Effects of Stochastic Environmental Variation on the Population Dynamics of Salmon Lice (*Lepeophtheirus salmonis)* in Newfoundland and Labrador

By
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Abstract

Salmon lice *Lepeophtheirus salmonis* are a marine parasite causing a significant economic burden in salmonid aquaculture. They experience both temperature-dependent growth and salinity-dependent mortality, impacting population dynamics. Many models have explored the effect of static or seasonal environmental conditions on salmon lice population dynamics, yet none have explored the impact of short-term daily environmental fluctuations. I derived a stochastic population model with daily variability in temperature and salinity, where these fluctuations effect population dynamics through temperature-dependent maturation and salinity-dependent mortality changes. I found that increasing variability in salinity slows population growth rates and decreases the logarithmic abundance of adult females, while increasing daily variability in temperature is a poor indicator of population dynamics, which is better predicted by seasonal temperature trends. Under all stochastic environmental scenarios salmon lice populations persisted and grew in Newfoundland, Canada. Population models are a valuable tool in the management of salmon lice and allow for more sustainable aquaculture practices.

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Chapter 1: General Introduction and Overview

Salmon lice *Lepeophtheirus salmonis* are parasitic copepod in the family Caligidae and are salmonid specialist parasite that consumes the blood, mucus and epidermal tissue of their host[1–3]. Globally, salmon lice cost salmonid aquaculture over 440 million CAD each year[4]. This cost is linked to the pesticides treatments required to manage populations of *L. salmonis* and lost profit from reduced fish growth and production quality[1,4,5]. Additionally, increased abundances of this parasite within aquaculture farms are linked to declines in wild salmon population, broadening the impact of *L. salmonis*[6,7]. Increased research into salmon lice population dynamics and management is needed to further improve management practices and produce more sustainable aquaculture. A United Kingdom aquaculture task force identified salmon lice management as the fifth most important research priority for sustainable aquaculture[8]. This thesis contributes to *L. salmonis* population dynamic modelling and explores the impact of short-term daily environmental variation on population dynamics.

Newfoundland's aquaculture industry is the third largest in Canada, having produced 17,655 tonnes of product in 2019[9]. The Newfoundland aquaculture industry has grown from a 50 million to a 300-million-dollar industry from 2007 to 2017, with predicted continued growth from government and industry stakeholders[9,10]. The provincial government shows significant interest in development opportunities for the aquaculture industry, which they believe has the potential to double production and expand in the province[10]. The Newfoundland aquaculture industry is comprised of both finfish and shellfish sectors, but is currently dominated by salmonid production (Atlantic salmon, Arctic char, and steelhead trout) along the south coast[9,10]. Newfoundland's *Sea Lice Integrated Pest Management Plan* list understanding pest and host biology and dynamics, preventative treatment strategies, monitoring, and research as key components salmon lice management, but currently does not include modelling components such as that in this thesis[11].

The aquaculture industry has increased its production of farmed product to keep up with increasing food demand by increasing the number of fish per pen and pen size over the last decade[12,13]. The aquaculture industry increased pen sizes from 500-2000 m^3 in the late 1980s to 12,000-80,000 m^3 today[12,13]. The depth of aquaculture pen sizes can vary from 10-25 m, but a study done by the Department of Fisheries and Oceans (DFO) for Bay d'Espoir found that the optimal salmonid cage depth for fish health and production ranged from 10-15 m[14]. A limitation of open-cage aquaculture pens is the lack of separation between fish and ocean conditions, resulting in easy immigration of marine parasites into pens and a lack of control of temperature, salinity and oxygen conditions. Thus, marine pests and parasites can never entirely be removed from aquaculture pens but rather can only be managed and controlled[15–17]. While some methods of physical barriers are used within salmonid aquaculture, these techniques have limitations and can place evolutionary pressure on salmon lice populations (see Coates *et al.* 2020 and Coates *et al.* 2021 for more information).

Salmon lice have a relatively simple life cycle with eight free-living juvenile and parasitic attached stages[1,18,19](Figure 1.1). Female salmon lice have high reproductive capacity, with the ability to produce up to ten pairs of eggs strings during their up to 210 day life-span[1,20]. Eggs produced by adult females hatch and produce three unattached life stages that do not feed: nauplius (I/II) and copepodids[1,18,19]. The length of development varies with temperature, but is time-limited by their endogenous energy supply[1,18,19] (Figure 1.1). Once a copepodid stage attaches to a host they develop through the chalimus and pre-adult life stages into adults[19,21–25] (Figure 1.1). During the chalimus stages, copepods attach to the host via frontal filaments, and during the preadult stages these filaments are believed to help individuals remain attached during molting[1,5]. Population abundance and dynamics vary seasonally and regionally due to differences in length of development and reproduction driven by environmental conditions.

Environmental temperature is the main determinant of the length of developmental time for each life-stage and reproduction rates of salmon lice[1,18,19,26,27]. Temperature changes impose performance constraints on individuals and even slight shifts can have population level effects[28–30]. Between lower and upper tolerance temperatures, basal metabolic rates increase with increasing temperature[28,29,31]. Outside this window, negative performance can be attributed to limited metabolic rate due to limited oxygen capacity and an increased stress on an individual[28–30]. Increasing temperatures produce shorter development times for salmon lice, a relationship seen across most ectothermic organisms[26–28,32]. Faster development of salmon lice makes juveniles viable for a shorter period as they consume their energy reserves faster[33]. Increased temperature also shortens the length of hatching, with one study finding that the length of hatching decreases from 45.1 days at 2°C to 8.7 days at 10°C[19]. However, temperature is not the only environmental condition that influences salmon lice biology and population dynamics.

The natural mortality and viable egg production rate are influenced by ocean salinity, which is also a driver of population dynamics. Individual life-stages respond differently to salinities, with unattached stages having a lower tolerance to salinity changes compared to attached adults[19,34]. Juvenile free-living salmon lice experience near instantaneous mortality when exposed to fresh-water (≤15 psu)[19]. Adult parasitic salmon lice are more tolerant of low salinities, and are able to tolerate unfavorable conditions for short periods of time. The ability of adult salmon lice to tolerate low salinities is hypothesized to be linked to their ability to osmoregulate using salt and blood from their host[19]. One study connecting ocean salinity and mortality by Brinknell *et al.* (2006) hypothesized that salmon lice are stenohaline and become negatively buoyant under low salinities, thus requiring more energy to remain in position, which leads to mortality[35]. Low salinities are also linked with reduced hatching success[19]. Brinknell *et at.* (2006) suggest that the attachment rate of copepodids and ability to identify host are reduced under low salinities, however it is debated if salinity interferes or if it is just an additional factor of reduced salmon lice survival[35]. Ocean salinity and temperature are such key drivers of population dynamics that they can largely explain variation in salmon lice abundances between estuaries, fjords and open oceans systems[1,19].

Seasonal environmental conditions are important aspects in all natural systems, and influence invertebrate and cyclic population dynamics[23,36,37]. The effects of seasonality can be seen across aspects of invertebrate biology ranging from sex ratio of offspring[38], ability of species to colonize new habitats[39], larval activity and behaviour[40], and developmental strategies[41]. In salmon lice, seasonality is known to influence life-stage developmental times, the production and viability of eggs and distance of larval dispersal[18,23]. Seasonal variation in salmon lice population dynamics are largely driven by seasonal variation in salinity and temperature[23,37]. Seasonal variations in population dynamics and growth are known to cause salmon lice populations to experience natural fluctuations in abundance[42].

Seasonal fluctuations are not the only form of variation that affects populations over time and space[43]. Nakaok (1996) found that when comparing stochastic and deterministic age-structured models, that populations experiencing stochastic population growth were never greater than the deterministic population growth rate estimated using average vital rates. He then went on to suggest that deterministic models may overestimate growth rates of populations in fluctuating environments, and these overestimated predictions can be exaggerated by the magnitude of variation in vital rates and frequency of random environmental events[43]. Additionally, stochastic environmental variation is a key driver in density-linked population variation[44]. Wootton *et al.* (2013) coined density-linked stochasticity as fluctuations in population cohort distribution that arise due to stochastic environmental conditions, such as stochastic variation in larval recruitment or dispersal and population age- and size-structure that influence population dynamics[44].

Climate change is predicted to have broad impact globally, affecting primary production, ocean chemistry and specie distribution and biomass[16,45–47]. During previous global warming events, an increase in temperature led to an influx of fresh glacial melt increasing sea surface levels and producing a layer of freshwater over denser salt water[46]. Changes in ocean stratification can lead to changes in primary production altering species biomass and distribution[47]. Salmon lice are predicted to benefit from increasing ocean temperatures through increased egg production and decreased development time[16]. However, predicting the effect of climate change is increasingly challenging for species comprised of multiple life-stages such as marine invertebrates[48]. A meta-analysis done by Pandori *et al.* (2019) of 287 different experiments found that while all invertebrate stages are sensitive to increased temperature events, embryo, larval and juvenile stages are more susceptible to environmental stressor which could lead increased mortality. An increase in temperature may increase maturation rates, but changes in ocean chemistry and salinity could have broad and hard to predict outcomes.

There are several methods to estimate population growth, however, the use of Floquet theory and Floquet exponents is an effective method for seasonal populations. Floquet theory is a method to analyze models with periodic seasonal components[49,50]. In ecological systems, Floquet theory has three potential applications: 1) defining fitness of structured populations in periodic environments, 2) calculating invasion criteria for interacting structured populations in periodic environments, and 3) testing the stability of a limit cycle (see Appendix S1 and Klausmeier, 2008 for more information). Within Floquet theory, Floquet multipliers approximate the multiplicative change in abundance of each life-stage, given that enough time has passed[49]. Floquet exponents describe the long-term rate of the system over time[49]. Floquet multipliers are related to the Floquet exponents by,

$$\rho_i = e^{\phi_i \omega} \qquad 1$$

where ρ_i are the Floquet multiplier and ϕ_i is the Floquet exponent for a given life-stage *i*, with period ω[49] (see Appendix S1 for further information on how to calculate Floquet exponents).

Among animals, individuals often develop through several life-stages that may respond differently to both deterministic and stochastic environmental conditions or contain stage-specific traits[18,19,51]. These populations then cannot be simplified into a single class structure model, and are better described by age-structured population models comprised of multiple stages[44,52–55]. Within these separate life-stages some traits maybe continuous, such as age and size, or more structured and discrete such as sex, reproductive state and instar stage[44,52,53]. Similar to other invertebrates, salmon lice undergo several structured instar stages that experience specific rates of maturation and mortality[2,18,19]. Representing populations through discrete age-structured models is typically easier to construct, analyze and interpret[52]. Information on how to construct structured population models can be found within Otto and Day (2007).

Mathematical models describe many biological systems, with dynamic models describing changes in biological variables over time, and with emergent properties arising at higher levels of biological organization. Dynamic models fall into two categories: deterministic, which represents future events as entirely predictable; and stochastic, which represents future events as random or stochastic events, with probabilities associated with various outcomes[52,56,57]. Both deterministic and stochastic dynamic models have been used to investigate the population dynamics of *L. salmonis*. The first mathematical model to describe *L. salmonis* population dynamics used delayed differential equations (DDEs) with constant delays, developed by Tucker *et al.* (2002). These models were expanded to include temperature-dependent maturation curves[21], salinity-dependent morality[22,23] and stochastic temperature-dependent maturation[24,58]. Advancements in computational power and availability of data have increasingly shaped these models.

Recent salmon lice models have explored seasonal timescales[23] and geographical regions[22,59] and show how population dynamics and management strategies are not static across time or space. The introduction of seasonality into models illustrates how population growth varies with time, with increased growth during warmer months[19,22,23]. Later models showed how regional populations experience different environmental conditions and a set treatment window is not adequate[22]. Instead, region-specific treatment strategies and treatment windows are required for effective pest management of salmon lice[22]. These findings can be expanded to investigate the reliability of recommendations made from models assuming deterministic environmental conditions[22–24]. Yet, to our knowledge no one has considered the effect that short-term or daily fluctuations in environmental conditions may have on salmon lice population dynamics. Understanding the impact of both deterministic seasonal and stochastic environmental variation on salmon lice population dynamics would strengthen management and treatment, and improve the understanding of salmon lice biology[22,23].

In this thesis, I derived a stochastic model for the farm-level population dynamics of salmon lice *L. salmonis* with temperature-dependent maturation and salinity-dependent mortality for a theoretical population along the southern coast of Newfoundland. In Chapter 2, the model explores the effect of daily stochastic salinity under deterministic seasonal temperature, and daily stochastic seasonal temperature under static salinity. Finally, in Chapter 3, I summarize the results, assumptions made in the model, and address how the model can optimize *L. salmonis* control and management and areas of future work.

1.1 Co-authorship Statement

The first manuscript in this thesis was co-authored with Dr. Amy Hurford. I am the principal author for all chapters of this thesis, and was the principal contributor to project design, model derivation, model analysis, and manuscript preparation.

1.2 Figures and Tables

Figure 1.1: Three stages of salmon lice, *Lepeophtheirus salmonis*. From top: Mature female with egg strings, a mature female without egg stings and an immature salmon louse. Picture taken by Thomas Bjønnøy at Norwegian Aquaculture Center, Brønnøy, Norway. Photo was taken from Wikipediae: https://commons.wikimedia.org/wiki/File:Salmonlouse.jpg.

Chapter 2: A Stochastic Model for Salmon Lice (*Lepeophtheirus salmonis*) Population Dynamics in Newfoundland, Canada with Temperature-Dependent Maturation Rates and Salinity-Dependent Mortality

Abstract

Species in the wild do not experience static environmental conditions and are exposed to natural variation on daily and seasonal timescales. Ignoring natural fluctuations around mean environmental conditions may produce models that over-or under-predict population dynamics, for example, owing to Jensen's inequality. Population dynamics can be predicted by considering the effect of environmental conditions on individuals. Several salmon lice *Lepeophtheirus salmonis* population dynamic models consider static conditions or deterministic seasonal trends; However, none have explored the effect of daily environmental variation. Environmental temperature and salinity conditions are predicted to shift and become more variable in future years due to climate change and global warming, leading to population dynamics shifts. To explore the effects of daily variation in temperature and salinity on population dynamics, I derived a stochastic discrete-time population model to study salinity-dependent mortality and temperature-dependent rates of maturation of theoretical salmon lice populations using environmental data for Newfoundland's southern coast. When isolating the impact of environmental variation, my results suggest that salmon lice growth rates decrease with increasing salinity variation and trends in abundance are better described by seasonal variation in temperature. Accounting for daily variation in salinity and temperature could lead to a more accurate understanding of population dynamics and abundance, and improved management and control within aquaculture systems.

2.1 Introduction

Environmental conditions, such as ocean temperature and salinity, influence population dynamics through rates of maturation and mortality[19,60,60–64]. Population dynamics can be predicted by understanding the effects that environmental conditions have on individuals, and this understanding is key to sustainable aquaculture and more broadly, species conservation. A prime example is the salmon lice *Lepeophtheirus salmonis*, a marine parasitic copepod that experiences temperature-dependent maturation and salinity-dependent morality, and is often modelled to improve management strategies and pest control within aquaculture systems.

Seasonal variation in environmental conditions plays a significant role in the spread and dynamics of diseases and host-parasite systems[65,66], with increasing climate change predicted to worsen these trends[16,67–70]. This link between environmental temperature and salinity and aspects of disease and parasite dynamics is a growing concern as environmental conditions shift due to climate change[67,68]. Recent *L. salmonis* models have explored the effect of seasonality[22,23,50,71], geographical location[22] and connectivity of farms[72,73]. However, *L. salmonis* and other parasites do not experience static conditions, but rather, are subject to short-term stochastic environmental conditions that fluctuate from day-to-day.

Newfoundland has patterns of seasonal and non-seasonal trends in salinity and temperature, along with variation between years[74–76]. Seasonal patterns in Newfoundland are associated with an influx of freshwater in early summer and late fall due to melting sea ice and snowmelt[74,75,77]. Globally, temperature and salinity have seen both increasing and decreasing trends in recent years, with salinity becoming more variable[78–81]. These trends and increased variability have been linked with global warming and climate change, and are predicted to continue and worsen[78–81].

Individuals in nature experience fluctuating conditions around the mean[66,82]. Depending on the direction of fluctuations, populations may experience short-term periods of beneficial, or limiting conditions[66]. A study done by Lambrecht *et al.* (2019) found that models using a realistic diurnal temperature range better explain seasonal variation in the transmission rates of the dengue virus (DENV) transmitted by *Aedes aegypti*. Another study found that the inclusion of seasonal variation supported the sustained presence of the Zika virus (ZIKV) in areas with non-optimal mean temperatures where other models predicted non-persistence[82]. The inclusion of daily variation in a population model for *L. salmonis* could strengthen the model estimates by accounting for short timescale variation that individuals naturally experience in the wild.

A variety of deterministic[22,23,73,83] and stochastic[24,72] mathematical models have been used to understand salmon lice population dynamics. While many of these studies have investigated the effects of temperature and salinity on salmon lice, none have considered fluctuations on short timeframes, i.e. daily, or changes in future salinity variability. Short-term daily variations in salinity are likely to affect mortality rates of salmon lice, while temperature will influence the rates of development and egg production. In this study, I consider independent daily fluctuations in salinity and temperature to explore current and future levels of environmental variation in Newfoundland and their effect on salmon lice population dynamics.

I hypothesize that salmon lice in areas with high daily salinity variability will have slower population growth rates. This is because very low salinities are more detrimental to salmon lice than higher salinities are beneficial, so I expect a decreasing and convex relationship between salinity and the population growth rate (see Methods and Figure 2.2 for further details). Owing to Jensen's inequality[84], the increase in mortality when salinity fluctuates below the mean is greater than the decrease in mortality when salinity fluctuates by the same amount above the mean, and so the overall effect of the fluctuations is a net increase in mortality. I also hypothesize that salmon lice in areas with higher daily temperature variability will have slower population growth rates, also owing to a net decrease in the maturation rate due to Jensen's inequality (see Methods and Figure 2.3 for further details). To test these predictions, I created a stochastic population dynamic model with the ability to alter and investigate current and future stochastic temperature and salinity variability scenarios. In the model, temperature is described by a deterministic seasonal function with a daily stochastic component and salinity is described by an asymmetric Laplace probability distribution. I will use Floquet theory to estimate structured population growth rates under stochastic salinity[22,36,49,50]. The model is applied to theoretical salmon lice populations in Bay d'Espoir and along the southern coast of Newfoundland, Canada.

2.2 Methods

This thesis aims to understand the effect of daily stochastic environmental variation on salmon lice population dynamics. I constructed a stochastic structured population dynamic model for salmon lice based on stage-specific rates of maturation and mortality from the literature (Table 2.1). Environmental salinity and temperature data for Newfoundland are used to construct two independent daily stochastic variables. An asymmetric Laplace distribution is constructed to explore daily stochastic salinity and a deterministic sinusoidal seasonal function with a random normal component controlling daily stochastic temperature fluctuations. The long term population dynamics and growth rates of salmon lice are calculated through Floquet theory and estimated by Floquet exponents.

2.2.1 Life cycle of *L. salmonis*

To inform the model derivation for the stage-structured dynamics of *L. salmonis*, I review the life cycle of salmon lice. Salmon lice *L. salmonis* transition through eight morphologically different life stages, which for the purpose of this model have been simplified into four relevant biological stages: P_t: nauplius I/II, I_t: copepodid, C_t: chalimus I/II, and A_t: pre-adult I/II and adult females[19,21–25,83] (Figure 2.1). The morphologically different life stages are simplified based on differences in maturation rates and mortality (Table 2.1). The length of time that an individual takes to mature in each life stage is temperature-dependent (Figure 2.1, solid lines), and decreases under higher temperatures[5,18,19,24]. The natural mortality rates for each life stage increase under lower salinity conditions[18,19,24] (Figure 2.1, dashed lines). See Chapter 1 for further information on salmon lice life-stage biology and information on modelling stage structured populations.

The change in the natural mortality of a single life stage to a range of salinity conditions can cascade through the entire population and affect population dynamics. All salmon lice life-stages show varying decreasing convex relationships between the natural mortality and salinity (Figure 2.2). The relationship curves between natural mortality and salinity suggest that a fluctuation above the mean decreases the mortality rate less than a fluctuation below the mean, of the same size, increases the mortality rate (Figure 2.2). Therefore, I hypothesize that salinity fluctuations around a mean have a net negative effect on the population growth rate due to periods of exposure to highly detrimental low salinities.

Additionally, the influences of ocean temperature on the viable egg production rate, $\eta_t \epsilon_t \nu_t$, and the nauplii and chalimus maturation rates, γ_t^P and γ_t^C respectfully, may provide valuable insight into further population dynamics (see Table 2.1 for units and rate definitions). The rate of maturation for both the nauplii, γ_t^P, and chalimus, γ_t^C, suggest a strong linear relationship with increasing temperature (Figure 2.3, Table 2.1). The relationship between temperature and the viable egg production rate, $\eta_t \epsilon_t \nu_t$, is non-linear (Figure 2.3, Table 2.1). Similar to the relationship between natural mortality and salinity, I hypothesize that temperature fluctuations below the mean will be more detrimental than equal fluctuations above, thus temperature fluctuations around a mean from a symmetric distribution have a net negative effect on the population growth rate (Figure 2.3, Table 2.1).

2.2.2 Salinity

Salinity data was collected by the Department of Fisheries and Oceans Canada (DFO) starting in 1956 and ending in 2013 in Bay d'Espoir, Newfoundland (47.63N, 56.21W to 47.97N, 55.70W, Figure 2.4a,b). Data were collected using mechanical bathythermograph at various depths and locations throughout the bay. See Appendix S2 for additional information on salinity data. Bay d’Espoir is a fjord-like bay located in the Coast of Bays region on the south coast Newfoundland and Labrador and connects into the Atlantic Ocean through Hermitage Bay[85] (Figure 2.4a). The Coast of Bays region can be divided into three distant geographical, hydrologic and oceanographic regions: a deep, long and narrow fjord (Bay d’Espoir), a deep and wide bay (Belle Bay) and a shallower region, more exposed to the open ocean (Connaigre Peninsula)[86].

Outside of Bay d’Espoir, the southern coast is fed by several large bays and inlets, influencing the salinity and temperature profiles of the water column[85]. A hydroelectric generating facility located at the head of the bay is the main source of freshwater runoff, and influences both the salinity and temperature profiles[85]. Salinity ranges from 0 psu at the head and increases towards an average of 32.25 at the mouth of the bay[85]. Within the Coast of Bays region, Bay d’Espoir experiences the highest annual average freshwater discharge of these three regions of about 252 $\frac{m^3}{s}$, with large spring freshet in April-May, low runoff in the summer (July-August) and a small speak in late-fall/early-winter (November-December)[86]. A salinity gradient is known to exist in Bay d’Espoir that varies in depth seasonally[86,87]. Salmonid aquaculture has increased and expanded out of Bay d’Espoir into Fortune and Hermitage Bay, with 81 salmonid licences in 2011[85,86].

To introduce realistic descriptions of salinity variation into the model that mirrors that seen in Bay d’Espoir, I only considered daily stochastic salinity variability since no relationship between the month sampled and observed salinity was found (Spearman correlation $r_S{}^2$= -0.08) . Thus, I fitted an asymmetric Laplace distribution,

$$S_t = \frac{\lambda}{k + \frac{1}{k}} \begin{cases} exp(\frac{\lambda}{k}(x - m)), & \text{if } x < m \\ exp(-\lambda k(x - m)), & \text{if } x \geq m \end{cases} \tag{2}$$

to salinity data taken from Bay d'Espoir (Figure 2.4b,c), where m is the location parameter, λ is the scale parameter, k is the asymmetry parameter, and x is a given salinity value (see Table 2.1 for parameter values). An asymmetric Laplace distribution was selected since the variance and skewness are affected by changing λ and k respectively, with increasing λ corresponding to smaller variance and $k > 1$ corresponding to increasing left-skewness. Within the model, a stochastic salinity value is sampled from the asymmetric Laplace distribution for each time, t.

Only salinity between 15-40 psu were fit to the distribution, as salinity data lower than 15 psu was sparse, and resulted in a poor fit (1948 observations were removed, leaving 168867 remaining). I estimated the location parameter, m, as the most frequently recorded salinity when all recorded values where binned into 0.5 psu increments (Figure 2.4b, Table 2.1). The parameters λ and k were estimated using maximum likelihood, assuming a normal distribution of errors, and using the bblme package in R[88].

Two separate mean salinity values are used in this thesis: mean ocean salinity for Bay d'Espoir, $s_{\mu_{BDE}}$, and the highest frequency salinity bin, m_{SC}, for Newfoundland's southern coast. Mean ocean salinity for Bay d'Espoir, $s_{\mu_{BDE}}$, is used to compared stochastic salinity scenarios, λ, to predictions made using a constant salinity. The highest frequency salinity bin salinity, m_{SC}, is used under daily stochastic deterministic seasonal temperature scenarios.

2.2.3 Daily Stochastic Seasonally Deterministic Temperature

Ocean temperature data for Bay d'Espoir were sparse and thus I used temperature data up to a depth of 10 m for the southern coast of Newfoundland collected by the Department of Fisheries and Oceans Canada (DFO) using drifting buoys spanning ten years from 2009 to 2019. See Appendix S2 for additional information on temperature data set. Only temperature data from the southern coast between (59°50'00.0"N, 48°04'00.0"W) and (54°00'00.0"N, 46°10'00.0"W) were fitted to the deterministic temperature functions (1,093,344 observations were removed leaving 87,722 specifically along the southern coast, Figure 2.5a). Ocean temperatures show seasonal patterns, with temperatures dropping in the winter and rising during spring and summer (Figure 2.5b).

To realistically describe temperature variation seen along the southern coast of Newfoundland in the model, I considered two sources of temperature variability: deterministic seasonal fluctuations in mean temperature and daily stochastic variations around these mean values. Temperature data were fit with a periodic function (one period = one year) with a random component,

$$T_t = a + b_1 sin(2\pi \frac{t}{365}) + b_2 cos(2\pi \frac{t}{365}) + \theta_t \tag{3}$$

where a is the mean annual temperature, b_1 and b_2 are the amplitudes for the sine and cosine functions, θ_t is a random variable, t is time, and is integer-valued (for parameter values see Table 2.1. Related parameters are estimated in Hurford *et al.*, 2019; and Rittenhouse *et al.*, 2016). A total of 87,722 observations were fitted (Figure 2.5a). The mean annual temperature parameter a was estimated by taking the mean of all observations, and the temperature amplitude parameter values for b_1 and b_2 were fit using the lm() function in R[89].

The random component of daily temperature, θ_t, is drawn from a normal distribution with a mean of zero, given by,

$$\theta_t \sim \frac{1}{\sigma_\theta\sqrt{2\pi}}e^{-\frac{1}{2}(\frac{t}{\sigma_\theta})^2} \qquad 4$$

where σ_θ is the standard deviation and values are sampled for each time t and added to the deterministic temperature value. The random components introduces daily stochastic variation around the deterministic seasonal temperature function. A normal distribution with a mean of 0, was used as variation is assumed to have an equal chance to cause temperature fluctuations above or below the deterministic seasonal temperature function. Changing the standard deviation, σ_θ, controls the level of variation within the daily stochastic temperature function (Table 2.1). For each time, t, the deterministic temperature is calculated and then the stochastic variation is added from the daily random temperature component, θ_t. I used the residual standard error, β, from our deterministic temperature function to estimate the baseline level of variation in observed temperature data (Figure 2.6).

To isolate the impact of stochastic salinity, when I investigate stochastic salinity, I do not consider stochastic temperature. The deterministic temperature function is,

$$T_t = c + d_1 sin(2\pi \frac{t}{365}) + d_2 cos(2\pi \frac{t}{365}) \tag{5}$$

where c is the mean annual temperature, and d_1 and d_2 are the amplitudes for the sine and cosine functions (Table 2.1).

2.2.4 Population dynamics

This model expands upon results from Rittenhouse *et al.* (2016) where they showed how population growth of salmon lice varied seasonally with temperature and salinity. However, Rittenhouse *et al.* (2016) did not include a method to incorporate short-term environmental variation, which is known to exist in Newfoundland and globally[23,87]. Here, I introduce the daily stochastic salinity variation and daily stochastic fluctuations around deterministic seasonal temperature trends into the model to explore its effect on population dynamics and simulate time in discrete intervals. Several parameters were first derived in the Rittenhouse *et al.* (2016) study and describe salmon lice life history, while others are site-specific corresponding to environmental conditions (see Table 2.1 for additional information such as units and parameter values).

Different aspects of salmon lice life-history are affected by temperature and salinity differently and need to be parameterized. As summarized in Chapter 1, salinity affects the egg viability and natural mortality and temperature affects the development and egg production rate of salmon lice[1,18,19,35,90]. The rate of maturation for a given life stage, x, is represented by the function $\gamma^x(T_t)$, where x is equal to P or C (Figure 2.1, Table 2.1). For notational simplicity, I write γ_t^x, where the dependence on t is implicit via the dependence of the maturation rate on temperature, which depends on time, t. All life history parameters that I write as depending on t, have an implicit dependence on temperature or salinity. The natural rate of mortality occurring in a given life-stage, i, is dependent on salinity, and is described by the function μ_t^i, where i is equal to P, I, C, or A (Figure 2.1, Table 2.1). The egg string production rate and the number of eggs per string depend on salinity and are described by the functions ϵ_t and η_t (Table 2.1). The proportion of eggs that produce viable nauplii depends on temperature and salinity and is described by the function ν_t (Table 2.1).

The model assumes the attachment rate is independent of temperature and salinity, occurs at a constant rate, and is given by $\iota f I_t$ where ι is the attachment rate, f is the number of fish within a given pen and I_t is the abundance of copepodid at time t (Table 2.1). The complete population model for *L. salmonis* is given by equations 6-9,

$$P_{t+1} = P_t + \eta_t \epsilon_t A \nu_t - \mu_t^P P_t - \gamma_t^P P_t \qquad 6$$

$$I_{t+1} = I_t + \gamma_t^P P_t - \iota f I_t - \mu_t^I I_t \qquad 7$$

$$C_{t+1} = C_t + \iota f I_t - \gamma_t^C C_t - \mu_t^C C_t \qquad 8$$

$$A_{t+1} = A_t + \gamma_t^C C_t - \mu_t^A A_t \qquad 9$$

As the maturation rates, γ_t^x, depend on temperature, which is periodic with annual seasonal cycles (see equation 3), I quantify the population growth rate by calculating the Floquet exponent (see Appendix S1 for full details and Table 2.1 for additional information on parameters).

2.3 Results

2.3.1 Stochastic Salinity Under Deterministic Temperature

The Floquet exponents, ϕ, are positive for all stochastic salinity scenarios, λ, investigated, indicating that the salmon lice extinction equilibrium is unstable and that salmon lice will persist and increase yearly (Figure 2.7b & 2.8b). I found that increasing daily stochastic salinity slows growth rates, represented by decreasing Floquet exponents, ϕ (Figure 2.8b). Increasing daily salinity increases the probability of unfavorable salinity conditions that correspond to higher mortality. Under all stochastic salinity variation scenarios salmon lice population growth was slower compared to that under a constant salinity of 32.25 psu, but all populations persisted and grew with time (Figure 2.8b). Smaller abundances of adult females were predicted under increasing stochastic salinity (Figure 2.8b). The difference in the logarithmic abundance of adult females between stochastic salinity scenarios, λ, grew as $t \rightarrow \infty$ (Figure 2.7b). See Appendix S2 for information for all model simulation predictions.

I found that extreme right-skewed stochastic salinity distributions, $k = 0.1$, had the fastest population growth rates of all salinity scenarios, λ and k, and was the only scenario to have population growth rates faster than those under static salinity conditions (Figure

2.8b, 2.9c). Increasing left-skewed stochastic salinity (salinities having a higher probability falling below the location parameter, m=32.25), $k > 1$, slowed population growth rates as stochastic variation moved to the right of the location parameter, m, and corresponds to higher mortality rates (Figure 2.9). Right-skewed stochastic salinity (salinities having a higher probability of falling below the location parameter, m=32.25) produced fast growth rates as they increased the probability of beneficial salinity conditions corresponding to lower mortality.

2.3.2 Daily Stochastic Seasonal Temperature Under Static Salinity

I found that under all stochastic temperature variation scenarios, σ_θ, population abundance grew with time t and persisted along Newfoundland's southern coast (Figure 2.10b,c). I considered daily temperature variation standard deviations of σ_θ = 0,1, 2, 3, 4, and 5°C and found no relationship between mean logarithmic abundance of adult females and increasing temperature variability. Increasing stochastic temperature did not provide an indication of mean logarithmic abundance overall (Figure 2.10c). Increasing temperature variation did increase the variation in the two-year logarithmic differences (Figure 2.10d). The seasonal effect of the deterministic seasonal temperature function was observed in both the individual salmon lice abundance realizations and in the mean logarithmic abundance and was the strongest determinant of population dynamics despite the level of daily temperature variation (Figure 2.10). Populations have local peaks in abundance during the late summer to early spring and local valleys during winter (Figure 2.10).

2.4 Discussion

Environmental conditions affect the rate of morality and maturation of salmon lice and daily variation in salinity and temperature have varying impacts on population dynamics. Understanding the effects of environmental conditions is key to controlling salmon lice populations and to producing more sustainable aquaculture. In the contexts of salinity-dependent mortality and temperature-dependent maturation, I found that increasingly variable salinity levels and increasingly left-skewed salinity distributions (i.e., the potential for very low salinity values) decreases salmon lice growth rates, while increasingly variable temperature had no effect, as seasonal temperature patterns were a bigger driver of population dynamics than daily variability. Compared to predictions made using static salinity conditions, the majority of populations under variable salinities were smaller and had slower growth rates. Comparing variable daily temperature variation scenarios to only deterministic temperature ($\sigma_\theta = 0°C$) no clear trend in population dynamics or abundance could be seen. Under levels of salinity variation, λ, and temperature variation, σ_θ, investigated in this thesis salmon lice populations grew with time, t, and are predicted to persist in Bay d'Espoir and along Newfoundland's southern coast.

2.4.1 Stochastic Salinity

I found that both the level of daily salinity variability and the direction of skewness affected population dynamics[43,44]. Under most salinity scenarios investigated, ignoring variation and skewness over estimates population abundance and growth. When looking at the base levels of variation in Bay d'Espoir, I found salinity tended to be more left-skewed or having lower salinity values, which corresponds to slower population growth. Quantifying levels and direction of variation is important in areas with well-defined daily variation (estuaries, fjords, and bays)[19] or seasonal trends such as temperate and polar regions[91].

Under all salinity scenarios investigated salmon lice are predicted to persist along Newfoundland's southern coast and grow with time, indicating that they will remain a problem for Newfoundland aquaculture industries and wild fish stocks. When only looking at the role of salinity variability on salmon lice population dynamics, our results suggest that management may become easier if globally salinity patterns continue to become more variable. However, this applies only to salinity-dependent mortalities and temperature-dependent maturation rates as tested in this thesis. It does not consider other complex factors such as the role of temperature variability on larval dispersal, directional variability of salinity and specific biological and evolutionary responses to physical and chemotherapeutants management strategies[67,69,92]. Aquaculture industries should not depend on predicted increased salinity variability and increased rates of natural mortality as a possible advantage for salmon lice management and control[67]. Rather, they should consider the inclusion of daily variability in population models as an effective tool to understand and mange salmon lice populations and outbreaks.

Our results suggest that salmon lice will persist in Newfoundland and Labrador under all temperature and salinity scenarios investigated in this thesis. This contrasts a similar theoretical population in a Hurford *et al.* (2019) study, which predicted that salmon lice should not persist in Newfoundland and Labrador. Hurford *et al.* (2019) considered lower mean salinity stemming from data for only the top four meters of water and these conditions are most similar to predictions made by our model with a low scale parameter, λ. While all variable salinity scenarios investigated in this study indicated that salmon lice will persist, populations from scenarios with high variation ($\lambda < 1.82$) and more symmetric salinity distributions ($k \geq 1.22$) had the slowest growth rates. It can be hypothesized that if I investigated greater levels of variation ($\lambda < 0.1$) or higher levels of left-skewed ($k > 10$) salinity that I could began to see annual decreases in salmon lice abundance in Newfoundland. Additionally, when Hurford *et al.* (2019) assumed a constant salinity of 31 psu both their model and this model predicted persistence and growth of salmon lice populations in Newfoundland.

2.4.2 Daily Stochastic Deterministic Seasonal Temperature

Despite the level of daily variation, seasonal trends in temperature was the most significant driver of population dynamics and could be seen in all simulations. The response in temperature- and salinity-dependent salmon lice life-history traits may explain and help predict the response in variable environments. Two similar increasing relationships are seen between the maturation rates of the nauplii and chalimus life-stages and increasing temperature, however an increasing linear relationship was not found across all temperature-dependent life traits. The viable egg production rate peaked around 20°C and decreased for temperatures above 20°C. The majority of both observed temperatures and temperatures produced by the simulations were under 20°C. For temperature variability, I assumed a symmetric distribution of the deviation of daily temperatures from the mean value. Variation corresponding to lower temperature have a larger negative impact thus corresponding to a net decrease in population growth rate. Rittenhouse *et al.* (2016) found in their sensitivity analysis that eggs per clutch was the third biggest driver of population dynamics and adult females were more sensitive to changes in developmental time of chalimus and pre-adults then to nauplius[23], all factors influenced by temperature, and have lower values under 20°C.

Short-term temperature variation is known to allow some species to persist and thrive in fluctuating conditions that otherwise are unfavourable[93–97]. A study by Tian and Dong (2006) found that the growth rate of Chinese shrimp *Fenneropenaeus chinensis* varied between constant and fluctuating temperatures, with small fluctuations (± 2-3°C) being the most beneficial to their growth[97]. Other studies have also investigated the effect of environmental fluctuations on a diverse number of species[50,93–96]; however, outcomes are broad and can be hard to predict.

2.4.3 Limitations and Future Work

Our model only accounts for daily fluctuations in salinity, not seasonal, which may not be appropriate for other regions. Without seasonal changes in the mean or variance of salinity over time the effect of daily fluctuations is easier to interpret, and to apply to Newfoundland; although there are patterns of seasonal salinity variation[74,75] these differences between the seasonal peaks and valleys in salinity are not considered large enough to effect population dynamics and are not correlated[23,98]. For the application of this model onto areas with both daily and seasonal variation in salinity, a similar sinusoidal function to the one used here to describe temperature may be appropriate. I recommend that future work should consider other methods or combination of stochastic environmental conditions in new regions and not be limited to the structure used in this thesis.

In this thesis, I account for variation with time but not for three-dimensional space in the ocean. A salinity gradient is known to exist in Newfoundland, and globally, which produces heterogonous environmental conditions with depth[74,86,87]. In Newfoundland, the salinity gradient varies throughout time and space with a smaller unstratified gradient in the winter months, with increasing stratification throughout the spring and reaching a maximum in around August[74,86,87]. Hydrodynamic models that account for changes in ocean conditions due to tidal and wind forces provide insight into environmental conditions through space[99,100]. These models also provide useful information about current and future aquaculture site hydrodynamics which would affect population dynamics. Farms in locations with well-defined salinity gradients may provide salmon lice with more or less favourable conditions for salmon lice[100–102]. Additionally, I recommend future work to explore the use of hydrodynamic models in Newfoundland and possible integration with stochastic population models.

My last recommendation for future models is to consider possible interactions between multiple stochastic environmental conditions. In this thesis, I only explored the independent effect of stochastic temperature or salinity; in reality correlations between ocean temperature and salinity likely occur. Baseline environmental salinity and temperature variation should be estimated and included into the model for more realistic environmental descriptions. Interactions between these two variables on population dynamics could produce a broad range of outcomes, depending on the level of each and should be further investigated in future models. It can be predicted that high values of one environmental condition may dominate population dynamics, but it becomes harder to hypothesize outcomes for more intermediate values.

Laboratory studies have quantified the impact of rapid exposure to freshwater on the mortality rates of *L. salmonis*[21,24,103], but only look at the effect of static temperature on the development and egg production of salmon lice. The parameters in this thesis were estimated by finding the rates of maturation[7,21,23], mortality[18,23], and viable egg production[18,23] along spectrums of static temperature and salinity conditions and is extrapolated between. Future laboratory studies should consider variable temperature regimes. Some conditions experienced in the thesis are outside those explored in laboratory studies, either due to barriers faced in the lab or at the extremes of wild conditions. Laboratory studies investigating the effect of environmental conditions face barriers such as realistic conditions and the length of time required to produce results. However, these studies would improve the understanding in the relationship between fluctuating and extreme temperature conditions and salmon lice. I recommend that future laboratory studies investigate salmon lice response to fluctuating and environmental cycling conditions along a wide range of conditions and lengths to increase model parametrization and quantify any delayed effects.

Lastly, several different pesticide treatments are currently used to control salmon lice abundances, including chemical pesticides, physical barriers, in-feed treatments, and thermal delousing[104–107]. Increased use of thermal delousing, exposing salmon to either warm or cold water to remove salmon lice[105,106], to detach salmon lice may place evolutionary pressure on salmon lice to have a higher thermal tolerance[92]. Regional populations are already experiencing local environmental conditions which require regional treatment strategies[22]. Additionally, salmon lice experience relatively high gene flow and levels of heritable basis[92]. Increasing tolerance to extreme conditions is unlikely to lead to advantages for salmon lice in natural conditions; however, it may cause an increase sensitivity at lower temperatures[92,108,109]. This in theory could limit the viable dispersal range of salmon lice as they natural disperse over large geographical and thermal ranges outside of their control[92,110,111]. Additionally, regional populations that acclimate to thermal delousing may experience population specific temperature-maturation relationships, lowering the efficacy of thermal treatments[92,110,111].

2.4.4 Conclusion

The ability to accurately predict the future abundances of *L. salmonis* population using models is dependent on the inclusion of realistic environments that mimic real word conditions, and is key to their management and control within aquaculture farms[1,18,85,103]. Through the inclusion of stochastic salinity and temperature I found that the use of static salinity over-predicts population growth rates, while seasonal temperature provided a stronger indicator of population dynamics than daily levels of variation. When looking at salinity-dependent mortality and temperature-dependent maturation rates, salmon lice are predicted to persist along Newfoundland's southern coast under all possible environmental scenarios investigated and remain an economic and environmental pest. However, I found that increasing daily salinity variation is predicted to decrease population growth rates. For these reasons future work should prioritize the inclusion of realistic fluctuating environmental conditions over static conditions into *L. salmonis* population models and explore additional multi-stage species.

2.5 Figures and Tables

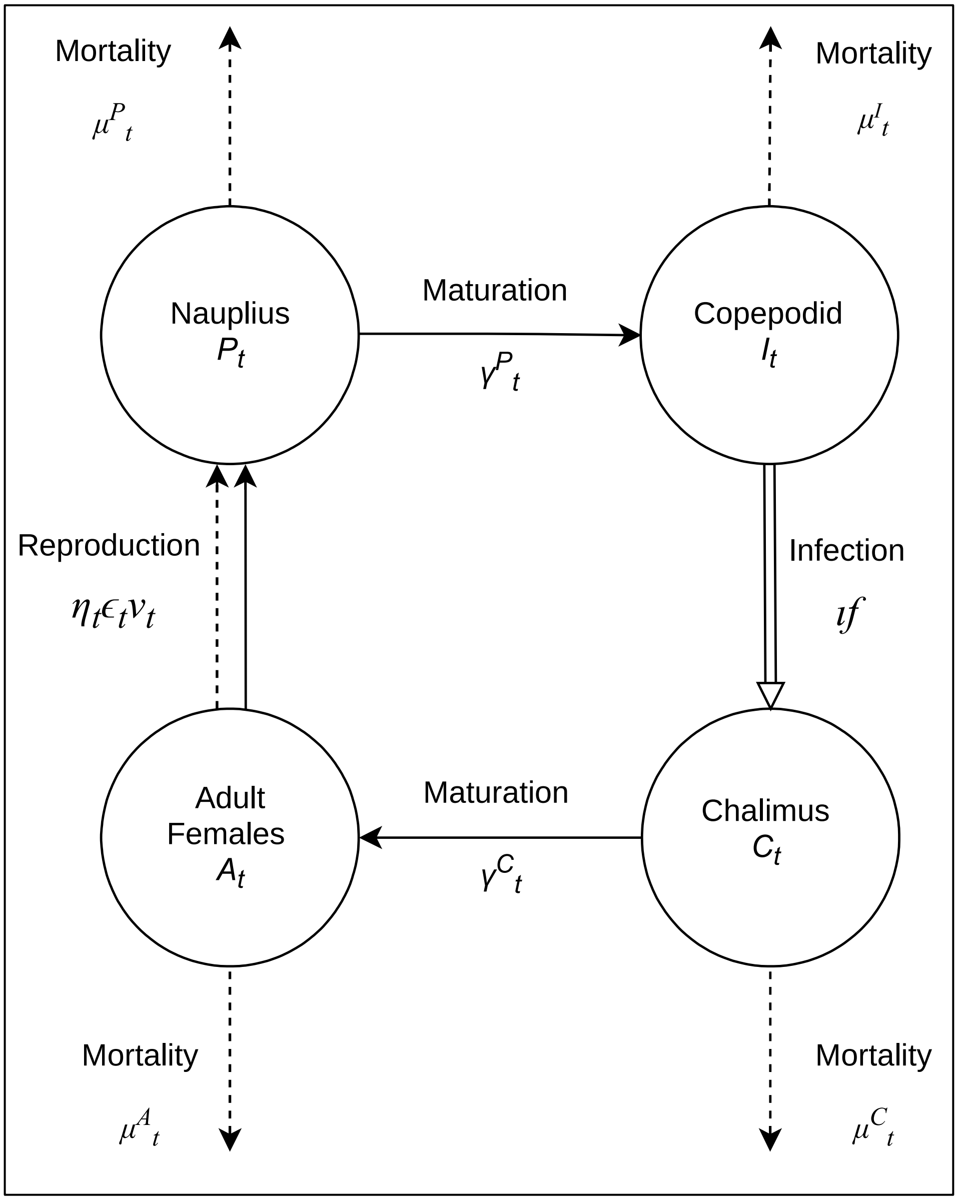

Figure 2.1: Modelled life cycle of *L. salmonis*. Dashed arrows indicate aspects of life history affected by salinity, and solid arrows are aspects affected by temperature. Double solid line arrow indicate aspect of life history independent of temperature and salinity.

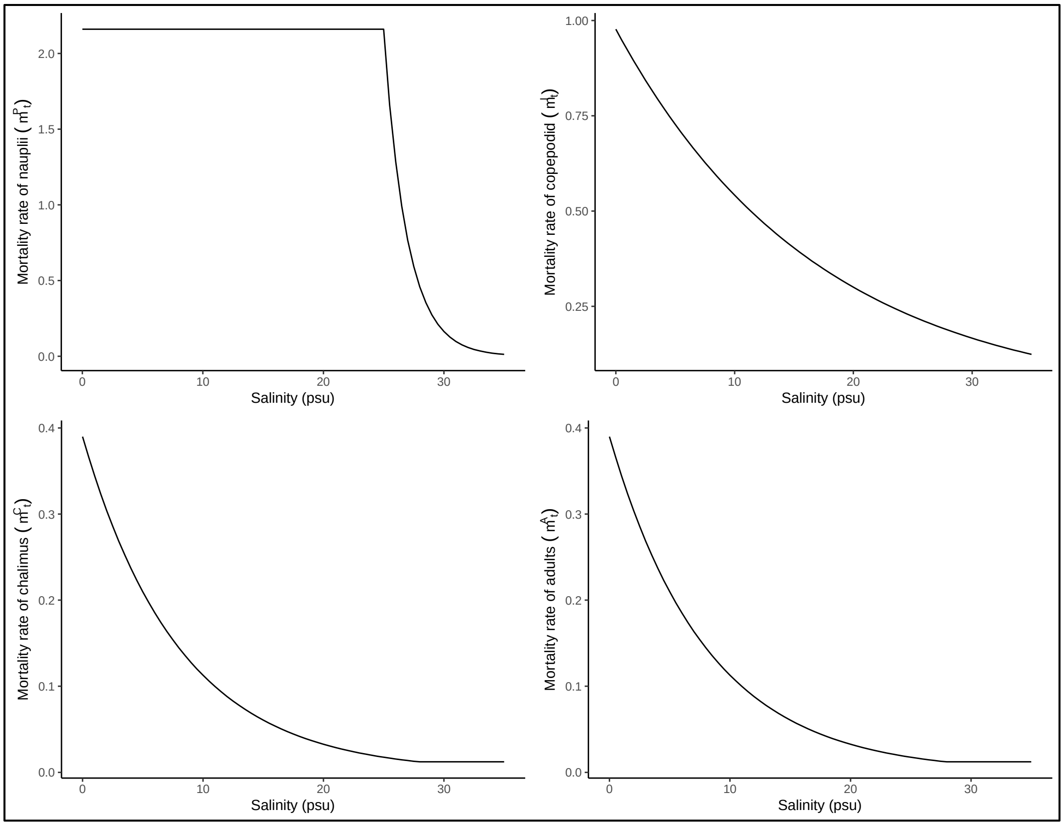

Figure 2.2: Mortality rate for nauplii, μ_t^P, copepodid μ_t^I, chalimus, μ_t^C, and pre-adults and adult females μ_t^A under salinity ranging from 0 psu (freshwater) to 35 psu (ocean salinity). The mortality rates of nauplii for salinity less than 25 psu is not known, and so is approximated as equal to the mortality at 25 psu. Data sources and fitting of these functions is described in Hurford *et al.* (2019).

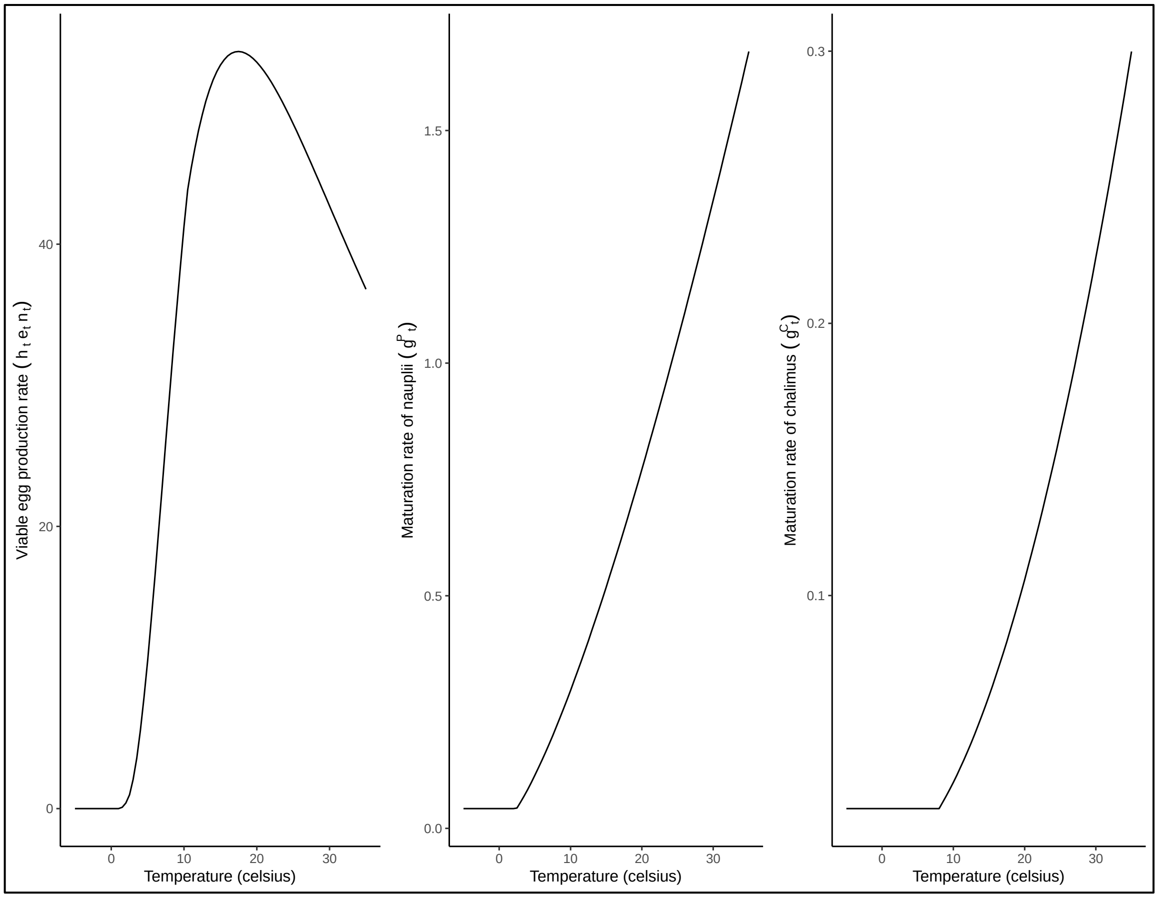

Figure 2.3: Viable egg production rate, $\eta_t \epsilon_t \nu_t$, and the maturation rate for nauplii, γ_t^P, and chalimus, γ_t^C, under temperature from -5 to 35 °C. The viable egg production rate, $\eta_t \epsilon_t \nu_t$, peaks around 20°C, and both the maturation rate for nauplii, γ_t^P, and chalimus, γ_t^C, peak at 35 °C. Data sources and fitting of these functions is described in Hurford *et al.* (2019).

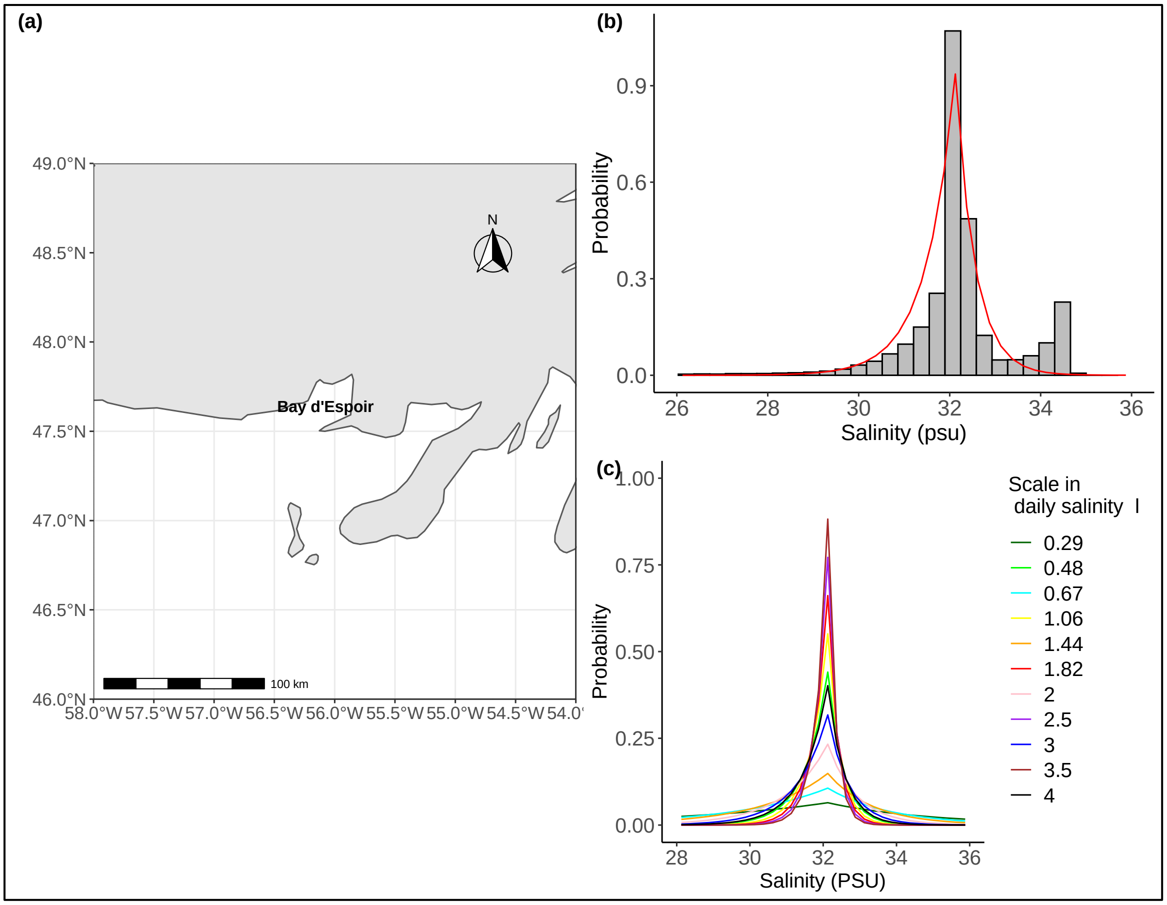

Figure 2.4: (a) A map highlighting Bay d'Espoir, (b) the fitted asymmetric Laplace distribution overlaid on the empirical salinity histogram, and (c) the effects of different scale parameters, λ, on the asymmetric Laplace salinity distributions. (a) Bay d'Espoir is a fjord-like bay located on the southern coast of Newfoundland and Labrador (47°40'36.9 “N 56°06'35.9 “W). Salinity data was recorded for each month but is not recorded for some years. (b) The histogram is separated into 0.5 psu bins. The fitted asymmetric Laplace distribution has parameters $m = 32.25$, $\lambda = 1.91$ and $k = 1.22$. (c) Increasing scale parameters produce a narrower distribution with higher probabilities located around the location parameter value, m, while smaller positive scale parameters produce a flatter, more even probability overall.

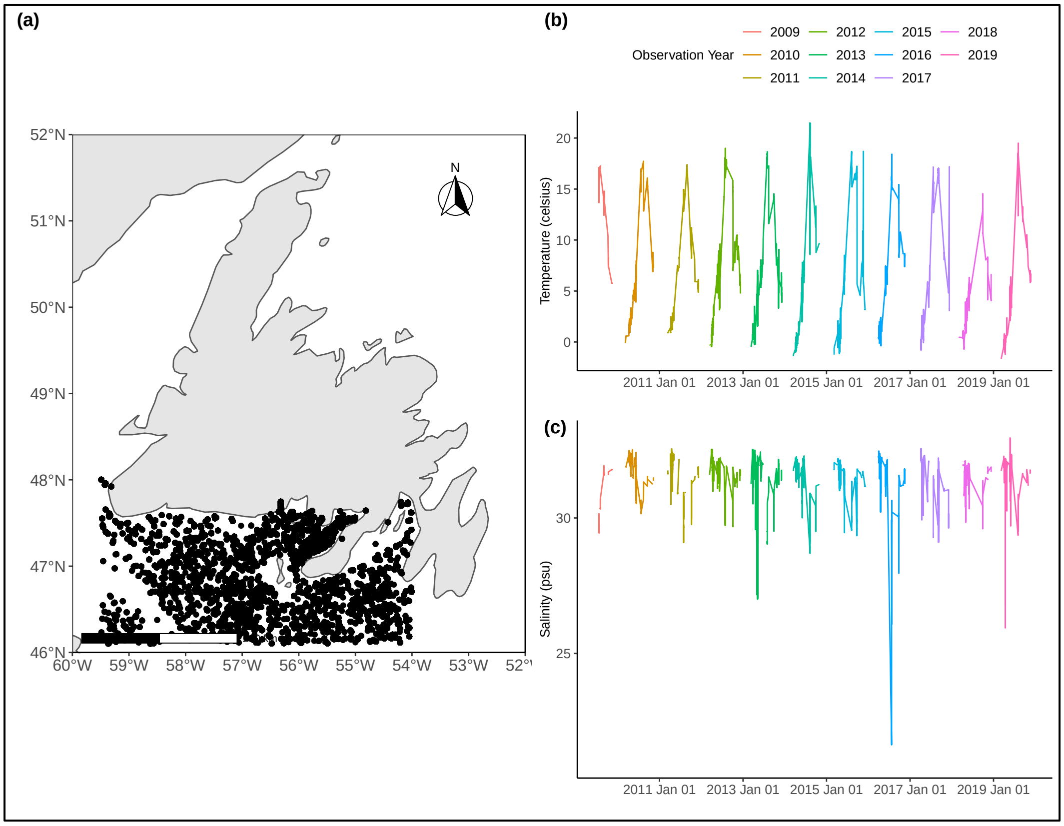

Figure 2.5: (a) A map of Bay D'Espoir Newfoundland showing the locations of the environmental samples, and (b) temperature and (c) salinity for these samples each year. (a) Only observations off the southern coast of Newfoundland were fit to the temperature and salinity functions (a total of 87,722). Each black dot represents one sample site with some sites having more than one sample taken overtime. The first observation was on July 20th, 2009, and the last on November 23rd, 2019. (b) All temperature observations, plotted chronologically from the first observations to the last. Observations are separated by colour based on year of observation. (c) All the salinity observations plotted chronologically from the first observations to the last, and follows the same colour index of panel b.

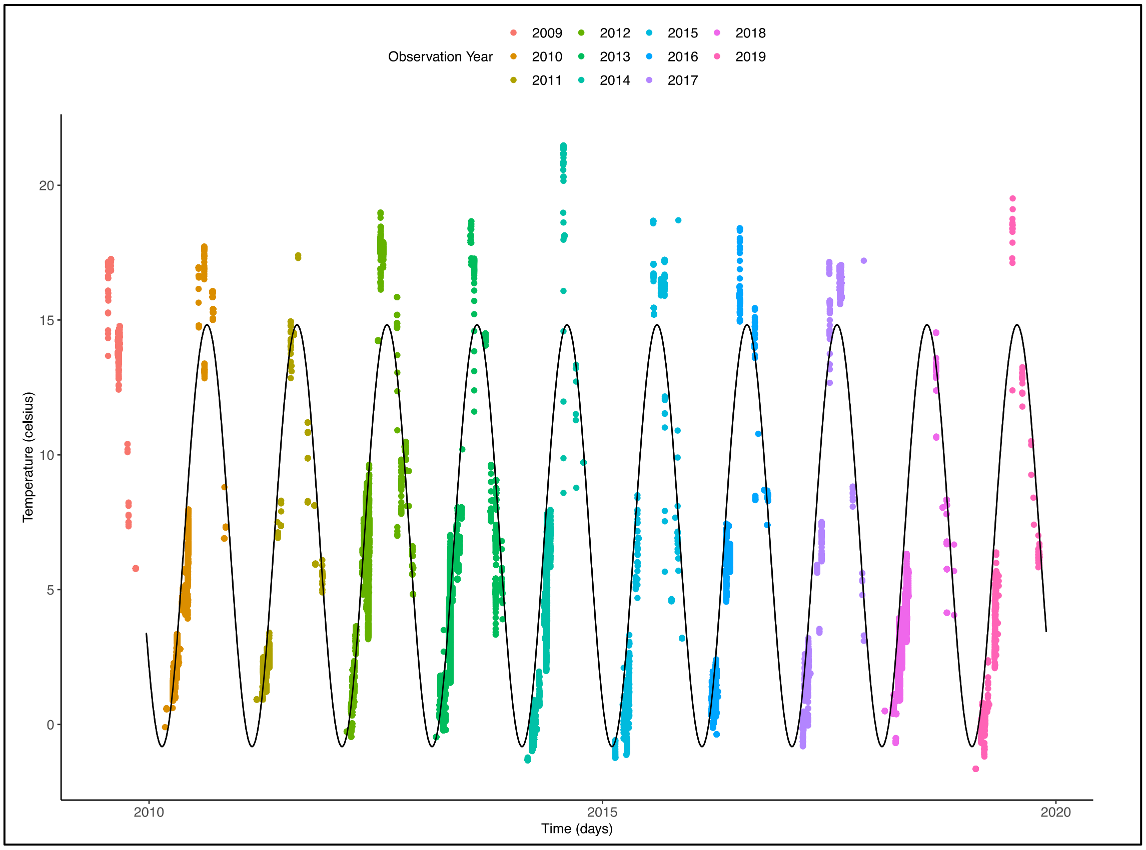

Figure 2.6: Observed ocean temperature for Newfoundland's southern coast between (59°50'00.0"N, 48°04'00.0"W) and (54°00'00.0"N, 46°10'00.0"W) from 2009-2019 and the fitted deterministic seasonal temperature function, see Equation 3. Parameter values for a, b_1 and b_2 can be found in Table 2.1.

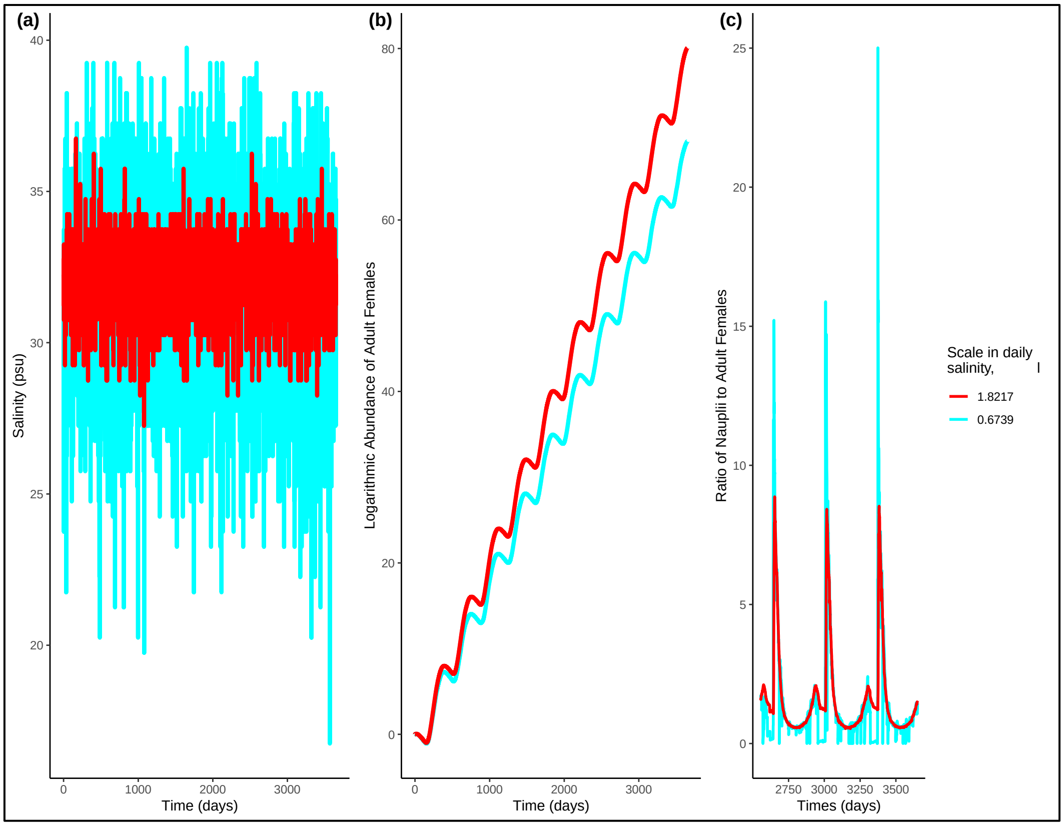

Figure 2.7: Smaller logarithmic abundances of adult females and greater ratios of nauplii to adult females were observed under decreasing variability. The plots represent (a) the stochastic salinity values over time for two realizations, (b) the logarithmic abundance of adult females and (c) the ratio of nauplii to adult females under two different salinity variability scenarios, and (c) the last three years of nauplii to adult females ratio. Red lines correspond to predictions made by the model using a scale parameter, $\lambda = 1.82$ (less variable salinity) and teal lines use a scale parameter value of $\lambda = 0.67$ (increased stochastic salinity).

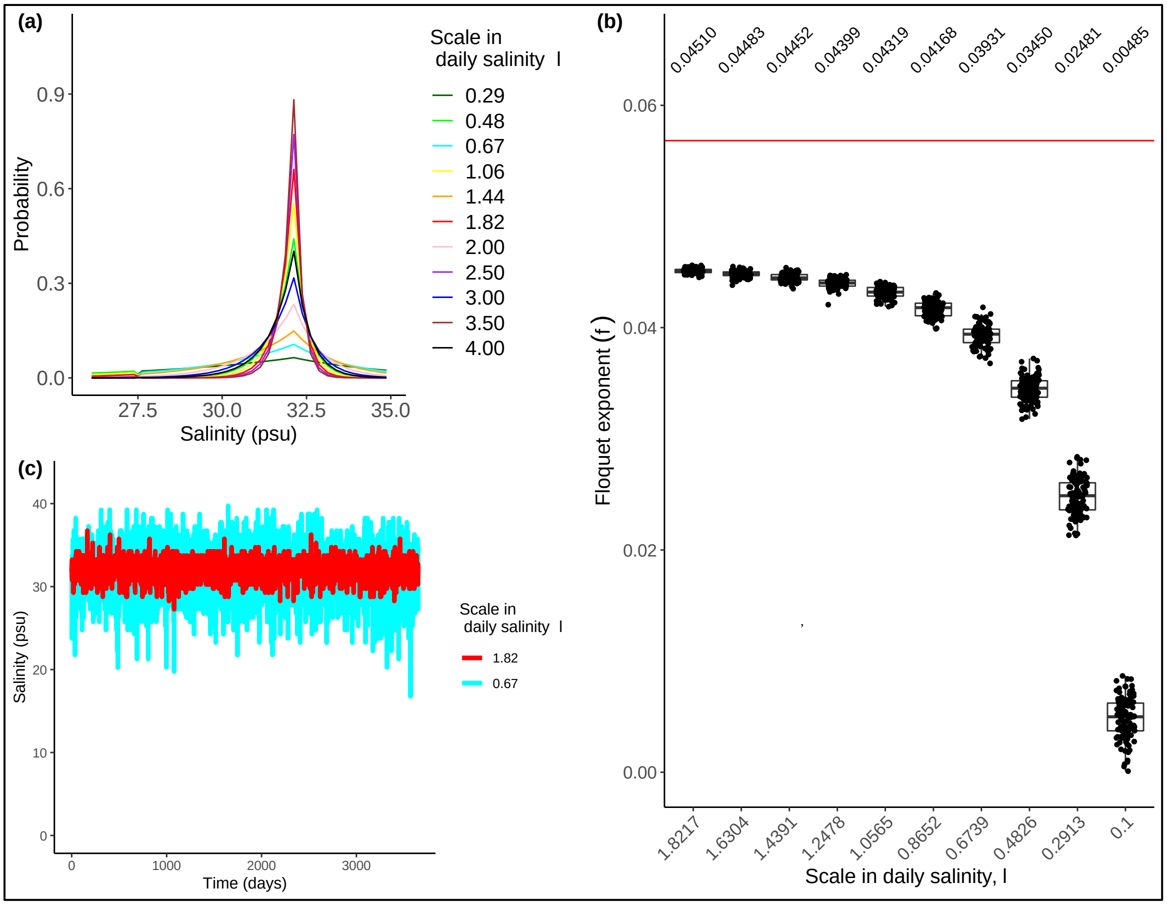

Figure 2.8: Salmon lice population growth rates slows with increasing stochastic salinity. (a) Scale stochastic salinity scenario, λ, values and their impact on the asymmetric Laplace distribution. Larger scale parameters produce a narrower distribution with higher probabilities located around the location parameter value, m, while smaller positive scale parameters produce a flatter, more even probability overall. (b) Floquet exponents ϕ measure annual growth rates, and were calculated for 100 simulations per stochastic salinity scenario, λ. Mean Floquet exponent values are listed above. All Floquet exponents under all salinity variability scenarios were less than the Floquet exponent, $\phi_c = 0.0569$, under 32.25 psu, constant salinity (red line). (c) The stochastic salinity values over time for one simulation using scale parameters $\lambda = 1.82$ (red) and $\lambda = 0.67$ (teal).

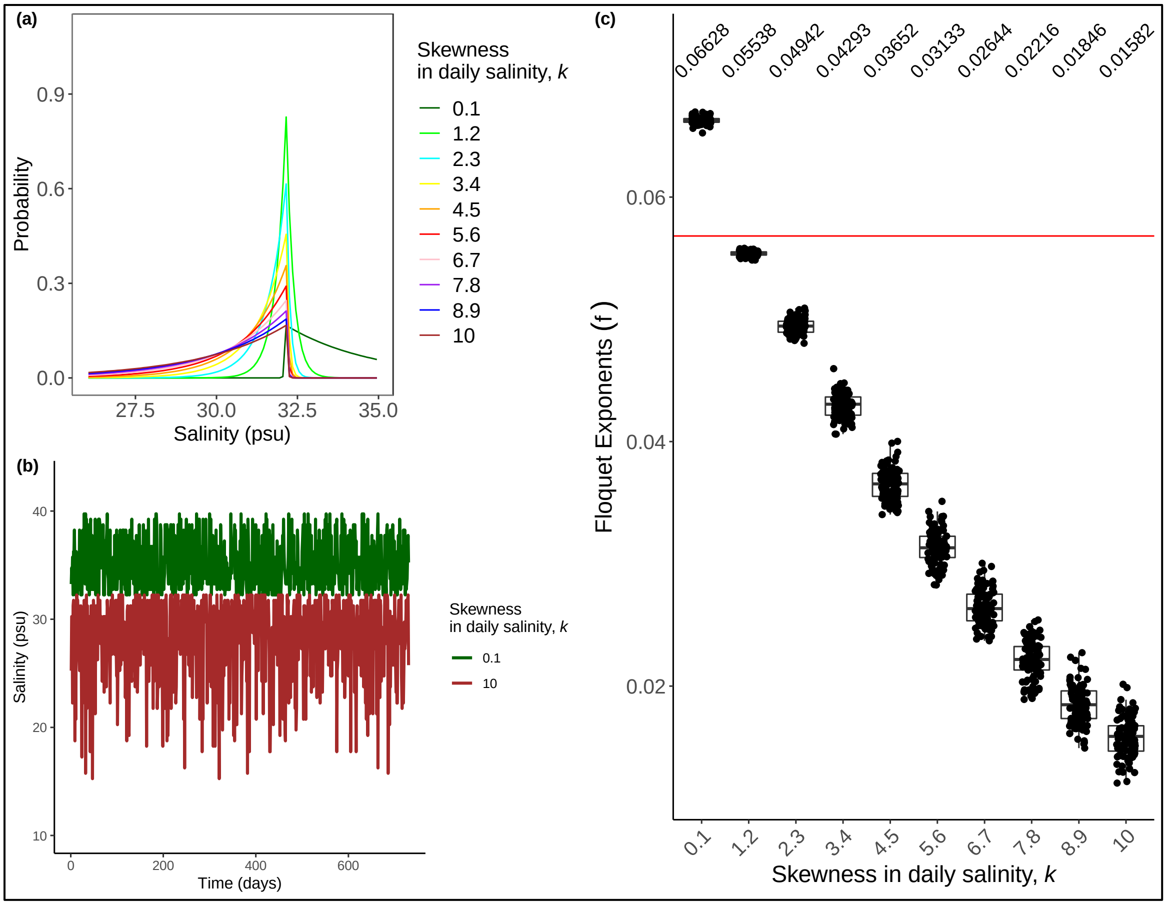

Figure 2.9: Salmon lice population growth rates decrease with increasing left-skewed stochastic salinity. Multipanel plot of (a) the effects of different stochastic salinity skewness, k, on the asymmetric Laplace salinity distributions, (b) stochastic salinities for one simulation under two skewness parameters, k, and (c) Floquet exponents, ϕ, measuring annual growth rates. (a) Skewness parameters less than one produce a right skewed distribution, where skewness parameters greater then 1 produce a left skewed parameter. The further that the skewness parameter is from 1, in either direction, results in a stronger skewness in the respective direction. (c) Floquet exponents were calculated for 100 simulations per stochastic salinity skewness scenario, k, where the mean Floquet exponent per skewness parameter are listed above. Floquet exponents from stochastic salinity skewness k =0.1 was the only Floquet exponents greater than the Floquet exponent, ϕc = 0.0569, under a constant salinity of 32.25 psu (red line).

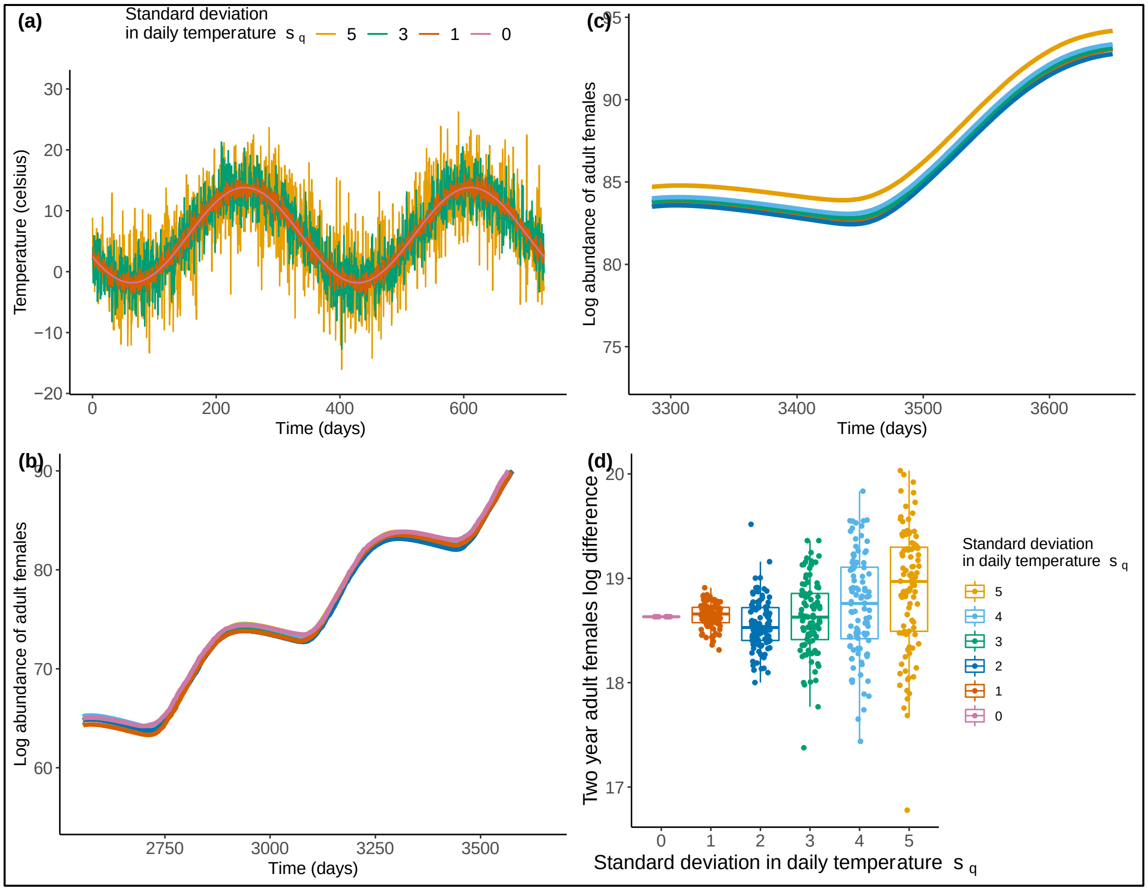

Figure 2.10: The abundance of *L. salmonis* under increasing daily temperature variation. (a) The daily temperature values over time for one realization, (b) the logarithmic abundance of adult females over a 10 year period focused on the last three years for a one randomly selected simulation under levels of daily variation of $\sigma_\theta = 0, 1, 3$ and 5, (c) the mean natural logarithmic abundance across 50 simulations for six temperature scenarios (σ_θ = 0, 1, 2, 3, 4, and 5°C) and (d) the difference in natural logarithmic abundance between the end of year 10 ($t = 3650$) and the start of year 8 ($t = 2920$) under six temperature scenarios (σ_θ = 0, 1, 2, 3, 4, 5°C).

Table 2.1: Parameter descriptions, units, and values

Parameters	Description	Unit Definition	Values	Reference
ι	Attachment rate	$\frac{1}{day}$	2.41×10^{-9}	Hurford *et al.* (2019)
f	Number of fish per pen	Numeric	5×10^{5}	-
a	Average annual temperature	°C	3.77	-
b_1	Temperature amplitude	°C	-6.95	-
b_2	Temperature amplitude	°C	-3.567	-
β	Residual Standard Error	°C	1.266	-
σ_θ	Sigma parameter for theta distribution	°C	6.07	-
μ_θ	Mean parameter for theta distribution	°C	0	-
m_{SC}	Highest frequency salinity bin	psu	31.75	-
$s_{\mu_{BDE}}$	Mean Salinity Bay d'Espoir	psu	32.25	-
c	Average annual temperature	°C	6.01	-
d_1	Temperature amplitude	°C	-4.79	-
d_2	Temperature amplitude	°C	-2.52	-
m	Asymmetric Laplace distribution location parameter	unitless	32.25	-
k	Asymmetric Laplace distribution skewness parameter	unitless	1.22	-
λ	Asymmetric Laplace distribution scale parameter	unitless	1.91	-
γ	Maturation rate	$\frac{1}{day}$	$\gamma^{x}(T(t))$	Hurford *et al.* (2019)
μ	Mortality rate	$\frac{1}{day}$	$\mu^{i}(T(t))$	Hurford *et al.* (2019)
η	Egg per clutch	eggs	$\eta(T(t))$	Hurford *et al.* (2019)
ϵ	Egg string production rate	$\frac{1}{day}$	$\epsilon(T(t))$	Hurford *et al.* (2019)
v	Proportion of viable eggs	unitless	$v(T(t), S(t))$	Hurford *et al.* (2019)

Parameters	Description	Unit Definition	Values	Reference
ϕ	Population growth rate	unitless	See Appendix S1	-

Chapter 3: Summary and Conclusion

The increasing diversity and use of environmental data is increasingly shaping salmon lice *L. salmonis* models. The work in this thesis incorporated salinity-dependent mortality and temperature-dependent maturation rates to understand and quantify the effect of short-term environmental variation on salmon lice population in a stochastic framework. The advantage of this approach is that it allows for natural fluctuation to be mimicked and explored. Population modelling is one of the few management strategies that salmon lice may not evolve a resistance.

In Chapter 2, I derived a stochastic population dynamic model with salinity-dependent mortality and temperature-dependent maturation. I applied the model to two theoretical populations of *L. salmonis,* one in Bay d'Espoir, Newfoundland, and the other more broadly along Newfoundland's southern coast. I used the model to demonstrate that when only considering salinity-dependent mortality and temperature-dependent maturation: 1) salmon lice growth rates are negatively affected by increasing stochastic salinity, λ (Figure 2.8); 2) increasing left-skewed stochastic salinity, k, negatively affects salmon lice population growth rates (Figure 2.9); 3) increasing temperature variation increased the range in abundances differences between years (Figure 2.10d); 4) increasing temperature variation, σ_θ, was a poor indicator of population dynamics and better described by seasonal temperature trends (Figure 2.10); and 5) salmon lice are predicted to persist and increase with time under all stochastic salinity scenarios, λ, and stochastic temperature scenarios, σ_θ, investigated (Figure 2.8-2.10).

Salmon lice are not the only marine parasite that will be affect by climate change, and impacts are seen across many taxa[37,48,112]. It is predicted that the transmission of parasites and disease will increase with increasing temperature[16,113], with an increased number of individual per stage and quicker development times[16]. Some studies hypothesis that climate change may affect direct and indirect parasites differently, with indirect parasites having a higher chance of extinction or extirpation due to their dependence on precise vector transmission to occur[91,114]. The thermal tolerance of the parasite also determines their tolerance to climate change. It is predicted that parasites located closer to the equator with smaller thermal tolerance ranges will be more susceptible compared to temperate and artic species[91,115]. One study estimated that while most oceans expect to see biomass decreases the Arctic ocean is predicted to see increased biomass as a result of global warming. However, one study exploring parasitic nematodes *Marshallagia marshalli* found that the populations in the arctic were more negatively affected by a small increase of 2°C compared to parasites from temperate regions[115]. Yet, impacts are species specific and is harder to predict for multi-stage species[91], such as salmon lice.

Demographic stage structured species are a widespread source of heterogeneity in ecosystems due to life-stage specific niche roles and responses to abiotic and biotic factors[116]. Parasites such as salmon lice with structured life-stages that fill different roles of infection and transmission[117]. Under static conditions, ignoring life-stage sensitivity to environmental conditions has smaller impacts then under fluctuating conditions, where they become magnified[43,44,48]. For example, larval salmon lice have been found to be a key drive in transmission of salmon lice between farms and the persistence within aquaculture sites[16,39,117,118]. Toorians and Adam (2020) found that the dispersal potential of larvae is related to temperature, and thus, temperature is critical for determining connectivity or incoming connections onto a site[16,117]. Similar to the introduction of seasonal conditions, ignoring daily variation can either over- or under-estimate population dynamics.

Aquaculture pests are inherently adaptable to pesticide treatments, and as these parasites transition from wild populations to farmed environments they have the ability to evolve and interact with hosts in new ways[92]. In this model, assumptions were made to simplify the understanding of daily environmental variation on salinity-dependent mortality and temperature-dependent maturation rates. One assumption in my model was that no pesticides treatments were included, despite levels being higher than those normally needed to trigger intervention treatments. Despite aquaculture being around for a relatively short-time period, there is strong evidence for salmon lice evolving resistances to all of the current chemotherapeutants treatments, expect for benzoylphenyl ureas[92,119]. Due to the limited selection of chemotherapeutants at salmonid farms disposal and relatively high gene flow, mutations increasing the resistances have the ability to rapidly disperse through populations[92,119,120]. As chemotherapeutant treatments efficacies continues to decline, the aquaculture industries is further limited on treatment and salmon lice management strategies. Additional focus should be put on modelling as a tool to manage salmon lice populations.

Another assumption of my model is that all salmon lice pens are closed systems and all juvenile salmon lice originate from within pens. This assumption ignores salmon lice immigrating from wild and other farms, which is strongly influenced by connectivity, proximity, and environmental conditions such as ocean temperature[72,120]. A study by Aldrin *et al.* (2013) found that 28% of salmon lice within Norwegian farms originate from nearby farms[72]. Proper management is limited if connectivity is not considered, especially when farms are packed within fjords and bays such as those in Newfoundland, New Brunswick and British Columba (Canada's three biggest aquaculture industries)[9,17]. While our model did not consider the role that larval dispersal and connectivity plays in the spread and sustained precise of salmon lice within farms, future work within Newfoundland would be strengthened by understanding the connectivity of farms along the southern coast and the Coast of Bays region. Future work could consider the role that farm connectivity has on Newfoundland's current and future aquaculture sites through hydrodynamic models, and in addition to estimating future population dynamics through stochastic population models.

An increasing amount of research is done into preventing salmon lice from immigrating into pens. One method, cage barriers, attempted to limit the contact between farmed salmon and copepodids, interrupting this link of the salmon lice lifecycle and eliminating the ability of lice to find a host[92,121]. Salmon lice aggregate at shallow depths in the water column as it is theorized to improve host encounter rates[120,122,123]. Barrier based strategies segregate salmon lice from farmed salmonids through physical barriers (i.e. lice skirts) at the upper several meters of cages, while leaving deeper sections of the cages open for water circulations. However, these practices can place section pressure on individual salmon lice's swimming depth. A study by Coates *et al.* (2020) found that the response to pressured varied strongly among salmon lice families, suggesting copepodid swimming depth is an heritable trait and physical barrier within aquaculture pens could lead to an evolutionary shift in vertical distributions[92,120]. This could lead to fitness trade-offs and lead to salmon lice having new interactions with ecosystems and wild salmonid populations.

A number of diverse mathematical models have been developed to address a range of fisheries, agriculture, and aquaculture indurates. Early models explored the impact of pest on crop production[124,125], and abiotic and biotic factors on plant growth, yields and evolution[125–127]. Later models then included temperature as a key driver of egg production and development rate of terrestrial[128] and marine invertebrate pests[19,21], and temperature is also known to influence activity levels and species distributions. Aquaculture pest management models are increasingly used to combat profit and stock losses[8,17,23,103,129] and can focus on the transmission of disease agents, such as salmonid pancreas disease[130,131], to ectoparasites, such as salmon lice[24,99,101,106,132]. Applied use of pest management models is largely within the agriculture sector, however, and a growing number of private companies are showing interest in applying mathematical models into the aquaculture sector. Despite a large level of mathematical models to estimate salmon lice, there is a lack information on the application within government or industry framework.

Within Newfoundland's aquaculture industry, further importance should be put on salmon lice population dynamic modelling. Currently, Newfoundland is using salmon lice count data to guide veterinarians in treatment methods and timing[11]. Yet, in this chapter I have mentioned some current treatment and management strategies and highlighted the evolutionary concern and decreasing efficacy on salmon lice populations. While the development of computer models may be expensive and take time, they are useful in identifying differences in population dynamics across time and space, and are useful in the selection of new farm locations[11]. Additionally, several salmon lice models have already been built for Newfoundland that could guide decision making[22,23]. The inclusion of models into pest management plans should consider and evaluate the effectiveness of long-term management strategies and new site placement[133].

The outcome of an individual species' population size or growth rate in the face of changing or fluctuating ocean conditions is a complex interaction between biological and ecological processes and evolutionary traits. These include traits such as: 1) plasticity: the ability for an individual of a species to alter their behaviour or physiology; 2) dispersal: the ability of species to produce new offspring to colonize new locations; and 3) evolution or adaptation: changes in gene frequency within a population as successful individuals out-reproduce others[134,135]. Within the framework of population modelling, many traits may influence population dynamics and should be considered. In this work, I provided a baseline understanding of the impact of daily variation in salinity and temperature on the population dynamics of salmon lice. However, in terms of response to climate change, future work needs to consider the combined effect of changing climate and abiotic factors impacting population dynamics.

In summary, population models with temperature-dependent maturation rates and salinity-dependent mortality are valuable tools in analyzing salmon lice *Lepeophtheirus salmonis* population dynamics. Increasing stochastic salinity slowed population growth and negatively affected population growth rates, while stochastic temperature has beneficial effects on population growth rates and increases the mean logarithmic population abundance. Applying population dynamic models to current and near future environmental conditions can provide useful insights into population dynamics benefiting salmon lice management, and leads to more sustainable aquaculture. In closing, I hope the work in this thesis adds to the understanding of salmon lice population dynamics and is expanded on by future researchers.

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Appendix S1

S1.1 Floquet theory

Floquet theory is the study of linear systems of differential equations with periodic coefficients, allowing for the extension of linear stability analysis onto periodic systems[49,50]. Within ecological systems, Floquet theory has three potential applications: 1) defining the fitness of a structured population in a periodic environment, 2) calculating the invasion potential for interacting structured populations in periodic environments, and 3) testing the stability of a limit cycle[49]. In this study, Floquet theory is applied to calculate the fitness of a structured *Lepeophtheirus salmonis* population in Bay d'Espoir Newfoundland with seasonal temperature and stochastic salinity. For more information on Floquet theory and applications to ecological theory, see Klausmeier (2008).

S1.2 Calculating Floquet exponents

To calculate Floquet multipliers and exponents numerically, here, I describe the monodromy matrix method applied to the *L. salmonis* population equations. Recall that the equations for the *L. salmonis* dynamics are:

$$\frac{d}{dt}\begin{bmatrix} A_{t+1} \\ C_{t+1} \\ I_{t+1} \\ P_{t+1} \end{bmatrix} = \begin{bmatrix} -\mu_t^A & \gamma_t^C & 0 & 0 \\ 0 & -\gamma_t^C - \mu_t^C & if & 0 \\ 0 & 0 & -if - \mu_t^I & -\gamma_t^P \\ \eta_t \epsilon_t v_t & 0 & 0 & -\mu_t^P - \gamma_t^P \end{bmatrix} \begin{bmatrix} A_t \\ C_t \\ I_t \\ P_t \end{bmatrix}$$

which are equations 6-9 from the main text written in matrix notation. I note that the periodically varying parameters are written with the function argument, *t*, and the period is ω = 365 days.

To calculate the Floquet exponents, I use the *L. salmonis* population matrix from above, and numerically solve the difference equation,

$$\mathbf{F}_{t+1} = \begin{bmatrix} -\mu_t^A & \gamma_t^C & 0 & 0 \\ 0 & -\gamma_t^C - \mu_t^C & if & 0 \\ 0 & 0 & -if - \mu_t^I & -\gamma_t^P \\ \eta_t \epsilon_t v_t & 0 & 0 & -\mu_t^P - \gamma_t^P \end{bmatrix} \mathbf{F}_t$$

from t = 0 to t = ω = 365 days, where $\mathbf{F}_t$ is a 4 by 4 matrix (the monodromy matrix), and with the initial condition,

$$\mathbf{F}(0) = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

The Floquet multiplier ρ_i is then computed as the dominant eigenvalue of $\mathbf{F}_{365}$, while the Floquet exponent is defined as $\phi_i = \frac{log(\rho_i)}{\omega}$. The complete R script can be found in the following GitHub repository: https://github.com/jakep962/MSc_salmon_lice.git.

Appendix S2

S2.1: Quantitative data summary

The theoretical salmon lice populations in this thesis are simulated over a 10 year (3650 days) period, with results shown in Figures 2.8-2.10 being the combination of multiple simulations. Floquet exponents in Figures 2.8 and 2.9 are calculated for 100 simulations per level of daily stochastic variation, λ, and salinity skewness, k, scenarios. The results for the effect of daily temperature fluctuations around deterministic seasonal trends in Figure 2.10 are calculated from 50 simulations. All model prediction data can be found in the following GitHub repository: https://github.com/jakep962/MSc_salmon_lice.git.

S2.2: Temperature and Salinity Data

Salinity and temperature data used throughout this thesis were compiled from two main sources as described below:

Salinity: **Salinity data for Bay d'Espoir along Newfoundland's Southern Coast.** Monthly temperature and salinity day for Hermitage Bay-Bay d'Espoir collected by the Department of Fisheries and Oceans. This data was acquired by my supervisor Dr. Amy Hurford and was used in Hurford *et. al.* (2019). These salinity data were collected between 1956 and 2013 and appears in Figures 2.4, 2.7-2.9.

Temperature: **Marine environmental data (MEDS) for the Atlantic Ocean.** Temperature and salinity profile data for the Atlantic ocean collected by the Department of Fisheries and Oceans in partnership with the Global Temperature and Salinity Profile Programme (GTSPP). Data was access through a data request to the Government of Canada: https://isdm.gc.ca/isdm-gdsi/request-commande/form-eng.asp. Data from this request appears in Figures 2.5, 2.6, 2.10.