



Effect of temperature on development rate and egg production in *Caligus elongatus* and other sea louse species

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ABSTRACT: The sea louse *Caligus elongatus* (Siphonostomatoida, Caligidae) is a generalist ectoparasite commonly found on farmed salmonids in the Atlantic Ocean. Together with the salmon louse *Lepeophtheirus salmonis* and the Chilean sea louse *Caligus rogercresseyi*, they represent a major challenge to sustainable farming of Atlantic salmon *Salmo salar*. Here, the development rate, egg production, and copepodid survival time of *C. elongatus* are described at 6, 9, 12, and 15°C, and compared to available data for *L. salmonis* and *C. rogercresseyi* in a seminal attempt to qualitatively compare how these life-history traits and epidemiological factors vary among the 3 caligid sea louse species. A development model for *C. elongatus* was established by applying a constant scaling factor to the published model for *L. salmonis* and compared to the data obtained. The model assumes that caligid sea lice with similar zones of temperature tolerance share a common basic physiology, and that their rate of development is equally affected by changing temperatures within the interval where their temperature tolerances overlap. Present data, and data from the literature, suggest that *C. elongatus* develops to adult at approximately 63% of the time required by *L. salmonis* females and, compared to *L. salmonis*, they produce about 1/3 of the eggs per day over the temperature interval studied. This study represents a new experimental approach for establishing caligid development models and demonstrates how important life-history parameters can be scaled by constants and used as temperature-independent measures to characterize and compare the biology and epidemiology of sea lice species.

KEY WORDS: *Salmo salar* · Molt rate · Thermal tolerance · Reproduction · *Lepeophtheirus salmonis* · *Caligus rogercresseyi*

1. INTRODUCTION

The sea louse *Caligus elongatus* (Siphonostomatoida, Caligidae) is a generalist ectoparasite recorded from more than 80 fish species (Kabata 1979) and is considered to be one of the most common sea louse species in the North Atlantic (Kabata 1979, Jackson et al. 2000). Their first 3 developmental stages are planktonic and consist of 2 nauplius stages and the infective copepodid stage. On the host, they develop

through the parasitic phase of the copepodid stage and 4 chalimus stages before becoming adult. Parasitic development can take place on a range of hosts, and the fate of the adult after the final molt is determined by host size. Small fish species, or fry too small to sustain adult individuals, are used as intermediate hosts from which they detach after the final molt to adult. An example of this is the abundant presence of developing larvae, but absence of free-living adults on age-0 gadoids (Neilson et al. 1987). In this case, an

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additional pelagic host search phase is required for the adults to find a larger and more suitable sized host (Jackson et al. 2000, Maran et al. 2016). This is not required if the parasitic development takes place on fish large enough to sustain the adult lice. It is evident from reports on the presence of juvenile chalimus stages (Wootten et al. 1982, Treasurer & Wadsworth 2004) that Atlantic salmon *Salmo salar* can become infected via 2 infection routes: (1) settling of planktonic adults and (2) settling of copepodids that complete development to adults. Although *C. elongatus* is often present on Atlantic salmon in fish farms (Jackson et al. 2000, Revie et al. 2002), the salmon louse *Lepeophtheirus salmonis* represents the dominant problem for wild salmonid populations, and thus for salmon farmers, in the Atlantic (Forseth et al. 2017). However, in recent years, higher numbers of *C. elongatus* have been reported from fish farms in northern Norway (Imstrand et al. 2019a,b), and anecdotal reports of sudden epidemics of infections with adult *C. elongatus* on salmon in sea cages are numerous.

Although the infection success of *C. elongatus* copepodids in laboratory cultures and trials can be variable, *C. elongatus* most often infect the fish and develop to adults with a success rate similar to the salmonid specialist *L. salmonis* (L. A. Hamre pers. obs.). However, there are no published studies that have verified the development rate of *C. elongatus* on Atlantic salmon. One study has been conducted on the development rate of *C. elongatus* on a salmonid host (*Salvelinus alpinus*) at 10°C (Piasecki & MacKinnon 1995); however, little is known about whether the rate of development differs between host species and how the development rate changes within a wider temperature range. Studies describing the relationship between temperature and growth rate of caligids are not abundant. The development of *Lepeophtheirus hippoglossi* has been described for temperatures ranging from 7.5 to 13.1°C in Douglas (2001), and more comprehensive development models are available for *L. salmonis* over a wider temperature range (Stien et al. 2005, Hamre et al. 2019). Comparisons of the data available for *L. salmonis* and *L. hippoglossi* show that the development rates of the 2 species are similar and change with temperature in a near identical manner. While the models for *L. salmonis* demonstrate a significant reduction in the number of degree-days required for development with increasing temperature (Hamre et al. 2019), a development model for *Caligus rogercresseyi* (Gonzalez & Carvajal 2003) assumes that the number of degree-days required for development is independent of temperature, thus describing a slightly different relationship between growth rate and temperature.

All developmental phases in *L. salmonis* (embryonal, planktonic, and parasitic) appear to be equally affected by changes in temperature, suggesting that their duration can be expressed independent of temperature as constant fractions of the time required to become adult on the host. This way, all development events can be described in terms of relative age units (RAU), where 1 RAU% represents 1% of the development time to adult on the host fish (Hamre et al. 2019). A temperature-independent development pattern can thus be established, characterizing development events or phases with a set of constants, allowing for comparison of temperature-independent developmental characteristics among louse species. Furthermore, once characterized in terms of RAU, simple models for the duration of phases or the timing of developmental events can be established (Hamre et al. 2019).

It has been suggested that the metabolism of all organisms can be described by one equation and that the temperature dependence term in this equation is universal for all organisms (Gillooly et al. 2001, 2002). However, Clarke (2004) points out that this excludes the opportunity for organisms to either acclimate or evolutionary adapt to temperature regimes, and that the level of resting metabolism is not purely mechanistic, it is also governed by evolutionary trade-offs and adaptations. According to the temperature–size rule, ectotherms tend to develop quicker at higher temperatures while their size decreases. Zuo et al. (2012) explained this by a general model where the rate of biomass accumulation and the rate of development depend differently on temperature.

The present study aimed to establish and verify a model for embryonic, planktonic, and parasitic development of *C. elongatus* as a function of temperature, and to compare relative aspects of development and planktonic survival to *L. salmonis* and *C. rogercresseyi*. These sea lice are all members of the same family (Caligidae), and they share a common anatomy and lifestyle. While embryonic and planktonic phases are lecithotrophic, the stages attached to a host have constant and unlimited food resources at their disposal. Based on the fundamental principles related to temperature and rate of development described in Gillooly et al. (2001), but also the near-identical relationship between growth rate and temperature displayed by *L. hippoglossi* and *L. salmonis* (see Douglas 2001, Hamre et al. 2019), we tested whether a development model for *C. elongatus* can be established by scaling the *L. salmonis* development model by a constant. Additionally, we incorporated new data on egg string production, planktonic development, and planktonic

copepodid survival for *C. elongatus*. Development, egg production, and survival data obtained were then compared to published data for *C. elongatus*, *L. salmonis*, and *C. rogercresseyi* to further evaluate how to characterize and compare relationships between temperature and rates of physiological processes among caligids.

2. MATERIALS AND METHODS

A simple theoretical development model for *Caligus elongatus* was generated based on published development data for *C. elongatus* and the model for another well-studied caligid, *Lepeophtheirus salmonis*. This model was used to design a sampling regime evaluating planktonic and parasitic development across 4 temperatures to validate whether model predictions were correct. Embryonic development rate and fecundity were also measured across temperatures from a limited number of females. The same louse population was used for all datasets, i.e. females from the parasitic development trials provided egg strings to determine embryonic and planktonic measures. Because of the variable and low sample sizes among temperatures, statistical models were not applied to the data, and thus results are qualitatively reported and compared to available data published on *L. salmonis* and *Caligus rogercresseyi*. The body size of adults was measured when ~100% of the population had become adults.

Experiments were conducted in accordance with the Norwegian legislation for animal welfare at Matre Research Station of the Institute of Marine Research, Norway (ethics approval ID 23820).

2.1. Theoretical development model

A theoretical development model for *C. elongatus* was generated based on the *L. salmonis* development model presented in Hamre et al. (2019) and modified using data from Piasecki & MacKinnon (1995). Development of *L. salmonis* and *C. elongatus* at 10°C, as described in these 2 papers, is summarized in Table 1. *C. elongatus* becomes adult at 74% of the development time it takes *L. salmonis* females to become adult (26.8 vs. 36 d). Thus, this factor of 0.74 is hereafter termed the scaling factor and is assumed to be constant over the entire temperature range where their natural temperature tolerance overlaps. As with all caligids, *C. elongatus* develops through 5 parasitic stages before the adult stage, and where $rM(T)$ is the average daily population molt rate, the expression $5/rM(T)$ gives the number of days before the population is adult. For *L. salmonis*, $rM(T) = aT^2 + bT + c$, where T is temperature in °C and a , b and c are constants. For females, the constants are $a = 0.000485$, $b = 0.008667$, and $c = 0.003750$ (Hamre et al. 2019). The theoretical development time to adult at temperature T for *C. elongatus* is thus $0.74 \times (5/rM(T))$.

A development pattern for *C. elongatus* was derived from Piasecki & MacKinnon (1995) (Table 1). To do so, data from Piasecki & MacKinnon (1995) were extracted from their Fig. 2 using image analysis software (ImageJ, <https://imagej.nih.gov/ij/>). A high degree of asynchrony in their data made it difficult to define a precise development pattern, thus the development pattern in Table 1 represents our interpretation of the data. The age at which most of the population had become adults in their study was assumed to be 26.8 d.

Table 1. Development pattern of *Lepeophtheirus salmonis* and *Caligus elongatus* summarized from the literature. The *L. salmonis* development pattern is a slightly modified version (L. A. Hamre unpubl. data) of the pattern reported in Hamre et al. (2019). The *C. elongatus* pattern is derived from tables and graphs in Piasecki & MacKinnon (1995) showing the development of *C. elongatus* on arctic charr *Salvelinus alpinus*. The point where the majority of the population (>85%) had become adult was set by the last sampling point in Fig. 2F in Piasecki & MacKinnon (1995). Relative age is given as a fraction of time it takes before the majority of the population reaches the adult stage. First: first appearance of a stage; All: when the majority of lice in the cohort has reached a stage. The timing of developmental events at 10°C is also given. dpi: days post-infection; F: female; ch: chalimus; pa: preadult; ad: adult

Parameter	Species	First ch1	All ch1	First ch2	All ch2	First pa1/ch3	All pa1/ch3	First pa2/ch4	All pa2/ch4	First ad	50% ad	All ad
Relative age	<i>L. salmonis</i> (F)	0.13	0.16	0.29	0.36	0.48	0.56	0.66	0.76	0.87	0.94	1.00
	<i>C. elongatus</i>	0.11	0.27	0.27	0.47	0.41	0.58	0.61	0.81	0.81	0.92	1.00
dpi (10°C)	<i>L. salmonis</i> (F)	4.7	5.8	10.4	13.0	17.3	20.2	23.8	27.4	31.3	33.7	36.0
	<i>C. elongatus</i>	2.9	7.4	8.2	12.6	13.7	15.5	16.3	22.2	21.8	24.7	26.8

2.2. Infection trials

Atlantic salmon (farmed strain, Aquagen) from a single cohort were kept in 3 replicate tanks ($0.9 \times 0.9 \times 0.4$ m) at each of the temperatures 6, 9, 12, and 15°C, and acclimated for >14 d prior to infection. Each tank contained 10 fish (mean weight at sampling \pm SE: 477.5 ± 157 g) fed daily with Skretting Spirit S pellets according to standard production protocols and provided continuous light. The tanks were supplied with a continuous flow-through of filtered and UV-treated seawater (34.5 ppt) collected at 90 m depth from the adjacent fjord, and temperatures were measured continuously using digital thermometers within the header tanks that supplied the experimental tanks (1 header tank per 3 experimental tanks). These header tanks were temperature-adjusted automatically using the water supply system (Normatic AS, www.normatic.no); temperatures did not deviate by more than 1°C.

C. elongatus larvae used in the experiment originated from the CeSenja strain established at the Sea Lice Research Centre at the University of Bergen (Norway). The strain has been genotyped according to Oines & Schram (2008) and consists only of genotype 1 *C. elongatus*. Eggs (F8) from that population were transported from the source lab to the experimental facility and used to infect a separate stock group of salmon at 8°C. This population was then used to provide eggs for the present study (F9). Prior to infection of the experimental fish, egg strings were collected from mature adult females and incubated in continuous flow-through incubators (Hamre et al. 2019) at 8°C.

The same infection protocol was applied to all groups: copepodids were enumerated and divided among the replicate tanks (infection pressure depended on number of available copepodids; see Table 2). The water level in the tanks was decreased to 1/3 of the normal volume and in-flow reduced. Copepodids were then gently poured into the water and these conditions were held for 20 min until normal flow was reinstated. Oxygen levels were monitored continuously using the system's sensors and did not drop below 70% during this period. Due to limited access to eggs for production of copepodids, the experimental groups were infected on separate occasions and with separate batches of copepodids:

the 6°C and 9°C groups were infected with the first batch, then the 12°C group with the second batch, and finally the 15°C group with the third batch.

Because of the limited availability and low infection success of *C. elongatus* here, the same fish were assessed multiple times to determine the parasitic development rate by keeping the lice on the host. To minimize handling, we aimed to sample each fish tank once prior to the appearance of the adult stage, and intermittent times after this to capture when first and second egg strings were produced. The development model in Hamre et al. (2019) was used to establish a sampling scheme. This model predicts the number of days to adult (~100% of population) for *L. salmonis* females at the respective temperatures. These predictions were scaled by a factor of 0.74 to calculate the expected days to adult for *C. elongatus*. Sampling started when the population had reached 65% of the estimated development time to adult (relative age = 0.65), and thereafter successive samples at intervals of about 10 RAU (10%) until all lice carried their second pair of egg strings. For example, this translated in practical terms to start of sampling at 33.4 d post-infection (dpi) for the 6°C group, then continued sampling at intervals of 5.1 d, while at 15°C sampling started at 9.8 d and continued at intervals of 0.98 d.

To reduce handling and sedative effects of sampling the same fish frequently, a single replicate tank was used for measures at each sample point, so that a tank of fish was only sedated every third sample point. Tanks were processed sequentially. At sampling points, all fish in the tank were gently netted into a vessel holding full sedation (metomidate hydro-

Table 2. Infection success (%) among tanks and temperature groups. Infection pressure is the estimated number of copepodids per fish introduced into the tanks. CISS: combined infection and survival success, the percentage of copepodids added to the tank at infection that were recovered at sampling

Temp. (°C)	Tank	Infection pressure	No. fish	No. lice	CISS (%)	Mean CISS (%)
6	1	50	10	17	3.4	3.1
	2	50	8	15	3.8	
	3	50	7	7	2.0	
9	6	60	10	100	16.7	12.1
	7	60	8	41	8.5	
	8	60	10	67	11.2	
12	9	42	10	7	1.7	2.5
	10	42	10	12	2.9	
	11	42	10	12	2.9	
15	13	50	10	1	0.2	1.9
	14	50	10	7	1.4	
	15	50	10	20	4.0	

chloride, 0.01 g l^{-1}). All lice were staged and counted on the 10 fish. At the first sample when all lice had become adults, individual male and females were gently removed from the fish and photographed on wet paper (using a stereomicroscope, Olympus SZX16), then quickly returned to the host fish. Male lice were imaged only once at first appearance of adults; however, females and their egg strings (if present) were imaged at every sample point to determine egg production parameters.

The mean number of molts (MnM) for each sample was calculated including only the 2 most advanced stages (see Hamre et al. 2019). This number represents the average number of molts undertaken by the majority of lice in a sample from infection to sampling. This way, MnM becomes an unambiguous number where the number to the right of the decimal separator gives the fraction of lice that have reached the most advanced stage at the point of sampling (Hamre et al. 2019). For example, if $\text{MnM} = 1.30$, all the lice have molted at least once, and 30% of the lice have molted twice, thus 30% of the population have reached the chalimus 2 stage.

2.3. Embryonic and planktonic development, and copepodid survival

Once the sampling regime from the previous experimental part was completed, adult female lice were monitored for measurements of embryonic development rate. After the females were photographed at the last sample point (see Section 2.2), egg strings were removed and put into individual incubators, while the females were marked with unique color combinations on the genital segment using permanent markers (Edding 3000). The colors used were red, blue, and black, yielding 16 combinations when marking either one or both sides of the genital segment, or leaving a side unmarked. To apply the permanent marker, the genital segment was first gently dried with a piece of absorbent paper, then air dried. After applying the color, the genital segment was allowed to air dry for a few seconds before the louse was transferred to a container with fresh seawater to recover. The lice were allowed to recover for 2–3 h and thereafter re-attached to fish in the tank they came from. When the next egg string pair emerged, the lice were once again removed from the fish using the same method. The lice were identified, and the new pairs of egg strings were incubated. The time between hatching of eggs from the sequential clutches were used to estimate the embryonic development rate for individual females.

The incubators used were 32 mm flow-through incubators (Hamre et al. 2009, 2013) supplied with seawater at 6.2, 9.6, 12.0, or 15.0°C. Incubators were inspected for hatching 3 times a day until hatching, and thereafter checked once a day to record development of planktonic stages. During the nauplius 1 and 2 stages, lice were inspected under a stereomicroscope to confirm their stage. Once a cohort had molted to copepodids, the cohort was divided into replicate wells of 10 copepodids per well, in new incubators. This allowed rapid visual assessment of the viability of copepodids daily until all the copepodids were dead.

The average number of days each copepodid lived for, from here on termed copepodid-days, was calculated as the sum of days that each of the individuals lived, divided by the total number of individuals alive at start. This value circumvents confounding issues associated with non-normally distributed survival in a cohort, and, although more laborious to establish, it is a more precise measure of copepodid longevity than measures describing when a fraction of the copepodid population is dead. At each inspection, the number of copepodid-days since previous inspection was calculated: here it was assumed that the copepodids that died between inspections were alive for 50% of that time interval.

In the 6- and 9-degree groups, the water temperature was slightly higher in the incubators than in the fish tank (6.2 and 9.6°C, respectively). The fertilized egg strings had spent on average half the time in the fish tanks and the other half in the incubators, thus the average temperatures for the embryonic development rates were set to 6.1 and 9.3°C.

Lice and egg strings were measured in ImageJ (<https://imagej.nih.gov/ij/>) from the photographs calibrated using photo of a standard ruler. Cephalothorax length and total length were measured excluding the frontal plate and caudal rami due to poor visibility in some photos. Total length was measured from the front of the cephalothorax to the anus (Fig. 1).

Statistica V13 was applied for statistical analysis (TIBCO Software 2017, <http://statistica.io>). A one-way ANOVA was applied to test whether there were significant differences between temperatures in female length, egg string length, and copepodid survival time. An unequal N HSD test was applied for post hoc testing. Hartley F_{\max} values and normal probability plots were applied to assess the assumptions prior to running the ANOVA. Detailed results are given in the Supplement at www.int-res.com/articles/suppl/q016p227_supp.pdf.

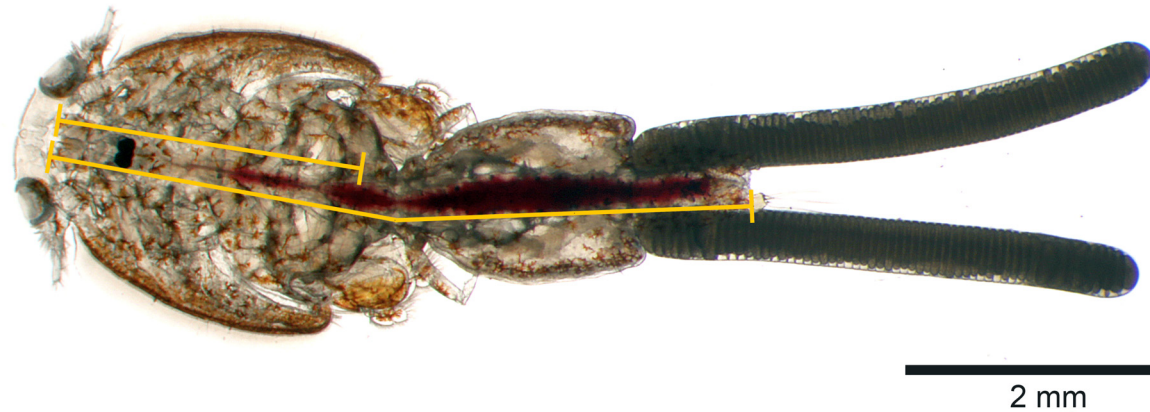


Fig. 1. Adult female *Caligus elongatus*. Orange lines indicate how measurements were obtained in ImageJ. The shorter line indicates cephalothorax length, and the longer line indicates total length

3. RESULTS

3.1. Parasitic development

3.1.1. Infection success

The overall infection and survival success of *Caligus elongatus* in the experiment was low. For the 6, 12 and 15°C temperature groups, ~2–4% of the copepods added to the tanks were recovered from the fish at sampling as chalimus 3 (ch3), ch4 or adults (Table 2). The highest number of lice was observed in the 9°C group, displaying a combined infection and survival success (CISS) between 8.5 and 16.7% (Table 2).

3.1.2. Parasitic development time

C. elongatus was sampled 3 times from Atlantic salmon for a brief period before the final development to the adult stage (Table 3). When the scaling factor of 0.74 was applied, lice in all temperature groups became adult at approximately 85% of the predicted time (Table 3). Thus, this model consequently overestimated the time to adult stage by approximately 15%, suggesting that the development rate of *C. elongatus* changes with temperature in the same manner as *Lepeophtheirus salmonis*. Reducing the scaling factor by 15%, from 0.74 to 0.63, provided a model that predicted time to adult correctly at all temperatures tested: $0.63 \times (5/rM(T))$.

3.2. Embryonic and planktonic development

The frequency at which new egg clutches were produced increased with temperature from ~12 d at

Table 3. Development of *Caligus elongatus* at different temperatures showing stage composition at 3 observation points (dpi) per temperature group. The relative age of the lice sampled was determined by scaling the *Lepeophtheirus salmonis* development model in Hamre et al. (2019) with a scaling factor estimated from Piasecki & MacKinnon (1995) (0.74), and the scaling factor based on the present data (0.63). Stage composition is given by the mean number of molts (MnM) carried out per capita in a cohort of lice until the point of sampling. N: number of lice at each sample point. Note that all lice are adult when MnM = 5, and that only the 2 most advanced stages are included in the calculation of MnM

Temp. (°C)	dpi	N	MnM	Relative age	
				Piasecki & MacKinnon (1995)	Present study
6	33.6	17	3.88	0.65	0.78
	38.6	15	4.53	0.75	0.90
	43.7	7	5.00	0.85	1.01
9	19.7	112	3.81	0.64	0.76
	22.8	45	4.62	0.74	0.88
	26.6	70	4.99	0.86	1.02
12	13.7	29	3.57	0.66	0.77
	15.8	19	4.25	0.76	0.89
	17.7	15	5.00	0.85	1.00
15	9.9	1	4.00	0.65	0.76
	11.3	6	4.67	0.75	0.87
	12.8	21	4.90	0.85	0.99

6°C to ~3 d at 15°C, equivalent to an increase by a factor of 3.75 (Fig. 2). Additionally, new egg clutches were extruded with an interval approximately equivalent to about 27% of the total developmental time to adult, or in other words, at intervals lasting about 27 RAUs (27.01 RAU%). Similarly, the development time from hatching to copepodid also appeared to be a constant fraction of the total development time to adult, lasting about 19% of the time to adult (18.77 RAU%) (Fig. 2).

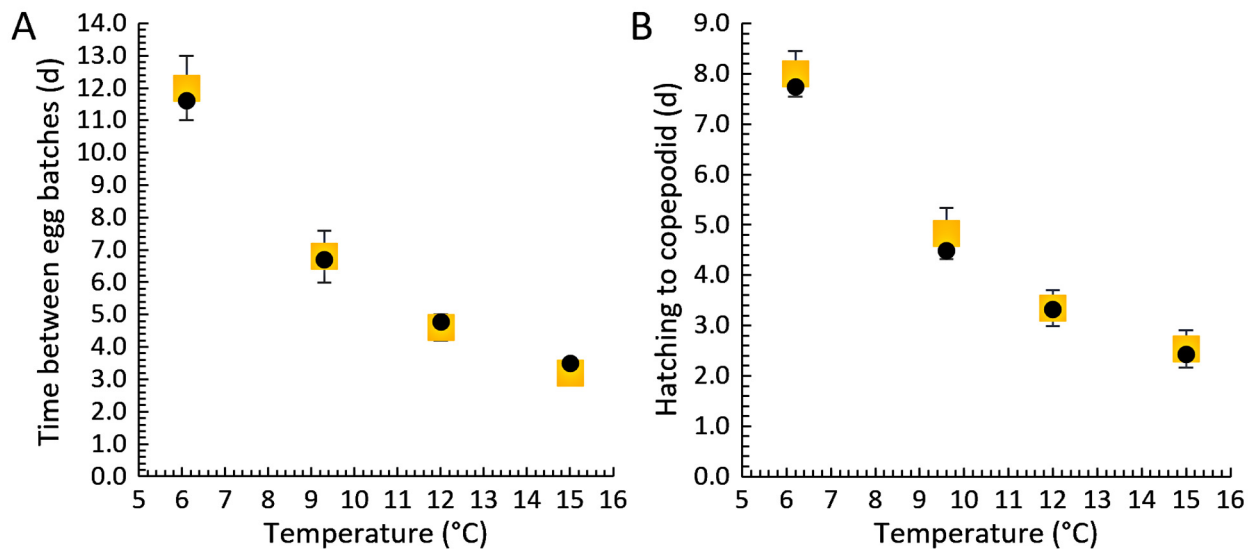


Fig. 2. (A) Time between egg batches and (B) time from hatching to the copepodid stage at the experimental temperatures, from 6 to 15°C. Sample size for each of the temperatures was (A) $n = 6, 21, 4,$ and 3 females at 6.1, 9.3, 12, and 15°C, respectively, and (B) $n = 16, 74, 20,$ and 8 egg string pairs at 6.2, 9.6, 12, and 15°C, respectively. Orange squares are the observed results, error bars indicate standard deviation, black filled circles are the predictions of the present model using a scaling factor of 0.63

3.3. Adult body size and egg production

The size of adult *C. elongatus* females was 5.6 mm at 6°C and approximately 20% smaller at 15°C (one-way ANOVA, $F_{3,114} = 26.4, p < 0.001$) (Fig. 3). Likewise, the general trend of egg string length was a decrease by a factor of 23% (one-way ANOVA, $F_{3,210} = 39.06, p < 0.0001$) in the same temperature interval, although with a somewhat higher length at 9°C (Fig. 3). Consequently, relative to body size, egg string length was

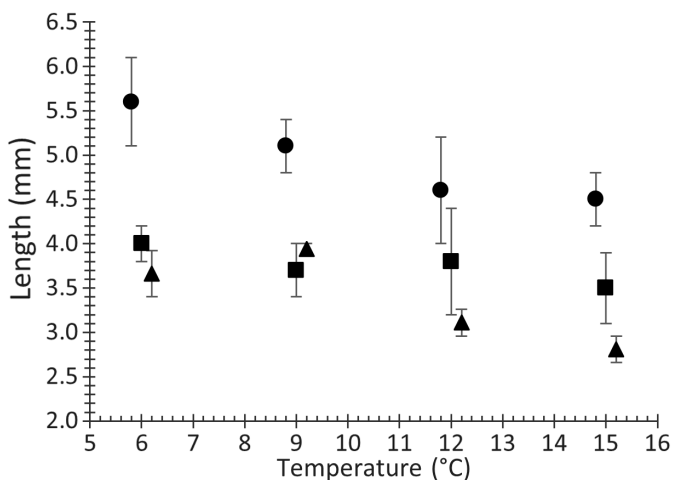


Fig. 3. Total length of adult *Caligus elongatus* and egg string length at temperatures from 6 to 15°C. Females = circles, males = squares, and egg strings = triangles. Markers are jittered along the x-axis to improve clarity. Error bars indicate standard deviations

greatest at 9°C. Statistical tests and details are given in Tables S1–S5 in the Supplement.

About 50% of the *C. elongatus* females carried only one egg string at 6°C, while only ~10–15% lacked an egg string at higher temperatures. The net and anesthetic bath were checked for detached lice after sampling but, in retrospect, the small and pale *C. elongatus* egg strings may have been overlooked. As a result, we were not able to ascertain whether the missing egg strings were lost due to handling or whether they were simply not produced. The mean daily egg production was estimated by dividing the number of eggs per egg string pair and number of days between extrusion of egg strings. For females carrying full egg string pairs, the mean daily egg production ranged from 10 eggs d^{-1} at 6°C to 24 eggs d^{-1} at 15°C (Fig. 4).

3.4. Life span of planktonic copepodids

The average life span of planktonic *C. elongatus* copepodids decreased from 8 to 3.4 d when temperatures increased from 6 to 15°C, representing a 57% reduction in survival time over this temperature interval. A steep decline in survival time was observed between 9 and 12°C (Fig. 5). However, in terms of degree-days, *C. elongatus* copepodid longevity appeared rather stable across the temperature range from 6 to 15°C, varying between 50 and 60 degree-days, with a peak of 60 degree-days at 9.6°C (Fig. 5).

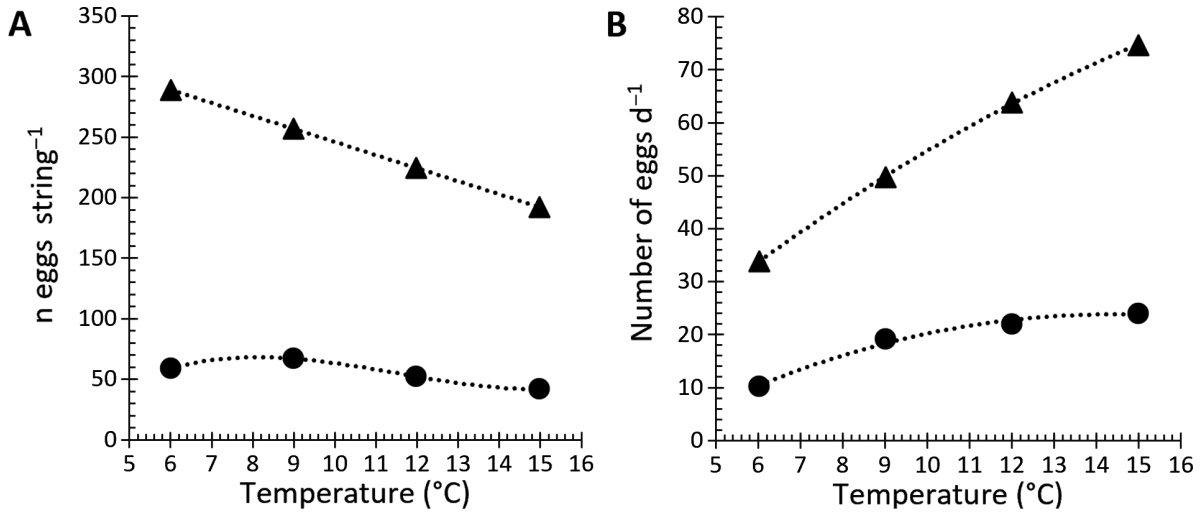


Fig. 4. (A) Mean number of eggs per egg string and (B) mean daily egg production in *Caligus elongatus* females carrying complete egg string pairs, at temperatures from 6 to 15°C (circles). Mean number of eggs per string and estimated mean daily egg production for *L. salmonis* females with complete egg string pairs are plotted for comparison (triangles; calculated based on data on egg batch production frequency in Hamre et al. 2019 and number of eggs per egg string in Samsing et al. 2016). The linear regression for number of eggs per string versus temperature for *L. salmonis* given in panel (A) was extrapolated from published data for temperatures 5–20°C (Samsing et al. 2016). Here, the 15°C data were excluded from the regression, because they appeared incorrect (Fig. 4 in Samsing et al. 2016) and deviate from other measurements at this temperature (unpubl. data from the experiment in Hamre et al. 2019). Second-order polynomials fitted to the mean daily egg production data are for *C. elongatus*, $\text{eggs d}^{-1} = -0.1933T^2 + 5.5346T - 15.768$, and for *L. salmonis*, $\text{eggs d}^{-1} = -0.1387T^2 + 7.4654T - 6.0078$, where T is temperature in °C

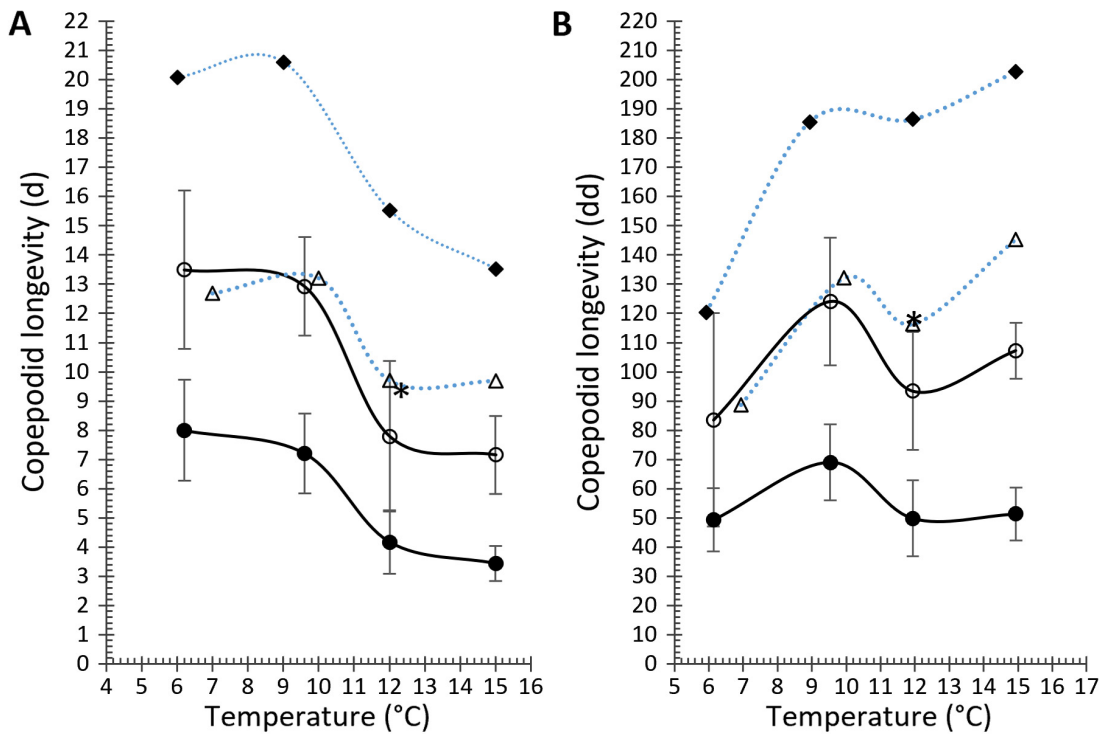


Fig. 5. Life span of planktonic *Caligus elongatus* copepodids at experimental temperatures 6–15°C; (A) in days and (B) in degree-days (dd). Filled black circles indicate the average life span, and open circles indicate the time when 80% of the copepodids are dead. Error bars indicate standard deviation, while lines are smoothed lines connecting the points. Survival time of *Lepeophtheirus salmonis* and *Caligus rogercresseyi* copepodids are plotted for comparison and indicate when 80% of *L. salmonis* copepodids are dead (open triangles, data extracted from Samsing et al. 2016), and when 50% of *C. rogercresseyi* are dead (filled diamonds, data extracted from Montory et al. 2018). *Unpubl. data on *L. salmonis* obtained from same laboratory and methods as in Samsing et al. (2016) and for *C. elongatus* herein. A statistical test for the *C. elongatus* survival data is given in Tables S6 & S7

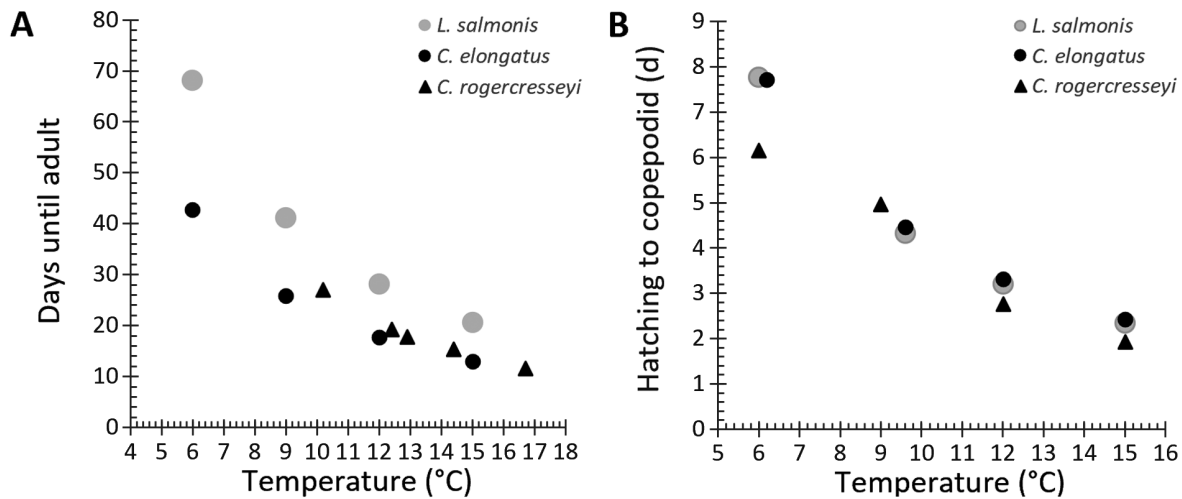


Fig. 6. (A) Predicted development time from infection to adult for *Lepeophtheirus salmonis* females (Hamre et al. 2019), *Caligus elongatus* (present study), and samples representing the time when the majority of *Caligus rogercresseyi* has become adult (Gonzalez & Carvajal 2003). (B) Planktonic development of *L. salmonis* (Hamre et al. 2019), *C. elongatus* (present study), and *C. rogercresseyi* (Montroy et al. 2018)

3.5. Life history parameters compared among three caligid species

As demonstrated above, *C. elongatus* developed to adult at about 63% of the time required for *L. salmonis* females to become adult, while *Caligus rogercresseyi* displayed a development rate similar to that of *C. elongatus*. These relationships were constant over the

temperature range tested (Fig. 6). The synchronicity of a developing larval cohort appeared to be far lower in *C. elongatus* than in *L. salmonis* (Fig. 7), while little data are available on the synchronicity in a developing cohort of *C. rogercresseyi*.

C. elongatus produced approximately 1/3 of the number of eggs produced by *L. salmonis* females per day over the temperature range studied (data from Fig. 4B).

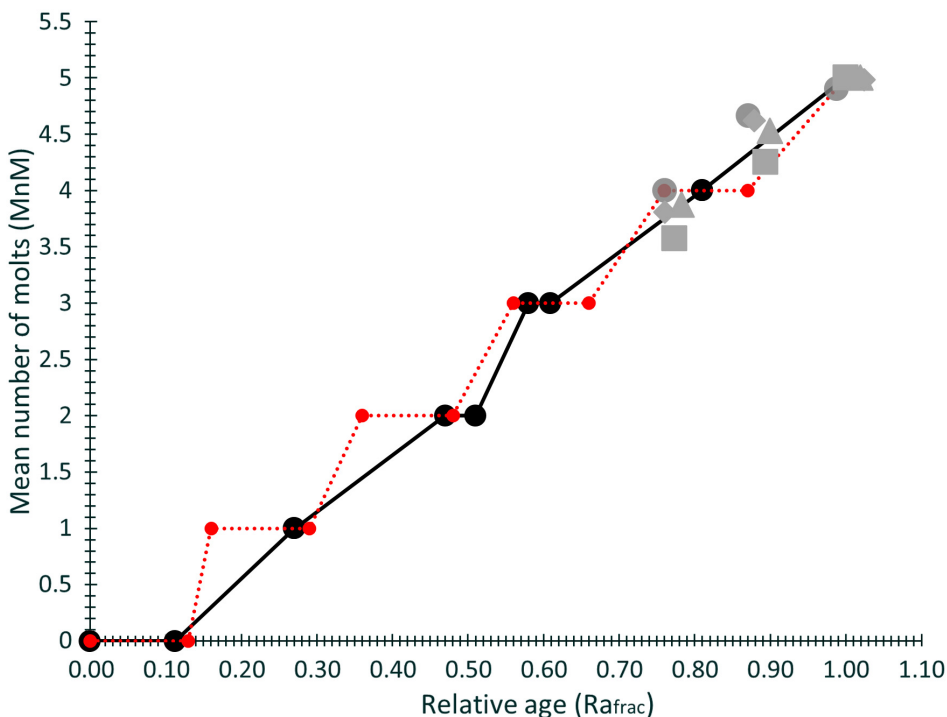


Fig. 7. Development pattern of parasitic stages of *Lepeophtheirus salmonis* and *Caligus elongatus*, combining results from previous literature and the present study. The relationship between relative age (fraction of life span where time to adult is defined as 1) and mean number of molts (MnM) from this experiment and previously published data are shown. Black solid line shows the development pattern of *C. elongatus* derived from Piasecki & MacKinnon (1995). The parasitic development pattern of *L. salmonis* females according to Hamre et al. (2019) is added for comparison (red dotted line). To evaluate how the model performed, the relative age of *C. elongatus* from each temperature group in all samples until adult was calculated under the assumption that *C. elongatus* becomes adult at 0.63 (or 63%) of the time it takes *L. salmonis* females to become adult, and plotted against MnM in each sample: observed development at 6°C (grey triangles), 9°C (grey diamonds), 12°C (grey squares), and 15°C (grey circles)

The egg string extrusion rate in *C. rogercresseyi* is comparable to that of *C. elongatus* at 13–14°C (Bravo 2010, Tables 2 & 3 therein); however, the egg strings contain fewer eggs ($n = 30\text{--}35 \text{ string}^{-1}$), resulting in a net production of 12–16 eggs d^{-1} for females carrying full sets of egg strings. This is equivalent to about 1/5 of the daily *L. salmonis* egg production at this temperature.

Planktonic *C. rogercresseyi* copepodids appeared to live about 2.5 times longer than *C. elongatus* at 6°C, but as temperature increased, *C. rogercresseyi* copepodids survived about 3.9 times longer than *C. elongatus* at 15°C (calculated from data in Fig. 5). Similar to *C. elongatus*, a steep decline in survival time between 9 and 12°C was also evident for *C. rogercresseyi*. *L. salmonis* copepodids appeared to survive approximately equally long as *C. elongatus* copepodids at 9°C, but slightly longer at temperatures above 12°C (Fig. 5). In terms of degree-days, *C. elongatus* survival time appeared approximately stable over the temperature range studied, but with a possible peak at 9°C. *C. rogercresseyi* survival time in degree-days (50% dead) was higher and approximately stable at 185–202 degree-days between 9 and 15°C but dropped considerably at 6°C (Fig. 5). For *L. salmonis*, survival in degree-days (80% dead) was somewhat stable between 10 and 15°C, with a similar drop towards lower temperatures (7°C).

4. DISCUSSION

The present study provides an overview of life history traits representing important epidemiological parameters for *Caligus elongatus*, including developmental rate, egg production and planktonic survival time of copepodids, covering relevant sea temperatures for its geographical range in the northeastern Atlantic Ocean. Based on existing development models for *Lepeophtheirus salmonis*, we have tested whether temperature has an equal effect on these parameters in *C. elongatus*. By this, we explored a new experimental approach for establishing caligid development models and attempted to explore whether important life history parameters can be scaled by constants and used as temperature-independent measures to characterize and compare the biology and epidemiology of sea lice species.

4.1. Infection success

A total of 15 tanks with Atlantic salmon were experimentally infected with *C. elongatus* copepodids,

and the infection success achieved was low in all tanks (Table 2). Typically for laboratory strains of *C. elongatus* maintained at the Sea Lice Research Centre from which the copepodids derived, the infection success is around 20–40%, although infections sometimes fail (L. A. Hamre pers. obs.). Piasecki & MacKinnon (1995) conducted 79 single fish infections, and of these 41 were considered successful. The reasons for low infection success in *C. elongatus* are unknown; however, in *L. salmonis*, copepodid age and temperature are known to be determining factors (Skern-Mauritzen et al. 2020). Further work on rearing of copepodids and infection protocols of *C. elongatus* is warranted.

4.2. Temperature and the effect of development rate on *C. elongatus* and *L. salmonis*

The results herein confirm that the development rate of *C. elongatus* changes with temperature in a similar manner to *L. salmonis* over the interval of 6–15°C. The scaling factor derived from Piasecki & MacKinnon (1995) consistently overestimated the time to adult by about 15%; however, reducing the scaling factor by 15%, from 0.74 to 0.63, provided a model that correctly predicted time to adult on Atlantic salmon (Table 3). Therefore, we propose that *C. elongatus* develops to adult on Atlantic salmon at about 63% of the time required for *L. salmonis* females to become adult. This applies within the temperature interval tested, and assumedly also within the entire temperature interval where their physiological temperature tolerance overlaps. The upper and lower temperature limits for *L. salmonis* were described in Hamre et al. (2019), whereas for *C. elongatus* these are yet unknown.

It was suggested in Hamre et al. (2019) that the rate of development changes in response to temperature in a similar way for the embryonic, planktonic, and post-infection stages of caligids. Hence, the duration of any developmental phase can be described independent of temperature in terms of relative age units or, in other words, as fractions of the total development time to adult. The present results support this and show that both the embryonic development time and the planktonic development time from hatching to copepodid for *C. elongatus* are constant fractions of the parasitic development time to adult (Fig. 2). Furthermore, this model on planktonic development concurs with the data on planktonic development for *C. elongatus* reported in Pike et al. (1993).

The highest mean number of eggs per string for *C. elongatus* was observed at 9°C. This was fewer than

observed by Hogans & Trudeau (1989) on *C. elongatus* from cultured salmon in the Lower Bay of Fundy in July ($n = 85$). A similar tendency is also observed in *L. salmonis*, where both body size and egg string lengths of lice hosted on wild fish are typically larger than lice hosted on farmed fish or in the laboratory (Jackson & Minchin 1992, Tully & Whelan 1993, Nordhagen et al. 2000). Knowledge of factors controlling the size of egg clutches in *C. elongatus* is scarce, and factors other than temperature may potentially play a role.

4.3. *C. elongatus* genotypes, host range, and rate of development

As mentioned in Section 1, *C. elongatus* is a generalist recorded from more than 80 fish species (Kabata 1979), but little is known about the ability of *C. elongatus* to exploit different host species. If *C. elongatus* can exploit all hosts equally well, then its development rate, adult size, egg string size, and mean daily egg production should be equal. However, 2 genotypes of *C. elongatus* were identified by Oines & Schram (2008), and based on molecular analysis of 2 mitochondrial genes *CO1* and *16S*, and 3 morphological characters, their results suggest that *C. elongatus* may consist of several sibling species. If true, there is most likely a variation among the sibling species with respect to which subset of hosts they can utilize optimally. In addition, species-specific and/or individual host factors within the range of hosts for each subtype may also have an influence, such as by limiting the conversion of host tissue to parasite growth (Michel et al. 1971). Moreover, as an integral part of host adaptation, there may potentially be a variation among subtypes of *C. elongatus* with respect to their evolved anabolic or metabolic rates (Clarke 2003, 2004, Clarke & Fraser 2004), this governed by their adopted level of virulence and thus determining food requirements, growth rates, and egg production.

From the present results, it appears that *C. elongatus* develops about 15% slower on Arctic charr (Piasecki & MacKinnon 1995) than on Atlantic salmon (present study). The factors responsible for this difference are unclear, and the development rate of *C. elongatus* on these 2 host species should be measured and compared in a controlled experiment including the 2 genotypes described by Oines & Schram (2008). The lice used by Piasecki & MacKinnon (1995) were of unknown genotype and collected from farmed salmon in Brandy Cove, St. Andrews, Canada. The irregular and asynchronous development of *C. elongatus* in their study is a striking contrast to the rather orderly and

synchronous development seen in a developing cohort of *L. salmonis* (Hamre et al. 2019). A variable degree of copepodid maturation at infection could potentially explain the asynchrony observed in Piasecki & MacKinnon (1995); however, in that study, 3-d-old copepodids (10°C) were used for the infection trials, suggesting that other factors may have played a role. The use of eggs of wild origin may thus have introduced different subtypes in that study, which may explain the highly variable infection success as well as the highly asynchronous development. The present study was conducted using a confirmed genotype 1 laboratory strain (CeSenja; L. A. Hamre unpubl. data). This strain was founded using 6 females and maintained for 8 generations in the lab prior to this study, and the genetic heterogeneity can thus be assumed to be limited.

4.4. Comparing life history parameters among sea louse species by temperature-independent measures

4.4.1. Development rate

The present results support the theory that a constant scaling factor can be applied to the *L. salmonis* development model to produce a valid model for *C. elongatus*. However, it should be kept in mind that the measurements for *C. elongatus* were generally based on low sample sizes from a laboratory strain with an assumedly limited genetic heterogeneity. Low sample sizes also leave some uncertainty regarding the exact value of the scaling factor, but also whether it is constant if analyzed at a finer scale. Furthermore, the duration of the parasitic phase of the copepodid on the host prior to the first molt is dependent on copepodid age at infection (L. A. Hamre, C. Eichner, A. C. Øvergård, H. L. Persson & E. Karlsbakk unpubl. data), and the present study was conducted using copepodids of mixed age, where the age distribution was unknown. Moreover, if there are variations in the development rate among *C. elongatus* subtypes and within their range of hosts, we expect that the rate of development will vary with temperature in a similar manner to *L. salmonis*, and that each combination of louse sub-type and host species can be assigned individual scaling factors.

Whether a simple scaling factor can be applied to predict development in other caligid species is not straightforward to assess based on the present literature. A similar relationship between temperature and rate of development in *L. salmonis* and *L. hippoglossi*

support this, suggesting that the development of *L. hippoglossi* can be predicted by applying a scaling factor close to 1, or slightly above, at least in the temperature range 7–13°C (see Douglas 2001, Hamre et al. 2019). For *C. rogercresseyi* and its similar sized congener *C. elongatus*, present data and published models (Gonzalez & Carvajal 2003) suggest that both species develop at approximately the same rate (Fig. 6). A direct comparison of their development rates on Atlantic salmon is difficult as Gonzalez & Carvajal (2003) used rainbow trout *Oncorhynchus mykiss* as the host. Also, in that study, the growth rates for *C. rogercresseyi* were obtained by averaging temperatures in experiments with wide variations in temperature during louse development. This approach provides a correct result if the number of degree-days required for parasitic development is temperature independent; however, for *L. salmonis* (Hamre et al. 2019) and *C. elongatus* (present study), degree-days is not a strictly temperature-independent measure for development, and this is most likely the case for *C. rogercresseyi* as well. The stage composition in samples of *C. rogercresseyi* obtained from Atlantic salmon maintained at a stable temperature of 11.3°C appeared to be perfectly predicted by the present *C. elongatus* model (see Gonzalez et al. 2015).

The planktonic development rates of *L. salmonis*, *C. elongatus*, and *C. rogercresseyi* are compared in Fig. 6B, demonstrating a remarkable similarity among the 3 species at temperatures at and above 9°C. At the lowest temperature, *C. rogercresseyi* appears to develop far quicker than both *L. salmonis* and *C. elongatus*. If correct, this would suggest that *C. rogercresseyi* is better adapted to cold temperatures. However, the overall change in planktonic development rate for *C. rogercresseyi* in temperatures from 6 to 15°C appears different than the simple parabolic slope evident for *L. salmonis* and *C. elongatus* (Fig. 6B), and new experiments are required to explore whether this deviation is consistent.

4.4.2. Egg production

The time between extrusion of new eggs is similar for *C. elongatus* and *L. salmonis* in terms of relative age units, and lasts for about 27% (present study) and 25% (Hamre et al. 2019) of the development time to adult, respectively. Whether this similarity suggests a shared physiological characteristic among the 2 species is unclear. However, since *C. elongatus* develops faster to the adult stage, the actual time between egg batches is shorter than in *L. salmonis*. For example,

according to the *L. salmonis* model (Hamre et al. 2019) and the present study, *L. salmonis* and *C. elongatus* extrude new egg string batches every 9 and 6.1 d, respectively, at 10°C. This implies that the actual mean daily egg batch extrusion rate is about 47.5% faster for *C. elongatus* than for *L. salmonis* over the entire temperature range studied. Despite a higher extrusion rate, the mean daily egg production of *C. elongatus* females is only approximately a third of that produced by *L. salmonis* females across this temperature range due to the smaller number of eggs per batch (see Fig. 4). For *C. rogercresseyi*, there is a lack of data on egg production across temperatures; however, at 13–14°C they extrude eggs at an interval similar to that of *C. elongatus*, but as *C. rogercresseyi* produces smaller egg clutches the mean daily egg production is only about 1/5 of that of *L. salmonis* at this temperature. Whether this ratio is constant over the range where their zone of temperature tolerance overlap is yet unknown and requires confirmation.

4.4.3. Planktonic survival time of copepodids

Available data on how the planktonic survival time changes with temperature have been collated in Fig. 5. The data herein originate from several different sources and experiments and represent slightly different descriptors of their longevity. Yet, the general pattern of how these descriptors change with temperature may provide information on this epidemiological factor, but perhaps also information on the ecology and zone of temperature tolerance for the different species of copepodids. Despite similar sized eggs and planktonic larvae, the planktonic survival time of copepodids appears to be substantially longer for *C. rogercresseyi* (Montory et al. 2018) than for *C. elongatus*, but also for the larger *L. salmonis* copepodids (Wootten et al. 1982, Johnson & Albright 1991, Gravil 1996, Bricknell et al. 2006, Samsing et al. 2016) at similar temperatures (Fig. 5). The impressive longevity of *C. rogercresseyi* copepodids measured by Montory et al. (2018) may suggest that *C. rogercresseyi* have a more energetically conservative lifestyle, through behavioral mechanisms and/or by having a lower basic metabolic rate (Clarke 2004, Clarke & Fraser 2004). However, as pointed out by Brooker et al. (2018), variation in the reported planktonic longevity may also be caused by the experimental conditions under which the copepodids were maintained, from continuous flow incubators (Samsing et al. 2016), to stagnant with aeration (Bricknell et al. 2006) and stagnant without aeration (Gravil 1996, Montory

et al. 2018), which could induce differences in swimming activity and hence energy expenditure.

Whereas development rates to a large extent depend on the effect at which digestive and anabolic processes can operate when temperature changes, the duration of planktonic survival is a measure of the total endogenous fuel storage, as well as the level of energy effectiveness the animal can operate at when temperature changes. Planktonic survival time may thus reflect a starvation process until death, where potential compensatory mechanisms stabilize energy use when temperature and metabolic rates increase (McCue 2010). As pointed out by Montory et al. (2018), temperature has a strong influence on the rate of development, but a weaker effect of planktonic survival time. Comparing the difference in planktonic survival time between species as temperatures change is difficult unless they are all measured and compared in one dedicated and controlled experiment. Nevertheless, the curves describing the duration of planktonic survival in Fig. 5 appear somewhat similar in shape and seem to be shifted along the y-axis by an absolute value, giving the impression that the relationship between the 3 species of copepodids may be better described by a constant and absolute difference in terms of days rather than by a scaling factor. This of course would apply only where their zone of temperature tolerance overlaps, and any change in this relationship over a temperature range could thus indicate that one or the other species enters a temperature zone where they become less energetically effective relative to the others. Another striking and common feature for all 3 species is a steep decrease in survival time over the temperature range from 9 to 12°C (Fig. 5). Whether this relates to rearing temperatures of mothers, other physical mechanisms and/or shared evolutionary adaptation is unclear.

This study provides basic knowledge on parameters governing the epidemiology of *C. elongatus* and presents a new and simple approach to characterize and compare caligids. It is evident that the 2 most troublesome species for the salmon farming industry globally, *L. salmonis* and *C. rogercresseyi*, are 2 very different species with respect to size, development rate, and egg production, yet they both possess qualities allowing them to establish as severe pests in salmonid fish farms. In our experience, laboratory cultures of genotype 1 copepodids most often infect Atlantic salmon with a success rate comparable to that of the salmonid specialist *L. salmonis* (L. A. Hamre unpubl. data). Moreover, compared to *C. rogercresseyi*, *C. elongatus* appears to have a similar development rate and higher

mean daily egg production. Despite this, *C. elongatus* for the most part still represents an infrequent and less serious problem to the fish farming industry. A key factor here may be the ability to complete a direct life cycle on farmed salmonids. While both the epipelagic *L. salmonis* copepodids and *C. rogercresseyi* copepodids have black pigments, the red pigments in *C. elongatus* copepodids suggest a deeper depth preference (Johnsen 2014), a trait likely to reduce the encounter rate with salmonids in traditional net pens. As such, a shift towards deep water intakes for enclosed, semi-enclosed or land-based systems to reduce *L. salmonis* infections (Oppedal et al. 2022) may potentially introduce additional challenges in the management of *C. elongatus*.

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