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Quantifying the influence of salinity and temperature on the population dynamics of a marine ectoparasite

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Running title: Environmental influences on sea louse population dynamics

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Abstract

Sea lice are common ectoparasites of farmed and wild salmonids and can cause substantial morbidity and mortality in their hosts. While sea lice infections are common in estuarine areas with variable salinity, the effects of salinity on population dynamics are poorly understood. We used existing literature to parameterize salinity-dependent logistic mortality curves for different life stages of sea lice. We then used population matrix models to characterize the effects of temperature and salinity on sea louse population growth. Our models showed that low salinity decreases survival, while low temperature retards sea louse development. In contrast to the linear effects of temperature on sea louse development, salinity has a non-linear effect on sea louse survival; values below 20 psu cause mortality, while values above 20 psu have little effect on survival. Simulations showed that sea louse population growth can be greatest in zones that are intermediate between estuarine and oceanic. In these cases population growth is not limited by the low salinities found in more estuarine sites or the low temperatures found in more oceanic sites.

Keywords: Population dynamics, parasite, aquaculture, disease, sea, salmon

Introduction

Marine diseases can have dramatic impacts on populations, with consequences for community structure, ecosystem function, and, when commercial species are involved, economics (Burge et al. 2014; Lafferty et al. 2015). Understanding the factors that influence the epidemiology of infectious diseases is critical for predicting and managing these impacts. In coastal and oceanic systems, environmental parameters such as salinity, temperature and hydrodynamic conditions have been found to influence the population dynamics of many species, however their impacts on infectious disease dynamics has only received limited consideration (e.g., Burge et al. 2014).

One host-parasite relationship that could benefit from an increased understanding of the influence environmental stressors is sea lice. Sea lice (e.g., *Lepeophtheirus salmonis* and *Caligus* sp.) are ectoparasites of salmonids and infect both farmed and wild salmon (Boxaspen 2006). Infections occur when larval copepodids attach to a host and molt into a chalimus stage, followed by preadult and adult stages. Preadults and adults are associated with damage to the skin and disruption of protective mucus layers, which can lead to morbidity, secondary infection, and, in some cases, death (Boxaspen 2006). Sea louse infections have been associated with declines of wild salmonids (Krkošek et al. 2013) and, on salmon farms, can be costly to control and may require the use of chemotherapeutants as part of a management strategy (Costello 2009).

Identifying and quantifying factors that influence the population dynamics of sea lice is critical for predicting epidemics and managing infestations on salmon farms. For this purpose, numerous population simulation models have been created to quantify the effects of temperature, hydrodynamics, and treatments on sea lice epidemiology (Revie et al. 2005; Gillibrand & Willis 2007; Amundrud & Murray 2009; Gettinby et al. 2011; Groner et al. 2013; 2014). While these models are often able to simulate general patterns of sea louse dynamics, they are not always successful at reproducing

site-specific trends. One factor that has been largely ignored in population models of sea lice is the influence of salinity (Bricknell et al. 2006; Stucchi et al. 2011). In coastal areas where wild salmon migrate and salmon are farmed, salinity can fluctuate on hourly levels due to precipitation and daily and seasonal levels due to run-off from snowpacks in the spring and summer. Salinity also fluctuates on local spatial scales, and is expected to be lower closer to freshwater riverine inputs, and along the water surface where fresher water forms a lens. Sea lice are unable to tolerate low salinity environments and, while it has not been well quantified, spatio-temporal variation in salinity likely impacts sea louse population dynamics. Numerous laboratory studies and analyses of infestations on salmon show that salinity can influence development, behaviour, infestation success, and survival of sea lice (Tucker et al. 2000; Bricknell et al. 2006; Genna et al. 2005; Sutherland et al. 2012). Moreover, field surveys often, but not consistently, find correlations between salinity and sea louse infestations on farmed and wild salmon (e.g., Johnson & Albright 2001; Revie et al. 2002; Heuch et al. 2002; 2009; Krkošek et al. 2006; Kristoffersen et al. 2013; Rogers et al. 2013; Rees et al. 2015). It is not clear whether this is due to a true lack of effect or an inability to detect an effect with the available data. These results suggests that incorporating these impacts into population simulation models will vastly improve our understanding of sea lice population dynamics and the accuracy of our predictions.

The goal of this study is to encourage the incorporation of salinity data into simulations of sea louse infections. Towards this end we: 1) review and parameterize the effects of salinity on different life stages of *L. salmonis* so that they will be accessible for population modelers; 2) use a population projection matrix model to quantify the roles of salinity and temperature on population vital rates; and 3) explore the effects of salinity and temperature on sea louse populations using environmental data from a range of habitats where farmed and wild salmon are commonly found. We focus this paper on *L. salmonis*, which occurs in the north Pacific and Atlantic oceans, has the greatest economic impact on farmed salmon and has been associated with declines of wild salmon (Boxaspen 2006).

Model

Parameterization of effects of salinity on sea lice

We were able to find sufficient data to parameterize the effects of salinity on the survival of eggs, copepodids, preadult, and adult sea lice. In all cases, we iteratively fit these data to a four parameter logistic curve in which the parameter for the maximum asymptote was 1 (for 100% survival) and the parameter for the minimum asymptote was 0 (for complete mortality). Iterations were performed to minimize the sum of squared differences between the actual data and the modelled curve. Logistic curves are commonly used to fit population growth and mortality data (Kingsland 1982) and reflect patterns seen in salinity tolerances of marine copepods (Lance 1963).

Eggs

A single study, by Johnson and Albright (1991), quantified the effects of salinity on egg hatching at 10 °C . They exposed sea louse eggs to four salinity levels (10, 20, 25, and 30 psu), and monitored hatching success. We calculated the proportion of death that was due to salinity (as oppose to other 'background' causes) by dividing the survival at 10, 20, and 25 psu salinity, by the survival at the highest salinity (i.e. 30 psu), which does not affect survival (Johnson and Albright 1991, Figure 1A). These data were then fit to a logistic curve. The resulting equation was:

$$M_{egg} = \frac{1}{1+(\frac{S}{20.82})^{13.98}}$$

[1]

Where M_{egg} is the mortality of eggs and S is salinity in psu.

Copepodids

Dalesman (2003) quantified the effects of salinity on the survival of copepodids by measuring survival after exposure to salinities of 5, 9, 12, 16, 19, 23, 26, 29, 33, and 36 psu (temperature = $12 \pm 1.5^\circ$ C). In these experiments the exposure lasted for 6 hours and mortality was assessed hourly. Most of the mortality due to low salinity occurred rapidly after the initial exposure, therefore these data are best expressed in terms of instantaneous mortality after exposure, as opposed to a constant mortality rate. We calculated this value by dividing the mortality after six hours by the mortality in the top three salinity treatments (where little to no mortality occurred), so that we could estimate the mortality due to salinity. We then fit a separate logistic curve to data from each trial (adjusted $R^2 > 0.95$ for each trial) and then took the means and standard errors of the resulting parameters to quantify copepodid mortality (Figure 1B):

$$M_{copepodid} = \frac{1}{1 + \left(\frac{S}{19.09 \pm 1.83}\right)^{7.11 \pm 1.31}} \quad [2]$$

where $M_{copepodid}$ is the mortality of copepodids and S is salinity in psu.

Decreased salinity has also been shown to reduce the attachment of copepodids to salmonid hosts (e.g. Tucker et al. 2000; Dalesman 2003; Genna et al. 2005; Bricknell et al. 2006). Some of this effect is due to mortality (described above), however, Dalesman (2003) and Bricknell et al. (2006) found that additional behavioral effects contribute to this reduced attachment. To quantify this effect, we used data from experiments by these authors, where copepodids were held at different salinities at a concentration of 0.75 individuals/ ml in 1L. After three hours, Atlantic salmon hosts were dipped into these suspensions for 30 seconds, and then placed in regular seawater for 30 min, after which all attached individuals were counted (Sevatdal 2001). We quantified the effect of salinity on the proportion of lice attaching by scaling the number of individuals attached by the median number of attached individuals at 34 psu (i.e. standard seawater). We then fit these data to a logistic curve so that

the effect of salinity on attachment due to mortality and behavioural effects was:

$$C_{proportion\ lice\ attaching} = 1 - \frac{1}{1 + (\frac{S}{21.22})^{5.82}} \quad [3]$$

As these equations are calculated based on only a 30 second exposure of the host to infective larvae, we consider them to show a proportional change in attachment.

Attached sea lice

In contrast to larval sea lice, which experience relatively rapid mortality after exposure to lower salinities, attached lice are more tolerant of reduced salinity. This is likely because sea lice are able to osmoregulate using salts in the blood and mucus of their host (Hahnenkamp & Fyhn 1985). We used data from Connors et al. (2008) to calculate mortality rates of motile lice as a function of salinity, host species, and the sex and life stage (pre-adult or adult) of the louse (Figure 1C). In this study, juvenile pink and chum salmon infected with male and female pre-adult and adult sea lice were exposed to salinities of 0, 7, 14, or 28 psu and mortality was measured. The temperature during these experiments was between 10 and 15°C (Connors et al. 2008). We fit these data to a mixed effect Cox proportional hazards model (using the 'coxme' function in the coxme package in R v. 3.1.0) with aquaria as a random effect. We then used model selection (by minimizing negative log likelihoods and AIC values) to choose the best fit. We found no violations of the assumption of proportional hazards. The best fit model for the daily mortality rate of motiles due to salinity was:

$$m_{motile} = 1 - (1 - e^{((-0.229 \pm 0.024) * S)})^{24} \quad [4]$$

This was calculated by solving for the survival function from the hazard ratio, where m_{motile} is the daily mortality rate and S is salinity in psu. These results are consistent with McLean et al. (1990), who showed that while attached sea lice could live up to six days in freshwater the majority die within 48

hours, and Connors et al. (2008), who found no difference in mortality between preadults and adults, or between males and females.

Population matrix models

We used a population projection matrix (PPM, Caswell 2001) of female sea lice to investigate the effects of salinity and temperature on sea lice population dynamics. We used the PPM from Groner et al. (2014) which already includes temperature-dependent development, added salinity-dependent mortality rates and removed equations for mate limitation because this was not a focus of the study. This updated model is described below.

L. salmonis transition through nine recognised life stages. After hatching from the egg, the sea louse goes through three unattached stages during which it does not feed: nauplii (two stages) and copepodid. Once the copepodid finds a host, it develops through two chalimus stages, two preadult and one adult stage. In our model, we simplified the life cycle to contain seven stages that reflect biologically important transitions: egg, larvae (consisting of nauplii I and II and copepodid), chalimus (stages I and II), preadult (I and II) and three adult phases which will be referred to as gravid I, between-clutch and gravid II (Figure 2). These three adult phases are separated here because they differ substantially in fecundity.

Transitions from stage to stage occur in one direction, with the exception that females can transition from gravid I or gravid II back to between-clutch, and then to gravid II, reflecting the observation that females can produce many successive pairs of egg strings (Heuch et al. 2000). The population projection matrix represents daily transitions and operates on the life stage state vector with elements [egg, larvae, chalimus, preadult, gravid I, between-clutch and gravid II] (Figure 2).

Entries on the diagonal (P_i) indicate the proportion of individuals remaining in a stage, entries on the sub- and super-diagonal (G_i) indicate the proportion of individuals developing into a new stage and

F_5 and F_7 indicate the fecundity of gravid I and gravid II adult females, respectively. P_2 and G_2 are a function of the rate that sea lice attach to the host (γ , described below), and G_5 , G_6 , and G_7 are a function of egg hatching and development (described below). The remaining P_i and G_i elements, together with the F_i elements, are defined as shown:

$$P_i = 1 - \frac{1}{\delta_{ij}} * (1 - \mu_i), \begin{cases} \text{for } i = \{1, 3-6\}, j = i + 1 \\ \text{for } i = 7, j = 6 \end{cases} \quad [5]$$

$$G_i = \left(\frac{1}{\delta_{ij}}\right) * (1 - \mu_i), \text{ for } i = \{1, 3, 4\}, j = i + 1 \quad [6]$$

$$F_i = \frac{\omega_i}{2}, \quad i = \{5, 7\} \quad [7]$$

where δ_{ij} = time to develop from stage i to stage j , μ_i = mortality rate at stage i , and ω_i = number of viable eggs in the clutch produced at stage i . The number of viable eggs is divided by two because the population matrix only models females and we assume a 1:1 sex ratio.

Developmental transitions: With the exception of copepodids, developmental transitions of sea lice were temperature-dependent. We parameterized developmental times in our model based on a review by Stien et al. (2005) of existing data on temperature-dependent development in *L. salmonis* (Table 1). This review uses developmental rates across a temperature range to parameterize a modified Belahrádek equation (Belahrádek 1935):

$$\tau_{ij}(T) = \left(\frac{\beta_{1ij}}{(T - 10 + \beta_{1ij}\beta_{2ij})}\right)^2 \quad [8]$$

where τ_{ij} is the minimum required developmental time for individual i in stage j at temperature T . β_{1ij} is a shape parameter and β_{2ij}^{-2} is the average for τ at 10 °C. Stochasticity in developmental rates was incorporated by randomly selecting values for β_{1ij} and β_{2ij} from normal distributions with means and standard deviations estimated by Stien et al. (2005). A stage-specific development time, ρ_j , representing

temperature-independent minimum development time was added to this temperature-dependent estimate, to represent additional time beyond the minimum developmental time needed to make developmental transitions. Total developmental time (δ_{ij}) of individual i at stage j is therefore:

$$\delta_{ij} = \tau_{ij} + \rho_j \quad [9]$$

Values of ρ_j were calculated using instantaneous development rates for (v_{ij}) from Stien et al. (2005) such that:

$$\rho_j = -\frac{\ln(0.5)}{v_j} \quad [10]$$

Developmental rates were calculated as the inverse of the developmental times. There is no evidence that copepodid developmental rates are temperature-dependent (Johnson & Albright 1991), so all copepodids in this model developed in 4.6 days, the mean value estimated by Stien et al. (2005). The developmental rate of larvae was calculated as the inverse of the sum of nauplii and copepodid developmental times.

Survival estimates: Survival was calculated as the product of two values, 'background survival' and 'salinity-induced survival'. As with many invertebrates, there is little evidence that survival of sea lice is directly dependent upon temperature (Stien et al. 2005; Revie et al. 2005) so background survival estimates ($1-\mu_i$) for all stages, except larvae, were stochastically drawn from a triangular distribution (based on data from Bjørn and Finstad (1998)) defined by the minimum, maximum and most probable survival times for each stage (Table 2).

Background survival of larvae was calculated as the product of nauplii survival (calculated as above) and copepodid survival. Survival of copepodids depends upon the attachment of copepodids to a host – a process that is sensitive to local host densities and abiotic factors including currents and

salinities (Bricknell et al. 2006; Stucchi et al. 2011; Jansen et al. 2012). We summarise this complex process in an attachment rate (γ) parameter and, with the development time (δ_c), calculate the daily mortality rate of copepodids (u_c) by distributing the attachment exponentially across the development time of this life stage.

$$u_c = 1 - \gamma^{\frac{1}{\delta_c}} \tag{11}$$

Salinity-dependent survival of eggs, copepodids and motile sea lice was calculated as described above in Equations 1, 2 and 3. The survival estimates for eggs and nauplii (Equations 1 and 2) are time-independent and were therefore converted into rates for the purpose of modelling by dividing each by the temperature-dependent development time for the respective stages. Because the salinity-dependent survival of motile sea lice was calculated as a daily rate, it included background survival. We had no data upon which to base salinity-induced survival for the nauplii or the chalimus stages. Therefore, we substituted values taken from the copepodid and motile stages respectively.

Fecundity: Sea lice reproduce sexually and females have two external egg strings in each clutch that are attached to them until hatching. Egg string production and hatching are synchronized on an individual louse. Estimates of egg viability, clutch size and time to hatching were based on data from (Heuch et al. 2000). Sea lice are estimated to have 152 ± 31 (mean $\pm$ SD) eggs per string in the first clutch and 296 ± 100 eggs per string in subsequent clutches (Heuch et al. 2000). Estimates of clutch size were chosen from these ranges (assuming a normal distribution of clutch sizes) and multiplied by two to account for both egg strings. The number of eggs produced was then multiplied by the estimated viability (Table 2) and divided by two because, like many population matrix models, this model only tracks female members of the population (Caswell 2001). There is little evidence for an effect of temperature or clutch order on egg viability (Heuch et al. 2000).

Because the first clutch of eggs is substantially smaller than subsequent clutches we divided the adult female stage into three components, gravid I to represent the first extrusion of eggs (represented by F_5), gravid II to represent subsequent extrusions of eggs (represented by F_7) and between-clutch to represent the time between the extrusion of eggs. After completing the gravid I stage (P_5), individuals will alternate between the between-clutch and gravid II stages represented by P_6 , P_7 , G_6 and G_7 in the PPM.

The time spent between clutches was the sum of the time needed for eggs to develop after egg string extrusion ($\delta_{egg}-\eta$) and the time between the hatching of one clutch and the release of the next egg string (ζ). Both of these values are temperature-dependent. The latter parameter was estimated with the following relationship:

$$\zeta = \max(1, -1.2T + 19.64) \quad [12]$$

This equation is based on hatching times at 7.2° C and 12.2° C (Heuch et al. 2000) and the observation that the shortest time between clutches, which was observed at temperature > 15° C, was ~24 hours (Johannessen 1978). Egg extrusion (η) (i.e. the time in the gravid I or gravid II stages) was set at one day (Johannessen 1978). G_5 , G_6 and G_7 are therefore defined as:

$$G_5 = G_7 = \frac{1}{\eta} * (1 - \mu_{adult}) \quad [13]$$

$$G_6 = \frac{1}{\zeta + \delta_{eggs} - \eta} * (1 - \mu_{adult}) \quad [14]$$

Attachment of larvae to host: The attachment rate of copepodids varies considerably in nature, and estimations of these rates is notoriously challenging (Boxaspen 2006). As understanding the role of attachment on sea louse infections was not the focus of this paper; we fixed the attachment rate at 1% for all scenarios (described in *Analyses*). Effects of varying attachment rates on sea louse population

dynamics are explored in Groner et al. (2014). We did not include behavioural effects of salinity on sea louse attachment. While these may occur, the data available on this topic are limited and it is unclear how they interact with other abiotic conditions.

Analyses

We analysed PPMs for a number of relevant temperature and salinity scenarios. To isolate the effects of specific conditions, we first examined fixed temperatures and salinities values. For each of these scenarios we calculated the following demographic parameters: population growth (λ), reproductive rate (R_0), generation time, and the sensitivity and elasticity of population growth to changes in matrix elements. To understand how salinity and temperature interact to alter sea louse population dynamics in more realistic scenarios, we then used the PPM to simulate sea louse population dynamics using temperature and salinity data collected daily on salmon farms from the top 5 m of the water column.

In our equations, λ was equal to the rate of population change over a day (i.e. the dominant eigenvalue of the matrix **A**). R_0 was equal to the average number of offspring by which an egg will be replaced within its lifetime (i.e. the rate at which the population increases from one generation to the next) and generation time was equal to the time necessary for the population to increase by R_0 (Caswell 2001). Population growth is stable when $\lambda = 1$, decreases for $\lambda < 1$ and increases for $\lambda > 1$. Sensitivity was calculated as the effect of absolute changes to matrix elements on the population growth rate,

$$s_{ij} = \left(\frac{\partial \lambda}{\partial a_{ij}} \right) \tag{15}$$

while elasticities were calculated as the effect of proportional changes in matrix elements on the population growth rate,

$$e_{ij} = \left(\frac{\partial \log \lambda}{\partial \log a_{ij}} \right) \quad [16]$$

where a_{ij} indicates the matrix element (Caswell 2001).

All analyses and simulations were implemented in R (v. 3.1.0) using the 'popbio' package (Stubben 2007). R-scripts for the population matrix models are available in the online appendix (ES1-ES5).

Effects of fixed salinity and temperature values on population vital rates

We calculated the matrix **A** and all relevant vital rates for sea lice for salinities of 16, 20, 24, 28, and 32 psu at temperatures of 4, 8, 12, and 16 °C. These are within the ranges of temperatures and salinities that salmon and sea lice experience. Each calculation was repeated 100 times in order to determine mean results.

Site specific simulations

We simulated sea louse populations for three different temperature and salinity profiles that were based on data collected daily from the first 5m of the water column at three Atlantic salmon farm sites in the Broughton Archipelago on the west coast of Canada. The sites were picked to represent three different types of conditions: (a) near rivers, (b) primarily affected by oceanic conditions, or (c) some transition between (a) and (b). There were occasional instances of missing data in these datasets; however this was usually in the winter, when salinity and temperature did not fluctuate much. In these instances, we interpolated the missing data by averaging temperature and salinity values for the days immediately preceding and following the missing data. We chose these sites to simulate in particular, because they exhibit substantial spatio-temporal variation in temperature and salinity and are within

the range temperature values that that can be interpolated from our parameters (e.g., greater than 4 °C).

To simulate sea louse populations, we calculated the population matrix A_1 for the temperature and salinity conditions at day one (defined as conditions on the 120th day of the year). We then seeded the population with ten larvae, to mimic the initial infestation of a salmon population with a small population of migrating sea lice. To simulate populations over time, we multiplied A_1 by a population vector with ten larvae. We then multiplied the resulting population vector by a new population matrix A_2 , which represented environmental conditions on day two, to get a population vector for day three. We continued this process until the population was simulated for one year. While it may be more realistic to include migration of sea lice after day 1, we were interested in quantifying the internal population dynamics of these sites in order to identify them as sources or sinks.

Results

Effects of fixed salinity and temperature values on population vital rates

Analysis of population vital rates at fixed temperature and salinity values showed that both abiotic factors influence the population demographics of sea lice (Figure 3). For each scenario in this category, we examined the demographic parameters of population growth (λ), generation time, reproductive rate (R_0), and the sensitivity and elasticity of population growth (Figure 4) to changes in matrix elements.

Salinity had a positive impact on daily population growth when temperature was greater than 4° C. At 4° C the sea louse population growth stayed between 0.92 and 0.99 for all salinities examined; while for higher temperatures, population growth increased with increasing salinities up to 24 psu and

plateaued at salinities above that. Population growth (λ) was greater than 1 and increased with increasing temperature when salinity was greater than 22 psu and the temperature was above 4° C. When salinity was less than 22 psu, populations were predicted to decrease (i.e., λ less than 1) for all temperatures.

The generation time of sea lice decreased with increasing temperature. At 16° C it was as low as 15 days, and at 4° C it was as high as 100 days. Salinity had a limited impact on generation time.

The basic reproductive ratio of sea lice increased with temperature if salinity was greater than 20 psu and increased with salinity if the temperature was 8° C or higher. At 4° C, there was no impact of salinity or temperature on the basic reproductive ratio. The highest basic reproduction ratio (37.8) occurred at 16° C and 32 psu.

Sensitivity analysis showed that (Figure 4: A-D), in cold, hyposaline conditions, λ is most sensitive to the survival and development of eggs. In cold conditions with oceanic salinity λ is most sensitive to the survival and development of preadults. In warmer conditions, at any salinity, λ is most sensitive to the survival and development of preadults and larvae. Salinity has a greater impact on the sensitivity of λ to sea louse life history stages in colder water.

Elasticity analysis indicated that at low salinity and temperature λ was most influenced by the proportional changes in survival and development of eggs (Figure 4: E-H). At temperatures 12° C and above, and salinities greater than 20 psu, the proportional changes survival and development of preadults and adults had a greater impact on λ .

Site specific simulations

The three sites chosen for simulations – an estuarine site, an oceanic site, and a transitional site – differed considerably from each other in temperature and salinity patterns (Figure 5: A-C). The most

estuarine site had an average temperature of $9.3 \pm 5.2^{\circ}\text{C}$ (mean $\pm$ 95% confidence interval) and an average salinity of 28.3 ± 13.0 psu (mean $\pm$ 95% confidence interval), the transitional site had an average temperature of $9.0 \pm 4.0^{\circ}\text{C}$ and an average salinity of 28.3 ± 9.9 psu, and the oceanic site had an average temperature of $8.2 \pm 1.9^{\circ}\text{C}$ and an average salinity of 30.3 ± 1.0 . In the estuarine and transitional sites, temperature was inversely correlated with salinity, with temperature highs and salinity lows occurring in July and August, corresponding to periods of snowmelt in nearby mountain ranges.

Simulations of specific temperature and salinity scenarios show that changes in these conditions across an estuarine to ocean gradient dramatically impacts the population dynamics of sea lice (Figure 5: E-F). In the most estuarine scenario, the sea louse population went extinct within 100 days, while in the transitional and oceanic scenarios, the sea louse population showed exponential growth. For the specific temperature and salinity profiles assessed in these simulations, sea louse population growth was greatest in the transitional scenario.

Discussion

Sea lice are a significant pest of wild and farmed salmon and understanding how external factors alter their population dynamics is important for predicting and controlling infections. In this study we explored the effects of temperature and salinity on sea louse population dynamics. We found that sea louse survival increases with salinity, while, as previously shown, sea louse development increases with temperature (e.g. Stien et al. 2005; Groner et al. 2014). Our parameterization of salinity impacts show that, in contrast to the fairly linear impact of temperature on the development rate of sea lice, salinity levels below key values strongly reduce sea louse survival, while salinity levels above those values have little effect on survival. Simulations of specific temperature and salinity conditions show that in estuaries, low salinities may limit or halt population growth, while in oceanic conditions, low temperatures may reduce population growth. Intermediate situations may provide a 'perfect storm' for

sea louse population growth if they have increased temperatures, which promote faster development, and salinity is not at low enough values to impact survival. By parameterizing the effects of salinity and temperature on survival, we hope to promote incorporation of these commonly variable environmental conditions into empirical and theoretical approaches to understanding regional variation in sea louse dynamics. More generally, we demonstrate the importance of parameterizing and evaluating the role of environmental variation in influencing epidemiological patterns.

While the impacts of temperature on sea louse life stages and populations dynamics are fairly well documented and quantified (e.g. Stien et al. 2005; Groner et al. 2014), the impact of salinity on sea louse population dynamics has received less attention. In this study, we parameterized the effects of salinity on the egg, copepodid, and motile life stages. The results of our parameter fitting are consistent with other studies that show salinity impacts motile sea lice below 27 psu, and causes significant mortality below about 15 psu (e.g. Tucker et al. 2000; Sutherland et al. 2012).

The existence of a 'salinity threshold' below which salinity impacts occur, may explain why salinity effects are detectable in some field data but not in others (Heuch et al. 2002; Revie et al. 2003; Krkošek et al. 2006; Rogers et al. 2013; Rees et al. 2015). In some locations with little freshwater run-off, salinity values may rarely dip below critical thresholds, while in others, for example, British Columbia, they frequently do. Studies of sea louse dynamics on wild salmon in Nootka Sound, British Columbia, Canada, could detect an effect of salinity below, but not above, 15 psu and sea louse infestations on farmed salmon in this area also tend to be low (Elmoslemany et al. 2015). The impacts of such threshold dynamics may not be detectable in studies where salinity values are averaged across a time period of interest. In a study of sea louse infections on Atlantic salmon farms in the Broughton Archipelago, in western Canada, Rogers et al. (2013) were unable to detect significant effects of monthly averages of salinity or temperature on monthly averages of sea louse infestations using a linear model.

Similarly, in the simulations of estuarine, oceanic and transitional conditions in this model, average conditions were not that different among sites; simulation of exact values allowed for the detection of strong effects of salinity and temperature. Moving forward, fitting salinity effects to nonlinear models (e.g. splines) and considering extreme values as oppose to averages may assist in detecting these effects, quantifying their impacts and validation of simulations such as in this paper.

Overall, this study presents a summary of the known temperature and salinity impacts on sea louse population dynamics. Further research on several specific impacts of salinity on sea louse life history will improve the parameterization of salinity impacts. Data is particularly lacking on the impacts of salinity on sea louse fecundity and the survival and attachment of larval stages. Moreover, while we were able to model combinations of temperature and salinity, there are few lab experiments that have manipulated both of these factors simultaneously. It is possible that these factors interact in non-additive ways that are inadequately captured in our model. For example, qualitative studies suggest that both light and temperature have been found to change attachment rates of copepodids and can interact with the effects of salinity on attachment (e.g., Tucker et al. 2000; Genna et al. 2005).

A second important research area is to understand population level variation in response to environmental conditions. Pacific and Atlantic subspecies of *L. salmonis* may show variation in life history responses to stressful salinity and temperature conditions, but, this has not been well-quantified (Skern-Mauritzen et al. 2014). The detection of a salinity threshold at 15 psu in Pacific sea lice as opposed to the threshold of 20 psu in the models here, which were based on studies from Atlantic sea lice, suggests that this may be the case. Low salinities and extreme temperatures place strong selective pressure on sea lice and, if there is genetic variation in tolerance to these conditions, local, regional or ocean-wide adaptation may occur. Our analysis of the sensitivity of population growth to different life stages (Caswell et al. 2001) shows that at low temperature, there is strong selective pressure for eggs to have increased tolerance to low salinity conditions; while at warmer temperature, the greatest selective

pressure for increased tolerance to low saline conditions is in the larval and preadult stages. The strong impact of salinity on sea louse population growth found here should justify and motivate further work on these topics.

Understanding the interactions between host behaviour, salinity and sea louse population dynamics will be important for site-specific estimations. For example, anadromous brown trout are able to control sea louse populations by spending time in fresh or estuarine water (Heuch et al. 2002), infected juvenile pink salmon have been shown to increase jumping, reduce feeding and prematurely return to freshwater when infected (Webster et al. 2007). Behavioural changes have been observed, but not quantified in farmed salmon infested with sea lice. If infested farmed salmon spend more time above the halocline, salmonids may be able to cause osmotic stress in their sea louse parasites, resulting in reduced fitness. Salinity has also been shown to alter behavioural patterns, attachment rates and development of free-swimming copepodids. Larval sea lice can make slight adjustments to their position in the water column in order to find more appropriate salinities by altering swimming behavior and changing their orientation during passive sinking (Bricknell et al. 2006). This behaviour is especially relevant in coastal areas where freshwater lenses from riverine inputs may cause abrupt haloclines. Therefore it may be relevant to farmed salmon and wild salmonids when they are migrating near the coasts. Understanding how these factors interact to alter exposure of sea lice to stressful conditions will improve our estimates of the effects of environmental conditions on sea louse population dynamics.

In contrast to other compartmental and individual-based models (Revie et al. 2005; Amundrud & Murray 2009; Gettinby et al. 2011; Stucchi et al. 2011; Groner et al. 2013) which aim to describe specific scenarios on specific host populations, the PPM here was more general, in that it examined, in the absence of host effects, and immigration, how environmental variation influences sea louse population dynamics in a closed population. The trade-off between this approach and more realistic models, is that, in PPMs general solutions for population growth, basic reproductive ratio, and

generation time can be calculated here and effects of specific factors can be more readily understood in the absence of complex metapopulation structures and host effects. Future site-specific models that expand upon the parameterization here could easily incorporate age-and species- specific properties of host populations, including mortality depending upon infection intensity and behaviors that modify exposure to or fitness of sea lice as well as varying patterns of sea louse immigration and emigration.

The effects of salinity and temperature that are illustrated in this study have numerous implications for management of farmed and wild salmonids. In many areas where salmon are farmed, run-off from large snowpacks is the main source of freshwater input in the spring and summer. Knowledge of winter snow conditions may allow managers to forecast the impact that freshwater run-off will have in controlling sea louse populations during warmer months, when temperatures may increase population growth. Similarly, placement of farms in areas affected by riverine input may help to control sea louse infestations if surface salinity reaches low enough levels to have an effect (Rees et al 2015). As the simulation in this study showed, when temperature is inversely correlated with salinity, intermediate input from estuaries can be a worst-case scenario for a salmon farm; temperatures exceed values seen in more oceanic conditions which leads to increased development, while salinity values are not low enough to be an effective control. The impact of temperature and salinity on sea louse populations at these transitional sites likely depends upon differences in conditions between years. Sea louse populations could experience exponential growth in years with little riverine run-off, but, in the absence of sea louse immigration, may decline when riverine input is high.

While the level of uncertainty in projected oceanic conditions is high, many climate change models predict increases in sea surface temperatures due to increased stratification, decreased upwelling, and altered circulation; and decreases in salinity, due to changes in the amount and timing of precipitation and melting of snow and altered oceanic circulation. These predictions are particularly

dramatic in the temperate and subarctic areas where salmon farming occurs and wild salmon migrate (IPCC 2007). Previous research has identified numerous marine diseases that are expected to increase with global climate change including *Vibrio tubiashii*, *Perkinsus marinus* and *Haplosporidium nelsonii* infections of oysters, seastar wasting, ichthyophthiriasis in various finfish and numerous coral diseases (Burge et al. 2014). This study provides a framework for identifying the conditions where sea louse infections may increase as a result of changing climatic and oceanic conditions and demonstrates how multiple interacting changes in environmental conditions can have complex epidemiological results. The population matrix modeling approach utilised here demonstrates the value of quantitative tools for determining the net effects of such complex interactions and highlighting areas for future research. Our research suggests that consideration of extreme values and variation (as oppose to averaged conditions) and nonlinear effects of environmental conditions will improve estimation of marine disease outbreaks in changing climatic conditions.

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Tables

598 **Table 1.** Parameters from Stien et al. (2005) used in Equations 8-10 to estimate developmental rates of
599 each stage.

600 **Table 2.** 'Background' survival rates for each life stage of the sea louse used in Equations 11-14. These
601 values do not include reductions in survival due to salinity. With the exception of nauplii, survival
602 estimates for individuals were randomly drawn from a triangular distribution with lower and upper
603 values shown.

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604 **Table 1**

Life Stage	θ_1 (Standard Error)	θ_2 (Standard Error)	v
Eggs	41.98 (2.85)	0.338 (0.012)	2
Nauplii	24.79 (1.43)	0.525 (0.017)	0
Chalimus	74.7 (33.64)	0.236 (0.007)	0.85
Pre-adult Female	67.47 (20.36)	0.177 (0.006)	0.34

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607 **Table 2.**

Parameters	Mean	Lower	Upper	Source
Egg Viability	0.90	0.75	0.96	Heuch et al. 2000
Nauplii Survival (daily)	0.83			Stien et al. 2005
Chalimus Survival (daily)	0.992	0.98	0.997	Bjorn and Finstad 1998
Preadult Survival (daily)	0.965	0.953	0.98	Bjorn and Finstad 1998
Adult Survival (daily)	0.965	0.904	0.997	Bjorn and Finstad 1998

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Figures

Figure 1. Effect of salinity on survival of eggs (A), copepodids (B) and motile sea lice (C). Data shown are for re-adjusted survival due to salinity from trials by Johnson and Albright (1991) for eggs and Dalesman (2003) for copepodids. Also shown are logistic regressions fit to data which were used in simulations. Because 3 trials were run for the copepodid survival data, we were able to calculate confidence intervals on regression value.

Figure 2. Diagram of the stage-structured population projection matrix used in simulations and analyses. P_i indicates the probability of staying in a stage in a single time-step, G_i indicates the probability of transitioning to a different stage in a single time-step and F_i is the fecundity of a particular stage. The time-step in the model is one day.

Figure 3. Effects of salinity and temperature on (A) sea louse population growth (λ), (B) generation time and (C) basic reproductive ratio (R_0)

Figure 4. Sensitivites (A-D) and elasticities (E-H) of population growth rate (λ) to sea louse life stages at different salinities and temperatures. Values presented for each life stage are the sum of the sensitivities or elasticities of remaining in and transitioning out of that stage.

Figure 5. Salinity and temperature profiles (A-C) and corresponding sea louse population simulation results (D-F) for three locations in the Broughton Archipelago, BC, Canada, where salmon farming occurs. Abiotic data was collected daily or extrapolated when daily collection wasn't possible. All data were collected from the top 5m of the water column during 2012. Sites were chosen to represent a range of conditions from highly or moderately influenced by riverine input (A, B) to independent of riverine discharge (C). Day 1 in all graphs refers to Julian day 120 (29 April). Note that the y-axis scale is smaller on figure D compared to figures E and F.

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$$A = \begin{bmatrix} P_1 & 0 & 0 & 0 & F_5 & 0 & F_7 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & G_7 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{bmatrix}$$