per capita rate that is the product of the rate of egg clutch production per day (ϵ) and the average number of eggs per clutch (η). The proportion of eggs that produce viable nauplii can be described as a linear function of salinity ($v(S(t))$), fitted to data from Johnson & Albright (1991). Thus,

$$Q_E(t) = \eta\epsilon v(t)A(t).$$

A.1.3 Infection

Copepodids transition into the chalimus stage by infecting salmonids. We assume infection success occurs at a constant per capita rate (ιN_f), where ι is the infection rate and N_f is the number of fish hosts in the area. Hence,

$$M_I(t) = Q_C(t) = \iota N_f I(t).$$

A.1.4 Maturation

The development times associated with maturation are such that a cohort exiting a state (x) at the same time (t) will all have entered that state at the same time ($t-\tau_x$), where $x \in \{P, C\}$. The maturation time (τ_x) is defined as the length of time it takes sea lice in a given state to reach a threshold development level ($q_x = q'_x$), where q_x

is a measure of development of sea lice in state x. Let $\gamma_x(T(t))$ be a function that describes the rate of change in the level of development (q_x) for a given state (x) as it depends on temperature (T). For notational simplicity, we write simply $\gamma_x(t)$, because given a function that describes temperature (T) at time, t, we can use this function to determine $\gamma_x(t)$ without explicitly needing to reference the dependence on temperature.

Maturation out of the nauplius stage is equal to recruitment into the copepodid stage and occurs when development level ($q_P = q'_P$) is reached. Therefore,

$$M_P(t) = Q_I(t) = \gamma_P(t)\rho(q'_P, t),$$

where $\rho(q'_P, t)$ is defined as the density of lice with development level q'_P at time t.

In a similar manner, maturation out of the chalimus stage and recruitment into the adult female stage occurs when development level ($q_C = q'_C$) is reached. We assume that the ratio of sexes between adult sea lice is equal and that both sexes mature at an equal rate. Thus, only half of the sea lice that mature out of the chalimus stage, when the threshold development level ($q_C = q'_C$) is reached, will develop into adult females. Therefore,

$$\frac{M_C(t)}{2} = Q_A(t) = \frac{\gamma_C(t)\rho(q'_C, t)}{2}.$$

The goal of the following section is, utilizing the derivation in Omori & Adams (2011), to find expressions for the time delays (τ_x) and, subsequently, the outflow variables associated with maturation of the nauplius (M_P) and chalimus (M_C) stages, in terms of the quantities $\gamma_x(t)$, $\rho(q'_P, t)$, q_x, and q'_x.

A.2 Finding Maturation into state x

The maturation rate into state x depends on the density of individuals that have reached the threshold development level (q'_x) at time t. This can be rewritten in terms of the durations of the states ($\tau_x(t)$) through the integral constraint,

$$q'_x = \int_{t-\tau_x(t)}^{t} \gamma_x(t)\,\mathrm{d}t. \tag{A.13}$$

This is done by using the McKendrick – von Forster PDE (Kot, 2001).

If $J(q_x, t)$ is the flux for sea lice with increasing development level (q_x) at time, t, then,

$$\frac{\partial \rho}{\partial t} = -\frac{\partial J}{\partial q_x} - \mu_x(t)\rho. \tag{A.14}$$

For $q_x < q'_x$, the rate of increase of development level is $G_x(t)$, therefore,

$$J(q_x, t) = \gamma_x(t)\rho(q_x, t). \tag{A.15}$$

So,

$$\frac{\partial \rho(q_x, t)}{\partial t} = -\frac{\partial}{\partial q_x}[\gamma_x(t)\rho(q_x, t)] - \mu_x(t)\rho(q_x, t). \tag{A.16}$$

The boundary condition for this PDE, for state x, is $\rho(q_x, t) = \frac{Q_x(t)}{\gamma_x(t)}$. With the boundary condition, this PDE can be solved via the appendix of Nisbet and Gurney (1983);

$$\rho(q, t) = \frac{Q_x(t - \tau_x(q_x, t))}{G_x(t - \tau_x(q_x, t))} \exp\left(-\int_{t-\tau_x(q_x,t)}^{t} \mu_x(t)\mathrm{d}t\right). \tag{A.17}$$

where $\tau_x(q_x, t)$ is the time already spent in state x by lice with development level q_x at time t. This can be simplified from a PDE to an integro-differential equation, since $\tau_x(t) = \tau_x(q_{x^+}, t)$. We also define $\phi_x(t)$ to be the proportion of a cohort entering state x at time $t - \tau_x(t)$ that actually mature at time t, rather than dying in-between

entering and exiting the state. So,

$$\phi_x(t) = \exp\left(-\int_{t-\tau_x(t)}^{t} \mu_x(t)\mathrm{d}t\right). \tag{A.18}$$

Substituting equation A.18 into equation A.17 gives,

$$M_x(t) = \gamma_x(t)\rho(q_{x^+}, t) = Q_x(t-\tau_x(t))\frac{\gamma_x(t)}{\gamma_x(t-\tau_x(t))}\phi_x(t). \tag{A.19}$$

A.3 Integro-Differential Equations

The overall system can be rewritten as a set of integro-differential equations,

$$\begin{aligned}
\frac{dP}{dt} &= \eta\epsilon v(t)A(t) - \eta\epsilon v(t-\tau_P)A(t-\tau_P)\frac{\gamma_P(t)}{\gamma_P(t-\tau_P)}\phi_P(t) - \mu_P(t)P(t), && \text{(A.20)}\\
\frac{dI}{dt} &= \eta\epsilon v(t-\tau_P)A(t-\tau_P)\frac{\gamma_P(t)}{\gamma_P(t-\tau_P)}\phi_P(t) - \iota N_f I(t) - \mu_I(t)I(t), && \text{(A.21)}\\
\frac{dC}{dt} &= \iota N_f I(t) - \iota N_f I(t-\tau_C)\frac{\gamma_C(t)}{\gamma_C(t-\tau_C)}\phi_C(t) - \mu_C(t)C(t), && \text{(A.22)}\\
\frac{dA}{dt} &= \frac{1}{2}\iota N_f I(t-\tau_C)\frac{\gamma_C(t)}{\gamma_C(t-\tau_C)}\phi_C(t) - \mu_A(t)A(t). && \text{(A.23)}
\end{aligned}$$

A.4 Transforming the Integrals into Differential Equations

Transforming the integrals (A.13 and A.18) into differential equations is desirable for numerical calculations. We transform the above system into a set of delay differential equations by finding differential equation forms for the integral definitions of $\tau_P(t)$, $\tau_C(t)$, $\phi_P(t)$, and $\phi_C(t)$.

Differentiating and rearranging the integral in (A.13) for $\tau_P(t)$ and $\tau_C(t)$ yields,

$$\frac{d\tau_P}{dt} = 1 - \frac{\gamma_P(t)}{\gamma_P(t-\tau_P(t))}, \tag{A.24}$$

$$\frac{d\tau_C}{dt} = 1 - \frac{\gamma_C(t)}{\gamma_C(t-\tau_C(t))}. \tag{A.25}$$

We also differentiate (A.18) for $\phi_P(t)$ and $\phi_C(t)$ to yield,

$$\frac{d\phi_P}{dt} = \phi_P(t)\left(\frac{\gamma_P(t)}{\gamma_P(t-\tau_P(t))} - \mu_P(t)\right), \tag{A.26}$$

$$\frac{d\phi_C}{dt} = \phi_C(t)\left(\frac{\gamma_C(t)}{\gamma_C(t-\tau_C(t))} - \mu_C(t)\right). \tag{A.27}$$

A.5 Initial Conditions

The initial conditions of the maturation delays, $(\tau_P(t_0))$ and $(\tau_C(t_0))$ are such that,

$$\int_{t_0-\tau_x(t_0)}^{t_0} \gamma_x(t)\,\mathrm{d}t = 1,$$

(Omori & Adams 2011).

The initial conditions of the survival proportions, $(\phi_P(t))$ and $(\phi_C(t))$ are,

$$\phi_x(t_0) = \exp\left(-\int_{t_0-\tau_x(t_0)}^{t_0} \mu_x(t)\mathrm{d}t\right),$$

(Omori & Adams 2011).

The initial conditions for the four sea lice stages are $P(t_0) = 0$, $I(t_0) \geq 0$, $C(t_0) = 0$, and $A(t_0) \geq 0$. Infection events occur when either a small number of copepodids and/or adult sea lice enter an aquaculture site. Nauplii do not actively seek out hosts and chalimi are non-motile; therefore, they are not expected to initiate infection

events. Unlike systems of ordinary differential equations, a history function describing the value of the sea lice variables ($P(t)$, $I(t)$, $C(t)$, $A(t)$) prior to t_0 is necessary to solve systems of delay differential equations, in addition to knowledge of initial conditions at t_0. For simplicity, we assume no sea lice of any stage are present in the system for any time $t < t_0$. Therefore, the history functions take the form $P(t < t_0) = 0$, $I(t < t_0) = 0$, $C(t < t_0) = 0$, and $A(t < t_0) = 0$.

A.6 The Maturation Rate, $\gamma_x(t)$

The maturation rate ($\gamma_x(T)$) is the inverse of the Bělehrádek function from Stien et al. (2005),

$$\gamma_x(T) = \left(\frac{T - 10 + \beta_1\beta_2}{\beta_1}\right)^2.$$

We reparameterized the function, so that ${}_xT_{min} = \beta_1\beta_2$ for stage x, and $\hat{d}_x = \beta_2^{-2}$ for stage x, to make the parameters' units and effects on function shape more intuitive. The shape of the reparameterized function is described by the duration of the life stage ($\hat{d}_x$), in days, at the reference temperature (T_{ref}), and by the location of a vertical asymptote at ($T_{ref} -_x T_{min}$), where T_{ref} and T_{min} have units of °C. The development function now takes the form,

$$\gamma_x(T) = \frac{1}{\hat{d}_x}\left(\frac{(T - T_{REF} +_x T_{min})}{{}_xT_{min}}\right)^2.$$

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Appendix B

Details on Numerical Methods and Simulations

B.1 General Notes

B.1.1 Software

All analyses were conducted with R (version 3.0.2). All model simulations utilized the dde() function found in the PBSddesolve (version 1.10.25) package in R. Figures were made using the R packages; ggplot2 (version 1.0.1), cowplot (0.3.1.9000), and scales (0.2.4). Unless otherwise noted, all parameter values come from Table 2 in the main text.

B.1.2 Initial Conditions & History Functions

The initial conditions of the maturation times ($\tau_P(t_0)$) and ($\tau_C(t_0)$) are such that,

$$\int_{t_0-\tau_x(t_0)}^{t_0} \gamma_x(t)\,\mathrm{d}t = 1. \tag{B.1}$$

We estimate $\tau_x(t_0)$ to the nearest day by finding the value closest to 1.

Unlike systems of ordinary differential equations, a history function describing the value of the sea lice variables (P, I, C, A) prior to t_0 is necessary to solve systems of delay differential equations, in addition to knowledge of initial conditions at t_0. For simplicity, we assume that the history functions of the variables are $P(t) = 0$, $I(t) = 0$, $C(t) = 0$, and $A(t) = 0$ for $t < t_0$. Practically, this is accomplished through simple "if else" statements in the R code.

B.2 The Time Dependent Reproductive Ratio ($R_0(t)$)

B.2.1 Fitting Seasonal Data

We fit sinusoidal curves to monthly temperature and salinity data from a salmon farm in the Broughton Archipelago of British Columbia and to quarter-hourly temperature and salinity data from a salmon farm in southern Newfoundland. The sinusoidal curves were fit using the lm() function in R, which assumes a normal error. The models for temperature and salinity took the forms,

$$T(t) = \bar{T} + \widetilde{T}_1 \sin\left(\frac{2\pi t}{365}\right) + \widetilde{T}_2 \cos\left(\frac{2\pi t}{365}\right),$$

and,

$$S(t) = \bar{S} + \widetilde{S}_1 \sin\left(\frac{2\pi t}{365}\right) + \widetilde{S}_2 \cos\left(\frac{2\pi t}{365}\right).$$

Data for the British Columbia site was acquired from Marty et al. (2010); data for the Newfoundland site was acquired through the Aquaculture Real-Time Integrated Environmental System (ARIES). The specific sites were chosen based on their completeness of temperature and salinity data over a period consisting of at least twelve months. Both sites are generally representative of the temperature and salin-

ity patterns of other sites within their regions. Data from December 14^{th} to January 20^{th} of the Newfoundland site was not used in the model fitting, due to the presence of highly erratic, below freezing temperatures, indicative of inaccurate readings. British Columbia was fitted to temperatures and salinities from "farm 3" during the November 2002 - September 2004 production cycle.

B.2.2 Numerically Calculating $R_0(t)$

We numerically calculated $R_0(t)$ for both sites at different times of the year. An additional variable, representing the number of adult female lice produced by the initial infection ($R(t)$), was introduced to record $R_0(t)$, consisting of,

$$\frac{dR}{dt} = \frac{1}{2}\iota N_f I(t-\tau_C)\frac{\gamma_C(t)}{\gamma_C(t-\tau_C)}\phi_C(t).$$

This way, sea lice reaching adulthood were recorded but did not contribute a second generation of offspring. For that reason, we also removed the influx of new adult female sea lice,

$$\frac{1}{2}\iota N_f I(t-\tau_C)\frac{\gamma_C(t)}{\gamma_C(t-\tau_C)}\phi_C(t),$$

from equation 6 of the main text,

$$\frac{dA}{dt} = \frac{1}{2}\iota N_f I(t-\tau_C)\frac{\gamma_C(t)}{\gamma_C(t-\tau_C)}\phi_C(t) - \mu_A(t)A(t),$$

so that it now consists of,

$$\frac{dA}{dt} = -\mu_A(t)A(t).$$

In this way we record the number of adult female sea lice produced by the initial infectious individual ($R_0(t)$).

The initial condition of the sea lice population was $P(t_0) = 0$, $I(t_0) = 0$, $C(t_0) = 0$,

and $A(t_0) = 1$. We simulated the model at 30 day intervals – from the 1^{st} day of the year to the 361^{st} day of the year – and we recorded $R_0(t)$ for each of those 13 dates.

B.2.3 Calculating Generation Time

The delays ($\tau_P(t)$ and $\tau_C(t)$) have so far been presented in terms of a cohort exiting a state (x) at the same time, t, having all entered that state at the same time, $t - \tau_x(t)$. The delays can be expressed in a forward looking manner ($\vec{\tau}_x(t)$), where $\vec{\tau}_x(t)$ is the number of days necessary for a sea louse entering a state (x) at time, t, to mature out of that state. The forward delays ($\vec{\tau}_P(t)$) and ($\vec{\tau}_C(t)$) can be inferred from $\tau_P(t)$ and $\tau_C(t)$ in the following manner,

$$\vec{\tau}_x(t) = \tau_x(t + \vec{\tau}_x(t)).$$

While this analytical expression seems circular, we can numerically calculate the forward delays for a set of times ($t_1 \leq t \leq t_2$), provided we know $\tau_x(t)$ for all times, t, between $t_1 + \vec{\tau}_x(t_1)$ and $t_2 + \vec{\tau}_x(t_2)$. While it is not possible to know the values of $t_1 + \vec{\tau}_x(t_1)$ and $t_2 + \vec{\tau}_x(t_2)$ in advance, simply extending the simulation for a large, but arbitrarily, long time after t_2 can accomplish this.

B.3 Sensitivity Analysis

We conducted a sensitivity analysis on seven model parameters to analyze the effects of their variation on the abundance of adult female sea lice (Table 2.3). Local sensitivity analyses are conducted by varying a single parameter, while holding all other parameters constant, then comparing the varied parameter's effect on a chosen output variable. However, model sensitivity to the variable of interest may depend on

variation in the other parameters. As such, we conducted a global sensitivity analysis on the seven aforementioned parameters, using latin hybercube sampling (LHS) and partial rank correlation coefficients (PRCC). The annual salinity cycle was aligned with the annual temperature cycle. All model runs were started on the coldest, least saline day of the year and were run through the warmest, most saline day of the year.

B.3.1 Latin Hypercube Sampling (LHS)

Parameter distributions were estimated from the literature (Table 2.3). A latin hybercube sampling (LHS) scheme was used to sample the parameter space for the seven selected parameters. The LHS scheme is a class of Monte Carlo sampling that requires fewer samples from the parameter distributions to provide a good representation of variability (Blower & Dowlatabadi 1994). The number of samples is suggested to be at least $4K/3$, where K is the number of parameters (Blower & Dowlatabadi 1994). We took 300 samples from the parameter distributions for our sensitivity analysis. The R packages, lhs (version 0.1), DoE.wrapper (version 0.8-9), and triangle (version 0.8), were used in the latin hypercube sampling.

B.3.2 Partial Rank Correlation Coefficients (PRCC)

We conducted a global sensitivity analysis, using partial rank correlation coefficients (PRCC) as the test statistic. Partial rank correlation coefficients are a good measure of sensitivity when the relationship between inputs and outputs is expected to be monotonic (Blower & Dowlatabadi 1994); the seven parameters were chosen due to their monotonic relationship with sea lice numbers. A PRCC value near unity indicates the output value has a high sensitivity to the input value, while a PRCC value near zero indicates the model outputs have a low sensitivity to the parameter. Negative PRCC values have a negative correlation and positive values have a positive

correlation between the parameter and the output variable. PRCCs were recorded every 10 days because sea lice sensitivity to parameters is expected to change early in the simulation, before reaching a stable, long term value. The R package, sensitivity (version 1.8-2), was used to calculate the PRCC values.

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