



Salmon lice detached during aquaculture practices survive and can reinfest other hosts

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ABSTRACT

Conventional net pens used in Atlantic salmon aquaculture are open to the environment, allowing infestation by salmon lice (*Lepeophtheirus salmonis*), and necessitating delousing treatments to keep within regulatory limits. These treatments, involving crowding and handling, can lead to detachment and loss of mobile louse stages to the surrounding water. It is not known to what extent these individuals pose a reinfestation risk for fish in surrounding net pens. We investigated the capacity of detached lice to survive off the host, and attach to a new host. Lice were placed in incubators at different temperatures (4, 8, 12, 16 °C) and at 12 °C, at three salinities (12, 24, 34 ppt). Once ~50 % mortality was reached, survivors were placed on salmon to quantify rates of reestablishment on a new host. Significantly shorter survival times were observed in warm and in low salinity conditions. Adult females survived longer (median 12 days at 12 °C, 34 ppt) than mixed-sex pre-adults or adult males (8–10 days), and were particularly long-lived in the coldest seawater (median 25 days at 4 °C, 34 ppt). Adult females were also better at reestablishing on a new host, with a 74 % success rate across all treatment combinations versus 52 % and 51 % for pre-adults and adult males, respectively. Together, these findings indicate that detached mobile lice may pose a reinfestation risk to downstream net pens. Management procedures should be developed to minimize infestation of new farmed salmon or wild salmonids in the surrounding environment.

1. Introduction

Salmon lice, *Lepeophtheirus salmonis*, are ectoparasitic copepods that pose significant challenges for the farming of Atlantic salmon (*Salmo salar*). Salmon lice occur naturally on wild salmonids in the north Atlantic and Pacific Oceans (Johnson et al., 1996; Torrissen et al., 2013), but the intensification of salmonid aquaculture in open net pens has created an ideal environment for their proliferation (Dempster et al., 2021; Nowak, 2007), leading to welfare impacts, economic losses, and environmental concerns (Barrett et al., 2022; Costello, 2009; Kragesteen et al., 2019; Krkosek et al., 2013; Overton et al., 2019; Thorstad et al., 2015; Vollset et al., 2018).

Salmon lice attach themselves to the fins and skin of fish, where they feed on the host's epidermis, blood and mucus (Grimnes and Jakobsen, 1996). They disperse and infest hosts as planktonic larvae, before progressing through five parasitic life stages (Hamre et al., 2013) with temperature dependent development (Hamre et al., 2019). The last three parasitic stages (pre-adult I, pre-adult II and adult) are mobile,

moving freely on the surface of the host. Whereas other ectoparasitic fish lice such as *Caligus elongatus* are known to switch host (Øines et al., 2006), salmon lice normally remain on the same host once attached and complete the lifecycle there. Nevertheless, detachment of lice from the surface of the fish and host switching is commonly observed when fish are in close proximity to each other in tanks and net pens (Bui et al., 2020; Ritchie, 1997; Stephenson, 2012; Todd et al., 2005; Todd et al., 2000).

Host-switching behaviour implies that mobile salmon louse stages also have the capacity to reattach to a new host after being accidentally dislodged from a previous host. This has implications for fish handling in salmon aquaculture, as any live lice that detach from the host could pose a (re)infestation risk for wild fish or farmed fish at the same or nearby sites. Direct transfer of lice between fish could also potentially lead to spread of fish disease. Although examples of such transfer have not been documented, some studies have demonstrated the presence of fish pathogens in lice (Barker et al., 2009). However other studies have found little evidence of pathogens or only pathogens associated with the

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louse itself (Dalvin et al., 2020b; Nylund et al., 2010; Øvergård et al., 2018).

Delousing treatments such as medicinal bathing, exposure to warm water, low salinity, or cleaning using water jets and/or brushes all have the potential to dislodge more lice than they kill (Andrews and Horsberg, 2020, 2021; Coates et al., 2021), some of which may pose a reinfestation risk if not immediately collected (Groner et al., 2019). Moreover, many aquaculture procedures, including delousing but also grading, splitting, transferring or harvesting, first require fish to be crowded by hauling a net around the cage population and gradually reducing the accessible volume. This facilitates capture or handling of fish, for instance by pumping, but also causes fish to brush alongside each other and against the crowding net, and can lead to lice, especially mobile stages, being dislodged and released into the environment (Guttu et al., 2025; Guttu et al., 2024; Powell et al., 2015). Furthermore, loss of lice weakened by the treatment is also likely to occur after treated fish are returned to net pens.

Ultimately, reinfestation risk depends on the detached lice remaining alive and at a suitable depth long enough to encounter a new host, and then being able to intercept and attach to that host. The salmon louse is a strictly marine organism. The free-living stages, nauplii and copepodids avoid low salinity water, as is commonly found in the upper meters of fjords in Norway, by sinking (Crosbie et al., 2019). Beyond the planktonic stages (nauplius and copepodite), salmon lice are parasitic. They normally remain on one host and are not adapted to swimming. Little is known about the response and behaviour of the parasitic stages when removed from the fish. Lice detached from fish are more vulnerable than their attached counterparts, likely because they can no longer gain salt from the host through feeding and have more surface area exposed to the low salinity environment (Hahnenkamp and Fyhn, 1985; Wright et al., 2016). Temperature is a strong regulator in ectotherm animals (Schulte, 2015). In salmon lice, temperature is a strong regulator of ability to infest, developmental success and developmental rate (Dalvin et al., 2020a, 2020b; Hamre et al., 2019; Skern-Mauritzen et al., 2020). Survival time is also strongly affected by temperature in the free-living non-feeding planktonic stages, where high temperatures increase developmental speed but also reduce the lifespan of copepodites (Samsing et al., 2016). Temperature is likewise expected to influence survival time of mobile lice by altering the metabolic rate in detached lice.

Here, we (i) establish some initial data on survival times of detached mobile salmon lice at a range of temperatures and salinity levels, and (ii) assess the ability of survivors to reattach when given access to a new host.

2. Methods

2.1. Production of lice

Fertilized eggs from salmon lice (*Lepeophtheirus salmonis*) were collected from farmed fish in Masfjorden during January 2023 and incubated in the laboratory at approximately 9 °C, with a salinity of 34 ppt until copepodites had developed. Infestation of fish to produce mobile lice was performed by lowering the water level to 20 cm and pouring copepodites into the tank. The water inlet and outlet were maintained and the water level in the tanks returned to normal within 10 min. The water temperature was adjusted to obtain required developmental speed and varied from 9 to 15 °C. Salinity was maintained at 34 ppt throughout. As the cohort of lice developed, individual fish were netted out of the tank and euthanized with a sharp blow to the head and placed in seawater. Anaesthesia was not utilized to avoid any negative effects on lice. Lice were carefully removed from the fish skin with forceps and sorted according to sex and stage into petri dishes containing 9 °C, 34 ppt seawater. From here, the mobile lice were carefully moved using forceps into individual wells for the survival experiment (see description below). All fish were monitored daily to ensure good welfare according to the approved permission to perform animal

experiments (Norwegian Food Safety Authority application ID 203748 and 275,263).

2.2. Survival experiments

L. salmonis were staged based on expected development (Hamre et al., 2019) and length measurement in case of doubt using illustrations of the lifecycle (Sea Lice Research Centre, 2020). Individual lice were placed in wells within incubators using a modified version of the formerly described hatching system (Hamre et al., 2009). In the present system, wells were reduced in size (diameter 26 mm; height 60 mm), enabling 16 wells per incubator with an approximate working water volume of 20 ml per well. The incubators were supplied with a continuous water supply at either of four temperatures (4, 8, 12 and 16 °C, all at 34 ppt salinity). Due to limitations in lice numbers and experimental logistics, the two lower salinities (12 and 24 ppt) were performed in the 12 °C condition only. This temperature mirrors common conditions in Norwegian fjords in late spring when brackish water from snow melt is most commonly present. For each combination of experimental condition and louse stage, 32 individuals were tested and allocated to wells across at least two incubators. Each well was inspected every business day to determine if lice were actively swimming or attached to the side of the incubators. Lice that remained unresponsive at the bottom of the well after movement of the incubator were designated as dead. Time of death was set as the first day the animal was scored as dead. Surviving lice were removed from the survival experiment once at least 50 % of their batch (i.e., a combination of stage, temperature, and salinity) had died, and were transferred to the reattachment experiment (described below). Therefore, the population of lice used in the reattachment experiment is made up of those that exceeded the median lethal time (LT50) under their specific incubation conditions.

2.3. Reattachment experiments

Given the artificial tank environment, the ability of detached and starved lice to detect and respond to host fish cues was not investigated here. Instead, lice that survived incubation during the survival experiment were tested to see if they could reestablish themselves on a new host, defined here as the ability to remain on a fish for 24 h after having been placed on the skin of an anaesthetised salmon. Reattachment was also tested for a procedural control group consisting of lice (26 pre-adults, 16 adult males, 16 adult females) that were removed from the host and then immediately replaced on the same host, without being incubated. The procedural control group was only tested at 12 °C and 34 ppt salinity.

Mobile salmon lice (pre-adults and the adult stage) can be removed and reattached to new fish or returned to the original fish with very high success rates. This technique is utilized for practical reasons during cultivation or for experimental work, including infestations with mobile lice (Braden et al., 2012) or injection of lice to perform RNA interference (Dalvin et al., 2021; Dalvin et al., 2009). Atlantic salmon smolts (160–250 g) were anaesthetized using metomidate (Aquacalm Vet), and lice taken from the survival experiment were placed on moist filter paper with their dorsal surface against the paper. The filter paper was then put against the skin of the anaesthetised salmon, gently pressed, removed, and the fish was immediately returned to the water, where normal swimming behaviour was observed within a few minutes. All lice from one batch (treatment combination) were applied onto a single fish maintained in an individual tank (75 L, 50 cm × 50 cm, filled to 30 cm) fitted with a filter over the outflow to collect any lice that failed to remain attached. Sealant was used around the edge of the filter to ensure effective filtration. The water supply to the tank was mixed to match the temperature and salinity of the incubators that the lice had been taken from (i.e., if a given batch of lice had been incubated at 8 °C and 34 ppt during the survival experiment, their ability to reattach was also assessed at 8 °C and 34 ppt). After 24 h, the fish was euthanised and any

lice attached to the fish or found elsewhere in the tank were recorded. Lice not accounted for were assumed to have been detached from and then consumed by the fish. Pre-adult lice which had moulted during the survival experiment were not utilized, as previous observations indicate that individuals that molt off the host have difficulty reattaching (pers. obs., S. Dalvin), believed to be due to malformation of the exoskeleton when the cuticle hardens in an incubator rather than on the surface of a host. Only a small fraction (4 %) of the pre-adults moulted during either experiment, and hence the experiment provided no usable data on the molt capacity of the preadults (Eichner et al., 2014).

2.4. Statistical analysis

We pooled data from all pre-adults (stages I and II, male and female) but kept adult male and adult female stages separate, yielding three distinct louse ‘classes’ for analysis: pre-adults, adult males, and adult females.

The survival dataset was converted to time-to-event format, with individuals as replicates (1 row per individual). The time-to-event dataset contained variables for experimental factors (louse class, incubator ID, well ID, temperature, salinity, and start date), and outcomes, namely the time-to-event (days) and type of event (mortality or censorship). Censorship occurred when individuals were removed from the trial while still alive, for instance when required for a reattachment trial. To model survival times while accounting for censored individuals, we fitted Kaplan-Meier step functions for combinations of temperature and salinity using the *Surv* and *survfit* functions in the *survival* package for R. We then fitted a Cox proportional hazards regression model using the *coxph* function from the same package (Team, 2023; Therneau, 2023; Therneau and Grambsch, 2000). To obtain smooth parametric survival curves, we also fitted a Weibull regression model using the *flexsurvreg* function in the *flexsurv* package (Jackson, 2016). To limit the complexity of the Weibull model while accounting for interactions between predictor variables, we fitted separate models for each salinity level, and therefore tested the effect of temperature within salinity level groups. As we have not characterized the shape of the temperature effect, we specified temperature as an unordered factor. Finally, stepped (Kaplan-Meier) and smooth (Weibull) survival curves were plotted together using *ggplot2* (Wickham, 2016) with assistance from *ggsurvfit* and *survminer* (Kassambara et al., 2021; Sjöberg et al., 2023).

Reattachment outcomes were formatted as counts of successes and failures within each batch of lice taken from a certain combination of conditions (class, temperature, and salinity). These outcomes were fitted with generalized linear models (binomial family, logit link function) using the *glm* function in base R. To limit model complexity, we fitted three separate models to the reattachment response variable. The first was designed to test whether extended incubation and starvation during the survival experiment affected reattachment rates by comparing reattachment rates for lice taken from the survival experiment to those taken directly off a host fish (procedural controls). This model contained predictors for group (incubated vs. control) and class (pre-adult (all), adult male, adult female), without interaction effects due to the small sample size of the control group. The second and third models tested the effect of salinity and temperature, respectively, on reattachment rates after incubation. The salinity model was fitted to data from lice incubated at 12 °C (the only temperature at which salinity was varied), and included factors for salinity (12, 24, 34 ppt) and class, including an interaction. The temperature model was fitted to data from lice incubated at 34 ppt, and included factors for temperature (4, 8, 12, 16 °C) and class, including an interaction. All three models related to reattachment success were evaluated and interpreted using inspection of simulated residuals via the DHARMA package (Hartig, 2019), generation of an analysis of deviance table with type II χ^2 tests using the *car* package (Fox and Weisberg, 2019), and extraction of conditional model predictions using the *ggeffects* package (Lüdtke, 2018).

Examples of data formatting and model specification are included in

the Supplementary Information.

3. Results

3.1. Survival off-host

The median survival time of detached salmon lice depended on temperature, salinity, and class, and ranged from 5 to 25 days (Table 1; Table 2). Temperature was the strongest predictor of survival time, with shorter survival times at higher (5–15 days) compared to lower temperatures (10–25 days). This pattern held across the range of realistic temperatures tested (longest survival times at 4 °C and shortest at 16 °C: Table 1; Fig. 1). Salinity was only varied within the 12 °C group, but at that temperature, strongly brackish water (12 ppt) halved the survival times of pre-adults, adult males and females relative to full salinity (34 ppt) conditions (Table 1; Table 2). Survival times remained high within the 24 ppt group (Table 1). Lack of model significance for adult females is likely due to many survivors at 24 ppt.

There was an interaction between class and temperature on survival times. Median survival times were very similar for pre-adults and adult males given the same conditions (Table 1; Fig. 1). By contrast, adult females survived twice as long as pre-adults and adult males in cold seawater (4 °C and 34 ppt) yet had similar survival times to the other classes in the warmest conditions tested (16 °C and 34 ppt), indicating that temperature is more important for off-host survival of adult females than for other mobile classes (Table 1; Fig. 1).

3.2. Reattachment to new host fish

Detached mobile lice can reattach in close proximity to the skin of host fish. Here starved lice from the survival experiment were tested for reattachment capacity. Averaged across all conditions (grand mean), the reattachment rate was 52 % for pre-adult, 51 % for adult male and 74 % for adult female lice (Table 3). This contrasted with reattachment rates of 88 % (pre-adults), 94 % (adult males) and 100 % (adult females) among lice that had not been incubated (i.e., the procedural control group), indicating that an extended time off the host, with starvation, impacts the viability and or ability to reattach of surviving individuals (Table 4). When salinity and temperature were taken into account, the probability of reattachment also depended on class (higher rates for adult females), although neither salinity nor temperature had significant effects in isolation (Table 4; Fig. 2). There was a significant interaction effect between temperature and class, indicating that adult females had higher success at higher temperatures (Table 4; Fig. 2), although this result should be treated with some caution given the relatively small sample sizes (between 12 and 47 lice per class and treatment combination) and multiple models applied to the same dataset.

4. Discussion

The present findings indicate that mobile salmon lice can survive for extended periods off host fish and reestablish themselves once placed onto a new host. Survival and reattachment were affected by interactions between environmental conditions and class (stage and sex), although survival and reattachment occurred within all lice classes and treatment combinations.

4.1. Survival as function of time

Most studies of environmental effects on the survival of parasites are focused on the free-living/off-host stages (Marcus et al., 2023). These studies include examples of survival above critical thermal limit and longevity as a function of temperature (Gannicott and Tinsley, 1998; Shodipo et al., 2020), and the effect temperature has on interactions between host and parasite (Amat-Valero et al., 2013). Similarly, the effect of environmental parameters on survival of salmon lice has

Table 1

Median survival times (i.e., time to 50 % mortality) for mobile salmon louse classes removed from host fish and incubated at combinations of 4 temperatures (4, 8, 12, 16 °C) and 3 salinity levels (12, 24, 34 ppt). Sample sizes are given for the number of lice that started the trial and the number that died during the trial (i.e., were not censored).

Class	Temperature (°C)	Salinity (ppt)	n (started)	n (died)	Median survival time (days)
Pre-adult	4	34	95	65	13
	8	34	96	46	11
	12	12	96	56	5
	12	24	110	58	7
	12	34	96	52	8
	16	34	95	46	5
Adult male	4	34	42	24	12
	8	34	41	22	10
	12	12	32	16	4
	12	24	32	17	7
	12	34	77	46	10
	16	34	37	25	7
	4	34	54	26	25
	8	34	54	27	14
Adult female	12	12	32	19	6
	12	24	32	16	15
	12	34	51	25	12
	16	34	43	26	7

Table 2

Results from Cox proportional hazards regression models testing the effect of temperature (4, 8, 12, 16 °C) and salinity (12, 24, 34 ppt) on survival time of salmon lice removed from host fish. Separate models were fitted for each louse class. The exponentiated regression coefficient ('exp(Coef)') gives the hazard ratio for the risk of mortality relative to the baseline condition (temperature: 4 °C, salinity: 12 ppt). Values <1 indicate a reduction in hazard (e.g., 0.90 = 10 % lower) and values >1 indicate an increase in hazard (e.g., 1.10 = 10 % higher) relative to the baseline condition. The statistical significance of each term is indicated by a *p*-value based on the Wald z-score.

Class	n (started)	n (died)	Term	Coef ± SE	exp(Coef)	z	<i>p</i>
Pre-adult	588	323	Temp (8 °C)	0.45 ± 0.22	1.57	2.09	0.037
			Temp (12 °C)	1.17 ± 0.22	3.22	5.26	<0.0001
			Temp (16 °C)	2.20 ± 0.25	9.03	8.76	<0.0001
			Sal (24 ppt)	-0.72 ± 0.19	0.49	-3.73	<0.0001
			Sal (34 ppt)	-1.04 ± 0.20	0.35	-5.08	<0.0001
			Temp (8 °C)	0.93 ± 0.35	2.53	2.65	0.008
Adult male	261	150	Temp (12 °C)	1.66 ± 0.33	5.26	5.08	<0.0001
			Temp (16 °C)	2.46 ± 0.38	11.7	6.41	<0.0001
			Sal (24 ppt)	-1.66 ± 0.41	0.19	-4.05	<0.0001
			Sal (34 ppt)	-2.01 ± 0.37	0.13	-5.40	<0.0001
			Temp (8 °C)	0.76 ± 0.31	2.14	2.46	0.014
			Temp (12 °C)	1.33 ± 0.33	3.78	4.08	<0.0001
Adult female	266	139	Temp (16 °C)	2.30 ± 0.36	9.97	6.45	<0.0001
			Sal (24 ppt)	-1.59 ± 0.38	0.20	-4.20	<0.0001
			Sal (34 ppt)	-1.04 ± 0.34	0.35	-3.08	0.002

focused on free-living stages or parasites on the host fish (Samsing et al., 2016; Sievers et al., 2019; Hamre et al., 2019). As such, the present study differs from related studies in that it investigates a situation where a parasite loses its host at a life stage where the louse is normally established on the host.

Overall, the survival times for all classes of lice were long, enabling the possibility of extended transport in the sea. It is possible that this experiment produced higher survival times than would occur in the sea, as the lice in this study spent most of their off-host time attached to the side of an incubator, which is likely to be less energetically demanding than swimming in open water under varying flow conditions. However, the behaviour of detached mobile lice in open water remains undescribed, and individuals that passively drift may not expend more energy than those held in incubators. Regardless, it is clear that mobile salmon lice can survive without their host, and hence food, for extended periods of time. Although beyond the scope of the present work, further investigations of mobile lice off-host behaviour are key to our understanding of the present result and how this will affect dispersal of lice in coastal areas. Furthermore, the laboratory conditions omit the aspect of predation, which would also reduce the survival of detached lice.

4.2. Salinity, temperature and class are major determinants of lice survival

Adult females survived longer than pre-adults and adult males, and warmer water and low salinity reduce off-host survival times for all classes. Low salinity appeared to affect all classes similarly and although not directly comparable the present results are in accordance with earlier findings of brackish water tolerance in chalimi developing on fish (Sievers et al., 2019). For the low salinity groups, 12 ppt, osmotic stress is likely to have contributed to accelerated mortality (Hahnenkamp and Fyhn, 1985). The brackish condition, 24 ppt, is commonly found in the upper layers of fjords with aquaculture activity e.g. Norway and Scotland: (Dalsøren et al., 2020; Rabe and Hindson, 2017) and had little or no effect on mortality relative to the full salinity condition. Hence detached mobile lice can be expected to have good survival even in fjords with moderately reduced salinity.

Higher temperatures reduced the off-host survival times of all stages, although the temperature effect was particularly strong for adult females, with a significant class × temperature interaction. While the data obtained here has very limited direct comparison in the literature, one study of the freshwater fish louse, *Argulus foliaceus*, showed a similar

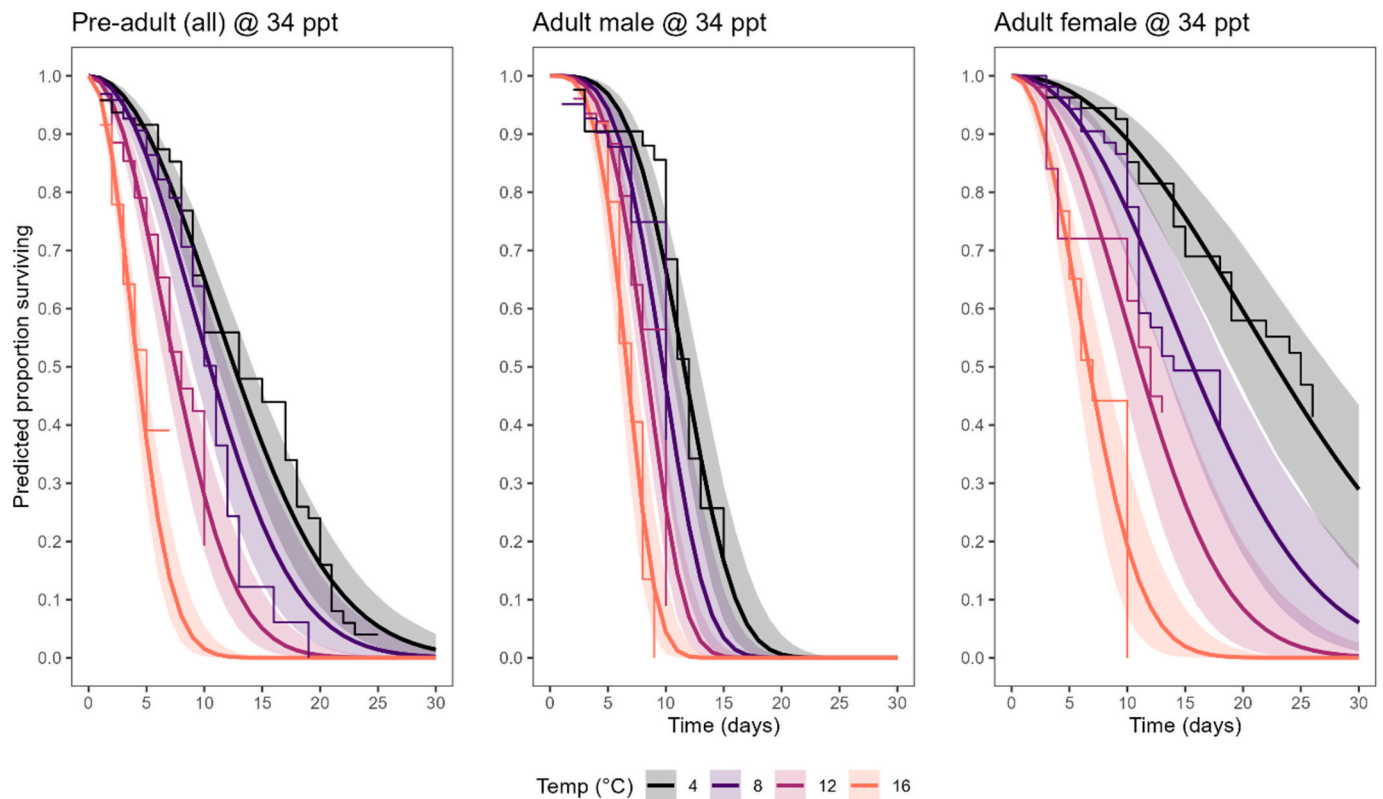


Fig. 1. Predicted survival over time for mobile salmon louse classes (pre-adult stages of mixed sex, adult males, and adult females) removed from host fish and incubated at 4 different temperatures (4, 8, 12, 16 °C) in 34 ppt seawater. Kaplan-Meier step functions and Weibull regression fits are plotted together. The shaded area indicates the 95 % confidence interval around the Weibull model fit.

Table 3

Reattachment rates among mobile salmon louse classes removed from host fish and incubated at combinations of 4 temperatures (4, 8, 12, 16 °C) and 3 salinity levels (12, 24, 34 ppt). The term ‘control’ denotes the procedural control group, in which lice were removed from a host and then immediately replaced on the host rather than being incubated. This was performed at 12 °C and 34 ppt salinity only.

Class	Temperature (°C)	Salinity (ppt)	n	Reattached	Reattachment rate
Pre-adult	4	34	28	19	0.66
	8	34	41	21	0.50
	12	12	38	16	0.43
	12	24	47	27	0.57
	12	34	42	17	0.40
	12 (control)	34 (control)	26	23	0.88
	16	34	44	24	0.54
	4	34	15	6	0.40
	8	34	12	9	0.75
	12	12	16	10	0.62
Adult male	12	24	15	11	0.73
	12	34	21	9	0.25
	12 (control)	34 (control)	16	15	0.94
	16	34	12	4	0.33
	4	34	15	10	0.67
Adult female	8	34	16	11	0.69
	12	12	14	9	0.64
	12	24	16	12	0.75
	12	34	15	10	0.67
	12 (control)	34 (control)	16	16	1.00
	16	34	17	17	1.00

Table 4

Results from 3 generalized linear models comparing reattachment rates of salmon lice according to treatments and class (pre-adults of mixed sex, adult males and adult females). The treatments are, respectively: (A) Incubation, comparing a group incubated and starved at 12 °C until ~50 % of their cohort had died, and a procedural control group, which was removed from the host and then immediately placed back on the host; (B) Salinity during incubation (12, 24, 34 ppt at 12 °C); and (C) Temperature during incubation (4, 8, 12, 16 °C at 34 ppt).

Model	Term	χ^2	df	p
A: Incubation effect	Group	36	1	<0.0001
	Class	5.0	2	0.08
	Salinity	5.9	2	0.052
B: Salinity effect	Class	7.3	2	0.03
	Salinity × Class	1.3	4	0.86
	Temperature	4.0	3	0.26
C: Temperature effect	Class	13	2	0.001
	Temperature × Class	17	6	0.007

reduction in off-host survival (Hunt and Cable, 2020). This temperature-dependency likely reflects energy depletion linked to metabolic rates. Similar responses are observed in the lecithotrophic larvae where copepodids have reduced lifespan at higher temperatures, presumably due to shortage of nutrients (Montory et al., 2018; Samsing et al., 2016; Tocher, 2010). Temperature can also affect behaviour: nauplii prefer colder water in a laboratory setting, perhaps reflecting an adaptation to conserve energy enabling extended transport with ocean currents until host cues are detected (Crosbie et al., 2020). Our observations also align with other documented temperature-dependent traits in salmon lice. For instance, lice attached to fish exposed to higher temperatures develop and transition into the next stages earlier and more successfully (Dalvin et al., 2020a, 2020b; Hamre et al., 2019). Equivalent observations of

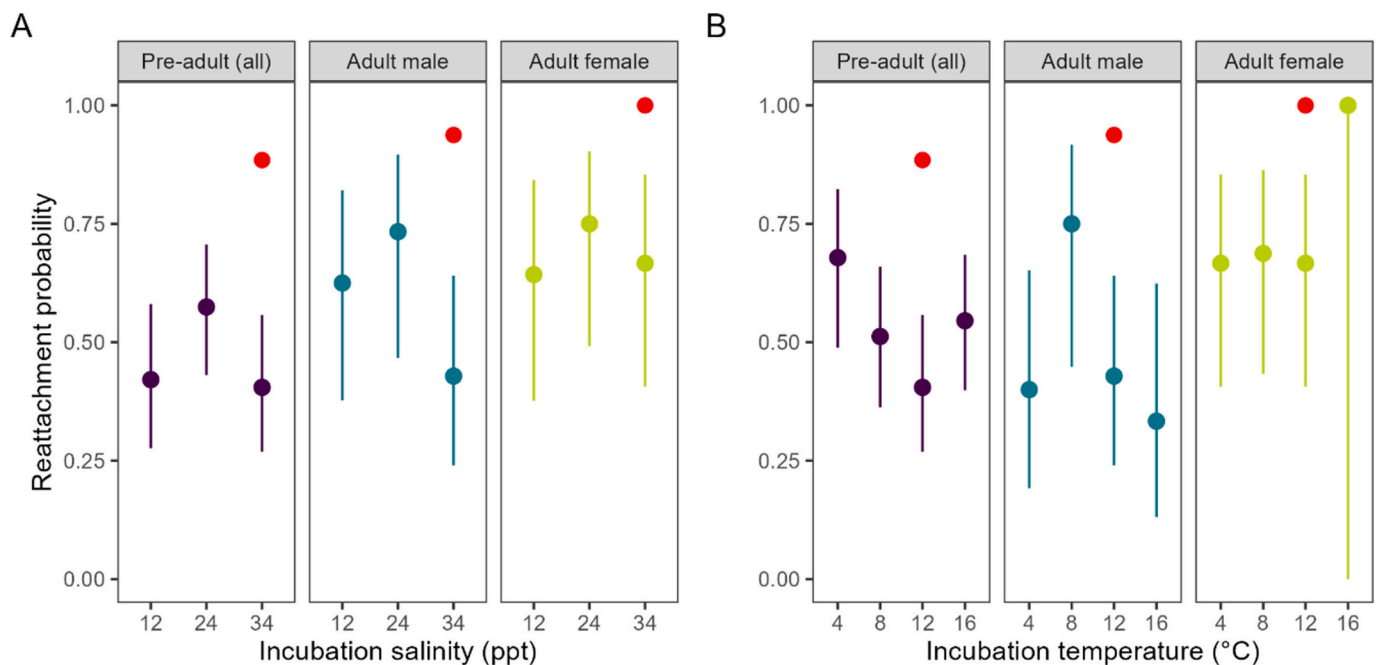


Fig. 2. Predicted probability of detached salmon lice successfully reattaching (mean \pm 95 % confidence interval). Lice were removed from the host, incubated until 50 % of the cohort had died, and then the surviving lice were placed back on a host. Reattachment probabilities are shown by louse class, according to incubation salinity at 12 °C (A) and incubation temperature at 34 ppt salinity (B). Red points indicate the reattachment rate of a procedural control group from each class (26 pre-adults, 16 adult males, 16 adult females), which were removed from the host and then immediately replaced on the host rather than being incubated. This was done at 12 °C and 34 ppt salinity only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperature dependence exist for other parasitic copepods (Jolma et al., 2024; Mardones et al., 2019).

Another significant difference between pre-adults, adult males and adult females is the much longer survival times of the latter. Comparing the adults only, fully mature female lice are approximately double the size of males (Schram, 1993) and hence, can be expected to have greater energy consumption. Furthermore, adult females have a significantly different metabolism as they produce large amounts of yolk proteins and lipids for the eggs (Dalvin et al., 2011; Tocher, 2010). Extrusion of eggs takes place in batches with a frequency dependent on temperature, e.g. weekly at 12 °C (Hamre et al., 2019). Adult females deposit approximately 30 % of their total body protein in each egg batch (unpublished personal observation) and are therefore likely to have a much larger energy requirement. One may speculate that females starved in the experimental setting may have been able to reabsorb energy from eggs maturing in their genital segment as can be observed in insects (Bell and Bohm, 1975). Pre-adults, which in this study were treated as one group regardless of stage (pre-adult I or II) and sex, represent sizes ranging from approximately 3.3 mm for the pre-adult I males to approximately 6.0 mm for pre-adult II females, which is almost identical to the adult males (Schram, 1993). The similar longevity of survival between pre-adults and adult male may reflect the similar size, although pre-adults are likely to expend energy as they prepare to molt. In conclusion, the present results remain open to interpretation and further studies are warranted to explore the exact mechanism.

4.3. Reattachment capacity is largely maintained in detached lice

Reattachment was successful for a relatively large proportion (50–75 %) of the detached and starved lice although less than procedural controls where almost all lice attached. The present experiment only investigated reattachment at one time-point; when 50 % of the group had died. I.e. conditions that may be described as prolonged detachment indicating that as long as the louse is alive, reattachment can be expected to be significant. The present experiment did however

only test the ability of the louse to reattach to the louse and did not explore the combined process of host finding and reattachment. The higher reattachment success observed in adult females may be attributed to the metabolic and size-related mechanisms presented above, which increase resilience to starvation and extremes in temperature and salinity. This high success rate has implications for downstream prevention, as understanding the dispersal of adult females is critical for infestation control (Kragestein et al., 2019). However, the reattachment success metric of the present experiment does not take into account the likelihood of a louse coming into close contact with a host salmon and initiation of attachment as lice were superficially placed on skin of the fish. Nor does it encompass the impact of moulting on reattachment or long-term capacity to remain on the new host.

4.4. Implications for management of sea lice

The high survival rate and reinfestation success of detached mobile salmon lice has implications for parasite management, and may increase parasite exchange both within and between farms, and between farms and wild fish (Bøhn et al., 2022; Groner et al., 2016). It is possible for lice detached from the farmed salmon to infest other salmon in cages nearby or wild salmonids swimming in close vicinity to cages. The distances travelled by the lice will depend on their sinking rate, the direction of the prevailing water currents and speed and temporary or long-term possibilities to attach to biological or physical structures. These details need to be investigated to reveal the full potential for reinfestation and to incorporate into hydrodynamic models predicting transmission of detached lice to nearby farms as is performed for the larval stages (Garnier et al., 2024). Even though little is known about the capacities of the mobile stages to attach to other surfaces, they are commonly observed to attach to tank or incubator well walls and they might therefore also have the ability to temporarily use structures around the cage, such as net, ropes, floaters and various seaweeds, between dislodging from the previous host and finding a new host. Salmon lice have also been observed on non-salmonid wild fish caught around salmon

farms (Lyndon and Toovey, 2001, Bruno and Stone, 1990)). Wild fish are known to move between farms (Uglem et al., 2014), suggesting as another potential transmission vector between farms.

Already, a clear recommendation for management practices involving crowding is to limit the spread of detached lice by considering flow regimes prior to the event and putting measures in place to collect lice that are dislodged. The present results are likely to be applicable also to other sea lice of farmed fish such as *Caligus rogercresseyi*, a major pathogen in salmon aquaculture in the Southern hemisphere. However, the specific biology and behaviour of each lice species needs to be accounted for. Another sea louse species observed in aquaculture, *C. elongatus*, exhibits voluntary detachment for host-switching (Hemmingsen et al., 2020), and survival and reattachment is thus likely to differ from the patterns observed here in salmon lice. For protection of wild fish, crowding events could be avoided during peak smolt out-migrations periods at the specific farms, although this may prove difficult in practice given the requirement for farmers to maintain low louse levels during the same period. The extent to which salmon lice at different stages detach during various operations and crowding events remains unknown and needs to be studied to reveal the potential for mitigation. The present results indicate that survival off the host and reattachment abilities are unlikely to be limiting factors for reinfestation potential.

CRedit authorship contribution statement

Sussie Dalvin: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Frode Oppedal:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition. **Minnie Harvey:** Writing – review & editing, Methodology, Investigation, Data curation. **Luke T. Barrett:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aquaculture.2024.742065>.

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