Received: 9 June 2020 | Revised: 5 August 2020 | Accepted: 6 August 2020

DOI: 10.1111/jfd.13253

ORIGINAL ARTICLE

Journal of Fish Diseases WILEY

The effect of temperature on ability of *Lepeophtheirus salmonis* to infect and persist on Atlantic salmon

Sussie Dalvin[1,2] | Lars Are Hamre[2] | Rasmus Skern-Mauritzen[3] | Tone Vågseth[4] | Lars Stien[4] | Frode Oppedal[4] | Samantha Bui[4]

[1]SLRC - Sea Lice Research Centre, Institute of Marine Research, Bergen, Norway

[2]Department of Biological Sciences, SLRC - Sea Lice Research Centre, University of Bergen, Bergen, Norway

[3]Institute of Marine Research, Bergen, Norway

[4]Institute of Marine Research, Matredal, Norway

Correspondence
Sussie Dalvin, SLRC - Sea Lice Research Centre, Institute of Marine Research, Bergen, Norway.
Email: sussie.dalvin@hi.no

Funding information
Fiskeri - og havbruksnæringens forskningsfond, Grant/Award Number: 90283; Norges Forskningsråd, Grant/Award Number: 203513

Abstract

The salmon louse (*Lepeophtheirus salmonis*) is an ecologically and economically important parasite of salmonid fish. Temperature is a strong influencer of biological processes in salmon lice, with development rate increased at higher temperatures. The successful attachment of lice onto a host is also predicted to be influenced by temperature; however, the correlation of temperature with parasite survival is unknown. This study describes the effects of temperature on infection success, and survival on the host during development to the adult stage. To accurately describe infection dynamics with varying temperatures, infection success was recorded on Atlantic salmon (*Salmo salar*) between 2 and 10°C. Infection success ranged from 20% to 50% and was strongly correlated with temperature, with the highest success at 10°C. Parasite loss was monitored during development at eight temperatures with high loss of lice at 3 and 24°C, whilst no loss was recorded in the temperature range from 6 to 21°C. Sea temperatures thus have large effects on the outcome of salmon louse infections and should be taken into account in the management and risk assessment of this parasite. Improving understanding of the infection dynamics of salmon lice will facilitate epidemiological modelling efforts and efficiency of pest management strategies.

KEYWORDS

aquaculture, infection success, moult, sea lice

1 | INTRODUCTION

The salmon louse (*Lepeophtheirus salmonis*) is a naturally occurring parasite on salmonid fish. The salmon louse has a direct life cycle consisting of two planktonic nauplius stages followed by the infective copepodid stage (Johnson & Albright, 1991; Schram, 1993). The remaining lifecycle takes place on the host fish, where the louse develops through the parasitic phase of the copepodid stage, two chalimus and two preadult stages before reaching adulthood (Hamre et al., 2013; Johnson & Albright, 1991). On the fish, salmon louse feeds on skin, blood and mucus (Brandal, Egidius, & Romslo, 1976) causing skin lesions, osmotic imbalance and stress to the fish with mortalities on heavily infected fish (Costello, 2006; Fjelldal, Hansen, & Karlsen, 2020). Due to the negative effects of infection, authorities impose strict regulations on the aquaculture industry to reduce the number of parasites produced on farmed fish and the spread of infective larvae to wild fish (Forseth et al., 2017; Olaussen, 2018). For example,

in Norway, aquaculture farm sites are required to quantify the level of infection on their fish (Nekouei et al., 2018; Torrissen et al., 2013; Vollset et al., 2017) and report these numbers weekly to the Norwegian Ministry for Food and Fisheries (Anon., 2012). Counting of salmon lice on fish is demanding due to the small size of the early parasitic stages, especially the copepodid and the first chalimus stage, which are ≤ 1.4 mm (Eichner, Hamre, & Nilsen, 2015). Counts of salmon lice in the field or on farm sites are often performed on live fish resulting in short inspection times to reduce the risk of harming the fish (Stien et al., 2020), and, in some cases, suboptimal conditions such as poor light, uncomfortable work positions (Thorvaldsen, Frank, & Sunde, 2019). In the laboratory, on the other hand, it is possible to plan sampling and optimize these parameters but counting of the smaller stages can, however, still be challenging (Fast et al., 2002). In Norway, extensive surveillance effort is also conducted on wild salmonids, with field assessments of the infection levels on Atlantic salmon (*Salmo salar*), Arctic char (*Salvelinus alpinus*) and sea trout (*Salmo trutta*) (Myksvoll et al., 2018; Serra-Llinares et al., 2014).

Salmon lice have been steadily studied across disciplines, including investigating the immunological (Braden, Koop, & Jones, 2015; Dalvin, Jørgensen, et al., 2020; Fast, Ross, Muise, & Johnson, 2006; Holm et al., 2017; Krasnov, Skugor, Todorcevic, Glover, & Nilsen, 2012; Skugor, Glover, Nilsen, & Krasnov, 2008; Øvergard, Hamre, Grotmol, & Nilsen, 2018) and the physiological effects on the host fish (Bui, Dempster, Remen, & Oppedal, 2016; Fjelldal et al., 2020; Grimnes & Jakobsen, 1996; Wagner & McKinley, 2004; Wagner, McKinley, Bjorn, & Finstad, 2003), furthermore, the ecological effects on wild salmonids (Arechavala-Lopez et al., 2015; Bøhn et al., 2020; Halttunen et al., 2018; Skilbrei et al., 2013; Vollset et al., 2016) and the use of hydrodynamic models to assess the risk of infection (Myksvoll et al., 2018; Sandvik et al., 2016). The infection pressure experienced by wild and farmed fish has been regarded as a function of copepodid density alone in oceanographic infection pressure models. These models incorporate sea temperature to calculate egg production, planktonic larval development, larval survival and sea currents to estimate the overall production and spread of *L. salmonis* infective copepodids (Johnsen, Stien, Sandvik, Asplin, & Oppedal, 2020; Myksvoll et al., 2018; Sandvik et al., 2016). However, although temperature is a known determining factor for the overall production of copepodids and their developmental rates and lifespan (Hamre, Bui, Oppedal, Skern-Mauritzen, & Dalvin, 2019; Samsing et al., 2016), a common theme here and in laboratory trial is that knowledge on the effects of temperature on copepodid infectivity and post-attachment survival is sparse.

Together with salinity, temperature is the major environmental factor affecting the developmental rate of salmon lice (Ljungfeldt, Quintela, Besnier, Nilsen, & Glover, 2017; Samsing et al., 2016; Tucker, Sommerville, & Wootten, 2000). As salmon louse growth and fecundity are driven by temperature, other factors of infection dynamics are also likely to be affected by temperature. Infection success varies widely between studies and is highly dependent on infection protocol, temperature, tank size, fish species, age, group density, water current velocity and host size (Glover, Hamre, Skaala, & Nilsen, 2004; Hamre, Glover, & Nilsen, 2009; Hamre & Nilsen, 2011; Samsing, Oppedal, Johansson, Bui, & Dempster, 2014; Samsing, Solstorm, Oppedal, Solstorm, & Dempster, 2015; Skern-Mauritzen et al., 2020; Tucker et al., 2000). Anecdotal evidence from salmon farmers indicates that new infections are absent at very low temperatures. Such observations are supported by experimental studies demonstrating an infection success of only 2% at 5°C compared to 40%–50% at higher temperatures at 15 and 20°C (Samsing et al., 2016). In the latter study, egg production had taken place at the same temperature as the subsequent infection. Similarly, another study demonstrated much lower infection success at 5°C compared to 10 and 15°C (Skern-Mauritzen et al., 2020). There is clearly a need to investigate infection success at lower temperatures in more detail.

Salmon lice can be long-lived and may remain on the host fish for extended periods of time under optimal conditions (Hamre et al., 2009); however, little concrete evidence is provided for the rate of loss of salmon lice after infection; it varies considerably between studies ranging from 30% to almost complete loss during development to adults (Bjørn & Finstad, 1998; Bui et al., 2018; Hamre et al., 2009; Hamre & Nilsen, 2011; Jones, Fast, Johnson, & Groman, 2007). Biological mechanisms have been explored whereby lice are likely to be lost from the host through host physiological or immune defences (Wagner, Fast, & Johnson, 2008), mate-searching behaviours in mature stages (Stephenson, 2012), natural mortality, or some cumulative interaction of these factors (Bui, Oppedal, Nola, & Barrett, 2020). Although some Pacific salmonids display resistance towards salmon lice, the most commonly farmed salmonids—Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*)—are susceptible (Dalvin, Jørgensen, et al., 2020; Fast et al., 2002; Gjerde & Saltkjelvik, 2009; Johnson & Albright, 1992; Jones et al., 2007; Sutherland et al., 2014). Salmon louse infection gives rise to a limited immune response in these species and does not lead to rejection of the lice (Braden, Barker, Koop, & Jones, 2012; Braden et al., 2015; Holm et al., 2015; Skugor et al., 2008; Øvergard et al., 2018). In order to estimate the potential damage inflicted on host fish, and the overall production of new parasites in the system through persistence of reproductively active lice, understanding the natural loss of salmon lice through their development and adult life on the host is essential.

In the natural environment, salmon lice are likely to experience a large range of temperatures including fast fluctuations as the free-living stages move through thermoclines and for parasitic stages as the host fish move in the water. Here, in two separate experiments, we explore the effect of temperature on the infection success and loss of salmon lice from Atlantic salmon during development from the infective copepodid until the lice become adult, at a range of relevant temperatures.

2 | MATERIALS AND METHODS

The study was divided into two trials, where the objective of the first was to identify infection success at low temperatures (from 2

to 10°C) with high resolution. The objective of the second trial was to investigate infestation success, survival and loss from infection to adults at a wide temperature scale (3 to 24°C) as a parallel aim of the more comprehensive study by Hamre et al. (2019).

2.1 | Experimental animals

All experiments were conducted at the Institute of Marine Research, Matre Research Station, Norway, with adherence to regulations maintained by the Norwegian Animal Research Authority (ID #9192). Atlantic salmon lice (*Lepeophtheirus salmonis salmonis*) (Skern-Mauritzen, Torrissen, & Glover, 2014) eggs used to initiate the culture of lice were collected from operating salmon farms (60°05N, 05°17E and 60°87N, 05°55E). Eggs were hatched and developed to copepodids in incubators (Hamre et al., 2009). For trial 1, eggs were collected in February 2017 at ambient temperature of 6–8°C and hatched at 8°C. For trial 2, eggs were collected in June 2016 at ambient temperature of 14–17°C from the same sites were used to establish an infection on a group of Atlantic salmon (*Salmo salar*) kept at 12°C. In August 2016, eggs from this culture were collected twice (10 days apart) and incubated at 12°C to produce copepodids in incubators (Hamre et al., 2009) kept at 12°C. Atlantic salmon (*Salmo salar*) post-smolts (AquaGen strain) used in the two trials ranged from 200 to 450 g (fork length 28–36 cm). Fish were monitored daily and fed to satiation (Skretting Spirit S, pellet size 75 and 150). They were held in tanks (0.9 m × 0.9 m × 0.4 m deep; volume ≈ 0.32 m^3) with a continuous flow-through of sea water (34 ppt) pumped from 90 m depth from the adjacent fjord (filtered, UV treated and aerated), with continuous lighting. Almost no mortality of fish was observed throughout trials apart from the 2°C (trial 1) where all fish were terminated early, and in the 24°C group (trial 2) where fish in one tank had to be terminated during the trial, due to unacceptable fish welfare.

2.2 | Experimental set-up and analysis of trial 1

Trial 1 aimed to investigate infection success at low temperatures with small increments in temperatures as the knowledge in this range is scarce. Copepodids (40 lice $fish^{-1}$) were used to infect Atlantic salmon at 1°C intervals from 2 to 10°C (9 groups total), which is a range resembling winter conditions for salmonids in Norwegian aquaculture. 360 fish were distributed between 36 tanks (4 replicates per temperature group). Fish were infected according to a standard procedure: tank water level was reduced to one-third of its total volume and water inflow was reduced to 6 L/min, before copepodids were added. Tank outlets were blocked until normal tank levels had been reached (45 min), whereby normal water flows were re-established to 12 L/min. Oxygen levels were monitored continuously to ensure good welfare of the fish. Due to poor welfare and mortality among fish kept at 2°C, lice were counted and the entire group was killed prematurely. On the few fish displaying good welfare, lice were present (1 to 11 $fish^{-1}$). Louse numbers from this group were not utilized in any further analysis. Louse levels on the remaining fish were assessed whilst lice were in the (late) copepodite stage to ensure that all lice on the fish were successfully attached and likely to proceed in development, but before loss processes had begun. These counts occurred 28–40 degree-days after infection (i.e. 4–11 days post-infection, depending on the treatment temperature). Prior to assessment, fish were lightly sedated in the tank and transferred by hand to a bucket containing an overdose of anaesthetics (1 g/L metomidate hydrochloride). Before counting, fish were killed by a sharp blow to the head. All counts were performed by careful inspection of fish by a single person trained and experienced in louse enumeration. The relative infection success (IS) was calculated at the tank level as copepodids were lost in the anaesthetic bath. IS was calculated as the percentage of salmon lice that successfully attached to a host from the population that were originally introduced to the tank.

2.3 | Experimental set-up and analysis of trial 2

Trial 2 aimed to investigate the effect of temperature on the key processes controlling louse density on individual fish. Therefore, an analysis of both loss of lice and a combined measure of infection success and survival was performed. Details of experimental set-up of trial 2 have been reported in Hamre et al. (2019), in a study that addressed the temperature-dependent developmental rate of salmon lice. In brief, the experiment explored the progress of louse infestations at eight temperatures: 3, 6, 9, 12, 15, 18, 21 and 24°C using a total of 1,280 fish. Each temperature group consisted of 160 fish distributed among 4 tanks. Fish followed the same infection procedure as in trial 1, but infection was performed with two different batches of eggs produced from the same females (3, 6, 9, 12, 15°C infected with 28 lice $fish^{-1}$ and 18, 21, 24°C with 30 lice $fish^{-1}$) of copepodids 10 days apart. Lice in these two batches may represent different age compositions at the time of infection; as copepodid age influences their infectivity (Skern-Mauritzen et al., 2020), comparison of infection success between the two batches of lice (i.e. 3–15 degree groups and 18–24 degree groups) is conducted with considerable caution. As infection success at the extreme temperatures was not expected to result in sufficient infection levels (Samsing et al., 2016), the 3 and 6°C groups were infected at 9°C and the 24°C group was infected at 21°C. The 3 and 6°C groups were adjusted to experimental temperature 6 hr post-infection, whereas the 24°C was adjusted 3 hr post-infection. Fish were sampled and killed as described in trial 1.

All temperature groups were sampled at 24 time-points equally distributed through the period during development from copepodids to adult females (Data S1). The 24°C group was, however, terminated early due to complete loss of salmon lice. Each sample consisted of five newly killed fish, and all lice were counted and staged by careful inspection by trained personnel. Because of the inconsistency in enumerating the smallest stages of lice attached to the host, the first two samplings that contained copepodids or chalimus I were

counted twice using two different methods. The fish was first placed in a tray of sea water, carefully inspected using strong light and lice counted. Subsequently, a second count was performed by a different person. This was done by carefully cutting off all fins and the tail of the fish, placing them in sea water and inspection under a microscope; these counts were added to the remaining lice attached to the body recorded as above. The latter method identified marginally more lice, and in most fish, we found identical or only slightly higher number of lice. In a few cases, fewer lice were found. This indicates that lice can be lost in the process of cutting the fins off the fish and that this method can also introduce new sources of error. Overall, there was a significant ($p = .03$), but negligible difference (less than 5%; Table 1) between count methods regardless of infection intensity, thus for practical purposes, we concluded that simple visual inspection of whole fish was adequate. All further counts were therefore performed by visual inspection only, and these data were used in the subsequent analyses.

Whereas the developmental rates calculated from Trial 2 have been reported elsewhere (Hamre et al., 2019), data were analysed here with respect to infection success and survival of lice during development. After infection, the number of lice remaining on a host at any given time is the result of two processes: copepodid attachment (measured as infection success: % of copepodids attaching the fish at infection) and the subsequent loss of lice prior to the time of sampling. Analysis of loss was performed by plotting numbers of lice found on the fish versus time for all samples where reliable louse counts could be obtained in all temperature groups. The Combined Infection Success and Survival (CISS) (Hamre et al., 2009) was defined as the total average percentage of copepodids added to the fish tank at infection that were present on the fish at sampling. Qualitative assessment of the data indicated that counts of copepodids and early chalimus 1 yielded slight underestimates; thus, loss and CISS were estimated for samples from the late chalimus I stage to the appearance of adult female lice (Relative age of females, RAF, between 30% and 115%) only. The definition and use of RAF to describe the developmental progression in a cohort has been comprehensively described (Hamre et al., 2019). In brief, relative age (RA) is a temperature independent measure of age, which is set to 100% at the time when the majority of a louse cohort (sex-specific) has become adult.

Sex ratio was calculated in samples from 6 to 21°C and given as the percentage of males. Only samples where sex could be determined were included, where the majority of lice were either preadult or adult, corresponding to samples where the relative age of females ranged from 56% to 115%. 56% RAF is the point where the majority of females have reached the preadult adult I stage; at 76%, the majority of females have reached the preadult II stage; and at 100%, the majority of females have become adults (Hamre et al., 2019). Data from the trial extended beyond the time-point of females becoming adults and were included (to 115%).

2.4 | The use of early counts

Preliminary analysis of counts from Trial 2 indicated that early counts of salmon lice including copepodites and chalimus 1 can lead to small underestimates of louse density compared to later counts. Consequently, these counts were excluded from further analysis in Trial 2. In Trial 1, all counts were performed at the same early time-point and can therefore be expected to be comparable hence was used for the analysis of infection success.

2.5 | Statistics

Counting method for copepodid stage: Louse count data were square-root transformed to stabilize the variance of the response variable before *t* test (paired) (Crawley, 2019). Analysis of infection success (Trial 1): infection success (IS) was calculated from the percentage of copepodids introduced to the tank that successfully attached to a host. The IS data were square-root and arcsine transformed to stabilize the variance before *t* test and regression analyses (Crawley, 2019). Plotting temperature versus IS suggested a logarithmic relationship (Figure 1), and temperature was therefore log-transformed before a linear regression test was applied. Assumptions of homogeneity of variance and normality

TABLE 1 Number of *L. salmonis* detected in early samples containing copepodids and early chalimus I at eight temperatures from 3 to 24°C (Trial 2)

Temperature (°C)	Average number of lice per fish		% infection success (visual inspection)
	Visual inspection	Microscope count	
3	9.3	9.6	31.0[a]
6	12.7	12.5	42.3[a]
9	11.3	12.2	37.7
12	17.0	17.5	56.7
15	19.0	18.4	63.3
18	10.8	11.6	38.6
21	14.3	16.8	51.1
24	11.3	12.0	40.4[b]
Mean	13.2	13.8	45.1

[a]The infection was performed at 9°C.

[b]The infection was performed at 21°C.

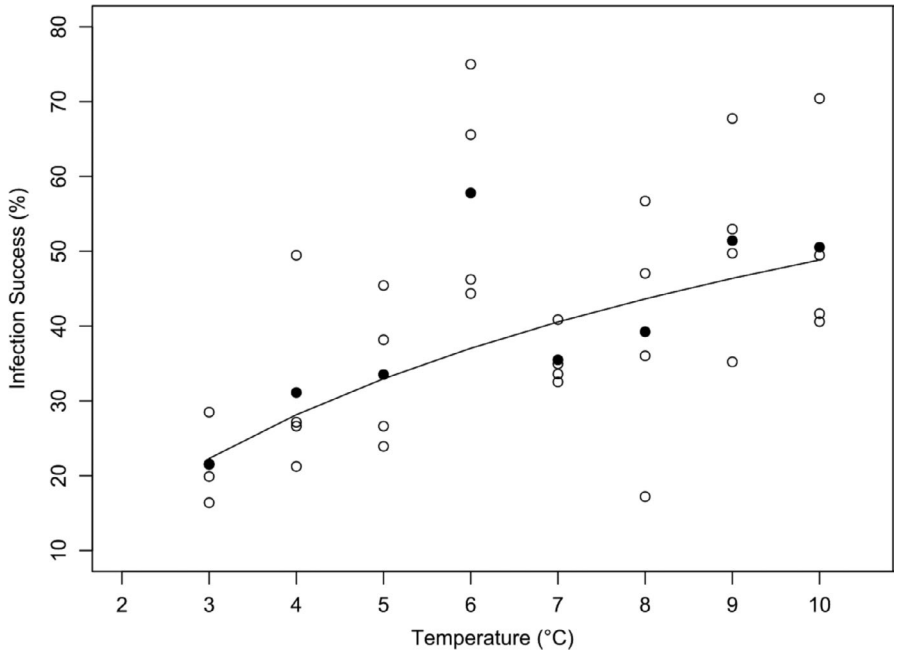

FIGURE 1 Infection success of salmon lice *(Lepeophtheirus salmonis)*. Percentage of salmon lice that successfully attached to a host per replica (open circles) and averaged across replicas (closed circles) at temperatures between 3 and 10°C, at temperatures between 3 and 10°C (Trial 1). The line shows the modelled *Infection success* = 100*((Sin(0.26376 + 0.23526*log(T))^2. Counts were performed at 28–40 degree-days before the lice had moulted to the chalimus I and are expressed as means of tanks. Each temperature group contained 4 tanks with 30 fish in each

of the data were satisfied before test was run. An additional analysis excluding the results from the 6°C group gave a higher R^2 value, but only minor changes to the regression line (data not shown). Analysis of loss (Trial 2): linear regression was applied to evaluate the mean abundance of lice versus relative age. Counts of lice were plotted against time and tank of origin to check for tank effects, to confirm that there was no correlation between tank of origin and number of lice. Linear regression was also used to evaluate whether sex ratio changes with development. Sex ratio was square-root and arcsine transformed before the regression analysis to achieve stable variance (Crawley, 2019). Both analyses were run using Statistica v. 13 (TIBCO Software, http://statistica.io). Analysis of CISS (Trial 2):only a qualitative analysis was used to investigate CISS in this trial, due to the limitations in the dataset (i.e. fish from the 6°C temperature group were infected at 9°C, and fish from the 18 and 21°C temperature groups were infected with a separate batch of copepodites). The two temperature groups with significant losses (3 and 24°C) were not included in CISS as calculations of a mean would be strongly affected by the sampling regime which was skewed due to the nonlinear effect of temperature on development.

3 | RESULTS

3.1 | Infection success of salmon lice on Atlantic salmon at low temperatures (Trial 1)

Infection success was tested in Trial 1 at temperatures from 2 to 10°C, calculated as the percentage of lice found on the fish compared to the number of lice introduced into the tank. The percentage of successfully infected copepodids varied from 20% to 50%, with the highest level of infection found at the warmest temperature tested (Figure 1). Fish infected at 10°C harboured twice as many copepodites as fish infected at 3°C. A linear regression model estimated the line: Infection success = 100*(Sin(0.26376 + 0.23526*log(T))^2 with a R^2 value of .58 and $p = .028$.

3.2 | Loss of salmon lice from Atlantic salmon between 3 and 24°C (Trial 2)

To quantify the loss of lice in Trial 2, mean number of lice fish^{-1} was monitored over the duration of their development period until adult. Loss was calculated during the developmental period from the end of the chalimus I stage (RAF > 30%) throughout development to the adult female stage (RAF < 115%) was used. Linear regression analysis showed no significant loss of lice during this period except for the 3 and 24°C groups, where most or all lice were lost before females became adult (Figure 2 and Data S2). At 3°C, loss occurred gradually whereas at 24°C, high rates of loss occurred at the transition from chalimus II to preadult I around 8 days after infection. Further inspection of the data (Data S1) revealed that loss of lice primarily occurred after the final moult to adult lice, but due to the experimental set-up, there were not sufficient data to compare loss rates of adults among temperature groups.

Furthermore, analysis of the sex ratio to determine whether one sex had a higher rate of loss found that the percentage of females was close to 50% in all temperature groups and linear regression revealed no significant effects of temperature or time on the sex ratio

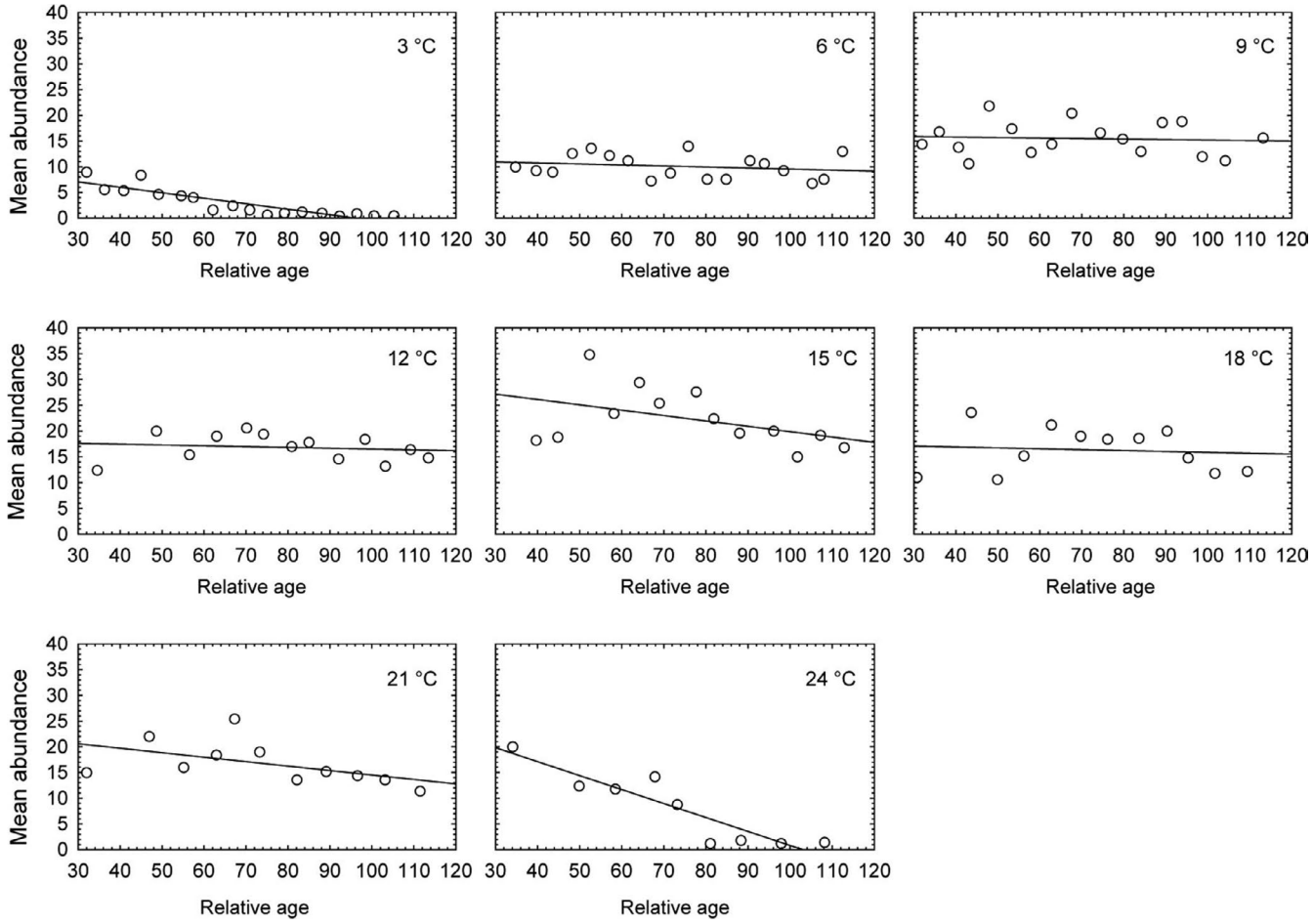

FIGURE 2 Mean abundance of developing salmon lice (*Lepeophtheirus salmonis)* (Trial 2). Each chart shows mean abundance of all salmon lice during development from end of chalimus I to just after females had reached the adult stage. The x-axis indicates the relative age of the female lice in the population

over the investigated period as the lice developed under the present experimental conditions (Figure 3).

3.3 | Infection success and survival of salmon lice as a function of temperature

There were large differences observed in the combined infection and survival success (CISS) between temperature groups (Figure 4) with the smallest CISS recorded at 6°C and the highest at 15°C. It should be noted that fish from the 6°C temperature group were infected at 9°C, and fish from the 18 and 21°C temperature groups were infected with a separate batch of copepodites than the remaining groups making a direct comparison difficult.

4 | DISCUSSION

Similar to its impact on development rate, temperature affected infection success; however, loss of parasites from the host was not induced by any of the intermediate temperatures tested. Below 10°C, increasing temperatures had a strong positive effect on the infection success of salmon lice on Atlantic salmon (Trial 1). Temperatures at the extreme ends of the natural range of the host fish (3 and 24°C) lead to significant losses under this experimental set-up, whereas negligible loss was recorded at temperatures between 6 and 21°C during the period from the first attached chalimus stage to development of adults (Trial 2).

Combined Infection Success and Survival expresses the combined infection and survival success, and thus reflects the actual number of lice which can be expected to be found on a fish; this also appeared to be positively correlated with temperature from 6°C up until 15°C in one louse cohort. Overall, these results emphasize the effect of seawater temperatures on salmon louse and extend the formerly reported effects on developmental rate to also encompass effects on infection success and CISS.

The observed infection success in trial 1 showed a significant gradual increase with temperature from 25% to 50% at temperature ranging from 3 to 10°C. Although not directly comparable, a similar trend was detected in Trial 2 where median CISS values were at 35% at 6°C and 71% at 15°C in trial 2. The observed increased infection success/CISS at higher temperatures is in accordance with

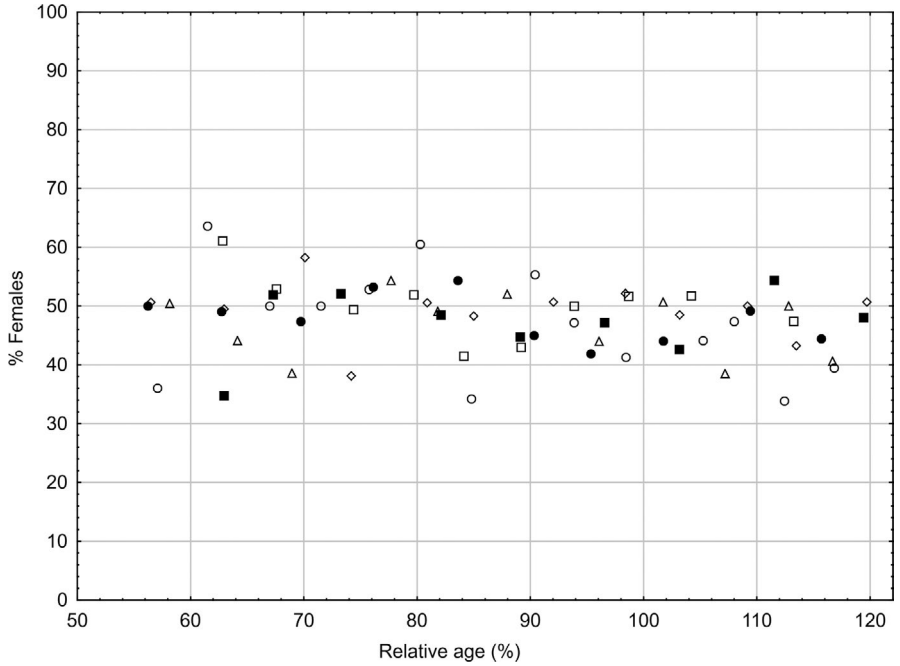

FIGURE 3 Sex ratio of preadult and adult salmon louse (*Lepeophtheirus salmonis*)(Trial 2). Percentage of female lice in all samples where the sex ratio could be determined visually (majority of lice either preadult or adult) from 6 to 21°C. The x-axis indicates the relative age of the female lice. Empty circle: 6°C, empty square 9°C, diamond: 12°C, triangle: 15°C, filled circle: 18°C, filled square: 21°C

earlier studies (Delfosse et al., 2018; Skern-Mauritzen et al., 2020; Tucker et al., 2000). The actual infection success in Trial 1 may be higher than the recorded numbers, as data in Trial 2 suggest that early counts are likely to underestimate the number of lice due to their small size and indistinguishable coloration against the salmon skin and fins. However, as all groups were counted at the same time (late copepodid stage) of development, this underestimation would apply across all temperatures and thus would not alter the conclusions. Interestingly, infection was also demonstrated at 2°C although this could not be quantified due to low sample size. Development from eggs to copepodids is severely reduced or completely impeded at 3°C (Boxaspen & Næss, 2000; Samsing et al., 2016), and copepodid production can be expected to be low below 3°C. However, the present finding demonstrates that copepodids produced at higher temperatures may still be capable of infecting a host even if transported into very cold water. The salmon lice used for this study were collected in western Norway, a region where sea temperatures below 6°C are relatively infrequent at 3 m depth (Data S3) and probably even less so in deeper water where the fish prefer to swim (Johnsen et al., 2020). It is therefore possible that the decrease in CISS levels observed here is, at least in part, caused by local adaptations to intermediate temperatures although previous work does not indicate a geographic component in temperature adaptation (Ljungfeldt et al., 2017). Nevertheless, the results presented here indicate that the chances of new infection on fish are reduced at low seawater temperatures.

At higher temperatures in Trial 2, the trial design only allowed comparison between temperature groups from 6 to 15°C as the higher temperatures were infected with a different cohort of copepodids. Furthermore, it should be noted that lice in the 6°C group had been exposed to an additional temperature adjustment. However, a gradual increase in louse levels with temperature was detected, reflecting the observed increase in infection success and high level of retention of lice in the respective temperature groups.

In this study, the loss of lice was quantified by the change in mean abundance of lice in consecutive samples until the lice were adult. The loss of lice from tanks between 6 and 21°C was insignificant under the experimental conditions applied here, though the analysis did not include the potential loss before the chalimus II stage and after development to adults. The remarkably low louse loss observed contrasts other reports. Whereas several experiments have observed little loss of lice in fish from infection to development of preadults (Bui et al., 2018; Fast et al., 2002; Grimnes & Jakobsen, 1996), considerable loss was reported during the preadult to early adult phase (Bjørn & Finstad, 1998; Bui et al., 2016; Dawson, Pike, Houlihan, & McVicar, 1997; Hamre et al., 2009; Hamre & Nilsen, 2011). Loss is likely to be a result of a number of processes including behaviour and response of the fish, accidental detachment of parasites from the fish through contact with tank surfaces, and movement of the parasite. Given the tank environment, detached lice may also re-attach to other fish in the tank (e.g. Bui et al. (2018)). Retention of lice is highly dependent on the size and density of host fish and tank environment (Hamre et al., 2009) and therefore varies between experiments. Comparisons between experiments are further hindered by differences in how copepodids are counted and infection protocol, resulting in highly variable infection success. Apart from good tank design and careful handling of the fish, the low loss reported here may in part have resulted from the relatively low louse density on each fish and the gradual decrease in host density due to the regular removal of fish samples from the tanks. Further, the repeated use of low doses of metomidate hydrochloride could have influenced the results but is unlikely to have reduced the rate of loss.

Loss of lice from the fish was notable in the extreme ends of the temperature range tested, 3°C and 24°C, as previously reported in

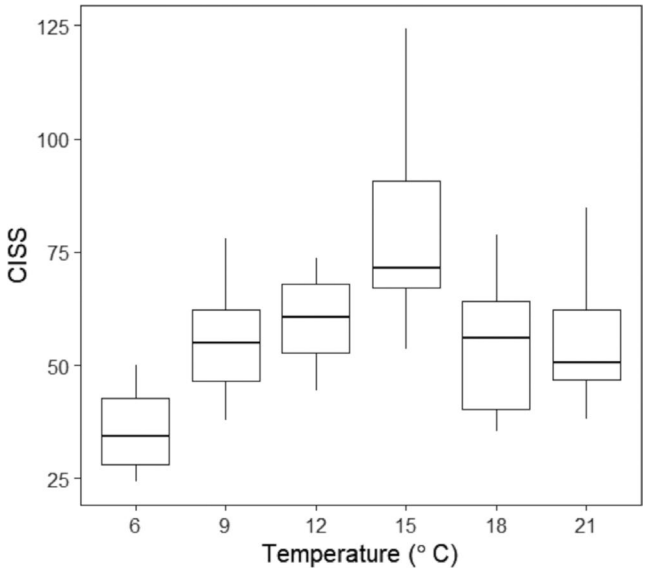

FIGURE 4 The combined infection and survival success (CISS) of salmon lice (*Lepeophtheirus salmonis)* (Trial 2). Samples were obtained from end of the chalimus I stage until all females were adult (30 < RAF < 115%) in each temperature group

Hamre et al. (2019). The pattern of loss differed between the two groups. Fish kept at 3°C had low levels of lice throughout the observation period and displayed a stable rate of loss over time, whereas fish from the 24°C group, which initially displayed an infection level similar to the 21°C group, experienced high rates of loss as the first mobile stage developed. At these extreme temperatures, the lice likely reach their physiological thermal tolerance limits, and thus strive to physically remain, feed and persist on the host fish. The complete loss of salmon lice at 24°C may also have been triggered by disease in the lice. A range of pathogens and associated organisms have been detected in salmon louse although none has been demonstrated to cause mortality (Dalvin, Skaftnesmo, et al., 2020; Økland et al., 2014; Økland, Nylund, Overgard, Skoge, & Kongshaug, 2019; Øvergard et al., 2018; Sveen, Overland, Karlsbakk, & Nylund, 2012). The parasites and pathogens may exhibit increased virulence when louse physiology is compromised as temperature approach the thermal limits of the louse. Loss of parasites could also be due to changes in the host–parasite interactions or host behaviour; both the innate and the adaptive immune system in teleost fish are influenced by temperature, where lower temperatures generally reduce wound healing and the ability to respond to pathogens (Abram, Dixon, & Katzenback, 2017; Alcorn, Murray, & Pascho, 2002; Jensen et al., 2015). The persistence of parasites during the infection reported here also indicates that the ability of Atlantic salmon to reject salmon lice is limited, independent of temperature in the range from 6 to 21°C under the present experimental conditions. Further studies of the fish immune response at low temperatures are needed to characterize such effects on salmon louse infections.

The sex ratio of salmon lice is generally 1:1 (Carmichael et al., 2013), but females develop slower than males (Eichner et al., 2015), and thus, at the end of the analysis period females were newly moulted to the adult stage, whereas males had been adult for a longer period. Earlier studies have reported a higher loss of adult males than females possibly due to mating-associated behaviour (Bui et al., 2020; Hamre & Nilsen, 2011; Stephenson, 2012). Nevertheless, no differences from a 1:1 sex ratio were detected in the present study, possibly due to the relatively short experimental period. Furthermore, temperature did not appear to affect male and female CISS differently.

Although several studies have reported an effect of temperature on infection success and survival of salmon lice, this is the first study that has systematically analysed this effect at a wide range of temperatures. The present study shows that temperature influences infection pressure, by reducing infectivity of copepodids at lower temperatures. Low temperatures can thus be expected to limit new infections. In contrast to this, development and loss of lice from fish was not affected by temperatures between 6 and 21°C (Hamre et al. (2019) and data presented here) indicating that once lice have settled on the fish, further development is not hampered by temperature. These effects should be accounted for in the management of the parasite in sea cages and natural ecosystems.

ACKNOWLEDGEMENTS

The authors thank Daniel Wright, Francisca Samsing and the staff at the Matre Research Station, especially to Simon Flavell, for excellent help during sampling of lice. This project was funded by the TEMPLUS project (project number 90283, Norwegian Seafood Research Fund) and carried out in collaboration with the SFI-Sea Lice Research Centre (grant number 203513, Research Council Norway).

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

ORCID

Sussie Dalvin https://orcid.org/0000-0002-6092-4710
Samantha Bui https://orcid.org/0000-0002-7885-2989

REFERENCES

Abram, Q. H., Dixon, B., & Katzenback, B. A. (2017). Impacts of low temperature on the teleost immune system. *Biology-Basel*, *6*(4), 1–15. s10.3390/biology6040039

Alcorn, S. W., Murray, A. L., & Pascho, R. J. (2002). Effects of rearing temperature on immune functions in sockeye salmon (*Oncorhynchus nerka*). *Fish & Shellfish Immunology*, *12*(4), 303–334. https://doi.org/10.1006/fsim.2001.0373

Anonymous. (2012). *Regulations on combating salmon lice in aquaculture farms (In Norwegian: Forskrift om bekjempelse av lakselus i akvakulturanlegg)*. Norway. https://lovdata.no/dokument/SF/forskrift/2012-12-05-1140

Arechavala-Lopez, P., Thorstad, E. B., Todd, C. D., Uglem, I., Bjorn, P. A., Gargan, P. G., … Finstad, B. (2015). Effects of salmon lice *Lepeophtheirus salmonis* (Copepoda: Caligidae) on sea trout (Salmo

trutta) populations from the NE Atlantic coast. *Revista de Biologia Marina y Oceanografia*, *50*(3), 411–426. https://doi.org/10.4067/S0718-19572015000400002

Bjørn, P. A., & Finstad, B. (1998). The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected post smolts of sea trout (Salmo trutta). *Canadian Journal of Zoology*, *76*(5), 970–977. https://doi.org/10.1139/cjz-76-5-970

Bøhn, T., Gjelland, K. O., Serra-Llinares, R. M., Finstad, B., Primicerio, R., Nilsen, R., … Bjørn, P. A. (2020). Timing is everything: Survival of Atlantic salmon *Salmo salar* postsmolts during events of high salmon lice densities. *Journal of Applied Ecology*, *57*(6), 1149–1160. https://doi.org/10.1111/1365-2664.13612

Boxaspen, K., & Næss, T. (2000). Development of eggs and the planktonic stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. *Contributions to Zoology*, *69*(1–2), 51–55. https://doi.org/10.1163/18759866-0690102005

Braden, L. M., Barker, D. E., Koop, B. F., & Jones, S. R. M. (2012). Comparative defense-associated responses in salmon skin elicited by the ectoparasite *Lepeophtheirus salmonis*. *Comparative Biochemistry and Physiology D-Genomics & Proteomics*, *7*(2), 100–109. https://doi.org/10.1016/j.cbd.2011.12.002

Braden, L. M., Koop, B. F., & Jones, S. R. M. (2015). Signatures of resistance to *Lepeophtheirus salmonis* include a T(H)2-type response at the louse-salmon interface. *Developmental and Comparative Immunology*, *48*(1), 178–191. https://doi.org/10.1016/j.dci.2014.09.015

Brandal, P. O., Egidius, E., & Romslo, I. (1976). Host Blood - Major Food Component for Parasitic Copepod *Lepeophtheirus-Salmonis Kroyeri*, 1838 (Crustacea-Caligidae). *Norwegian Journal of Zoology*, *24*(4), 341–343.

Bui, S., Dalvin, S., Dempster, T., Skulstad, O. F., Edvardsen, R. B., Wargelius, A., & Oppedal, F. (2018). Susceptibility, behaviour, and retention of the parasitic salmon louse (*Lepeophtheirus salmonis*) differ with Atlantic salmon population origin. *Journal of Fish Diseases*, *41*(3), 431–442. https://doi.org/10.1111/jfd.12707

Bui, S., Dempster, T., Remen, M., & Oppedal, F. (2016). Effect of ectoparasite infestation density and life-history stages on the swimming performance of Atlantic salmon *Salmo salar*. *Aquaculture Environment Interactions*, *8*, 387–395. https://doi.org/10.3354/aei00184

Bui, S., Oppedal, F., Nola, V., & Barrett, L. T. (2020). Where art thou louse? A snapshot of attachment location preferences in salmon lice on Atlantic salmon hosts in sea cages. *Journal of Fish Diseases*, *43*(6), 697–706. https://doi.org/10.1111/jfd.13167

Carmichael, S. N., Bekaert, M., Taggart, J. B., Christie, H. R. L., Bassett, D. I., Bron, J. E., … Sturm, A. (2013). Identification of a Sex-Linked SNP Marker in the Salmon Louse (*Lepeophtheirus salmonis*) Using RAD Sequencing. *PLoS One*, *8*(10), e77832. https://doi.org/10.1371/journal.pone.0077832

Costello, M. J. (2006). Ecology of sea lice parasitic on farmed and wild fish. *Trends in Parasitology*, *22*(10), 475–483. https://doi.org/10.1016/j.pt.2006.08.006

Crawley, M. J. (2019). *The R book*. London, UK: John Wiley & Sons.

Dalvin, S., Jørgensen, L. V. G., Kania, P. W., Grotmol, S., Buchmann, K., & Øvergård, A.-C. (2020). Rainbow trout *Oncorhynchus mykiss* skin responses to salmon louse *Lepeophtheirus salmonis*: From copepodid to adult stage. *Fish & Shellfish Immunology*, *103*, 200–210. https://doi.org/10.1016/j.fsi.2020.05.014

Dalvin, S., Skaftnesmo, K. O., Malde, K., Glover, K. A., Leong, J. S., Koop, B. F., … Sandlund, N. (2020). Microbial communities associated with the parasitic copepod *Lepeophtheirus salmonis*. *Marine Genomics*, *49*, 100688. https://doi.org/10.1016/j.margen.2019.05.003

Dawson, L. H. J., Pike, A. W., Houlihan, D. F., & McVicar, A. H. (1997). Comparison of the susceptibility of sea trout (Salmo trutta L.) and Atlantic salmon (Salmo salar L.) to sea lice (Lepeophtheirus salmonis (Krøyer, 1837)) infections. *Ices Journal of Marine Science*, *54*(6), 1129–1139. https://doi.org/10.1016/S1054-3139(97)80018-5

Delfosse, C., Lafont-Lecuelle, C., Barthelemy, H., Chabaud, C., Teruel, E., Bienboire-Frosini, C., & Pageat, P. (2018). Study of the hooking behaviour of Lepeophtheirus salmonis (Kroyer, 1837) copepodids on Atlantic salmon, Salmo salar L., using a novel in vivo test system. *Journal of Fish Diseases*, *41*(6), 969–972. https://doi.org/10.1111/jfd.12747

Eichner, C., Hamre, L. A., & Nilsen, F. (2015). Instar growth and molt increments in *Lepeophtheirus salmonis* (Copepoda: Caligidae) chalimus larvae. *Parasitology International*, *64*(1), 86–96. https://doi.org/10.1016/j.parint.2014.10.006

Fast, M. D., Ross, N. W., Muise, D. M., & Johnson, S. C. (2006). Differential gene expression in Atlantic salmon infected with *Lepeophtheirus salmonis*. *Journal of Aquatic Animal Health*, *18*(2), 116–127. https://doi.org/10.1577/H05-043.1

Fast, M. D., Ross, N. W., Mustafa, A., Sims, D. E., Johnson, S. C., Conboy, G. A., … Burka, J. F. (2002). Susceptibility of rainbow trout *Oncorhynchus mykiss*, Atlantic salmon *Salmo salar* and coho salmon *Oncorhynchus kisutch* to experimental infection with sea lice *Lepeophtheirus salmonis*. *Diseases of Aquatic Organisms*, *52*(1), 57–68. https://doi.org/10.3354/dao052057

Fjelldal, P. G., Hansen, T. J., & Karlsen, O. (2020). Effects of laboratory salmon louse infection on osmoregulation, growth and survival in Atlantic salmon. *Conservation Physiology*, *8*, 1–10. https://doi.org/10.1093/conphys/coaa023

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., … Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. *Ices Journal of Marine Science*, *74*(6), 1496–1513. https://doi.org/10.1093/icesjms/fsx020

Gjerde, B., & Saltkjelvik, B. (2009). Susceptibility of Atlantic salmon and rainbow trout to the salmon lice *Lepeophtheirus salmonis*. *Aquaculture*, *291*(1–2), 31–34. https://doi.org/10.1016/j.aquaculture.2009.03.006

Glover, K. A., Hamre, L. A., Skaala, O., & Nilsen, F. (2004). A comparison of sea louse (*Lepeophtheirus salmonis*) infection levels in farmed and wild Atlantic salmon (*Salmo salar* L.) stocks. *Aquaculture*, *232*(1–4), 41–52. https://doi.org/10.1016/S0044-8486(03)00454-X

Grimnes, A., & Jakobsen, P. J. (1996). The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. *Journal of Fish Biology*, *48*(6), 1179–1194. https://doi.org/10.1111/j.1095-8649.1996.tb01813.x

Halttunen, E., Gjelland, K. ø., Glover, K. A., Askeland Johnsen, I., Serra-Llinares, R. M., Skaala, Ø., … Skilbrei, O. T. (2018). Migration of Atlantic salmon post-smolts in a fjord with high infestation pressure of salmon lice. *Marine Ecology Progress Series*, *592*, 243–256. https://doi.org/10.3354/meps12403

Hamre, L. A., Bui, S., Oppedal, F., Skern-Mauritzen, R., & Dalvin, S. (2019). Development of the salmon louse *Lepeophtheirus salmonis* parasitic stages in temperatures ranging from 3 to 24 degrees C. *Aquaculture Environment Interactions*, *11*, 429–443. https://doi.org/10.3354/aei00320

Hamre, L. A., Eichner, C., Caipang, C. M. A., Dalvin, S. T., Bron, J. E., Nilsen, F., … Skern-Mauritzen, R. (2013). The Salmon Louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) life cycle has only two chalimus stages. *PLoS One*, *8*(9), 1–9. https://doi.org/10.1371/.pone.0073539

Hamre, L. A., Glover, K. A., & Nilsen, F. (2009). Establishment and characterisation of salmon louse (*Lepeophtheirus salmonis* (Krøyer 1837)) laboratory strains. *Parasitology International*, *58*(4), 451–460. https://doi.org/10.1016/j.parint.2009.08.009

Hamre, L. A., & Nilsen, F. (2011). Individual fish tank arrays in studies of *Lepeophtheirus salmonis* and lice loss variability. *Diseases of Aquatic Organisms*, *97*(1), 47–56. https://doi.org/10.3354/dao02397

Holm, H., Santi, N., Kjoglum, S., Perisic, N., Skugor, S., & Evensen, O. (2015). Difference in skin immune responses to infection with salmon louse (*Lepeophtheirus salmonis*) in Atlantic salmon (*Salmo salar* L.) of families selected for resistance and susceptibility. *Fish & Shellfish Immunology*, *42*(2), 384–394. https://doi.org/10.1016/j.fsi.2014.10.038

Holm, H. J., Skugor, S., Bjelland, A. K., Radunovic, S., Wadsworth, S., Koppang, E. O., & Evensen, O. (2017). Contrasting expression of immune genes in scaled and scaleless skin of Atlantic salmon infected with young stages of *Lepeophtheirus salmonis*. *Developmental and Comparative Immunology*, *67*, 153–165. https://doi.org/10.1016/j.dci.2016.10.008

Jensen, L. B., Wahli, T., McGurk, C., Eriksen, T. B., Obach, A., Waagbø, R., … Tafalla, C. (2015). Effect of temperature and diet on wound healing in Atlantic salmon (*Salmo salar* L.). *Fish Physiology and Biochemistry*, *41*(6), 1527–1543. https://doi.org/10.1007/s10695-015-0105-2

Johnsen, I. A., Stien, L. H., Sandvik, A. D., Asplin, L., & Oppedal, F. (2020). Optimising the estimated release of salmon lice from aquaculture. *Aquaculture Environment Interactions*, *12*, 179–191. https://doi.org/10.3354/aei00358

Johnson, S. C., & Albright, L. J. (1991). The Developmental Stages of *Lepeophtheirus-Salmonis* (Krøyer, 1837) (Copepoda, Caligidae). *Canadian Journal of Zoology*, *69*(4), 929–950. https://doi.org/10.1139/z91-138

Johnson, S. C., & Albright, L. J. (1992). Comparative susceptibility and histopathology of the response of naive atlantic, chinook and coho salmon to experimental-infection with *Lepeophtheirus-Salmonis* (Copepoda, Caligidae). *Diseases of Aquatic Organisms*, *14*(3), 179–193. https://doi.org/10.3354/dao014179

Jones, S. R. M., Fast, M. D., Johnson, S. C., & Groman, D. B. (2007). Differential rejection of salmon lice by pink and chum salmon: Disease consequences and expression of proinflammatory genes. *Diseases of Aquatic Organisms*, *75*(3), 229–238. https://doi.org/10.3354/dao075229

Krasnov, A., Skugor, S., Todorcevic, M., Glover, K. A., & Nilsen, F. (2012). Gene expression in Atlantic salmon skin in response to infection with the parasitic copepod *Lepeophtheirus salmonis*, cortisol implant, and their combination. *Bmc Genomics*, *13*, 130. https://doi.org/10.1186/1471-2164-13-130

Ljungfeldt, L. E. R., Quintela, M., Besnier, F., Nilsen, F., & Glover, K. A. (2017). A pedigree-based experiment reveals variation in salinity and thermal tolerance in the salmon louse, Lepeophtheirus Salmonis. *Evolutionary Applications*, *10*(10), 1007–1019. https://doi.org/10.1111/eva.12505

Myksvoll, M. S., Sandvik, A. D., Albretsen, J., Asplin, L., Johnsen, I. A., Karlsen, Ø., … Ådlandsvik, B. (2018). Evaluation of a national operational salmon lice monitoring system-From physics to fish. *PLoS One*, *13*(7), e0201338. https://doi.org/10.1371/journal.pone.0201338

Nekouei, O., Vanderstichel, R., Thakur, K., Arriagada, G., Patanasatienkul, T., Whittaker, P., … Revie, C. W. (2018). Association between sea lice (Lepeophtheirus salmonis) infestation on Atlantic salmon farms and wild Pacific salmon in Muchalat Inlet, Canada. *Scientific Reports*, *8*, 1–11. https://doi.org/10.1038/s41598-018-22458-8

Økland, A. L., Nylund, A., Øvergård, A.-C., Blindheim, S., Watanabe, K., Grotmol, S., … Plarre, H. (2014). Genomic characterization and phylogenetic position of two new species in rhabdoviridae infecting the parasitic copepod, Salmon Louse (*Lepeophtheirus salmonis*). *PLoS One*, *9*(11), e112517. https://doi.org/10.1371/journal.pone.0112517

Økland, A. L., Nylund, A., Overgard, A. C., Skoge, R. H., & Kongshaug, H. (2019). Genomic characterization, phylogenetic position and in situ localization of a novel putative mononegavirus in *Lepeophtheirus salmonis*. *Archives of Virology*, *164*(3), 675–689. https://doi.org/10.1007/s00705-018-04119-3

Olaussen, J. O. (2018). Environmental problems and regulation in the aquaculture industry. Insights from Norway. *Marine Policy*, *98*, 158–163. https://doi.org/10.1016/j.marpol.2018.08.005

Øvergard, A. C., Hamre, L. A., Grotmol, S., & Nilsen, F. (2018). Salmon louse rhabdoviruses: Impact on louse development and transcription of selected Atlantic salmon immune genes. *Developmental and Comparative Immunology*, *86*, 86–95. https://doi.org/10.1016/j.dci.2018.04.023

Samsing, F., Oppedal, F., Dalvin, S., Johnsen, I., Vagseth, T., & Dempster, T. (2016). Salmon lice (*Lepeophtheirus salmonis*) development times, body size, and reproductive outputs follow universal models of temperature dependence. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(12), 1841–1851. https://doi.org/10.1139/cjfas-2016-0050

Samsing, F., Oppedal, F., Johansson, D., Bui, S., & Dempster, T. (2014). High host densities dilute sea lice Lepeophtheirus salmonis loads on individual Atlantic salmon, but do not reduce lice infection success. *Aquaculture Environment Interactions*, *6*(1), 81–89. https://doi.org/10.3354/aei00118

Samsing, F., Solstorm, D., Oppedal, F., Solstorm, F., & Dempster, T. (2015). Gone with the flow: Current velocities mediate parasitic infestation of an aquatic host. *International Journal for Parasitology*, *45*(8), 559–565. https://doi.org/10.1016/j.ijpara.2015.03.006

Sandvik, A. D., Bjørn, P. A., Ådlandsvik, B., Asplin, L., Skarðhamar, J., Johnsen, I. A., … Skogen, M. D. (2016). Toward a model-based prediction system for salmon lice infestation pressure. *Aquaculture Environment Interactions*, *8*, 527–542. https://doi.org/10.3354/aei00193

Schram, T. A. (1993). Supplementary descriptions of the developmental stages of Lepeophtheirus salmonis (Krøyer, 1837) (Copepoda: Caligidae). In G. A. Boxshall, & D. Defaye (Ed.), *Pathogens of Wild and Farmed Fish Sea Lice* (pp. 30–47). New York: Ellis Harwood.

Serra-Llinares, R. M., Bjorn, P. A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M., & Asplin, L. (2014). Salmon lice infection on wild salmonids in marine protected areas: An evaluation of the Norwegian 'National Salmon Fjords'. *Aquaculture Environment Interactions*, *5*(1), 1–16. https://doi.org/10.3354/aei00090

Skern-Mauritzen, R., Sissener, N. H., Sandvik, A. D., Meier, S., Sævik, P. N., Skogen, M. D., … Bui, S. (2020). Parasite development affect dispersal dynamics; infectivity, activity and energetic status in cohorts of salmon louse copepodids. *Journal of Experimental Marine Biology and Ecology*, *530–531*, 151429. https://doi.org/10.1016/j.jembe.2020.151429

Skern-Mauritzen, R., Torrissen, O., & Glover, K. A. (2014). Pacific and Atlantic Lepeophtheirus salmonis (Kroyer, 1838) are allopatric subspecies: Lepeophtheirus salmonis salmonis and L. salmonis oncorhynchi subspecies novo. *Bmc Genetics*, *15*. 1–9. https://doi:10.1186/1471-2156-15-32

Skilbrei, O. T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F., & Strand, R. (2013). Impact of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 19972009. *Journal of Fish Diseases*, *36*(3), 249–260. https://doi.org/10.1111/jfd.12052

Skugor, S., Glover, K. A., Nilsen, F., & Krasnov, A. (2008). Local and systemic gene expression responses of Atlantic salmon (*Salmo salar* L.) to infection with the salmon louse (*Lepeophtheirus salmonis*). *Bmc Genomics*, *9*, 498. https://doi.org/10.1186/1471-2164-9-498

Stephenson, J. F. (2012). The chemical cues of male sea lice *Lepeophtheirus salmonis* encourage others to move between host Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, *81*(3), 1118–1123. https://doi.org/10.1111/j.1095-8649.2012.03347.x

Stien, L. H., Tørud, B., Gismervik, K., Lien, M. E., Medaas, C., Osmundsen, T., … Størkersen, K. V. (2020). Governing the welfare of Norwegian farmed salmon: Three conflict cases. *Marine Policy*, *117*, 103969. https://doi.org/10.1016/j.marpol.2020.103969

Sutherland, B. J. G., Koczka, K. W., Yasuike, M., Jantzen, S. G., Yazawa, R., Koop, B. F., & Jones, S. R. M. (2014). Comparative transcriptomics of Atlantic *Salmo salar*, chum *Oncorhynchus keta* and pink salmon *O. gorbuscha* during infections with salmon lice *Lepeophtheirus salmonis*. *Bmc Genomics*, *15*, 200. https://doi.org/10.1186/1471-2164-15-200

Sveen, S., Overland, H., Karlsbakk, E., & Nylund, A. (2012). *Paranucleospora theridion* (Microsporidia) infection dynamics in farmed Atlantic salmon *Salmo salar* put to sea in spring and autumn. *Diseases of Aquatic Organisms*, *101*(1), 43–49. https://doi.org/10.3354/dao02464

Thorvaldsen, T., Frank, K., & Sunde, L. M. (2019). Practices to obtain lice counts at Norwegian salmon farms: Status and possible implications for representativity. *Aquaculture Environment Interactions*, *11*, 393–404. https://doi.org/10.3354/aei00323

Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O. T., Nilsen, F., … Jackson, D. (2013). Salmon lice - impact on wild salmonids and salmon aquaculture. *Journal of Fish Diseases*, *36*(3), 171–194. https://doi.org/10.1111/jfd.12061

Tucker, C. S., Sommerville, C., & Wootten, R. (2000). The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases*, *23*(5), 309–320. https://doi.org/10.1046/j.1365-2761.2000.00219.x

Vollset, K. W., Halttunen, E., Finstad, B., Karlsen, O., Bjorn, P. A., & Dohoo, I. (2017). Salmon lice infestations on sea trout predicts infestations on migrating salmon post-smolts. *Ices Journal of Marine Science*, *74*(9), 2354–2363. https://doi.org/10.1093/icesjms/fsx090

Vollset, K. W., Krontveit, R. I., Jansen, P. A., Finstad, B., Barlaup, B. T., Skilbrei, O. T., … Dohoo, I. (2016). Impacts of parasites on marine survival of Atlantic salmon: A meta-analysis. *Fish and Fisheries*, *17*(3), 714–730. https://doi.org/10.1111/faf.12141

Wagner, G. N., Fast, M. D., & Johnson, S. C. (2008). Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. *Trends in Parasitology*, *24*(4), 176–183. https://doi.org/10.1016/j.pt.2007.12.010

Wagner, G. N., & McKinley, R. S. (2004). Anaemia and salmonid swimming performance: The potential effects of sub-lethal sea lice infection. *Journal of Fish Biology*, *64*(4), 1027–1038. https://doi.org/10.1111/j.1095-8649.2004.0368.x

Wagner, G. N., McKinley, R. S., Bjorn, P. A., & Finstad, B. (2003). Physiological impact of sea lice on swimming performance of Atlantic salmon. *Journal of Fish Biology*, *62*(5), 1000–1009. https://doi.org/10.1046/j.1095-8649.2003.00091.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Dalvin S, Are Hamre L, Skern-Mauritzen R, et al. The effect of temperature on ability of *Lepeophtheirus salmonis* to infect and persist on Atlantic salmon. *J Fish Dis*. 2020;43:1519–1529. https://doi.org/10.1111/jfd.13253