Aquaculture Reports 42 (2025) 102784

Contents lists available at ScienceDirect

Aquaculture Reports

journal homepage: www.elsevier.com/locate/aqrep

Crowding causes detachment and loss of mobile sea lice: Fine-meshed crowding nets may mitigate spread

Lena Geitung [a,*], Luke T. Barrett [b], Velimir Nola [a], Sussie Dalvin [a], Line Vatne Martinsen [a], Adele Dahlgren [a], Frode Oppedal [a]

[a] Institute of Marine Research, Postboks 1870 Nordnes, Bergen 5817, Norway
[b] Sustainable Aquaculture Laboratory – Temperate and Tropical (SALTT), Queenscliff Marine Science Centre, Deakin University, Victoria 3225, Australia

ARTICLE INFO

Keywords:
Parasite control
Salmo salar
Lepeophtheirus salmonis
Caligus elongatus
Handling

ABSTRACT

Detachment of mobile lice from salmon during crowding and handling procedures in sea-cage fish farms may lead to loss and unwanted spread of ectoparasitic sea lice to other cages, farms or wild fish. However, rates of detachment and loss of lice during crowding are not well understood. We conducted a series of replicate crowding events in 125–2000 m^3 sea-cages, using either a standard coarse-meshed crowding net, or a more fine-meshed crowding net intended to retain detached mobile lice. Lice that were detached during crowding and passed through the crowding net were collected using a 350-μm plankton net positioned around the crowding net (in some cases pumps and filters were also used), allowing lice 'lost' from the crowding net to be directly quantified. Detachment of lice during crowding varied from 2 % to 38 %, with higher detachment rates for smaller life stages (highest for pre-adult 1 salmon lice) and in trials involving larger fish and/or longer crowding durations (up to 2 h). In most cases, the type of crowding net did not affect detachment rates, but the fine-meshed crowding net did retain some detached lice, including 75 % of adult female salmon lice. The fine-meshed crowding net also improved welfare outcomes for crowded fish, including significantly reduced scale loss, fin damage and bleeding. Provided dissolved oxygen levels can be maintained, fine-meshed crowding nets may be the most promising means of limiting the spread of mobile lice into the surrounding environment, while also reducing injuries to fish. Supplementary benefits may be achieved by minimising crowding time but also ensuring filter collection on the water used to bring fish into wellboats and delousing systems.

1. Introduction

Ectoparasitic salmon lice (*Lepeophtheirus salmonis*) have been a challenge for the Atlantic salmon (*Salmo salar*) industry for decades and are the primary obstacle to continued production growth (Vollset et al. (2018). Salmon lice are adapted to live on salmonid fish and feed on their skin, mucus and blood (Kabata, 1974; Brandal et al., 1976; Bjørn and Finstad, 1998). Without any intervention, lice infestation can negatively affect the welfare of their host as they can cause skin erosion, increased energetic cost, physical damage, osmoregulatory failure and ultimately death (Grimnes and Jakobsen, 1996; Tully and Nolan, 2002; Costello, 2006; Torrissen et al., 2013; Bui et al., 2016; Fjelldal et al., 2020; Hvas, Bui, 2022). Salmon louse infestations not only affect the growth and welfare of farmed salmon, but also pose a serious risk for wild salmon populations, as the constant availability of farmed salmonid hosts have caused a proliferation of salmon lice to the environment (Krkošek et al., 2011, 2013; Kristoffersen et al., 2018; Dempster et al., 2021). To minimize the effect of salmon lice on wild fish, the Norwegian government have enforced production volume limits and mandatory treatments if lice levels exceed the permitted thresholds of 0.2–0.5 adult female lice per fish (Lovdata, 2012; Myksvoll et al., 2018; Vollset et al., 2018; Dean et al., 2021), resulting in substantial costs for the farming industry (Liu and Bjelland, 2014; Abolofia et al., 2017; Iversen et al., 2020; Walde et al., 2023), and severe effects on fish welfare (Overton et al., 2019; Moltumyr et al., 2021; Walde et al., 2021, 2022; Bui et al., 2022b)

The life cycle of salmon lice consists of eight life stages, with two planktonic nauplius stage, followed by the infective copepodite stage and the remaining five stages on the host fish (attached chalimus I/ II, mobile preadult I/ II and adult) (Hamre et al., 2013). Salmon lice usually complete their life cycle on the same host, but it has been observed that the final mobile stages can switch between hosts, especially when in

---

* Corresponding author.
E-mail address: lena.geitung@hi.no (L. Geitung).

https://doi.org/10.1016/j.aqrep.2025.102784
Received 22 January 2025; Received in revised form 28 March 2025; Accepted 28 March 2025
Available online 5 April 2025
2352-5134/© 2025 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

close proximity in tanks and cages (Jaworski and Holm, 1992; Ritchie, 1997; Hull et al., 1998; Stephenson, 2012; Bui et al., 2020), but also between wild fish (Birkeland and Jakobsen, 1997). This is particularly true for adult males, which are likely stimulated to move between hosts to improve their reproductive chances, either because of lack of reproductive females on current host (Ritchie, 1997), too high competition from other adult males on the same host (Stephenson, 2012), or finding new reproductively active females once they have interacted with the females on their current host (Todd et al., 2005). This host switching behaviour is probably a voluntary action, which is also supported by the observation that lice were more likely to move to other fish in the dark, when susceptibility to predation was lower (Connors et al., 2011). However, involuntarily detachment can also occur, especially when farmed salmon are handled or crowded.

Handling procedures involving crowding (e.g. treatments, grading, splitting, transferring or harvesting) occur repeatedly throughout the production cycle for Atlantic salmon. The main purpose of crowding is to increase fish density and make it easier to collect or transfer fish (Føre et al., 2018). This is often done by either raising the net wall in gradual steps, using seine/cast nets, or a combination of both, to reduce the accessible cage volume (Føre et al., 2018; Stien et al., 2024). There are concerns that the mechanical impact from crowding where fish are brushing alongside each other, the net or other equipment, can lead to mobile lice voluntarily or involuntarily becoming detached from host fish and being released into the surrounding environment (Reynolds, 2014; Powell et al., 2015; Guttu et al., 2024). Few studies have captured how many lice are actually detached from fish during crowding, but there have been reports of reductions in lice numbers after fish were pumped from the cage, but before being exposed to treatments, ranging from 22–70 % (Reynolds, 2014; Powell et al., 2015; Guttu et al., 2024, 2025). Additionally, there are indications that the total number of lice on the fish can be reduced with increasing crowding time (unpublished data, Lars H. Stien et al.) and a sudden increase in the abundance of mobile lice in submerged cages following treatment of neighbouring surface cages (Olafsen et al., 2021).

The infestation risk posed by detached mobile lice depends on how long mobile lice can survive without a host while remaining at a suitable depth to encounter a new host, as well as their ability to intercept and attach once a new host is encountered. Mobile lice can survive without a host for days to weeks, depending on the life stage and temperature (Andrews and Horsberg, 2020; Dalvin et al., 2025). Further unpublished data based on sinking rates between 0.5–1.5 cm reveals a clear risk of reinfestation to cages at the farm of origin, but possibly further depending on currents and tides (Barrett et al., 2025a). Lastly, the reinfestation success of mobile salmon lice after detachment has been observed to range between 40–100 % (Barrett et al., 2025a; Dalvin et al., 2025). Based on this, mobile lice lost from fish can be expected to survive for extended periods, be transported over long distances and infest new hosts. This poses a serious risk for the salmon industry, as treatments and other handling procedures can increase lice infestation in the surrounding environment. There is a need to understand how many lice detach during handling procedures such as crowding and to develop methods to collect them or otherwise prevent their spread.

Here, we estimated stage-specific rates of detachment from fish during four different crowding trials, and simultaneously documented the use of a commercially available louse collection crowding net intended to reduce detachment and/or loss of mobile lice during crowding. We use the term ‘detachment’ to describe both voluntary and involuntary processes, and ‘loss’ where detached lice escape into the surrounding environment rather than being collected. Proper characterisation of detachment, loss and collection rates using crowding nets will support the optimisation of handling and crowding procedures, limiting releases of mobile lice into the environment while maintaining or improving welfare outcomes.

2. Methods

The study was carried out at the Institute of Marine Research sea-cage farm in Austevoll (Norway; 60°05’17.8"N 5°15’55.8"E). It consisted of four different crowding trials, to test two different crowding nets under different conditions, the detachment of mobile salmon lice and possibilities to collect them. The four trials differed in terms of crowding time, fish size and louse density spanning from short time trials with small fish to more commercially realistic crowding with large fish and two hours crowding time (Table 1; Table S1). Salmon were reared and fed following standard procedures for salmon aquaculture. All crowding and sampling were done following standard farm practices, with guidelines from the relevant national authority (The Norwegian Food Safety Authorities) and thus no special permission was necessary.

2.1. *Experimental setup*

Fish were crowded using either a standard coarse seine/cast net (5 m × 5 m, nominal mesh opening 30 mm) or a more fine-meshed nylon net (catchLICE: 5 m × 6 m, nominal mesh size 2 mm; Askvik Aqua AS and OK Marine AS) to potentially reduce injuries, detachment of lice and collect lice that are detached. For each of the four trials, three replicate crowding events was performed with both crowding nets (Table 1). Only naïve individuals were used in each crowding replicate as all crowded fish were removed and euthanised during sampling. Crowding intensity were planned to be at level 3–4 on the 1–5 (good-unacceptable) scale (Noble et al., 2018; Stien et al., 2024) to resemble commercial crowding situations. However, in Trial 1 (9 August 2022) where only a few, small fish were crowded for 10 minutes, we only managed to reach level 1–2. Therefore, during Trial 2 (10 August 2022), more fish were crowded for a longer duration (1 h) to reach level 3–4. Unfortunately, this trial was only done with the catchLICE net. On 24–25 August 2022, Trial 3 was carried out with larger fish, but still 1 h crowding, while in Trial 4 (14–17 November 2023) more fish were crowded for 2 h (Table 1). Lice infestations in all four trials were natural, hence fish were infested with “wild” salmon lice copepodids from the surrounding water.

During each sample, two layers of netting were used: an inner crowding net (either the standard or the catchLICE net), and an outer finely meshed plankton net (350 μm; Fiizk AS) to collect any lice that passed through the crowding net. Each crowding event involved hanging the nets vertically within the cage, and then attracting fish to the surface by throwing feed pellets. When enough fish were visible near the surface, the bottom of the crowding net was brought up to the surface at the edge of the cage, creating an envelope that trapped the salmon. The plankton net was thereafter quickly introduced under the crowding net before further volume reduction created crowding next to a cage corner. This procedure mimic standard procedures at commercial fish farms. To keep crowding levels between 3–4 (Noble et al., 2018; Stien et al., 2024), regular disturbance was created by pulling at the net throughout the crowding period, simulating the gradual reduction of the available volume (as would occur if fish were being continuously removed from the crowding volume for treatment or transfer), and to provoke fish movement. Dissolved oxygen was monitored throughout and added if necessary to keep oxygen saturation above 80 %. This was only necessary when using the catchLICE net, for which an oxygen diffusor stone was placed at the net bottom.

In Trial 4, two pumps (FLYGT Ready 4 L, max 192 l/min) with protection grid and padding, were added inside and outside the crowding net with lice collecting filters mounted at the outlet. One pump was placed inside both crowding nets to collect lice and fish scales in the free water mass, mimicking a well-boat suction pump situation. The second pump was placed between the crowding net and plankton net, reducing the likelihood for some of the lice to potentially pass back into the crowding net, which could have otherwise caused the collection efficiency of the crowding net to be overestimated. Both pumps were positioned at the deepest part of the net to maximise collection rates.

Table 1
Overview of the conditions for each of the four trials. The measuring of net mesh openings for both net types were performed according to the Norwegian Standard (NS) 9415:2021.

Trial	Duration (min)	Replicate x treatment	Fish per replicate		Cage size (m^3)	Treatment 1			Treatment 2		
			Number	Size (kg)		Net type	Inner length (mm)	Inner height (mm)	Net type	Mesh opening (mm)	Bar length (mm)
1	10	3×2	7–10	0.5 ± 0.05	5 × 5 × 5	CatchLICE	1.98	3.39	Cast net	30.5	19.1
2	60	3×1	22–24	0.5 ± 0.05	5 × 5 × 5	CatchLICE	1.98	3.39	NA		
3	60	3×2	17–32	2.8 ± 0.03	5 × 5 × 5	CatchLICE	1.98	3.39	Cast net	30.5	19.1
4	120	3×2	60–108	2.7 ± 0.07	12 × 12 × 12	CatchLICE	1.98	3.39	Cast net	30.5	19.1

2.2. Sampling protocol

At the end of the crowding period in Trial 1–3, all fish were carefully netted out using a dip net and euthanized in individual buckets with a lethal dose of anaesthetic (Finquel MS-222, 500 mg/L). Mobile stages of salmon lice were counted and classified according to life stage: preadult I, preadult II (male and female) and adult (male, and female with and without egg-strings). *Caligus elongatus* were also recorded but was only present in Trial 4. After all fish were processed, the catchLICE and the plankton nets were carefully examined to count detached lice. At the start, the standard crowding net was examined repeatedly, but as no lice were found, further checks were random and still no lice were detected.

In Trial 4, fish were continuously sampled throughout the crowding period, to determine the temporal effect on detachment rates. All fish were carefully captured using a dip net, 2–3 fish at the time at regular intervals of approximately 30 fish per hour. After two hours of crowding, timely within recommended standard commercial procedures (RSPCA, 2021), all remaining fish were sampled. All fish were counted as in Trial 1–3 except that we used a common anaesthetic bath that was emptied through a lice collection filter and counted for lice after every 15 fish. The content from pump filters were collected and counted for lice halfway through the crowding (1 h) and at the end of crowding (2 h).

In addition to lice counts, length, weight and fish welfare scores were noted on all fish in Trials 1–3 and on 30 fish per crowding event in Trial 4. Fish welfare was evaluated according to the FISHWELL scoring system (Noble et al., 2018), with a scoring system from 0 = ideal, 1 = lightly affected, 2 = moderately affected to 3 = extremely affected.

2.3. Data analyses

All analyses were performed using R software v.4.4.1 (R Core Team, 2024). Unless otherwise stated, summary values are mean ± SE. We fitted generalised linear models using the glmmTMB package (Brooks et al., 2017; R Core Team, 2023), with model fit assessed via residual diagnostics from the DHARMa package (Hartig, 2019). Proportional detachment rates were compared between crowding net types (2 levels: standard, catchLICE) and louse classes (4–5 levels: pre-adult I, pre-adult II, adult male and adult female *L. salmonis* in all trials, and in Trial 4, also adult *C. elongatus*). It was expected that the catchLICE net would result in fewer lice falling off the fish, due to finer net and smaller mesh size. A net type × louse class interaction term was included, as the effect of the crowding net was expected to vary among louse classes. Because conditions differed substantially between trials (e.g., environmental conditions, infestation densities, crowding time, fish size), we fitted separate models to each trial. Crowding events were treated as statistical replicates, with detachment rates (proportion data) fitted as the response variable using a beta regression. To allow 0 s and 1 s to be fitted, we applied the following transformation to the response variable:

$$y_t = \frac{y \bullet (n-1) + 0.5}{n}$$

where n is the sample size of lice (Smithson and Verkuilen, 2006; Cribari-Neto and Zeileis, 2010). Collection rates of detached lice were compared between louse classes using the same approach as for detachment rates. It was expected that the catchLICE net would collect some smaller lice, and most adult female lice. Because the standard crowding nets were not checked for lice throughout (even though no lice were found inside or on standard crowding nets during early trials and random checks), we did not test for an effect of net type. We also did not fit a model to collection rates from Trial 1, as too few lice detached during that trial.

Two additional models were fitted to louse data from Trial 4, the first of which compared numbers of detached lice (count data) collected by filtering pumps placed inside or outside the crowding net, and as the filters were replaced halfway through the crowding procedure, also compared numbers of lice collected during the first (0–60 min) and second (60–120 min) half of the crowding procedure, while accounting for net type and louse class. The model therefore included terms for filter position (2 levels: inside, outside), filter number (2 levels: 0–60 min, 60–120 min), crowding net type, and louse class. Two- and three-way interactions were also tested between filter position, net type and louse class. A negative binomial model family provided a good fit. The second model compared remaining densities of lice on the fish sampled over the course of each crowding event. It was expected that fish sampled later in the crowding event would have fewer mobile lice remaining. The mean total infestation density (lice fish^{-1}) was used as the response variable, with crowding events as replicates. The model was specified with predictors for time (continuous, crowding duration to nearest ~15 min), net type, and louse species (2 levels: *L. salmonis*, *C. elongatus*). A Tweedie model family provided a good fit for the slightly zero-truncated distribution.

Four welfare indicators typically associated with crowding injuries (fin condition, scale loss, skin haemorrhaging, mouth/jaw/snout wounds) were compared between fish crowded using either the standard or catchLICE net. A single univariate model was fitted for each welfare indicator, with a factor for trial ID, and to account for differing crowding durations and fish sizes between trials, a net type × trial interaction term. Welfare indicators were represented by ordinal scores from 0 to 3 but were acceptably fitted by a gaussian model family.

3. Results

3.1. Environmental conditions during trials

During the three first trials in August temperature was between 14.8–16.6 °C at 5 m depth and had been stable at 14–16 °C the month prior to sampling. At Trial 4 in November, temperatures were between 10–11 °C at 5 m depth and had been decreasing from 13 °C about a month prior to sampling. Salinity ranged, between 30–32 ppt at 5 m depth in all trials.

3.2. Detachment of lice during crowding

Averaged across all trials (grand mean ± SE), detachment rates of salmon lice during crowding were 11.9 ± 4.4 %, and for individual trials (Trial 1–4) 2.3 ± 0.3 %, 7.0 ± 1.5 %, 21.2 ± 2.4 %, and 17.1 ± 2.2 %. Infestation densities varied between trials, from 6–31 lice fish^{-1}, ranged within same level for trial replicates (Table S1). Detachment rates varied between 1.8–37.5 % depending on the combination of louse stage, net type, and trial (Fig. 1A, S1). The detachment rate of *C. elongatus* during crowding was 20.3 ± 2.8 %, (Trial 4 only) (Fig. 1A). Across all four trials, detachment rates significantly differed among salmon louse stages (Fig. 2, Table S2). In general, pre-adult 1 had the highest likelihood of detaching from fish during crowding (20.0 ± 5.4 % averaged across all trials) and rates decreased as louse size increased (pre-adult 2: 13.3 ± 3.4 %; adult male: 8.6 ± 2.0 %; adult female: 8.2 ± 2.7 %) (Fig S1). There was no significant difference in detachment rates between the two crowding net types (Fig. 2, Table S2), with the exception of Trial 3, where more adult females were detached when using the standard crowding net than the catchLICE net (Fig. 2, Table S2, S3). Because several parameters were changed between each trial, it is difficult to isolate the effects of fish size and crowding time, but both may be influential. For instance, during Trial 1, with few, small fish and only 10 min crowding, very few lice became detached, and as crowding time, fish size and numbers were increased in later trials, detachment rates also increased (Fig. 1 A). More specifically, the detachment rate in Trial 3 was more than double that of Trial 2, which was run under similar conditions but with larger fish (Fig. 1 A). In Trial 4, the cumulative detachment rate increased with crowding time (Fig. 3, Table S4), which adds support to the previous observations that longer crowding time will lead to more detachment.

3.3. Collection of detached lice in catchLICE net

Collection rates in Trial 1 were not analysed due to insufficient numbers of detached lice. In Trial 2–4, adult females were captured by the catchLICE net at a higher rate than any of the other louse stages (Fig. 4, Table S5), with an average collection rate of 74.7 ± 13.5 % across the three last trials (Trial 2–4), while average rates for the other louse stages were below 20 % (preadult 1: 11.5 ± 11.5 %; preadult 2: 14.8 ± 10.9 %, adult male: 16.4 ± 10.2 %), regardless of differences in lice intensities between trials. No pre-adult 1 salmon lice were collected by the catchLICE net during either Trial 2 or 3 (Fig. 1B). Collection rate for *C. elongatus* was 31.3 ± 15.8 %, being collected at similar rates to the smaller mobile salmon louse stages, i.e. preadults and adult males (Fig. 1B, Table S6), based on counts from Trial 4 with inclusion of the pump. During Trial 4, there was a higher collection rate for all louse stages, whereby 24–68 % was collected by the pump inside the crowding net (Fig. 5). In accordance with the previous trials the number of preadult 1 and *Caligus elongatus* caught was similar regardless of net type, corresponding with the fine-meshed crowding net not trapping this louse size. However, a slightly higher proportion preadult 2, adult male, and especially adult female were captured by the pump inside the

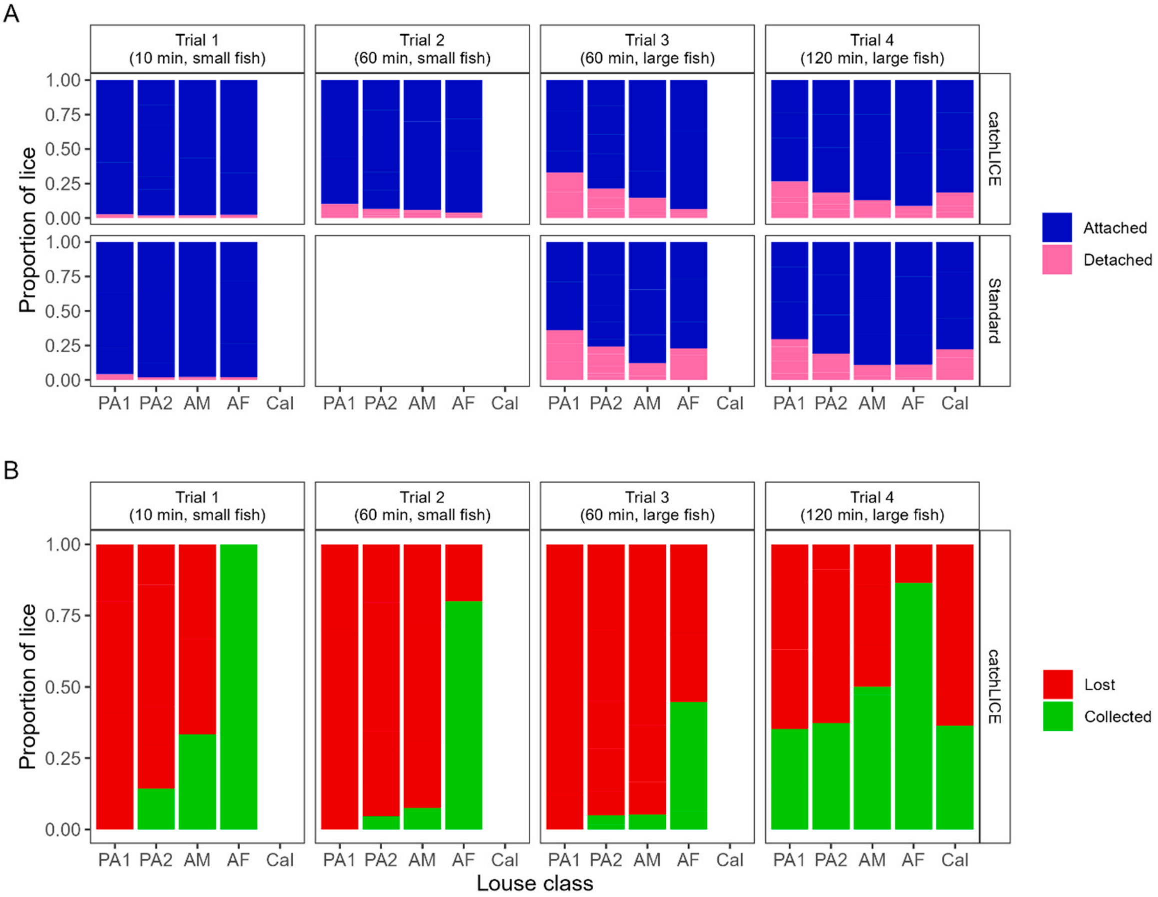

Fig. 1. Outcomes for mobile louse stages during crowding in Trials 1–4. (A) Initial outcome, showing the proportion of lice that either remained attached through crowding and were counted when their host was sampled from the crowding net ('Attached'), or detached during crowding ('Detached'). (B) Where the catchLICE net was used, secondary outcomes showing the proportion of detached lice that passed through the crowding net ('Lost') or were retained within the crowding net for collection ('Collected'). Within these trials, 'lost' lice were collected using a plankton net, yet in a typical crowding scenario, would have been lost into the surrounding environment. Louse classes denote: *Lepeophtheirus salmonis* life stages: PA1 = pre-adult I, PA2 = pre-adult II, AM = adult male, AF = adult female; Cal = *Caligus elongatus.*

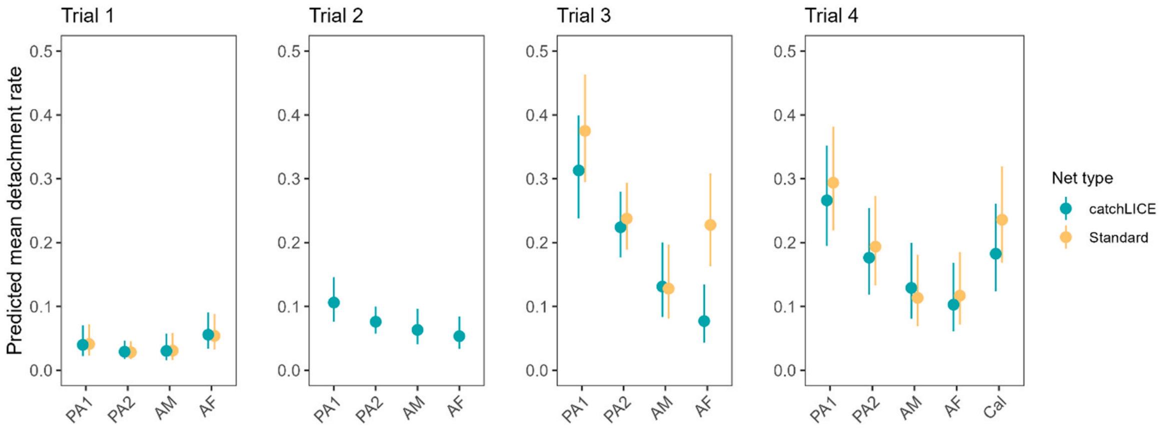

Fig. 2. Predicted mean detachment rates during crowding events in Trials 1–4. A separate model was fitted to detachment rates from each trial. Predictions are shown by crowding net type and louse class: *Lepeophtheirus salmonis* life stages: PA1 = pre-adult I, PA2 = pre-adult II, AM = adult male, AF = adult female; Cal = *Caligus elongatus* (only present in Trial 4). Error bars indicate 95 % confidence intervals.

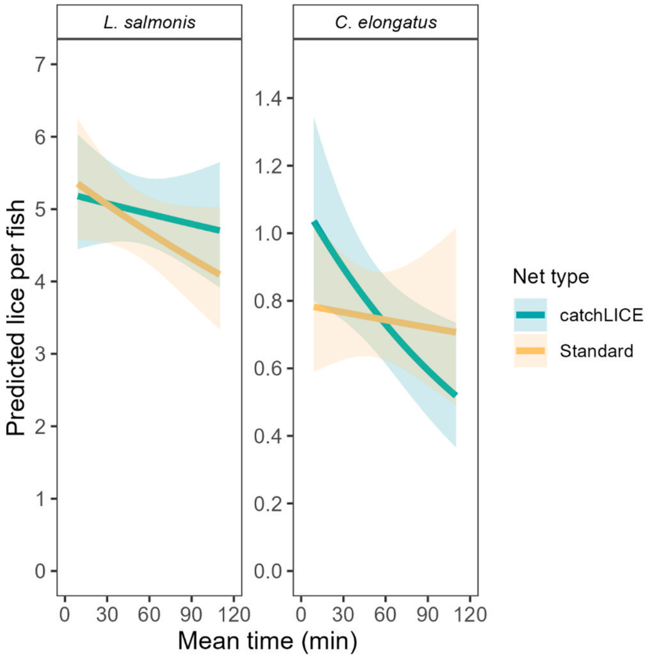

Fig. 3. *Predicted* mean lice per fish over time during the sampling for Trial 4. Fish were binned at ~15 min intervals during sampling, corresponding to increasing crowding time for fish that were sampled later. Salmon louse (*L. salmonis*) life stages were pooled, but separate counts were kept for salmon lice and *C. elongatus*. Marginal predictions are given according to louse species and crowding net type. Shaded ribbons indicate 95 % confidence interval.

catchLICE net than in the standard crowding nets (Fig. 5).

3.4. Fish welfare after crowding

The fish included in the trial exhibited good welfare, with most fish obtaining a score of either 0 (ideal) or 1 (lightly affected) (Fig. 6). In Trial 4, where salmon were crowded for the longest duration (2 h), fish crowded using the catchLICE net displayed slightly better welfare scores than those crowded using the standard crowding net (Fig. 6, Table S7). The only exception was snout damage, for which there was no difference between net types (Table S7). There were also differences in welfare outcomes between trials, with the main difference being that the smaller fish in the first two trials displayed better welfare scores for both snout damage and skin haemorrhage than the larger fish in the later trials (Fig. 6, Table S7).

4. Discussion

Detachment and loss of lice was observed across all four trials, ranging from 10-min crowding durations with small fish to 2-h crowding durations with larger fish. This indicates that any form of crowding and handling of fish poses a risk of releasing mobile lice into the surrounding environment. This introduces a new risk of reinfestation of lice on both wild and farmed salmon (Guttu et al., 2025), as salmon lice are able to survive for several weeks and have a high likelihood of reattaching if a host is encountered (Barrett et al., 2025a; Dalvin et al., 2025). Collection of detached adult females was relatively efficient using the catchLICE net (~75 %), while a different method may be required to reliably collect smaller louse stages.

Detachment rates during crowding varied considerably from 2–38 %, with an overall mean of 12 %, depending on several factors such as lice species, lice stage, crowding time and fish size. The findings are slightly lower than those from previous studies, which reported up to 30 % of mobile lice detaching due to crowding procedures on farms (Powell et al., 2015; Guttu et al., 2025). This was true even in the final trial, which most closely resembled commercial crowding conditions with larger fish and a 2-h crowding duration. One possible explanation could be that the previous studies were conducted in a commercial scale setting, with higher fish densities and likely more mechanical impact. For instance, in Powell et al. (2015) the last lice counting was done after fish had been pumped into the treatment vessel, subjecting them to additional crowding and mechanical stress through pumps, pipes and the water draining section. To our knowledge, ours is the only study that has focused solely on the impact of crowding, which is likely to be the primary cause of loss of mobile lice to the surrounding environment, as any lice that become detached during pumping would typically be retained by the filters on the boat. However, this study was conducted in a small-scale setting, and there was some indication that more lice were lost when larger salmon and more fish were crowded, possibly due to higher densities. In tanks, it has been observed that lice detachment was higher with many, small fish compared to few large fish, indicating that densities and number of fish has an influence on lice loss. The low fish numbers and densities in these trials, compared to large-scale commercial settings, could explain why less lice were observed to be lost here compared to previous studies. However, more data is needed to isolate the effects of fish size and higher fish densities on detachment rates.

There was large variation in detachment rates among life stages. Pre-adult 1 consistently had the highest detachment rate across all trials, regardless of fish size or crowding time, while adult males and females

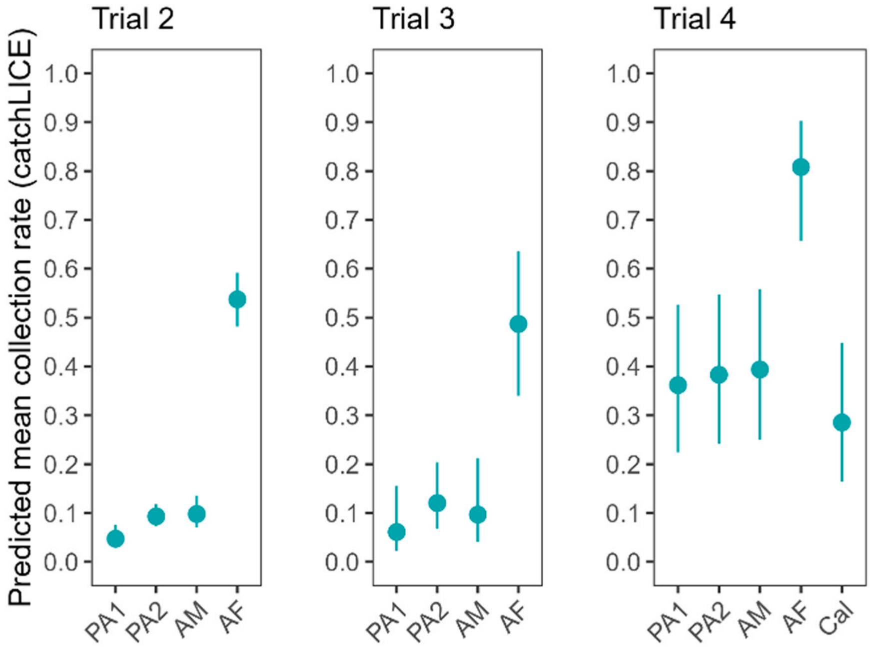

Fig. 4. *Predicted* mean collection rates of detached lice using the catchLICE crowding net in Trials 1–4. A separate model was fitted to collection rates from each trial. Predictions are shown by louse class: *Lepeophtheirus salmonis* life stages: PA1 = pre-adult I, PA2 = pre-adult II, AM = adult male, AF = adult female; Cal = *Caligus elongatus* (only present in Trial 4). Error bars indicate 95 % confidence intervals.

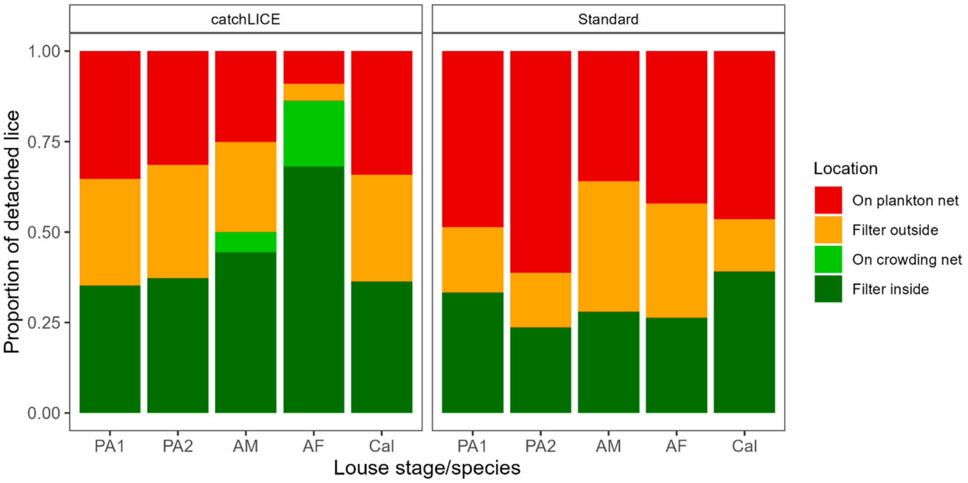

Fig. 5. *Detailed* outcome for mobile lice stages during trial 4, showing the proportions of detached lice that passed through the crowding net and was caught 'on the plankton net' or by the pump outside the crowding net ('Filter outside') and lice that were retained within the crowding net for collection ('On crowding net') or caught by the pump inside the fine-meshed crowding net ('Filter inside'). Within these trials, lice that passed through the crowding net were collected using a plankton net or 'Filter outside', yet in a typical crowding scenario, these would otherwise have been lost into the surrounding environment. Note, only the catchLICE net was checked for lice (the standard crowding net was not).

typically had the lowest detachment rates. This was even true over very different lice infestation levels, from more commercially realistic levels (5 lice per fish and 1 adult female) to very high lice levels (30 lice per fish and 8 adult females) which are almost never experienced during commercial production. No prior studies have compared detachment or loss rates by life stage, but Powell et al. (2015) similarly found that fewer adult females were lost from fish compared to a mix of pre-adults and adult males. Additionally, they observed that sessile lice were lost at twice the rate of mobile lice, and it was suggested that larger lice may be more resilient to mechanical impact, or they may attach to areas of the fish where they are less likely to be dislodged. Adult females and males are often found on more protected areas, such as the head region, along the dorsal line or in the area behind the anal or adipose fin (Wootten et al., 1982; Jaworski and Holm, 1992; Bui et al., 2020). Since adult females are larger and do not move around in search of mates, they can outcompete other lice and claim the best locations (Ritchie et al., 1996; Todd et al., 2000; Bui et al., 2022a). In contrast, adult males need to be more mobile in their search for mates, which may lead to suboptimal attachment sites (Todd et al., 2000; Bui et al., 2022a) or less secure attachment, potentially increasing their chances of detachment compared to adult females. This could also be the reason for high detachment rates of *C. elongatus*, which were similar to the rates for the smallest salmon louse stages (preadult 1 and preadult 2). *C. elongatus* are much less host specific than salmon lice and are more likely to move between hosts (Pike and Wadsworth, 1999; Øines et al., 2006), which may lead to higher detachment rates during crowding due to voluntary

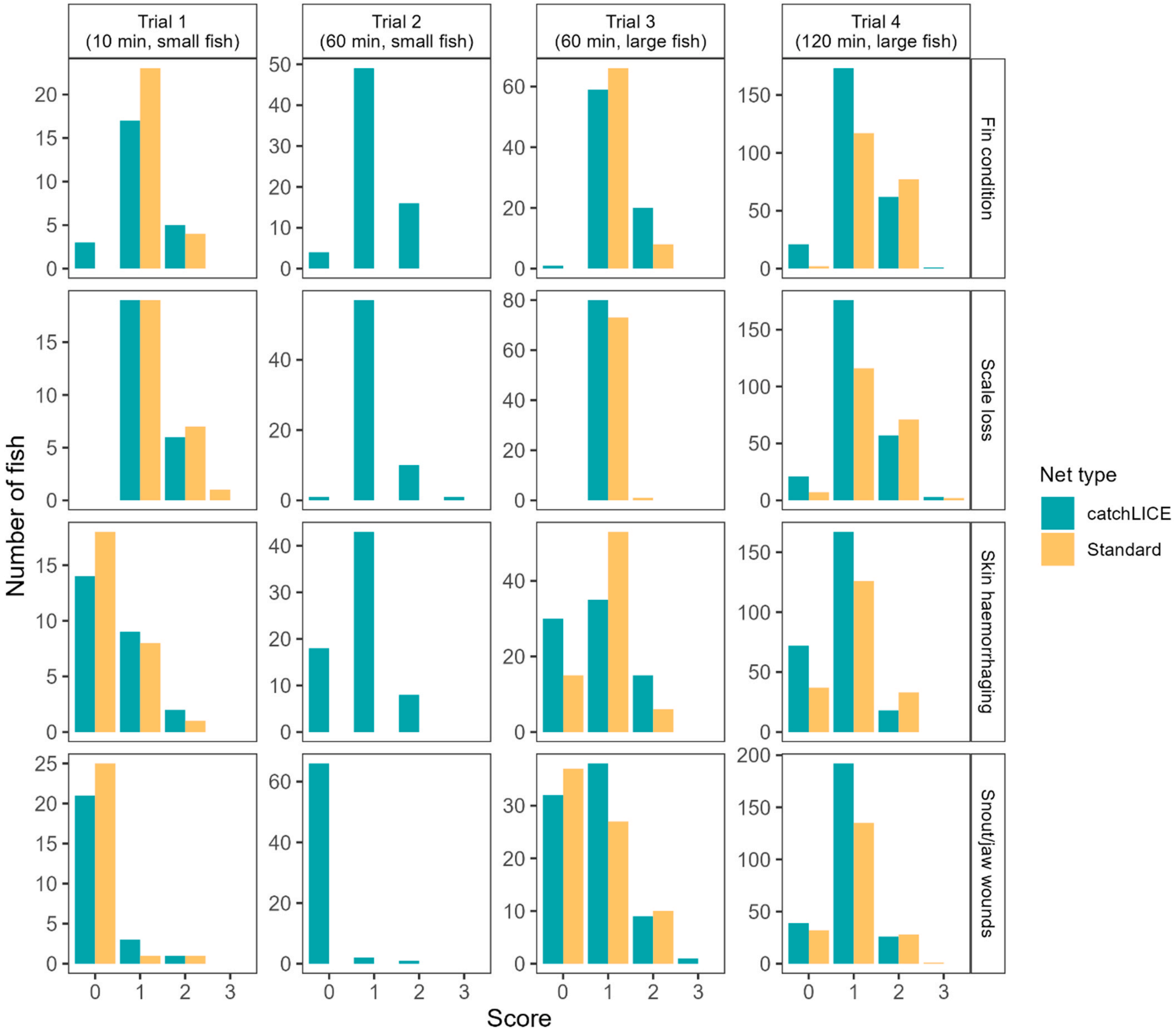

Fig. 6. *Distribution* of welfare scores among fish crowded using a standard seine net or catchLICE net in each of the four trials. Welfare metrics commonly associated with net abrasion are selected for display. Scores ranged from 0 = ideal, 1 = lightly affected, 2 = moderately affected to 3 = extremely affected. Note, only a catchLICE net was used in Trial 2.

host-switching and/or a vulnerability to dislodgment by mechanical forces. Data on the relative attachment strength of louse species, sexes and life stages are currently lacking.

There was no consistent difference in detachment rates between the standard crowding net and the catchLICE net. We expected that the catchLICE net, with its finer and more complex weave, would either dislodge more lice than standard nets due to increased contact area with the skin of the salmon, or fewer lice due to reduced peak mechanical forces. In practice, rates only differed during Trial 3, in which the standard net led to a significantly higher detachment rate of adult females than the catchLICE net.

Using a fine-meshed crowding net during crowding reduced the number of lice lost to the environment by an average of 30 %. Most of the lice collected were adult females (75 % collection rate). Adult females are by far the largest lice stage, with a cephalothorax width of 3.6–4.5 mm (Schram, 1993) making them very likely to be caught by the fine-meshed crowding net. In contrast, no pre-adult 1 lice and only a few pre-adult 2 and adult males were captured. The catchLICE mesh size, measured at 1.98 mm × 3.39 mm, likely allowed all preadult 1 (1.4–2.0 mm cephalothorax width) to pass through, as well as most pre-adult 2 (2.0–3.5 mm cephalothorax width) and adult males (2.5–3.3 mm cephalothorax width) (Schram, 1993). The observed collection rates were lower than those recorded in laboratory studies, where the catchLICE net retained 100 % of adult females (Barrett et al., 2025b). Reasons why more adult female individuals passed through the catchLICE net in this study may be due to greater deformation of either the net mesh or the lice exoskeleton, which is somewhat flexible under mechanical/hydromechanical forces (Christiane Eichner, pers. comm.). These forces may be more pronounced in a field setting. Adult *C. elongatus* were collected at the same rate as preadult 1 salmon lice in Trial 4. There were no *C. elongatus* present in previous trials without the pumps but based on their similarity in size (cephalothorax length 3.5–4.5 mm (Eichner et al., 2018; Hamre et al., 2024)) and collection rates of salmon lice preadult 1 in previous trials, it can be assumed that they would not be collected at a high rate by the catchLICE net itself. To achieve 100 % collection of all mobile stages of salmon lice and

C. elongatus, 0.8 mm square mesh openings would be required (Barrett et al., 2025b). However, this would significantly decrease water flow and could negatively impact oxygen levels within the net (this was also a challenge for the catchLICE net, which required oxygen bubbling during crowding to maintain adequate saturation). Additionally, logistically handling of the net would also become more challenging as the mesh size decreases, the net is more affected by water currents and more prone to fouling, although such issues may be solved by innovative designs or techniques. Having a suction pump inside the fine-meshed crowding net may improve lice capture, as the crowding net will slow their escape (especially larger lice stages), allowing more lice to be collected by the suction pump, while the suction pump may also create negative pressure inside the crowding net to further slow the loss of lice through the net. Additionally, salmon lice size are dependent on temperature, with lice generally growing larger at lower temperatures (Samsing et al., 2016). There was a slight difference in temperature between Trials 1–3 and Trial 4, which could have affected the size of salmon lice (larger in Trial 4 due to lower temperatures) and thereby collection rates, but likely not to a high degree.

Standard crowding nets were not checked during the trial, as it was time consuming and earlier checks had revealed no lice on the net. However, mobile salmon lice do sometimes prefer to attach to surfaces rather than remain swimming when off the host (pers. obs., all authors), and therefore some lice might have been missed if they were attached to the crowding net when it was taken out of the cage. The crowding net was always rinsed above the plankton net before being removed, so any lice attached to the crowding net would likely have been collected, but then registered as lice lost to the surrounding environment (along with all other lice found between the crowding net and plankton net). Accordingly, there is a possibility that standard crowding net could have a collection rate of more than 0 %. In an industrial setting, the fate of lice attached to the crowding net will depend on the handling of the net, including if or how it is rinsed.

When introducing new technology in the industry, it is important to maintain and assure good fish welfare. During delousing operations, crowding is considered to be a major factor contributing to poor fish welfare and increased mortality (Overton et al., 2019). In this study, salmon crowded for up 2 h within the catchLICE net experienced better welfare conditions than salmon crowded in a standard net. It is likely that smaller mesh sizes provide better support for fins and other body parts compared to larger meshes, leading to reduced fin splits (De Lestang et al., 2008; Lizée et al., 2018; Moltumyr et al., 2024). However, smaller meshes also increase the contact area with the fish, and could increase scale loss (Lizée et al., 2018). In the present study, fish crowded using the catchLICE net had similar or better skin condition compared to those in the standard crowding net. One possible explanation could be that the fine-meshed crowding net used in this study used very fine threads, woven into a complex, high surface area material, meaning there are fewer ‘pressure points’ than with a knotted mesh or one woven from coarser thread. Anecdotal reports from farmers also suggest that fish are calmer when crowded within the catchLICE net (pers. comm., Steffen Kildal, Askvik Aqua AS), and calmer fish are less likely to sustain injuries, even when crowded at high intensities (Stien et al., 2024). Although superficial skin damage during crowding might not be directly detrimental to the fish (Stien et al., 2024), it can increase vulnerability to secondary infections and further wound development (Ingerslev et al., 2010). Reducing these injuries could therefore greatly improve fish welfare following a crowding event. Differences in welfare outcomes between trials are likely due to fish size or accumulation of small injuries over a longer period in the cage.

This study provides clear evidence that mobile lice are lost from fish during crowding. Although there are still many uncertainties regarding their abilities to re-attach to salmon after being dislodged, there are strong indications that some lice will reattach (Dalvin et al., 2025; Guttu et al., 2025), however likely only within the farm of origin (Barrett et al., 2025a). There are several management strategies that could help mitigate the loss and spread of dislodged lice. Detachment of lice occurred over time, meaning that the longer fish were crowded, the more lice will be lost from the fish. Reducing the duration of crowding could therefore be an effective strategy to minimize the risk. Although not tested here, another strategy could be to use barriers, such as skirts around cages, to limit horizontal spread of lice until they have sunk below the depth of the barrier. However, the swimming depth of fish in neighbouring cages should be considered, especially if neighbouring cages are submerged or also have skirts – there have been reports of mobile lice reattaching to submerged fish after treatments of neighbouring standard cages (Olafsen et al., 2021). The aim should be to create a barrier or vertical mismatch between the detached mobile lice and fish in neighbouring cages. The most effective management practice would be to limit the number of lice released into the environment by using a relatively fine-meshed crowding net (catchLICE or other nets with a similar mesh size), preferably coupled with a suction pump inside the crowded volume to collect lice of all sizes and create a negative pressure gradient through the crowding net. Obviously, this will mean that all the water taken from the crowd and pumped into the well-boat or de-lousing system need to pass a filter that collect all mobile stages of the lice. Normally this would be used after the point where the pump water is separated from the fish for them to go into the well or delousing chambers. To illustrate the management effect of collecting lice during crowding a calculated example is given. In a cage with 200,000 salmon and a density of 0.5 adult females per fish, there would be 100,000 adult females. Based on findings from the present study, approximately 10 %, or 10,000 adult females, are likely to fall off during crowding. If 10 % of these re-attach and produce one pair of egg strings (around 570 eggs per pair; (Thompson et al., 2023), that would give rise to more than half a million new infectious copepodites within one to two weeks. Using a fine-meshed crowding net during crowding could capture 7500 of these adult females, reducing the potential egg production by over 400,000. If this approach were scaled across an entire farm or if all farms used fine-meshed crowding nets during crowding events, it would prevent the release of millions of adult females into the environment.

CRediT authorship contribution statement

Geitung Lena: Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Oppedal Frode:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Dahlgren Adele:** Writing – review & editing, Methodology, Investigation. **Nola Velimir:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Barrett Luke T.:** Writing – review & editing, Formal analysis, Data curation, Conceptualization. **Martinsen Line Vatne:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **Dalvin Sussie:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the staff at Austevoll research station for animal production, technical assistance and farm management during the trial, with special thanks to Simon Søreide, Andreas Habbestad and Glenn Sandtorv. Special thanks also to Florian Sambraus for excellent measurements of net mesh sizes. The experiment was funded by FHF project "Collection technology for lice that fall off during crowding and the ability of mobile lice to spread and reinfect new salmon (#901784) and

Institute of Marine Research (#14597–19). The work was conducted in accordance with the laws and regulations controlling experiments and procedures on live animals in Norway, following the Norwegian Regulations on Animal Experimentation 1996.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2025.102784.

Data availability

Data will be made available on request.

References

Abolofia, J., Asche, F., Wilen, J.E., 2017. The cost of lice: quantifying the impacts of parasitic sea lice on farmed salmon. Mar. Resour. Econ. 32, 329–349.

Andrews, M., Horsberg, T.E., 2020. Sensitivity towards low salinity determined by bioassay in the salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae). Aquaculture 514, 734511.

Barrett, L.T., Jensen, M.F., Dalvin, S., Oppedal, F., 2025a. Behaviour and dispersal of mobile salmon lice when detached from the host. Zenodo.

Barrett, L.T., Oppedal, F., Harvey, M., Eichner, C., Sambraus, F., Dalvin, S., 2025b. Collection rates of detached mobile sea lice according to net mesh and body size: a benchtop model. Aquacult. Eng. 110, 102514.

Birkeland, K., Jakobsen, P.J., 1997. Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. Environ. Biol. Fishes 49, 129–137.

Bjørn, P.A., Finstad, B., 1998. The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected post smolts of sea trout (*Salmo trutta*). Can. J. Zool. 76, 970–977.

Brandal, P.O., Egidius, E., Romslo, I., 1976. Host blood - major food component for parasitic copepod *Lepeophtheirus salmonis* Krøyer, 1838 (Crustacea: Caligidae). Norwegian. J. Zool. 24, 341–343.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9, 400.

Bui, S., Hamre, L.A., Skern-Mauritzen, R., Dalvin, S., Bron, J.E., 2022a. Sea lice behaviour. In: Bricknell, I.R., Bron, J.E. (Eds.), Sea lice biology and control. 5 m Books Ltd..

Bui, S., Madaro, A., Nilsson, J., Fjelldal, P.G., Iversen, M.H., Brinchman, M.F., Venås, B., Schrøder, M.B., Stien, L.H., 2022b. Warm water treatment increased mortality risk in salmon. Vet. Anim. Sci. 17, 100265.

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. J. Fish. Dis. 43, 697–706.

Bui, S., Oppedal, F., Stien, L., Dempster, T., 2016. Sea lice infestation level alters salmon swimming depth in sea-cages. Aquac. Environ. Interac 8, 429–435.

Connors, B.M., Lagasse, C., Dill, L.M., 2011. What's love got to do with it? Ontogenetic changes in drivers of dispersal in a marine ectoparasite. Behav. Ecol. 22, 588–593.

Costello, M.J., 2006. Ecology of sea lice parasitic on farmed and wild fish. Trends Parasitol. 22, 475–483.

Cribari-Neto, F., Zeileis, A., 2010. Beta Regression in R. J. Stat. Softw. 34, 1–24.

Dalvin, S., Oppedal, F., Harvey, M., Barrett, L.T., 2025. Salmon lice detached during aquaculture practices survive and can reinfest other hosts. Aquaculture 598, 742065.

De Lestang, P., Griffin, R., Allsop, Q., Grace, B.S., 2008. Effects of Two Different Landing Nets on Injuries to the Barramundi Lates calcarifer, an Iconic Australian Sport Fish. N. Am. J. Fish. Manag. 28, 1911–1915.

Dean, K.R., Aldrin, M., Qviller, L., Helgesen, K.O., Jansen, P.A., Bang Jensen, B., 2021. Simulated effects of increasing salmonid production on sea lice populations in Norway. Epidemics 37, 100508.

Dempster, T., Overton, K., Bui, S., Stien, L.H., Oppedal, F., Karlsen, Ø., Coates, A., Phillips, B.L., Barrett, L.T., 2021. Farmed salmonids drive the abundance, ecology and evolution of parasitic salmon lice in Norway. Aquac. Environ. Interac 13, 237–248.

Eichner, C., Dondrup, M., Nilsen, F., 2018. RNA sequencing reveals distinct gene expression patterns during the development of parasitic larval stages of the salmon louse (*Lepeophtheirus salmonis*). J. Fish. Dis. 41, 1005–1029.

Fjelldal, P.G., Hansen, T.J., Karlsen, Ø., 2020. Effects of laboratory salmon louse infection on osmoregulation, growth and survival in Atlantic salmon. Conservation. Physiology 8.

Føre, M., Svendsen, E., Alfredsen, J.A., Uglem, I., Bloecher, N., Sveier, H., Sunde, L.M., Frank, K., 2018. Using acoustic telemetry to monitor the effects of crowding and delousing procedures on farmed Atlantic salmon (*Salmo salar*). Aquaculture 495, 757–765.

Grimnes, A., Jakobsen, P.J., 1996. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. J. Fish. Biol. 48, 1179–1194.

Guttu, M., Båtnes, A.S., Aunsmo, A., Bjørnland, T., Olsen, Y., 2025. Detachment and re-attachment of Salmon lice during full-scale delousing operations on Salmon farms. Aquaculture 594, 741372.

Guttu, M., Gaasø, M., Båtnes, A.S., Olsen, Y., 2024. The decline in sea lice numbers during freshwater treatments in salmon aquaculture. Aquaculture 579, 740131.

Hamre, L.A., Dalvin, S., Myhre, G., Bui, S., 2024. Effect of temperature on development rate and egg production in *Caligus elongatus* and other sea louse species. Aquac. Environ. Interac 16, 227–240.

Hamre, L.A., Eichner, C., Caipang, C.M.A., Dalvin, S.T., Bron, J.E., Nilsen, F., Boxshall, G., Skern-Mauritzen, R., 2013. The salmon louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) life cycle has only two chalimus stages. PLoS One 8, e73539.

R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org.

Hartig, F., 2019. DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.2.

Hull, M.Q., Pike, A.W., Mordue, A.J., Rae, G.H., 1998. Patterns of pair formation and mating in an ectoparasitic caligid copepod *Lepeophtheirus salmonis* (Krøyer 1837): implications for its sensory and mating biology. Philos. Trans. R. Soc. Lond. B Biol. Sci. 353, 753–764.

Hvas, M., Bui, S., 2022. Energetic costs of ectoparasite infection in Atlantic salmon. J. Exp. Biol. 225.

Ingerslev, H.C., Lunder, T., Nielsen, M.E., 2010. Inflammatory and regenerative responses in salmonids following mechanical tissue damage and natural infection. Fish. Shellfish Immunol. 29, 440–450.

Iversen, A., Asche, F., Hermansen, Ø., Nystøyl, R., 2020. Production cost and competitiveness in major salmon farming countries 2003–2018. Aquaculture, 735089.

Jaworski, A., Holm, J.C., 1992. Distribution and structure of the population of sea lice, *Lepeophtheirus salmonis* Krøyer, on Atlantic salmon, *Salmo salar* L., under typical rearing conditions. Aquac. Res. 23, 577–589.

Kabata, Z., 1974. Mouth and mode of feeding of caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. J. Fish. Res. Board Can. 31, 1583–1588.

Kristoffersen, A.B., Qviller, L., Helgesen, K.O., Vollset, K.W., Viljugrein, H., Jansen, P.A., 2018. Quantitative risk assessment of salmon louse-induced mortality of seaward-migrating post-smolt Atlantic salmon. Epidemics 23, 19–33.

Krkošek, M., Connors, B.M., Morton, A., Lewis, M.A., Dill, L.M., Hilborn, R., 2011. Effects of parasites from salmon farms on productivity of wild salmon. Proc. Natl. Acad. Sci. 108, 14700–14704.

Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B., Todd, C.D., 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B: Biological Sciences. 280, 20122359.

Liu, Y., Bjelland, Hv, 2014. Estimating costs of sea lice control strategy in Norway. Prev. Vet. Med. 117, 469–477.

Lizée, T.W., Lennox, R.J., Ward, T.D., Brownscombe, J.W., Chapman, J.M., Danylchuk, A.J., Nowell, L.B., Cooke, S.J., 2018. Influence of Landing Net Mesh Type on Handling Time and Tissue Damage of Angled Brook Trout. N. Am. J. Fish. Manag. 38, 76–83.

Lovdata, 2012. Regulations on combating salmon lice in aquaculture facilities (in Norwegian: Forskrift om bekjempelse av lakselus i akvakulturanlegg) ⟨https://lovdata.no/dokument/SF/forskrift/2012-12-05-1140⟩ (accessed September 2020).

Moltumyr, L., Nilsson, J., Madaro, A., Seternes, T., Winger, F.A., Rønnestad, I., Stien, L.H., 2021. Long-term welfare effects of repeated warm water treatments on Atlantic salmon (*Salmo salar*). Aquaculture, 737670.

Moltumyr, L., Stien, L.H., Madaro, A., Nilsson, J., 2024. Increasing Dip Net Mesh Size Results in More Fin Splits in Post-Smolt Atlantic Salmon (*Salmo salar*. J. Appl. Anim. Welf. Sci. 27 (4), 666–678.

Myksvoll, M.S., Sandvik, A.D., Albretsen, J., Asplin, L., Johnsen, I.A., Karlsen, Ø., Kristensen, N.M., Melsom, A., Skardhamar, J., Ådlandsvik, B., 2018. Evaluation of a national operational salmon lice monitoring system—From physics to fish. PLoS One 13, e0201338.

Noble, C., Nilsson, J., Stien, L.H., Iversen, M.H., Kolarevic, J., Gismervik, K., 2018. Welfare Indicators for farmed Atlantic salmon: tools for assessing fish welfare. ⟨http://hdl.handle.net/11250/2575780⟩.

Øines, Ø., Simonsen, J.H., Knutsen, J.A., Heuch, P.A., 2006. Host preference of adult *Caligus elongatus* Nordmann in the laboratory and its implications for Atlantic cod aquaculture. J. Fish. Dis. 29, 167–174.

Olafsen, T., Holm, H., Ottesen, E., Tjølsen, J.I., Sæternes, R., Øren, T.-O., Oppedal, F., Walaunet, J., 2021. Rapport fra produksjon på lokaliteten Otervika 2021. Kunnskap fra utviklingsprosjektene. Fiskeridirektoratets utviklingstillatelser. ⟨www.fiskeridir.no⟩.

Overton, K., Dempster, T., Oppedal, F., Kristiansen, T.S., Gismervik, K., Stien, L.H., 2019. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. Rev. Aquac. 11, 1398–1417.

Pike, A.W., Wadsworth, S.L., 1999. Sealice on Salmonids: Their Biology and Control. In: Baker, J.R., Muller, R., Rollinson, D. (Eds.), Advances in Parasitology. Academic Press, pp. 233–337.

Powell, M.D., Reynolds, P., Kristensen, T., 2015. Freshwater treatment of amoebic gill disease and sea-lice in seawater salmon production: considerations of water chemistry and fish welfare in Norway. Aquaculture 448, 18.

R Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reynolds, P., 2014. Ferskvannsavlusing i brønnbåt: The use of freshwater to control infestations of the sea louse *Lepeophtheirus salmonis* K on Atlantic salmon *Salmo salar*

L. Report for NCE funded project in collaboration with Nova Sea: avlusing i ferskvann. Rapp. fra GIFAS.

Ritchie, G., 1997. The host transfer ability of *Lepeophtheirus salmonis* (Copepoda: Caligidae) from farmed Atlantic salmon. *Salmo salar* L. J. Fish. Dis. 20, 153–157.

Ritchie, G., Mordue, A.J., Pike, A.W., Rae, G.H., 1996. Observations on mating and reproductive behaviour of *Lepeophtheirus salmonis*, Krøyer (Copepoda: Caligidae). J. Exp. Mar. Biol. Ecol. 201, 285–298.

RSPCA, 2021. RSPCA welfare standards for farmed Atlantic salmon. RSPCA Horshum.

Samsing, F., Oppedal, F., Dalvin, S., Johnsen, I., Vågseth, T., Dempster, T., 2016. Salmon lice (*Lepeophtheirus salmonis*) development times, body size, and reproductive outputs follow universal models of temperature dependence. Can. J. Fish. Aquat. Sci. 73, 1841–1851.

Schram, T.A., 1993. Supplementary descriptions of the developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837)(Copepoda: Caligidae). In: Boxshall, G.A., Defaye, D. (Eds.), Pathogens of wild and farmed fish: sea lice. Ellis Horwood, New York, pp. 30–47.

Smithson, M., Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol. Methods 11, 54–71.

Stephenson, J.F., 2012. The chemical cues of male sea lice *Lepeophtheirus salmonis* encourage others to move between host Atlantic salmon *Salmo salar*. J. Fish. Biol. 81, 1118–1123.

Stien, L.H., Nilsson, J., Noble, C., Izquierdo-Gomez, D., Ytteborg, E., Timmerhaus, G., Madaro, A., 2024. Evaluating a crowding intensity scale and welfare indicators for Atlantic salmon in sea cages. Aquac. Rep. 37, 102211.

Thompson, C., Bui, S., Dalvin, S., Skern-Mauritzen, R., 2023. Disentangling the key drivers of salmon louse *Lepeophtheirus salmonis* fecundity using multiyear field samples. Aquac. Environ. Interac 15, 161–178.

Todd, C.D., Stevenson, R.J., Reinardy, H., Ritchie, M.G., 2005. Polyandry in the ectoparasitic copepod *Lepeophtheirus salmonis* despite complex precopulatory and postcopulatory mate-guarding. Mar. Ecol. Prog. Ser. 303, 225–234.

Todd, C.D., Walker, A.M., Hoyle, J.E., Northcott, S.J., Walker, A.F., Ritchie, M.G., 2000. Infestations of wild adult Atlantic salmon (*Salmo salar* L.) by the ectoparasitic copepod sea louse *Lepeophtheirus salmonis* Krøyer: prevalence, intensity and the spatial distribution of males and [2 pt] females on the host fish. Hydrobiologia 429, 181–196.

Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Horsberg, T. E., Jackson, D., 2013. Salmon lice - impact on wild salmonids and salmon aquaculture. J. Fish. Dis. 36, 171.

Tully, O., Nolan, D.T., 2002. A review of the population biology and host–parasite interactions of the sea louse *Lepeophtheirus salmonis* (Copepoda: Caligidae). Parasitology 124, 165–182.

Vollset, K.W., Dohoo, I., Karlsen, Ø., Halttunen, E., Kvamme, B.O., Finstad, B., Wennevik, V., Diserud, O.H., Bateman, A., Friedland, K.D., Mahlum, S., Jørgensen, C., Qviller, L., Krkošek, M., Åtland, Å., Barlaup, B.T., 2018. Disentangling the role of sea lice on the marine survival of Atlantic salmon. ICES J. Mar. Sci. 75, 50–60.

Walde, C.S., Bang Jensen, B., Stormoen, M., Asche, F., Misund, B., Pettersen, J.M., 2023. The economic impact of decreased mortality and increased growth associated with preventing, replacing or improving current methods for delousing farmed Atlantic salmon in Norway. Prev. Vet. Med. 221, 106062.

Walde, C.S., Jensen, B.B., Pettersen, J.M., Stormoen, M., 2021. Estimating cage-level mortality distributions following different delousing treatments of Atlantic salmon (*Salmo salar*) in Norway. J. Fish. Dis. 44, 899–912.

Walde, C.S., Stormoen, M., Pettersen, J.M., Persson, D., Røsæg, M.V., Jensen, B.B., 2022. How delousing affects the short-term growth of Atlantic salmon (*Salmo salar*). Aquaculture, 738720.

Wootten, R., Smith, J.W., Needham, E.A., 1982. Aspects of the biology of the parasitic copepods Lepeophtheirus salmonis and Caligus elongatus on farmed salmonids, and their treatment. Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences. 81, 185-197.