

Quantifying key parameters related to the life cycle of *Caligus rogercresseyi*

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Abstract

The salmon louse *Caligus rogercresseyi* (Boxshall and Bravo 2000) is a common ectoparasite of farmed salmonids in Chile. Sea lice can negatively impact the growth of hosts, adversely affecting aquaculture productivity. Unlike *Lepeophtheirus salmonis* (Krøyer, 1838), whose life cycle parameters have been well studied due to its importance in the northern hemisphere, for *C. rogercresseyi* no single source exists that quantifies the parameters required to model this ectoparasite's life cycle. Given that different species of sea lice have substantially different biological characteristics, it is important to parameterise the life cycle of *C. rogercresseyi* using appropriate observational data, rather than simply trying to adapt parameters developed for *L. salmonis*. Using data from existing literature we quantified the development and survival rates for each stage in the *C. rogercresseyi* life cycle. We illustrate how development rates are affected by water temperature and explore the important impacts of salinity on rates of survival. We present equations that can be used to model development periods and survival proportions given certain water temperature and salinity profiles. While key parameters to quantitatively model the life cycle of *C. rogercresseyi* are presented, further research is required to adequately model the complete population dynamics of this ectoparasite on Chilean salmon farms and consequently to support decision making to achieve effective control and mitigation.

Keywords: *Caligus rogercresseyi*, life cycle, population dynamics, salmon farms, sea lice,

1. Introduction

Sea lice (*Lepeophtheirus* spp. and *Caligus* spp.) remain a serious threat to aquaculture productivity and may have an impact on wild salmonids in salmon producing countries. Unlike countries in the northern hemisphere where *Lepeophtheirus salmonis* (Krøyer, 1838) is the major ectoparasite, *Caligus rogercresseyi* (Boxshall and Bravo 2000) is the most significant ectoparasite on Chilean Atlantic salmon (*Salmo salar* L.) farms. *C. rogercresseyi* on farmed salmon are widely distributed in many regions of Chile and pose a serious threat to salmonid aquaculture. Also, relatively high levels of *C. rogercresseyi* infestation on some farms need to be controlled to improve their productivity and to prevent wild hosts from being infested with farm-originated sea lice (Hamilton-West et al., 2012).

Given that model parameters for *L. salmonis* are well studied (Brooker et al., 2018; Groner, et al., 2016; Hamre et al., 2019; Johannessen, 1977; Revie et al., 2005; Samsing et al., 2016; Stien et al., 2005) and that the two species are both ectoparasites of salmonids, it may seem reasonable to use some parameter values from *L. salmonis* for *C. rogercresseyi* modelling studies. However, these two species of louse exhibit important biological differences. For example, *L. salmonis* are around twice the size of *C. rogercresseyi* (Burka et al., 2011); also *L. salmonis* has two pre-adult stages, while *C. rogercresseyi* does not (Burka et al., 2011). Due to their different evolutionary histories and differing host preferences, other characteristics such as duration of larval survival and depth preferences to maximise encounter rates also differ. Considering these differences, determining parameters for *C. rogercresseyi* population dynamics is a critical step to creating useful models for ectoparasitic development and control on salmon farms. A recent discovery around differing development rates between *L. mugiloidis* and *C. rogercresseyi* emphasised the necessity of robustly specifying the relevant parameters for *C. rogercresseyi* (Bravo et al., 2021).

The confluence of large datasets and robust models can inform our understanding of host-parasite interactions and help design effective intervention methods (Groner et al., 2016). To model *C. rogercresseyi* population dynamics, we need to know the parameters relating to the length of time spent in each life stage as well as how likely it is that a sea louse will survive to reach its next life stage. Here, we describe these parameters and analyse the available observational data from published studies. We then estimate the effects of water temperature and salinity on the parameters. The life cycle of *C. rogercresseyi* consists of the stages of egg, nauplius, copepodid, chalimus and adult (Fig. 1). Parameters to model the *C. rogercresseyi* life cycle are categorised into development, survival, and reproduction-related parameters.

2. Development

The development period was defined as time spent in a given stage before progressing to the subsequent stage. As the development periods for *L. salmonis* are known to depend on temperature (Johannessen, 1977; Rittenhouse et al., 2016; Stien et al., 2005), we generated estimates based on observational data around development periods for the life stages of *C. rogercresseyi* at different temperatures.

Montory et al. (2018) and Montory et al. (2020) observed the time until hatching of eggs and development time until moulting of Nauplius I and Nauplius II at five different temperatures

of 6, 9, 12, 15, and 18 °C (Fig. 2A-1 and 2A-2). González and Carvajal (2003) observed the frequency of occurrence of different stages in chalmus samples at temperatures of 10.2, 11.3, 12.4, 12.9, 14.4, and 16.7 °C (Fig. 2A-3). We estimated $\delta(T)$ of development periods of egg hatching, nauplius and chalmus via regression to a second-order polynomial function of temperature (Toorians & Adams, 2020) (Table 1):

$$\delta(T) = A_0 + A_1 * T + A_2 * T^2$$

In this quadratic regression, $\delta(T)$ is the predicted development time at temperature T, while A_0 , A_1 , and A_2 are constants.

The development period for copepodids at a variety of temperatures has not been observed. However, the time from hatching to infestation of *C. rogercresseyi* was observed in different temperatures (González & Carvajal, 2003). We calculated the developmental period of copepodid in different temperatures, by subtracting the period spent in the nauplius stage, which was calculated using equation (1), from the time from egg hatching to infestation. The copepodid developmental period was not found to be markedly affected by temperature and the period was estimated to be on average 3.07 days. This finding is in line with a temperature-independent developmental period that has been estimated for *L. salmonis* copepodids (4.6 days on average) (Groner, et al., 2016).

The development rates for adult males and females were quantified by González and Carvajal (2003), using linear regression. They showed that these rates linearly depend on temperature and that a minimum temperature of 4.2 °C is required for development of the reproductive stage of sea lice.

3. Survival

The survival of sea lice is known to be affected by salinity, and some will fail to survive even at ideal salinity levels (Arriagada et al., 2016; Groner et al., 2016). Thus, the proportion (ρ) of *C. rogercresseyi* surviving in a life stage and developing to the next stage was calculated as the product of the salinity-induced survival rate (σ) and the salinity-independent background survival rate (θ).

Montory et al. (2018) evaluated the effects of four salinities (14, 20, 24, and 32 PSU) on the success of egg hatching. We calculated the proportion of hatching that was dependent on salinity by dividing the hatching proportion at 14, 20, and 26 PSU salinities by the survival at the highest salinity (i.e., 32 PSU), which maximizes the survival and the hatching proportion at 32 PSU was assumed as the salinity-independent hatching proportion (Groner et al., 2016) (Fig. 2B-1).

Montory et al. (2018) also observed the survival of nauplius I and nauplius II in the same salinity setting as eggs. The survival proportion of nauplius was calculated by multiplying each survival proportion in nauplius I and nauplius II. The salinity-induced survival proportions of eggs and nauplius were fit to a logistic curve (Fig. 2B-2) (Groner, et al., 2016; Johnson & Albright, 1991) (Table 2).

Copepodid (infective stage) must survive in a free period without a host and must attach to its host (Burka et al., 2011). The time until the death of the free copepodid without a host $\kappa(S)$

was observed by Montory et al., (2018) in the same setting of salinities as eggs, and we fitted the time to a logistic curve (Fig. 2B-3).

$$\kappa(S) = 16.125 - \frac{16.125}{\left(1 + \frac{S}{21.462 \pm 0.098}\right)^{10.460 \pm 0.440}}$$

If the survival time without a host was shorter than the period of copepodid (i.e., which was estimated as 3.37 days), the survival of copepodid cannot be plausible. Although temperature and salinity influence the attachment probability (Bricknell et al., 2006; Tucker et al., 2000), quantification of attachment probability based only on temperature or salinity cannot be reliable because their ability to attach to a host is also affected by other numerous factors such as host density and water currents.

A group of chalimus I and II were observed at 31 PSU on fish for 48 hours, and 65%, 25%, and 11% of the group were observed to result in the condition of live, moribund, and dead, respectively (Marín et al., 2015). Chalimus were defined as moribund if they, “presented movement in extremities, the gut or other organs only when pressed” (Marín et al., 2015). We therefore assumed that half of the moribund chalimus would survive, resulting in an estimated salinity-independent survival proportion of 0.965 in chalimus I and II grouped. If the survival proportion is assumed to be similar for chalimus III and IV grouped, the background survival proportion for all chalimus stages could be estimated as 0.965². Survival of chalimus exposed to a range of salinities has not been studied; therefore, it is not currently possible to model any effect. However, in the case of *L. salmonis*, the survival rate of chalimus was found not to be significantly different to the survival rate of adults (Bjørn & Finstad, 1998; Groner, et al., 2016).

Regarding all stages, other than adults, survival involves staying alive until moulting to the subsequent life stage. In the survival of egg and nauplius, the proportions that successfully developed to the next stage were observed. However, the adult stage, (i.e., the terminal stage), does not have a subsequent stage. Thus, the way of dealing with survival must be expressed differently. Survival of adults is not about the proportion surviving but rather the period over which they survive. Also, the available data around adult survival based on salinity (Bravo et al., 2008) record the proportion that survived at each time point; data that are more appropriate for proportional hazard modelling. Thus, instead of fitting the data to a logistic curve as was carried out for eggs and nauplii, we fit these data to a Cox proportional hazards model (using the “coxph” function in the survival package in R version 3.4.4) (Lin & Zelterman, 2002). To parameterise the salinity-induced survival rate, we used experimental observations of the percentage survival of adult males and females at recorded exposure times (30 min, 1, 12, 18, and 24 hrs) over various salinities (Bravo et al., 2008). The best-fit model for the daily survival rate of adult lice due to salinity (S) was:

$$\sigma_{adult} = 1 - \left\{e^{(-0.168 \pm 0.010) * S}\right\}^{24}$$

This was calculated by solving for the survival function from the hazard ratio, where σ_{adult} is the daily survival rate, and S is salinity in PSU (Fig. 3A). Sex did not significantly affect the survival rate. To quantify the salinity-independent survival rate, we used another experiment that observed the survival percentages of adult males and females in the salinity between 28 and 31 PSU (Bravo, 2010). The data were fit to a parameter exponential curve, which is commonly used

to solve the survival rate in epidemic models (Vynnycky & White, 2010). Unlike salinity-induced survival, salinity-independent survival was found to significantly differ between males and females, and the average periods until death for adult males and females were estimated to be 17.83 days and 33.66 days, respectively (Fig. 3B).

4. Reproduction

Adult females of *C. rogercresseyi* were estimated to produce 35 ± 6.1 (mean \pm SD) eggs per string in the first clutch (Bravo, 2010), and 45 ± 16 eggs per string on average in subsequent clutches (Bravo et al., 2009). These are much lower than for *L. salmonis* which have been estimated to produce 152 ± 31 and 296 ± 100 eggs per string in the first and subsequent clutches, respectively (Heuch et al., 2000). The sex ratio in *L. salmonis* is 1:1 (Hamre et al., 2019), and this equal ratio seems reasonable for *C. rogercresseyi*. An experiment found that adult females and adult males emerged as 46% and 54% of the total population of adults respectively (González et al., 2015), which appears close to a 50/50 split.

The interval between clutches is temperature-dependent (Groner et al., 2014). This interval consists of the period of days for eggs to develop after egg string extrusion ($\delta_{\text{egg}}(T) - 1$) and the days between the hatching of one clutch and the extrusion of the next egg string (ζ) (Groner et al., 2014). This value was estimated using the following equation:

$$\zeta = \max(1, -0.59T + 12.39)$$

This equation is based on hatching times that have been estimated to hold from between 10.3 to 16.7 °C (González & Carvajal, 2003).

5. Conclusion

Here, we have used observed data to estimate appropriate parameter values for the developmental, survival and fertility rates of *C. rogercresseyi* at each life stage. The information summarised in this study also formed the basis for a model of *C. rogercresseyi* population dynamics that simulates its epidemiological properties and can be used to devise effective control measures on Chilean salmon farms (www.caligus.life).

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Table 1. Values for quadratic regressions of the development functions, $\delta(T) = A_0 + A_1 * T + A_2 * T^2$, where T indicates temperature. This function is temperature-dependent developmental periods of life stages.

Stage	A ₀ (standard error)	A ₁ (standard error)	A ₂ (standard error)
Egg, $\delta_{egg}(T)$	6.68 (0.76)	-0.68 (0.13)	0.02 (0.01)
Nauplius, $\delta_{nauplius}(T)$	11.30 (2.44)	-0.85 (0.40)	0.02 (0.02)
Chalimus, $\delta_{chalimus}(T)$	46.62 (25.71)	-3.73 (3.88)	0.08 (0.08)

Table 2. Estimates of salinity-induced survival (σ) and salinity independent background survival (θ). $\sigma(S)$ was quantified with the means and standard errors of the parameters. S indicates salinity in PSU.

	Salinity-induced survival proportion, $\sigma(S)$	Salinity independent survival proportion, θ
Egg hatching	$\sigma_{egg}(S) = 1 - \frac{1}{1 + \left(\frac{S}{14.42 \pm 0.03}\right)^{6.31 \pm 0.11}}$	$\theta_{egg} = 0.98$
Nauplius	$\sigma_{nauplius}(S) = 1 - \frac{1}{1 + \left(\frac{S}{26.36 \pm 0.31}\right)^{29.71 \pm 25.15}}$	$\theta_{nauplius} = 0.57$
Chalimus	-	$\theta_{chalimus} = 0.93$

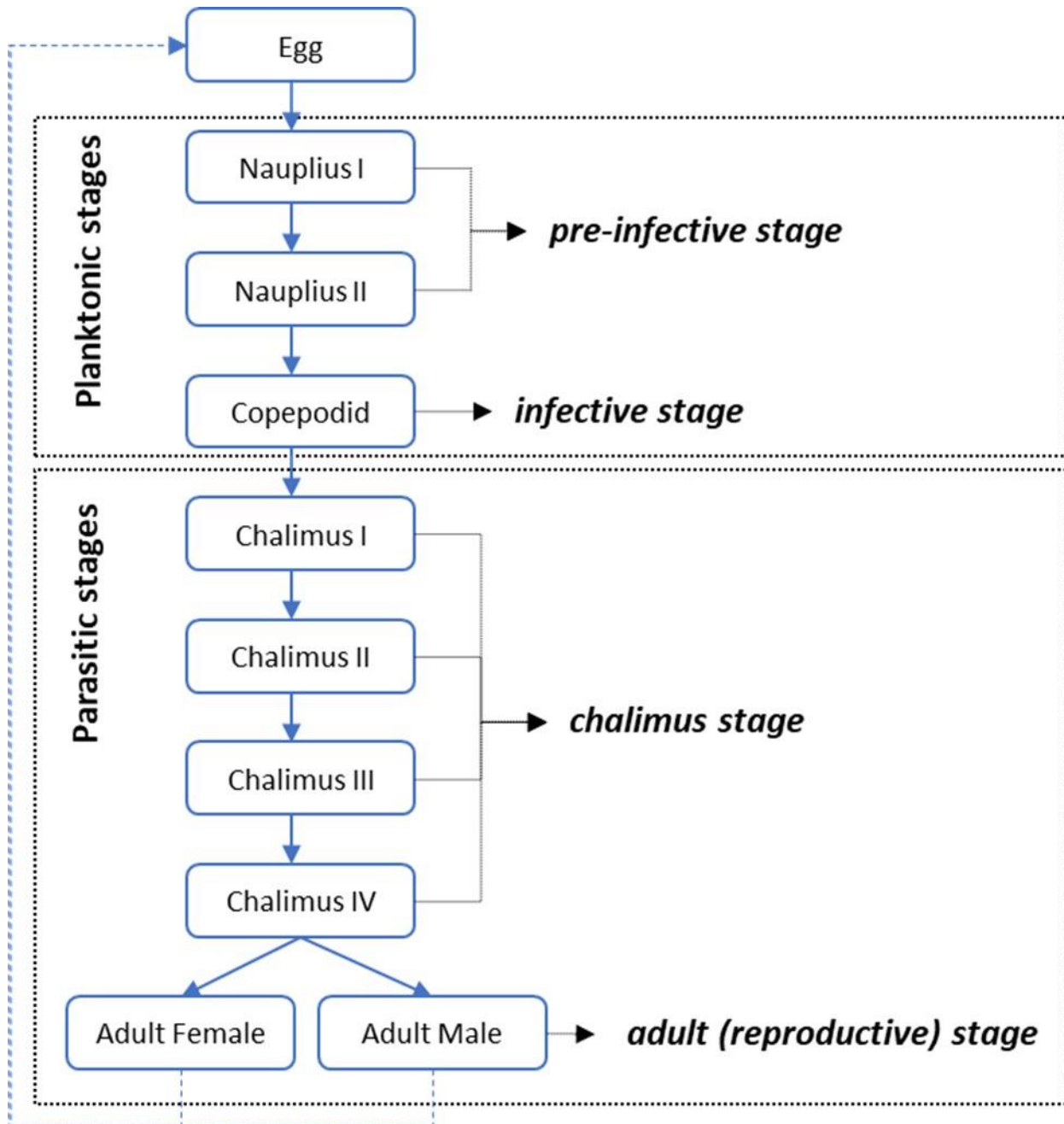


Fig. 1 The lifecycle of *Caligus rogercresseyi*.

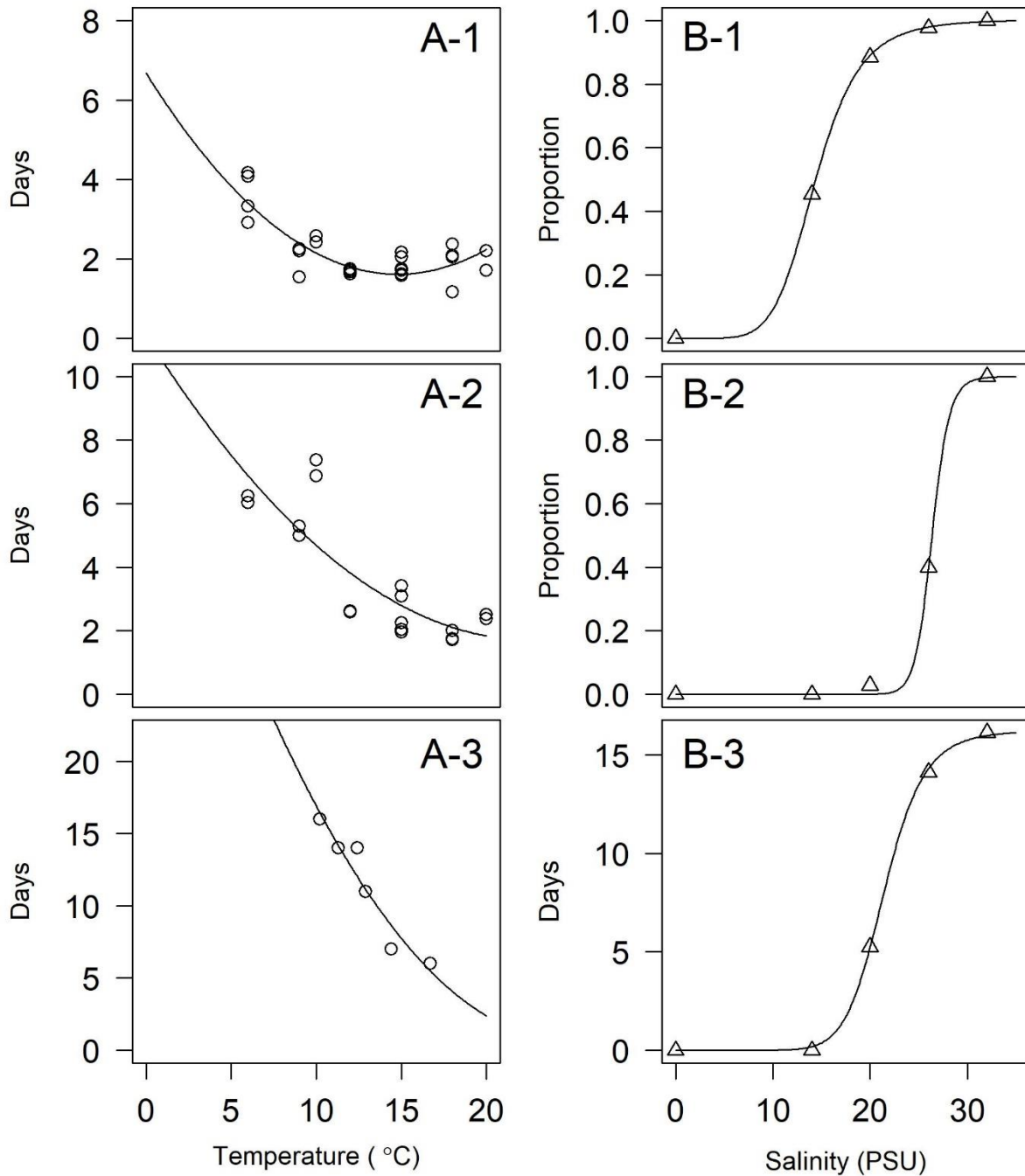


Fig. 2 Effect of water temperature (A) and salinity (B). Effect of water temperature on period until egg hatching (A-1), nauplius development period (A-2), and chalimus development period (A-3) was quantified. Dots and lines represent actual data from (Montory et al., 2018, 2020) and predicted values, respectively. The best-fit regression lines used a second-order polynomial function of temperature (T), $\delta(T) = A_0 + A_1 * T + A_2 * T^2$, with the parameter estimates given in Table 1. Effect of salinity on egg hatching proportion (B-1), nauplius survival proportion (B-2)

and days until copepodid dies without a host (B-3) was quantified. Triangles represent average values of actual data at each level of salinity, while lines represent their predicted values through logistic regressions that were fit to the actual data, which are given in Table 2. The actual data shown are for re-adjusted survival due to salinity from trials by (Montory et al., 2018), and zero salinity was assumed to result in zero values of the proportions and days.

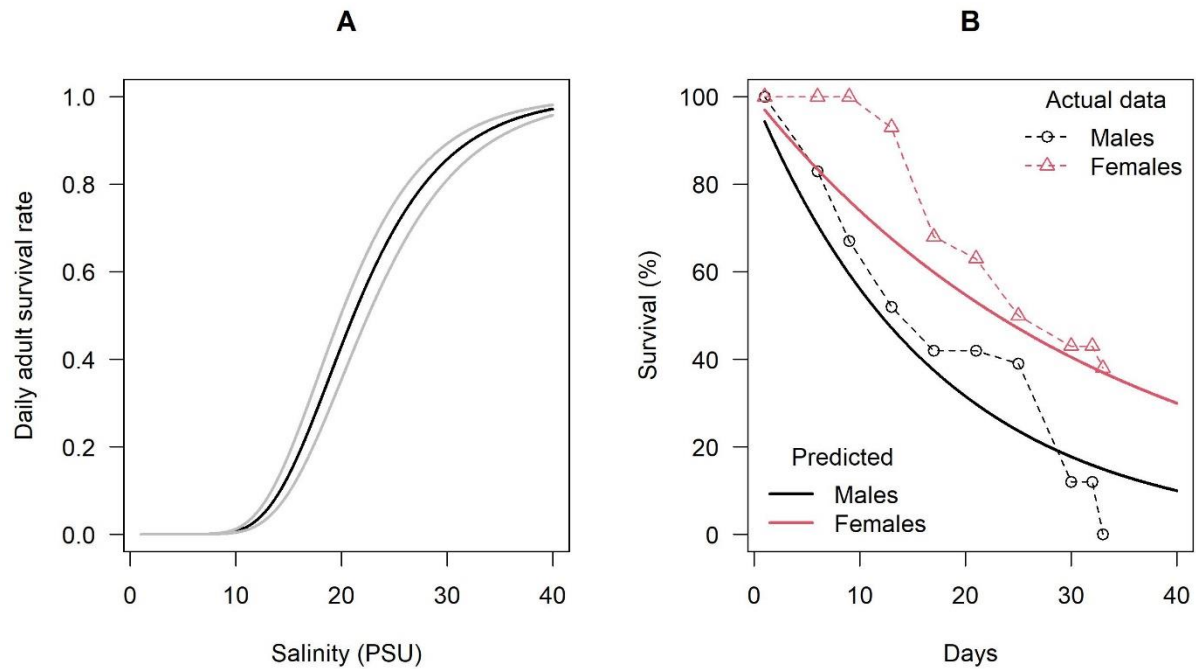


Fig. 3 Survival of adult lice. (A) salinity-induced daily survival rate was fit to data using the proportional hazard method and generated the average (black line) and 95 % confidence intervals (grey lines). (B) salinity-independent background survival percentage across days was fit using exponential curves giving average survival periods for males and females of 17.8 and 33.7 days, respectively. Daily mortality rates are their reciprocals of 0.056 and 0.03, respectively.