Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout

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ABSTRACT: The salmon louse *Lepeophtheirus salmonis* is a common ectoparasite of both farmed and wild salmonids in the marine environment, and can have a significant negative effect on the survival and growth of its host. To facilitate development of models of salmon lice population dynamics, we review the available experimental information on its demographic rates and highlight areas where further research is needed. For all stages, the reduced minimum development time of a stage with increasing water temperature (T) was well described by Belehrádek's function. However, detailed experimental studies of the development of the parasitic stages at low ($T < 7°C$) and high ($T > 15°C$) water temperatures are needed to cover the whole range of water temperatures experienced in the wild. Little information was available on mortality rates and distributions of developmental times after the initial minimum developmental times. These parameters could only be estimated for a narrow temperature range, but the available estimates suggested that distributions of development times may be assumed to be constant with respect to temperature. Factors affecting female fecundity are presently poorly understood, with a level of unexplained variability in both average egg numbers per string and egg viability, which demands further investigations. In addition, experiments on possible density-dependent effects on salmon lice fecundity and survival are required.

KEY WORDS: Stage-structured models · Demography · Survival · Development · Fecundity

INTRODUCTION

The salmon louse *Lepeophtheirus salmonis* Krøyer 1837 (Copepoda: Caligidae) is a common ectoparasite of both farmed and wild salmonids in the marine environment (Kabata 1979). *L. salmonis* feeds on the skin of its hosts and thereby causes mechanical damage (reviewed in Pike & Wadsworth 2000). The skin damage from the early parasitic (i.e. chalimus) stages is in general relatively small (Pike & Wadsworth 2000), while the larger and mobile pre-adult and adult stages can cause considerable skin erosion with associated osmoregulatory problems for the host and potentially host death (Grimnes & Jakobsen 1996, Bjørn & Finstad 1998, Nolan et al. 1999, Tully & Nolan 2002). The negative effect of salmon lice on farmed salmonids has resulted in considerable interest in its population dynamics and research into treatment strategies. However, the dramatic increase in salmon farming world-wide has also caused concern for increased transmission of salmon lice to wild salmonids (Bjørn et al. 2001, Heuch & Mo 2001, Butler 2002), of which the post-smolt stage is likely to be especially vulnerable to the pathogenic effects of salmon lice infections.

Lepeophtheirus salmonis has 10 morphologically distinct stages (Johnson & Albright 1991b, Schram 1993). Adult female salmon lice produce 2 egg strings, which are filled with embryos. These remain attached to the female as they develop. A pre-infective planktonic naupliar stage hatches from the egg and leaves the string as a planktonic larva. It moults to the second nauplius stage, from which the infective copepodid stage is reached (Fig. 1). These planktonic stages are non-feeding (Pike & Wadsworth 2000). After infection, the copepodid begins to feed on the host and develops through 4 chalimus stages and 2 pre-adult stages before reaching the reproducing adult stage (Kabata 1979). At the pre-adult and adult stages, male and
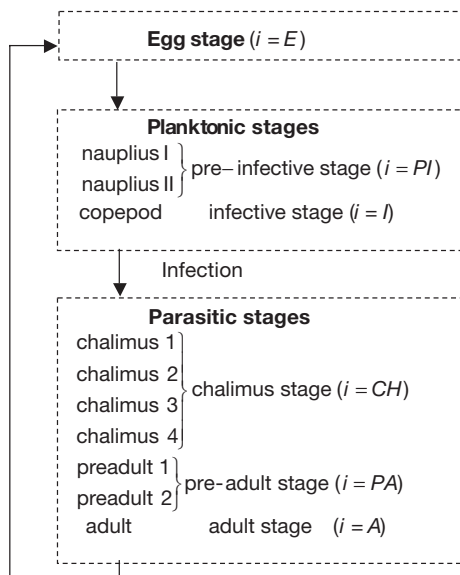
Fig. 1. *Lepeophtheirus salmonis*. The 11 morphological life cycle stages grouped into 6 functional groups of stages (subscript notation used for these stage groups in brackets)

female salmon lice can be distinguished morphologically (Johnson & Albright 1991b, Schram 1993).

Despite the economic and potential ecological importance of *Lepeophtheirus salmonis*, relatively little work has been carried out on population dynamic models for developing control strategies in fish farms and evaluating the potential impact of transmission from farmed fish to wild host populations (but see Tully 1992, Heuch & Mo 2001, Tucker et al. 2002). The life history of *L. salmonis* suggests that stage-structured population models could be developed along similar lines as models used for non-parasitic copepods (e.g. McCauley et al. 1996) and parasitic nematodes (e.g. Smith & Grenfell 1985). To facilitate such model development, we bring together the literature on *L. salmonis* in a quantitative review of the available experimental information on stage-specific development and mortality rates, and on fecundity of *L. salmonis* on Atlantic salmon *Salmo salar* L. and sea trout *Salmo trutta* L. Due to the low resolution of many datasets with respect to morphological stage and frequency of sampling, we group the 11 morphologically distinct stages into 6 functional groups (Fig. 1), with potential differences between the

sexes in survival and development being allowed for in the pre-adult and adult stages. We focus especially on the effect of water temperature on stage durations since we believe observations on stage durations in laboratory populations are more likely to be applicable to natural populations than estimates of survival. In addition, good estimates of stage durations allow for improved estimation of recruitment and stage-specific survival in analyses of stage-frequency data from natural populations (Wood 1994, Manly 1997).

MATERIALS AND METHODS

Basic stage-structured models of the development and survival of salmon lice. As a conceptual framework for evaluating available data, we used linear delay-differential equation models for the change over time t in the number of lice N_{ij} at developmental stage i (Fig. 1) and of sex j. For an overview of the notation used, see Table 1. The models were formulated to correspond closely to the study designs used to generate the available data. Stage durations were modelled by dividing the development within a stage into 2 periods: (1) a minimum development period (τ_{ij}) common to all individuals and (2) a distribution of development times $f_{ij}(t)$ that mimic the individual variation in actual

Table 1. Notation

Indices	
i	Louse developmental stage (see Fig. 1)
j	Sex of parasitic stages, m = males, f = females
k	Sample unit number
State variables	
$N_{ij}(t)$	Expected number of lice of stage i and sex j at time t
Observed variables	
n_{ijk}	Observed number of lice of stage i and sex j in sample unit k
m_k	Number of fish hosts grouped together in sample unit k
T_k	Water temperature (°C) associated with sample unit k
t_k	Sampling time of sample unit k
C_{lijk} and C_{uijk}	Lower and Upper limit of interval censored data on minimum developmental times
Parameters	
$\hat{N}_{CH.k}(0)$	Population size of lice in sample unit k at $t = 0$
μ_{ij}	Instantaneous mortality rate (ind.$^{-1}$ d^{-1}) of stage i and sex j
τ_{ij}	Minimum development time (d) for stage i and sex j
υ_{ij}	Instantaneous development rate (ind.$^{-1}$ d^{-1}) after minimum development time of stage i and sex j
p_j	Proportion of sex j among infective stages
ρ_E	Proportion of eggs that hatch and develop to viable nauplii larvae
q_j	Proportion of salmon lice at the chalimus stage of sex j that survive the transition to the pre-adult stage
λ_k	Average intensity of infection in sample unit k
a and b	Scale and shape parameters of gamma distribution
β_1 and β_2	Parameters in Belehrádek's function, $\bar{\tau}(T) = [\beta_1/(T - 10 + \beta_1\beta_2)]^2$
β_3 and β_4	Parameters describing time variation in female development rates in the function $\log[\upsilon_{CHf}(t)] = \beta_3 + \beta_4(t - \tau_{CHf})$

developmental times, where $f_{ij}(t)$ is the probability for an individual to have developed to the next stage at time t. In the basic model, we assumed $f_{ij}(t)$ to follow the exponential distribution, $f_{ij}(t) = 1 - e^{-v_{ij}t}$, giving a constant instantaneous rate of development v_{ij}. Similarly, we assumed that mortality within each stage could be modelled assuming a constant instantaneous mortality rate, μ_{ij}. However, for the egg stage, data suitable to estimate mortality over time within the stage have not been reported. Based on available data, we therefore summarised mortality as a constant proportion, ρ_E, of a batch of eggs that would hatch and develop to the pre-infective stage. For the egg and planktonic stages, we assumed no differences in demographic rates between males and females since the stages cannot be sexed, and we suppress the subscript j.

The basic model for the change over time in the number of viable eggs extruded at time $t = 0$, $\rho_E N_E$, was:

$$\frac{d\rho_E N_E}{dt} = \begin{cases} 0, & \text{for } t < \tau_E \\ -v_E \rho_E N_E, & \text{for } t \geq \tau_E \end{cases} \tag{1}$$

where τ_E is defined as the minimum number of days needed for egg development from egg string extrusion. With an initial value of $N_E(0)$, the analytical solution to this model is:

$$\rho_E N_E(t) = \begin{cases} \rho_E N_E(0), & \text{for } t < \tau_E \\ \rho_E N_E(0)e^{-v_E t}, & \text{for } t \geq \tau_E \end{cases} \tag{2}$$

Similarly, we modelled the change over time in the number of lice at the pre-infective stage in a cohort that hatched at time $t = 0$, and their subsequent development into the infective stage. In the experimental studies we review, there was no loss of infective stages due to infection events, giving:

$$\frac{dN_{PI}}{dt} = \begin{cases} -\mu_{PI} N_{PI}, & \text{for } t < \tau_{PI} \\ -(v_{PI} + \mu_{PI}) N_{PI}, & \text{for } t \geq \tau_{PI} \end{cases}$$
$$\frac{dN_I}{dt} = \begin{cases} 0, & \text{for } t < \tau_{PI} \\ v_{PI} N_{PI} - \mu_I N_I, & \text{for } t \geq \tau_{PI} \end{cases} \tag{3}$$

where τ_{PI} is defined as the minimum number of days needed for pre-infective stage development from egg hatching. With initial values of $N_{PI}(0)$ and $N_I(0) = 0$, the analytical solution to this model is:

$$N_{PI}(t) = \begin{cases} N_{PI}(0)e^{-\mu_{PI}t}, & \text{for } t < \tau_{PI} \\ N_{PI}(0)e^{-(v_{PI}+\mu_{PI})t}, & \text{for } t \geq \tau_{PI} \end{cases}$$
$$N_I(t) = \begin{cases} 0, & \text{for } t < \tau_{PI} \\ \dfrac{N_{PI}(0)v_{PI}e^{-\mu_{PI}\tau_{PI}}}{\mu_I - \mu_{PI} - v_{PI}}[e^{-(\mu_{PI}+v_{PI})(t-\tau_{PI})} - e^{-\mu_I(t-\tau_{PI})}], & \text{for } t \geq \tau_{PI} \end{cases} \tag{4}$$

Finally, the basic model for the change over time in the number of parasitic salmon lice of stage i and sex j in a cohort that infected the host at time $t = 0$ was:

$$\frac{dN_{CHj}}{dt} = \begin{cases} -\mu_{CHj} N_{CHj}, & \text{for } t < \tau_{CHj} \\ -(\mu_{CHj} + v_{CHj}) N_{CHj}, & \text{for } t \geq \tau_{CHj} \end{cases}$$

$$\frac{dN_{PAj}}{dt} = \begin{cases} 0, & \text{for } t < \tau_{CHj} \\ v_{CHj} N_{CHj} - \mu_{PAj} N_{PAj}, & \text{for } \tau_{CHj} \leq t < \tau_{PAj} \\ v_{CHj} N_{CHj} - (\mu_{PAj} + v_{PAj}) N_{PAj}, & \text{for } t \geq \tau_{PAj} \end{cases} \tag{5}$$

$$\frac{dN_{Aj}}{dt} = \begin{cases} 0, & \text{for } t < \tau_{PAj} \\ v_{PAj} N_{PAj} - \mu_{Aj} N_{Aj}, & \text{for } t \geq \tau_{PAj} \end{cases}$$

where τ_{CHj} is defined as the minimum number of days from infection needed for development at the chalimus stages, and τ_{PAj} defined as the minimum number of days from infection needed for development to the adult stage. With initial values of $N_{PAj}(0) = 0$, $N_{Aj}(0) = 0$, $N_{CHf}(0) = p_f N_{CH.}(0)$, $N_{CHm}(0) = p_m N_{CH.}(0) = (1 - p_f) N_{CH.}(0)$, where $N_{CH.}(0) = N_{CHf}(0) + N_{CHm}(0)$ and p_f is the proportion of female chalimus larvae at initial infection, the analytical solution to the model is:

$$N_{CHj}(t) = \begin{cases} p_j N_{CH.}(0)e^{-\mu_{CHj}t}, & \text{for } t < \tau_{CHj} \\ p_j N_{CH.}(0)e^{-\mu_{CHj}\tau_{CHj}} e^{-(\mu_{CHj}+v_{CHj})(t-\tau_{CHj})}, & \text{for } t \geq \tau_{CHj} \end{cases}$$

where:

$$N_{PAj}(t) = \begin{cases} 0, & \text{for } t < \tau_{CHj} \\ p_j N_{CH.}(0)a_{2j}(e^{-(\mu_{CHj}+v_{CHj})(t-\tau_{CHj})} - e^{-\mu_{PAj}(t-\tau_{CHj})}), & \\ \qquad\qquad \text{for } \tau_{CHj} \leq t < \tau_{PAj} \\ p_j N_{CH.}(0)(a_{1j}(e^{-(\mu_{CHj}+v_{CHj})(t-\tau_{PAj})} - e^{-(\mu_{PAj}+v_{PAj})(t-\tau_{PAj})}) + \\ \qquad a_{3j}e^{-(\mu_{PAj}+v_{PAj})(t-\tau_{PAj})}), & \text{for } t \geq \tau_{PAj} \end{cases}$$

$$N_{Aj}(t) = \begin{cases} 0, & \text{for } t < \tau_{PAj} \\ p_j N_{CH.}(0)(\dfrac{a_{1j}v_{PAj}}{\mu_{Aj} - \mu_{CHj} - v_{CHj}}(e^{-(\mu_{CHj}+v_{CHj})(t-\tau_{PAj})} - e^{-\mu_{Aj}(t-\tau_{PAj})}) + \\ \dfrac{(a_{3j}-a_{1j})v_{PAj}}{\mu_{Aj} - \mu_{PAj} - v_{PAj}}(e^{-(\mu_{PAj}+v_{PAj})(t-\tau_{PAj})} - e^{-\mu_{Aj}(t-\tau_{PAj})})), & \\ \qquad\qquad \text{for } t \geq \tau_{PAj} \end{cases}$$

where

$$a_{1j} = \frac{v_{Jj}e^{-\mu_{CHj}\tau_{CHj}}e^{-(\mu_{CHj}+v_{CHj})(\tau_{PAj}-\tau_{CHj})}}{\mu_{PAj}+v_{PAj}-\mu_{CHj}-v_{CHj}}, \quad a_{2j} = \frac{v_{CHj}e^{-\mu_{CHj}\tau_{CHj}}}{\mu_{PAj}-\mu_{CHj}-v_{CHj}} \text{ and}$$

$$a_{3j} = a_{2j}(e^{-(\mu_{CHj}+v_{CHj})(\tau_{PAj}-\tau_{CHj})} - e^{-\mu_{PAj}(\tau_{PAj}-\tau_{CHj})}) \tag{6}$$

The data. The data available on the demographic rates of the egg and planktonic stages of *Lepeophtheirus salmonis* were direct estimates of minimum developmental times (τ_i) and survival with associated average water temperatures over the course of the studies (Table 2). For the parasitic stages, data was frequently available from studies that were not primarily concerned with estimation of demographic rates. In these studies, hosts were infected by copepodids in the laboratory, and data on the stage structure on hosts

Table 2. *Lepeophtheirus salmonis* on *Salmo* spp. Summary of the sources of the data used to estimate the demographic rates of *L. salmonis*, the host species used, stages studied, demographic parameters that could be estimated for stage *i* and sex *j*, and average temperature used in the experiments. For experiments at >2 temperature levels, the range is given in brackets

Host species	Stages studied	Parameters	Temperature (°C)	Source
S. salar	All	$\tau_{ij}, \upsilon_{ij}, \mu_{ij}, \rho_E$	[5, 15]	Johnson & Albright (1991a)
S. salar	Egg	ρ_i	7.2, 12.2	Heuch et al. (2000)
S. salar	Egg	ρ_i	14	Ritchie (1993)
S. salar	Egg and planktonic	τ_i, υ_i	[2, 10]	Boxaspen & Næss (2000)
S. salar	Egg and planktonic	τ_i	[9, 19]	Johannessen (1978)
S. salar	Planktonic	τ_i	12	Wootten et al. (1982)
S. salar	Planktonic and parasitic	$\tau_{ij}, \upsilon_{ij}, \mu_{ij}$	[7.5, 8.8]	Tucker et al. (2002)
S. salar	Parasitic	τ_{ij}	9.5	Johnson (1993)
S. salar	Parasitic	τ_{ij}	9.7	Grimnes et al. (1996)
S. salar	Parasitic	$\tau_{ij}, \upsilon_{ij}, \mu_{ij}$	10.4	Grimnes & Jakobsen (1996)
S. salar and *S. trutta*	Parasitic	τ_{ij}	9.7	Dawson et al. (1997)
S. trutta	Parasitic	τ_{ij}	12.3	Dawson et al. (1998)
S. salar	Parasitic	τ_{ij}	15	Dawson et al. (1999)
S. trutta	Parasitic	$\tau_{ij}, \upsilon_{ij}, \mu_{ij}$	9.7	Bjørn & Finstad (1998)
S. salar	Parasitic	$\tau_{ij}, \upsilon_{ij}, \mu_{ij}$	8.9	Finstad et al. (2000)
S. salar	Parasitic	τ_{ij}	[6.9, 14.7]	Tucker et al. (2000a)
S. salar	Parasitic	τ_{ij}	6.5, 11	Tucker et al. (2000b)

were collected at different time intervals thereafter (Table 2). In most of these experiments, the data (Y_{ijk}) contained information on the minimum developmental times of stage *i* and sex *j* in experiment *k* (τ_{ijk}) in form of a time range, $Y_{ijk} = (c_{lijk}, c_{uijk})$ where τ_{ijk} was known to be within (c_{lijk}, c_{uijk}) with $c_{lijk} < c_{uijk}$ (interval censoring). However, for some experiments, it was only known that no lice had developed to stage *i* at the termination of the experiment (right censoring) giving $c_{uijk} = \infty$.

Four studies contained enough information for a more detailed analysis of the population dynamics of *Lepeophtheirus salmonis* on the host, giving estimates of most of the demographic parameters in the basic model (Eq. 5). In these experiments (Grimnes & Jakobsen 1996, Bjørn & Finstad 1998, Finstad et al. 2000, Trial 3 in Tucker et al. 2002), a group of fish were infected simultaneously by *L. salmonis* copepodids and sampled at different time intervals thereafter. The number of individuals of the different stages of *L. salmonis* were then counted from the sampled hosts. In most studies, the individual host fish were sampled destructively, so only 1 estimate was available of the salmon lice burden and demography on any individual fish. The study by Tucker et al. (2002) differed from this approach, in that the same 10 fish were repeatedly sampled over the course of the experiment. In both the study by Grimnes & Jakobsen (1996) and Bjørn & Finstad (1998), some parasite-induced host mortality occurred. The data from Bjørn & Finstad (1998) were obtained from the authors, while the others were extracted from their published tables and figures.

Dawson et al. (1997) also had a high frequency of sampling events, but the basic model (Eq. 5) could not reproduce some of the main patterns in the data. We suspect substantial fluctuations in water temperature may have occurred during the course of that experiment, and detailed temperature information would be needed to model the data well.

Modelling minimum development times (τ_{ij}) in relation to water temperature. For the relationship between average minimum development times ($\bar{\tau}$) and water temperature (*T*, measured in °C), we chose what has been called Belehrádek's function (Belehrádek 1935), which is commonly used in models of copepod development (Aksnes et al. 1997):

$$\bar{\tau}(T) = \alpha_1(T + \alpha_2)^{\alpha_3} \tag{7}$$

where α_1, α_2 and α_3 are parameters to be estimated from data. When analysing the censored data on the minimum developmental times of parasitic stages, a high correlation between the parameters caused problems in the estimation procedure. To overcome this problem, we simplified the model by assuming $\alpha_3 = -2$, centered the temperature variable around 10°C and reparameterised the model setting $\beta_1 = \sqrt{\alpha_1}$ and $\beta_2 = \alpha_2/\beta_1$, giving:

$$\bar{\tau}(T) = [\beta_1/(T - 10 + \beta_1 \beta_2)]^2 \tag{8}$$

With this parameterisation, β_2^{-2} is the average τ at 10°C, while β_1 is a shape parameter.

For the minimum development time of eggs (τ_E) and the pre-infective stage (τ_{Pl}), this model (Eq. 8) was fitted by minimising the squared residual error. For the censored data on the minimum development time of

the parasitic stages, we modelled the relationship between τ_{ijk} and water temperature (T_k) using Bayesian Markov chain Monte Carlo methods implemented in the program WINBUGS 1.4 (Spiegelhalter et al. 2003, Gómez et al. 2004), assuming a truncated lognormal distribution for the unobserved τ_{ijk}:

$\log(\tau_{ijk}) \sim N[\log(\bar{\tau}_{ij}(T_k), \sigma^2)]$ truncated in the interval $[\log(c_{l_{ijk}}), \log(c_{u_{ijk}})]$ (9)

where $\bar{\tau}_{ij}(T_k)$ is given by Eq. (8). We fitted the model using non-informative prior distributions for the parameters: $\beta_1 \sim$ gamma(0.001, 0.001), $\beta_2 \sim$ N(0.0, 1/0.0001), $1/\sigma^2 \sim$ gamma(0.001, 0.001).

Detailed statistical modelling of the population dynamics of parasitic stages. The detailed statistical modelling of the population dynamics of parasitic stages was performed by fitting the basic model for the parasitic stages (Eq. 5) to the available data. Since the sex of chalimi was not determined, the vector of observed frequencies for a given sampling unit had length 5, $\mathbf{n}_k = [n_{CH.k}, n_{PAfk}, n_{PAmk}, n_{Afk}, n_{Amk}]$. In addition, we included the estimated number of dead animals $n_{dead}(t_k) = N_{CH.k}(0) - \sum_{ij} n_{ijk}$ in $\mathbf{n}_k$. The data did not allow evaluation of sex differences in chalimus mortality, so it was assumed that $\mu_{CHf} = \mu_{CHm} = \mu_{CH.}$. For the data from Grimnes & Jakobsen (1996), Bjørn & Finstad (1998) and Finstad et al. (2000), the analytical solution to the model (Eq. 6) was fitted to the data by assuming:

$$\mathbf{n}_k \sim \text{multinomial}\ [\boldsymbol{\pi}(\boldsymbol{t_k}), N_{CH.k}(0)] \qquad (10)$$

where the vector of expected proportions of the initial population at stage i and sex j at time t_k is $\boldsymbol{\pi}(\boldsymbol{t_k}) = [N_{CHf}(t_k) + N_{CHm}(t_k), N_{PAf}(t_k), N_{PAm}(t_k), N_{Af}(t_k), N_{Am}(t_k), N_{dead}(t_k)]/N_{CH.}(0)$, and $N_{CH.k}(0)$ is the chalimus population size of sampling unit k at the onset of the experiment. Due to restrictions in the use of the multinomial distribution in WinBUGS, the likelihood was implemented as a sequence of conditional univariate binomial distributions (McCullagh & Nelder 1989).

A complication in the analysis of these studies was that the population size of sample unit k at the onset of the experiment, $N_{CH.k}(0)$, was unknown, and had to be replaced by its estimated value $\hat{N}_{CH.k}(0)$. As the distribution of lice was over-dispersed with respect to a pure Poisson distribution in all studies, we assumed that all sampling units consisted of infected fish drawn from a population with a negative binomial distribution for $N_{CH.k}(0)$. The negative binomial distribution of $N_{CH.k}(0)$ was assumed to be the result of a Poisson process with rate parameter λ, with λ having a gamma distribution in the population of fishes. For Bjørn & Finstad (1998), we had the lice data for each individual fish sampled, while from Grimnes & Jakob-

sen (1996) and Finstad et al. (2000), the total number of lice in each sex-stage class collected on all fish sampled at a given time were available. The information on the number of fish sampled was included in the model for λ by noting that for the gamma distribution with parameters a and b

$$\left(\text{gamma}(a,b) = \frac{a^b t^{b-1} e^{-at}}{\Gamma(b)} \right),$$

$$\sum_1^m \text{gamma}(a,b) = \text{gamma}(am,b)$$

giving the following model for $\hat{N}_{CH.k}(0)$:

$$\hat{N}_{CH.k}(0) \sim \text{Poisson}(\lambda_k) \qquad (11)$$

$$\lambda_k \sim \text{gamma}(am_k, b) \qquad (12)$$

where m_k is the number of infected fish included in sample unit k. For the analysis, we centered the time variable around the time of the first sample event (t_0) using $t =$ time since infection $- t_0$. For the studies by Grimnes & Jakobsen (1996) and Finstad et al. (2000), we estimated the shape and rate parameters of the gamma distribution from the mean $(\bar{N}_{CH.}(0))$ and variance in infection intensities at the first sample event, $b = \bar{N}_{CH.}(0)/[\text{var}(N_{CH.}(0)) - \bar{N}_{CH.}(0)]$ and $a = b\ \bar{N}_{CH.}(0)$. The estimates were $a = 2.759$ and $b = 0.03245$ for Grimnes & Jakobsen (1996), and $a = 5.12$ and $b = 0.142$ for Finstad et al. (2000). For the study by Bjørn & Finstad (1998), a and b were estimated with the other parameters of the model, giving the point estimates $a = 9.177$ and $b = 0.09445$. The model was implemented in WinBUGS 1.4 (Lunn et al. 2000) and fitted using Bayesian Markov chain Monte Carlo methods assuming non-informative uniform (U) prior distributions for the parameters with $\mu_{CH.} \sim$ U(0.0005, 1) and for other stage–sex combinations $\mu_{ij} \sim$ U(0.001, 1), $\upsilon_{ij} \sim$ U(0.003, 3), $\tau_{ij} \sim$ U($c_{l_{ij}}, c_{u_{ij}}$) and $p_f \sim$ U(0, 1). For the analysis of the data from Bjørn & Finstad (1998), the prior distributions for a and b were $a \sim$ gamma(0.01, 0.01) and $b \sim$ gamma(0.01, 0.01).

The models implemented in WinBUGS 1.4 (Eqs. 9 & 10) were fitted using burn in periods of 5000 iterations followed by sampling from the posterior distributions of the parameters over the subsequent 15 000 iterations. Convergence was assessed in WinBUGS using the Gelman-Rubin convergence statistic, as modified by Brooks & Gelman (1998). Parameter estimates from these analyses were summarised by their median values, 95% credible sets with limits defined by the 2.5% percentiles of their posterior distributions, and standard errors estimated from their posterior distributions (SE).

Inspection of the data from Trial 3 in Tucker et al. (2002) made it clear that the observed variance was due to the stochastic nature of the development and the survival processes, and also measurement error,
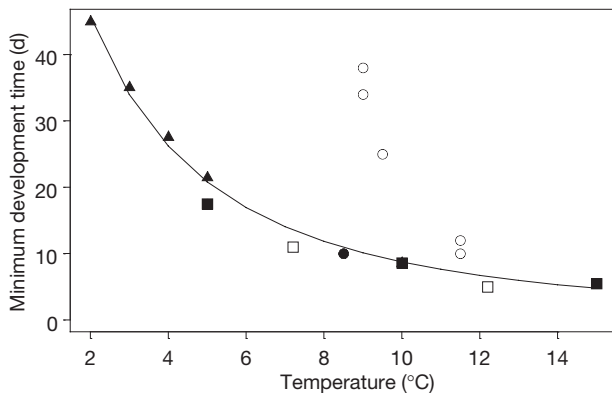
Fig. 2. *Lepeophtheirus salmonis*. Minimum egg-development times to hatching at different water temperatures as estimated by Johnson & Albright (1991a, ■), Boxaspen & Næss (2000, ▲), and Tucker et al. (2002, ●). The best fit regression line for the average time to stage, $\overline{\tau}_E = [\beta_1/(T - 10 + \beta_1\beta_2)]^2$, for these data is drawn using the parameter estimates given in Table 3. Also shown are the egg development times to hatching estimated by Johannessen (1978, ○), and egg string replacement times estimated by Heuch et al. (2000, □)
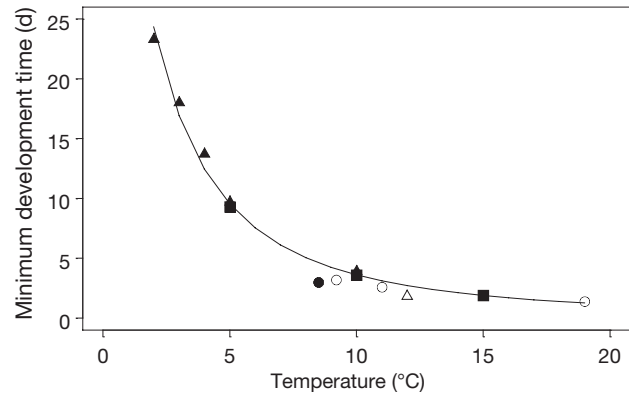

Fig. 3. *Lepeophtheirus salmonis*. Minimum development time from egg hatching to the infectious copepodid stage at different temperatures as estimated by Johannessen (1978, ○), Wootten et al. (1982, △), Johnson & Albright (1991a, ■), Boxaspen & Næss (2000, ▲) and Tucker et al. (2002, ●). The regression line for the average time to stage, $\overline{\tau}_{PI} = [\beta_1/(T - 10 + \beta_1\beta_2)]^2$, is drawn using the parameter estimates given in Table 3

because in some samples $\sum_{ij} n_{ij}(t_k) < \sum_{ij} n_{ij}(t_l)$ for $t_i < t_l$. To simplify model fitting, we ignored process error and fitted the model (Eq. 5) directly to the data from Day 8 to 74 assuming:

$$n_{ijk} \sim \text{Poisson}[N_{ij}(t_k)] \tag{13}$$

The model (Eq. 5) did not fit the data well, in that some extra mortality seemed to occur at the transition from the chalimus to the pre-adult stage, and the exponential distribution was a poor approximation for female development times to the pre-adult stage. To accommodate this, we assumed that only a proportion q_j of the lice survived the transition:

$$\frac{dN_{PAj}}{dt} = \begin{cases} 0, t < \tau_{CHj} \\ \upsilon_{CHj} q_j N_{CHj} - \mu_{PAj} N_{PAj}, \tau_{CHj} \leq t < \tau_{PAj} \\ \upsilon_{CHj} q_j N_{CHj} - (\mu_{PAj} + \upsilon_{PAj}) N_{PAj}, t \geq \tau_{PAj} \end{cases} \tag{14}$$

and we assumed $p_j = 0.5$, since p_j and q_j were confounded. For the distribution of female developmental times, we used a log-linear approximation: $\log(\upsilon_{CHf}(t)) = \beta_3 + \beta_4(t - \tau_{CHf})$, where β_3 and β_4 were parameters estimated by data. The model was solved numerically using the 4th order Runga-Kutta-Fehlberg method with 5th order error estimate as implemented in the GNU Scientific Library version 1.4 (Galassi et al. 2003), and fitted using the nlm function in R 1.8.1 (Anonymous 2003). Standard errors (SE) of parameter estimates were estimated as the square root of the diagonal of the inverse of the Hessian matrix, and 95% confidence limits were estimated as ±2 SE.

RESULTS

Egg and planktonic stages

Development

The minimum times needed for development at the egg (τ_E) and pre-infective stages (τ_{PI}) were strongly affected by water temperature (Figs. 2 & 3, Table 3). The estimates of Johnson & Albright (1991a) and Boxaspen & Næss (2000) of the minimum development times of eggs showed good agreement with the estimates of Heuch et al. (2000), regarding the egg string replacement period in females when the egg string was removed after extrusion (Fig. 2), suggesting that female salmon lice need approximately the same time to replace egg strings as for the embryos to develop to nauplii. Johannessen's (1978) estimates of minimum development times for eggs (Fig. 2) differed considerably from the others and were excluded from the analysis.

Johnson & Albright (1991a) found that from first to last hatching in a set of egg strings, took 18 to 65 h at 10°C. Boxaspen & Næss (2000) reported a similar range of within-egg–string hatching times, but with a wider range observed for eggs incubated in darkness than eggs incubated in light. A crude estimate of the development rate after the initial minimum development time, based on these observations and assuming that the probability of development is 0.995 in 2.7 d, would be $\upsilon_E = -\log(0.005)/2.7 = 2.0$ ind.$^{-1}$ d^{-1}. For development from the nauplii to the copepodid stage,

Table 3. *Lepeophtheirus salmonis.* Estimates of the parameters β_1 and β_2 ($\pm$SE) in the models for the relationship between water temperature (T) and average minimum development time $\overline{\tau}_{ij} = [\beta_1/(T-10 + \beta_1\beta_2)]^2$ of the stage. Estimates are given for the minimum development time of eggs $\overline{\tau}_E$, Fig. 2), pre-infective larvae ($\overline{\tau}_{PI}$, Fig. 3), males and females at the chalimus stage ($\overline{\tau}_{CHm}$ and $\overline{\tau}_{CHf}$, Fig. 5) and the period from infection to appearance of adult male and female lice ($\overline{\tau}_{PAm}$ and $\overline{\tau}_{PAf}$, Fig. 5)

Development time	β_1	β_2
$\overline{\tau}_E$	41.98 ($\pm$ 2.85)	0.338 ($\pm$ 0.012)
$\overline{\tau}_{PI}$	24.79 ($\pm$ 1.43)	0.525 ($\pm$ 0.017)
$\overline{\tau}_{CHm}$	74.70 ($\pm$ 33.64)	0.255 ($\pm$ 0.007)
$\overline{\tau}_{CHf}$	74.70 ($\pm$ 33.64)	0.246 ($\pm$ 0.007)
$\overline{\tau}_{PAm}$	67.47 ($\pm$ 20.36)	0.197 ($\pm$ 0.006)
$\overline{\tau}_{PAf}$	67.47 ($\pm$20.36)	0.177 ($\pm$ 0.006)

we found no information that allowed us to estimate the distribution of development times after the initial minimum development time.

Mortality

The proportion of active nauplii that survive to develop to active copepodids has been reported to be $\approx 50\%$ at 10°C and 30‰ salinity (Johnson & Albright 1991a). Given a residence time at the pre-infective stage of about 4 d at 10°C, this suggests a mortality rate of $\mu_{PI} = -\log(0.5)/4 = 0.17$ ind.$^{-1}$ d^{-1}. It is not known how this parameter depends on temperature. Boxaspen & Næss (2000) reported that few hatched eggs developed to the copepodid stage at 2 and 3°C. This is consistent with a constant mortality rate of 0.17 ind.$^{-1}$ d^{-1} due to the long development time needed at low temperatures (Fig. 3). Johnson & Albright (1991a) also estimated the geometric mean survival time of the infective copepodid stage at 5, 10 and 15°C. They found no clear trend in survival with increasing temperature at 30‰ salinity, and an overall mean survival time of 4.6 d. Assuming a constant mortality rate with age, this suggests a mortality rate of $\mu_I = 1/4.6 = 0.22$ ind.$^{-1}$ d^{-1}.

Parasitic stages

Development

The minimum times needed for development to the pre-adult and adult stages were also strongly affected by water temperature (Fig. 4). For both τ_{CH} and τ_{PA}, there was no evidence to suggest a sex difference in the shape parameter β_1 (p > 0.1). However, males developed faster than females to the adult stage and
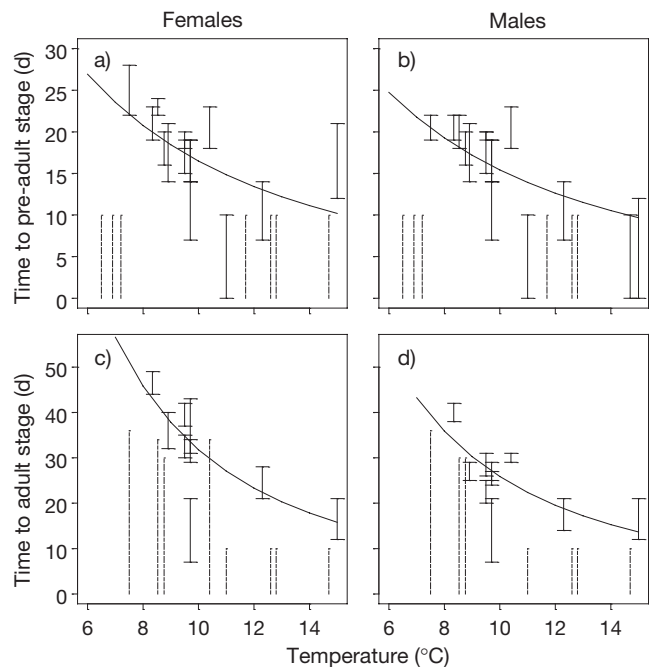

Fig. 4. *Lepeophtheirus salmonis.* Time from infection to the presence of (a,c) female and (b,d) male lice at the pre-adult (a,b) and adult stages (c,d). The time range within which individuals entered the stage is shown as bars. For studies where no individuals had entered the stage at the termination of the study, the study periods are shown as vertical dotted lines. The regression lines for the average time to stage, $\overline{\tau}_{ij} = [\beta_1/(T - 10 + \beta_1\beta_2)]^2$, are drawn using the parameter estimates given in Table 3

also showed a tendency to develop faster to the pre-adult stage, as reflected in a higher estimated value of β_2 (Table 3). The experiments carried out at average temperatures of 11°C by Tucker et al. (2000b) and 9.7°C by Dawson et al. (1997), were outliers in the analysis, showing faster development than in the other experiments. The study of Grimnes & Jakobsen (1996) at 10.4°C showed slightly slower development. However, excluding these data from the analysis had negligible effects on parameter estimates. It should be noted that no studies have investigated the development times of the parasitic stages at temperatures <7°C over a suitable time period.

For the distribution of development times after the initial minimum development time, we found that an exponential distribution fitted the data of Grimnes & Jakobsen (1996), Bjørn & Finstad (1998) and Finstad et al. (2000) reasonably well (Fig. 4). However, the relatively low sampling frequency in these studies gives low power for detecting deviations from the assumption of an exponential distribution. The estimates suggest relatively fast development after the initial minimum development times, both for development from the chalimus to the pre-adult stage (range of estimates

Table 4. *Lepeophtheirus salmonis*. Parameter estimates for demographic rates (with 95% CI in brackets) obtained by fitting Eq. (5) to the data from Grimnes & Jakobsen (1996, G&J), Bjørn & Finstad (1998, B&F), Finstad et al. (2000, Finstad) and Trial 3 in Tucker et al. (2002, Tucker). Average water temperatures in the experiments are given in the column heading. In Grimnes & Jakobsen (1996), no adult female lice had appeared at the end of the experiment, so associated parameters could not be estimated. In the analysis of Tucker et al. (2002), p_f was fixed to 0.5, and a log-linear model for υ_{CHf} was used (see text)

Parameter	G&J (10.4°C)	B&F (9.7°C)	Finstad (8.9°C)	Tucker (8.3°C)
$\mu_{CH.}$	0.005 (0.0008, 0.017)	0.008 (0.003, 0.020)	0.002 (0.0006, 0.0087)	0.01 (0.007, 0.017)
μ_{PAf}	0.047 (0.011, 0.074)	0.035 (0.020, 0.047)	0.074 (0.044, 0.102)	0.056 (0.047, 0.066)
μ_{PAm}	0.047 (0.015, 0.078)	0.048 (0.027, 0.074)	0.018 (0.002, 0.045)	0.18 (0.16, 0.21)
μ_{Af}	–	0.035 (0.003, 0.096)	0.38 (0.06, 0.70)	0.019 (0.011, 0.034)
μ_{Am}	0.10 (0.009, 0.26)	0.029 (0.008, 0.052)	0.16 (0.11, 0.22)	0.059 (0.043, 0.080)
υ_{CHf}	0.82 (0.73, 0.91)[a]	0.89 (0.75, 1.09)[a]	0.67 (0.59, 0.77)[a]	–
υ_{CHm}	0.82 (0.73, 0.91)[a]	0.89 (0.75, 1.09)[a]	0.67 (0.59, 0.77)[a]	0.27 (0.25, 0.29)
υ_{PAf}	–	0.34 (0.30, 0.40)	0.33 (0.27, 0.39)[a]	0.24 (0.19, 0.30)
υ_{PAm}	0.64 (0.49, 0.83)	0.80 (0.69, 0.90)	0.33 (0.27, 0.39)[a]	0.39 (0.23, 0.66)
τ_{CHf}	10.85 (10.22, 11.26)	10.64 (10.18, 10.98)	13.91 (13.86, 13.95)	23.0 (21.3, 24.9)
τ_{CHm}	10.00 (8.59, 10.7)	9.24 (7.34, 10.18)	11.6 (9.6, 12.4)	21.8 (21.6, 21.9)
τ_{PAf}	–	24.97 (24.90, 25.00)	29.5 (27.3, 31.0)	45.8 (45.0, 46.6)
τ_{PAm}	19.76 (19.65, 19.84)	19.84 (19.59, 19.95)	21.94 (21.86, 21.98)	40.5 (39.9, 41.0)
p_f	0.46 (0.43, 0.49)	0.48 (0.43, 0.52)	0.52 (0.45, 0.59)	–

[a]Male and female parameters were constrained to the same value

for $\upsilon_{CH.}$ = [0.67, 0.89], Table 4), and from the pre-adult to adult stage (range of estimates for $\upsilon_{PA.}$ = [0.33, 0.80], Table 4). The most frequent sampling of the parasitic stages of *Lepeophtheirus salmonis* (every 2 to 3 d) was reported in Tucker et al. (2002). For their study, we also found that an exponential distribution was a reasonable approximation for most stage transitions (Fig. 4d), with the exception of female development from the chalimus to the pre-adult stage (test for change over time: χ^2 = 28.07, df = 1, p < 0.0001). Female chalimi showed low development rates initially [$\upsilon_{CHf}(t = \tau_{CHf})$ = 0.03] increasing by a factor of 1.8 per day as time progressed after the minimum development time [$\log(\upsilon_{CHf}(t)) = -3.469 + 0.607(t - \tau_{CHf})$]. This model gives an average development time in addition to the minimum development time of 4.2 d for female chalami, an estimate only slightly higher than that for males (υ_{CHm}^{-1} = 3.7 d). For υ_{CHm}, υ_{PAm} and υ_{PAf}, the estimates from the analysis of Tucker et al. (2002) were generally lower than the estimates obtained from the other studies (Table 4). This may be due to the lower average water temperature in their study.

Mortality

The estimated mortality rate at the chalimus stage ($\mu_{CH.}$) was low in all the experiments analysed (range of estimates for $\mu_{CH.}$ = [0.002, 0.01], Table 4). However, in the experiment by Tucker et al. (2002), the data suggested additional mortality in that only a proportion q_j survived the developmental transition from the chalimus to the pre-adult stage (q_f = 0.44, 95% CI = [0.38,

0.51], q_m = 0.79, 95% CI = [0.65, 0.90]). This additional mortality may have been caused by the frequent handling and anaesthesia of fish and salmon lice infrapopulations.

The estimates of pre-adult female mortality rates were similar, around 0.05 ind.$^{-1}$ d^{-1}, across all 4 experiments (Table 4). Among pre-adult males, the estimated mortality rate was much higher in the experiment by Tucker et al. (2002) (μ_{PAm} = 0.18 ind.$^{-1}$ d^{-1}) compared to the other experiments (range of estimates for μ_{PAm} = [0.018, 0.048], Table 4).

Only the experiment by Tucker et al. (2002) contained enough measurements of adult abundances to give reasonable estimates of both adult male (μ_{Am} = 0.06 ind.$^{-1}$ d^{-1}) and female (μ_{Af} = 0.02 ind.$^{-1}$ d^{-1}) mortality rates (Fig. 5, Table 4). In addition, data allowed the adult male mortality rate (μ_{Am} = 0.03 ind.$^{-1}$ d^{-1}, Table 4) to be estimated reasonably well in the study of Bjørn & Finstad (1998).

Female fecundity

The fecundity of salmon lice can be defined as a function of the rate of egg string production, the number of eggs per string, and the proportion of these eggs that are viable. As noted above, the estimates by Heuch et al. (2000) suggest that the time it takes for an adult female louse to develop a new pair of egg strings is very similar to the time from egg string extrusion to egg hatching (Fig. 2). This supports the finding by Johannessen (1978) that females can extrude a new set of egg strings within 24 h after a set has hatched.

Heuch et al. (2000) also found that the number of eggs per string increased from, on average, 152 eggs per string in the first set of egg strings to 290 eggs per string in the second and later egg strings produced by a female. A similar increase in egg numbers with string number was found by Ritchie (1993) (in Pike & Wadsworth 2000). However, the average number of eggs per string was lower in his study, in which an increase from about 70 eggs per string to 150 eggs per string from the first to the fifth egg string was recorded. Water temperature (8.7 versus 12.2°C) was not found to have a significant effect on the number of eggs per string by Heuch et al. (2000). In addition, by visual inspection, Heuch et al. (2000) classified 7.5% of the eggs at 12.2°C and 10% of the eggs at 7.2°C as non-viable, suggesting little effect of temperature on hatching success. In comparison, Ritchie (1993) (in Pike & Wadsworth 2000) found 50% of the eggs in a female's first pair of egg strings and 30% in its second pair of egg strings to be non-viable at 14°C, with low frequencies of non-viable eggs thereafter, suggesting an age effect. A low frequency of viable eggs was also found at 10°C by Johnson & Albright (1991a) with, on average, 66 and 55% of the eggs in 2 different experimental set-ups developing into active nauplii.

DISCUSSION

We have suggested a set of models suitable for integrating the available experimental information relevant to the demographic rates of the functional stages of salmon lice. The models fit the experimental data well and particularly good estimates were obtained for the relationship between the minimum development times of the stages and water temperature (Figs. 2, 3 & 4). These are the best available estimates for these demographic processes and are, therefore, essential building blocks in the development of models for the population dynamics of salmon lice in the natural environment. However, our review also points out population processes that, at present, are poorly understood, and thereby suggest topics that should be given high priority in future studies of salmon lice.

Sea water temperatures off the south coast of Norway have been reported to vary seasonally from 1.5 to 19°C (Schram et al. 1998). Along other coasts of the Atlantic ocean, water temperatures seem to be generally within this range but with lower temperatures in the summer further north in Norway (seasonal temperature range: 2 to 13°C, Rikardsen 2004) and along the North-East Atlantic coast (seasonal temperature range: 2 to 14°C, Hogans & Trudeau 1989), and higher winter temperatures on the west coast of Scotland and Ireland (seasonal temperature range: 5 to 16°C, Tully 1992, Ritchie et al. 1993, Heuch et al. 2003). The minimum development times of both eggs (τ_E) and pre-infective planktonic larval stages (τ_{PI}) are well described over the whole of this ecologically relevant temperature range using the Belehrádek function, while models suggested previously (Tully 1992, Boxaspen & Næss 2000) poorly fit observations at high water temperatures ($T > 12$°C). A weakness in the current knowledge of the minimum development times of the parasitic stages is the lack of studies at low temperatures ($T < 7$°C). Some detailed studies at high water temperatures ($T > 15$°C) would also be needed to cover the whole temperature range in the sea.
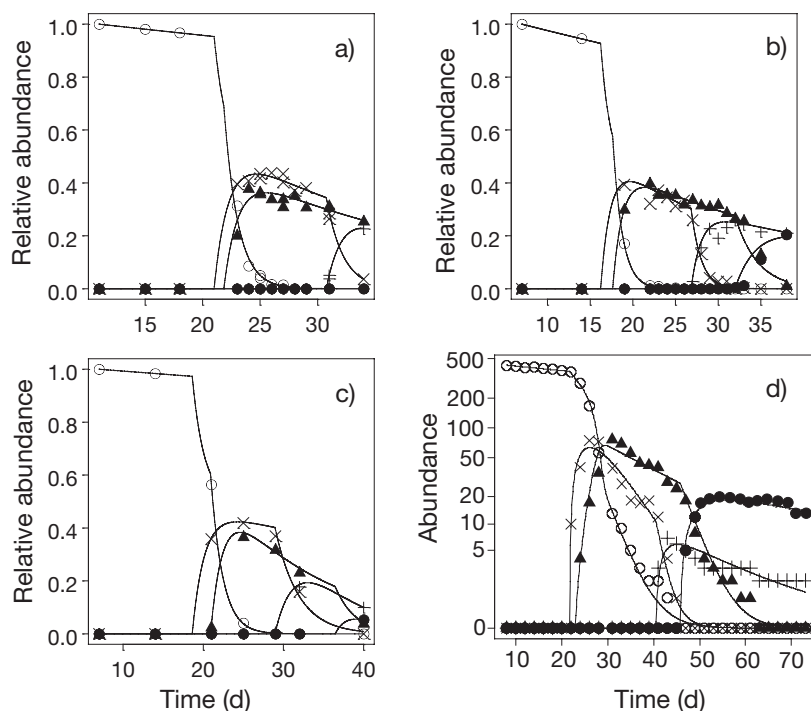

Fig. 5. *Lepeophtheirus salmonis*. Stage structure in salmon lice populations against time since infection in the experiments of (a) Grimnes & Jakobsen (1996), (b) Bjørn & Finstad (1998), (c) Finstad et al. (2000) and (d) Trial 3 of Tucker et al. (2002). In a–c, the abundance relative to the estimated abundance at the first sample event ($n_{ijk}/N_{CH.k}[0]$) has been plotted, since the study design gave a highly variable abundance of infection at different sampling events. Symbols used: ○: chalimus larvae; ×: pre-adult males; ▲: pre-adult females, +: adult males; ●: adult females. The lines give predicted abundances using estimated parameter values (Table 4) in Eq. (5)

Little information is currently available to evaluate the effect of water temperature on mortality rates (μ) and development rates after the initial minimum development times (υ). Studies of other invertebrates suggest that both μ and υ could be expected to show a positive relationship with temperature (e.g. Smith et al. 1986, Hirst & Kiørboe 2002). However, at least for the mortality rate of the infective stage, there was no evidence of a positive effect of temperature (Johnson & Albright 1991a). In Table 5, we have summarised what the experimental studies suggest as plausible values for mortality and development rates. These estimates suggest rapid development after the initial minimum development time, with average development times ($υ^{-1}$) in the range of 1.1 to 4.2 d at the parasitic stages. The temperature range used in the experiments is rather limited, but the narrow range of these average developmental times suggest that population dynamic model, which assume a constant, temperature-independent development rate, will give reasonable predictions. The main patterns in the estimates of mortality rates were a consistently lower mortality rate at the chalimus stage than at the pre-adult and adult stages, and high mortality rates at the planktonic pre-infective and infective stages. Detailed laboratory experiments over a wide range of water temperatures would be needed to properly characterise variability in distributions of development times. Survival is, in comparison, more likely to be seriously affected by laboratory conditions (e.g. Pike & Wadsworth 2000). Time series analyses of stage-frequency data from natural populations (Wood 1994, Manly 1997) may, therefore, be the preferred approach in future studies of mortality rates of the parasitic stages. Field studies of the planktonic pre-infective and infective stages are difficult to design, so laboratory experiments may be the only option for detecting relevant abiotic factors with respect to their mortality. For these planktonic stages,

Table 5. *Lepeophtheirus salmonis*. Plausible estimates of the mortality (μ) and development rates (υ) of the different stages based on experimental studies

Stage-sex combination	μ	υ
Eggs (*E*)		2.0
Pre-infective larvae (*PI*)	0.17	–
Infective larvae (*I*)	0.22	
Chalimus males (*CHm*)	0.002–0.01	0.27–0.89
Chalimus females (*CHf*)	0.002–0.01	0.24–0.89[a]
Pre-adult males (*PAm*)	0.02–0.18	0.30–0.80
Pre-adult females (*PAf*)	0.03–0.07	0.24–0.34
Adult males (*Am*)	0.03–0.06	
Adult females (*Af*)	0.02–0.04	

[a]An exponential distribution of development times was not supported in the study of Tucker et al. (2002)

a positive age effect on mortality could also be expected, since they are non-feeding, and nutrient reserves may become depleted at high ages. In support of age effects on the viability of the infective stage, Tucker et al. (2000b) found reduced infectivity in 7 d old copepodids when compared to younger copepodids. They also showed that increasing water temperature causes increased copepodid infectivity (Tucker et al. 2000a,b), suggesting positive effects of increasing water temperature on *Lepeophtheirus salmonis* transmission both through decreased development times and increased copepodid infection success.

Female salmon lice seem to use approximately the same time period to develop a new set of egg strings as a set of egg strings need to hatch, and produce fewer eggs in their first set of egg strings than in the later ones (Heuch et al. 2000, Ritchie 1993 in Pike & Wadsworth 2000). This age dependence in fecundity has also been found for other parasitic copepods (de Meeüs et al. 1993). In the experiment by Ritchie (1993) (in Pike & Wadsworth 2000), the average number of eggs per egg string was approximately half that found in the study by Heuch et al. (2000). It is not clear why these studies differ so much in the number of eggs produced per string. Field studies have suggested that water temperature during female development and egg production may explain some of this variation (Tully 1989, Ritchie et al. 1993, Tully & Whelan 1993), since low temperatures give rise to larger adult female salmon lice (Tully & Whelan 1993, Nordhagen et al. 2000) with a higher number of eggs per string (Tully & Whelan 1993). However, water temperature did not have a statistically significant effect on the number of eggs per string in the experiments by Heuch et al. (2000). Female salmon lice on farmed salmon have also been found to have a lower number of eggs per string than females on wild salmon (Jackson & Minchin 1992, Tully & Whelan 1993). Nordhagen et al. (2000) suggested that a size and fecundity difference could be due to wild salmon feeding on oceanic feeding grounds with lower temperature, whereas farmed salmon are bred in warmer coastal waters. When raised at the same temperature, the progeny from lice from both wild and farmed salmon attained the same size, thus indicating phenotypic plasticity rather than genetic control of egg numbers (Nordhagen et al. 2000). The lack of genetic structure in *Lepeophtheirus salmonis* populations sampled across the North Atlantic Ocean (Todd et al. 2004) supports this conclusion. Experimental studies also show great variability in the hatching success of eggs (Johnson & Albright 1991a, Heuch et al. 2000, Ritchie 1993 in Pike & Wadsworth 2000). Low hatching success may be due to poor water quality in some of these experiments. Overall, factors affecting female fecundity seem to be

poorly understood at present, with a level of unexplained variability in both average egg numbers per string and egg viability that suggests that further investigations are needed. Factors of potential importance are water temperature during female and egg development, female age, infection intensities and host size, sex and age (Johnson 1993).

Several potentially important factors in the population dynamics of salmon lice have been poorly investigated to date. Studies of density-dependent processes at the parasitic stages are particularly needed. Such processes could operate both within and between stages, and may have significant effects on both survival and fecundity. Heavy lice infections may kill a smolt and hence its lice (Bjørn et al. 2001), and the chalimus stages may strip the dorsal fin of skin and thus remove the food supply and attachment possibilities. Acquired immunity following infection with parasitic copepods has also been reported (Woo & Shariff 1990), but not at present for the salmon lice–salmonids interaction. Repeated observations of the demography of salmon lice populations on individual fish will be needed to study such processes. Previous studies have also suggested that salinity and photoperiod may be of importance. The egg and planktonic stages are likely to be more vulnerable to low salinities than the parasitic stages, as the latter may use ingested substances from the host to maintain osmotic pressure (Hahnenkamp & Fyhn 1985). For the planktonic infective stage, salinities <20‰ reduce survival (Johnson & Albright 1991a) and also cause behavioural avoidance (Heuch 1995). Boxaspen & Næss (2000) also showed that eggs develop faster in 24 h of daylight than in total darkness. However, the small effects detected suggest no significant effects on the overall population dynamics of the salmon lice. Furthermore, Ritchie et al. (1993) found no relationship between photoperiod and the numbers of eggs per egg string on farmed Atlantic salmon.

Even though the experimental studies have shown a strong effect of temperature on the development times of *Lepeophtheirus salmonis*, the effect of water temperature has not been very clear in many long-term epidemiological studies at salmon farms (Tully 1989, Revie et al. 2002, 2003). This is particularly true for studies from the coast of Scotland (Revie et al. 2002, 2003), where high abundances of salmon lice at the chalimus stage are found throughout the winter months (Heuch et al. 2003). In comparison, there is a clear drop in infection rates over the winter months along the coasts of Norway (Heuch et al. 2002, Rikardsen 2004) and the North-East Atlantic (Hogans & Trudeau 1989), a pattern which is also seen for wild sea trout (Heuch et al. 2003). The lack of a clear temperature signal in the extensive dataset from Scotland may

be partly due to the higher water temperature in winter, allowing high transmission rates throughout the year. In addition, the high frequency of salmon lice treatments used in Scottish fish farms (Heuch et al. 2003) may make the effect of treatments and temperature on transmission rates difficult to tease apart statistically. Alternatively, the generally higher water temperature in Scottish waters may cause processes that affect the survival of the planktonic stages (e.g. predation), or contact rates between the infective stage and farmed fish (e.g. weather and sea current systems), to be more important for transmission rates than the temperature-dependent development rates.

In free-living copepod species, the proportionate amount of time used at each stage is generally the same at all temperatures (equiproportional development; Hart 1990, Kiørboe & Sabatini 1995, Campbell et al. 2001). In our parameterisation of the Belehrádek function, equiproportional development would imply that the product $\beta_1\beta_2$ is constant across all stages and sexes. Using the estimates and standard errors given in Table 3, we found no evidence for any stage or sex deviating significantly from the overall average value of $\beta_1\beta_2$ (Fig. 6). This suggests that the pattern of equiproportional development also holds for *Lepeophtheirus salmonis*. Consistent with the general pattern for copepods (Hart 1990, Kiørboe & Sabatini 1995), our analysis also reproduces the fact that male lice develop to the adult stage more rapidly than females (e.g. Johnson & Albright 1991a).

This study has obtained good estimates of the minimum development times of the different functional stages of salmon lice using data from laboratory studies performed at fairly constant temperatures. However, to analyse the situation in natural populations, models have to allow for fluctuating temperatures. To obtain predictions for minimum development times
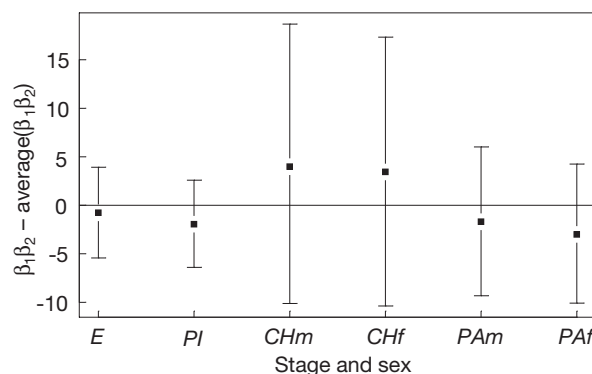

Fig. 6. *Lepeophtheirus salmonis*. Estimates with 95 % CI of the discrepancy between the stage and sex-specific estimates of the products $\beta_1\beta_2$ (see Table 3) and the overall average estimate of $\beta_1\beta_2$

under a fluctuating temperature regime, one commonly used approach is to assume that development within the stage occurrs at a rate $\tau_{ij}[T(t)]^{-1}$. This implies the assumption that previous development history has no effect on the current developmental rate within the stage. Individuals that enter the stage at time t_0 will then reach their minimum development time at the stage at time t_1 when $\int_{t_0}^{t_1} \tau_{ij}[T(x)]^{-1}\mathrm{d}x = 1$ (Smith et al. 1986, Gurney & Nisbet 1998). Using this approach, our estimates (Table 3) can be implemented in models for the population dynamics of *Lepeophtheirus salmonis* in farmed and wild host populations. It is our belief that such models will improve both our understanding of salmon lice population dynamics, our ability to evaluate different treatment stategies in fish farms, and allow better analyses of available longitudinal data on lice demography and abundances.

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