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Behavioural responses of wild anadromous Arctic char experimentally infested *in situ* with salmon lice

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Salmon lice can impact the marine behaviour, growth, and survival of salmonids, but little is known about their effects on Arctic char. We present behavioural responses from the first dose-response experiment with wild anadromous Arctic char ($n = 50$) infested *in situ* with salmon lice (0.0–1.2 lice g^{-1} fish) in an area with low natural infestations. Infested fish spent less time at sea (mean $\pm$ SD = 22 $\pm$ 6 d) than non-infested fish (mean $\pm$ SD = 33 $\pm$ 5 d), and a significant dose response was evident, with even very low louse burdens (<0.05 lice g^{-1} fish) reducing the marine feeding time. Furthermore, a negative correlation was present between time spent close to their native watercourse and parasite burden, suggesting that salmon lice influence the marine habitat use of Arctic char. No impact of salmon lice was evident on the return probability, i.e. marine survival. However, the presence of louse-induced mortality cannot be excluded as the modest sample size was only sufficient to detect extreme effects. Reduced marine feeding time and altered marine habitat use will likely have substantial negative effects on growth and fitness, suggesting that impacts of salmon lice must be considered in the conservation of anadromous Arctic char.

Keywords: Anadromous salmonids, aquaculture environment interactions, manipulative field experiments, marine feeding migration, parasite-induced behaviour, salmon lice.

Introduction

The increasing demand for fish has, in conjunction with the global decline in ocean fisheries, facilitated a >500% rise in aquaculture production since 1990 (FAO, 2020). Aquaculture currently constitutes ∼50% of the global aquatic food production and among the fishes cultured globally Atlantic salmon *Salmo salar* represents one of the most important species with a production of 2.5 million tonnes in 2018 (FAO, 2020). Atlantic salmon aquaculture is dominated by three countries, Norway, Chile, and Scotland, where fish are predominately raised in open marine cages within fjords and in coastal areas. This practice poses several environmental risks and among the key threats to the industry's sustainability is the transmission of salmon lice *Lepeophtheirus salmonis* from cultured Atlantic salmon to wild anadromous salmonids (Forseth *et al.*, 2017; Bøhn *et al.*, 2021; Shephard and Gargan, 2021).

Salmon lice are natural marine ectoparasites that feed on the skin and mucus of anadromous salmonids, causing osmoregulatory dysfunction, physiological stress, growth reduction, behavioural changes, compromised reproduction, and increased mortality (Wells *et al.*, 2006; Tveiten *et al.*, 2010; Bøhn *et al.*, 2020; Fjelldal *et al.*, 2020; Serra-Llinares *et al.*, 2020). Although disentangling the negative effect of salmon louse infestation from other factors can be challenging in natural environments, it is well documented that infestations can alter the physiology, behaviour, and increase the mortality of anadromous salmonids in areas with Atlantic salmon aquaculture (Bjørn *et al.*, 2001; Krkošek *et al.*, 2011; Bøhn *et al.*, 2020).

How salmon lice impact wild salmonids depend on the timing of the marine migration, as well as species' migratory and life history strategy. For Atlantic salmon, an obligate anadromous species with rapid migrations toward the open ocean, the most important consequence of high infestations is reduced survival (Vollset *et al.*, 2016; Bøhn *et al.*, 2020). Although louse-induced mortality may also impact facultative anadromous species with coastal migrations (Shephard and Gargan, 2021), the negative effects of salmon lice are often less direct. For sea trout *Salmo trutta*, infested fish may respond by residing closer to their natal river or by returning prematurely to fresh water (Birkeland and Jakobsen, 1997; Halttunen *et al.*, 2018; Serra-Llinares *et al.*, 2020). This reduction in marine habitats and marine feeding times will likely curtail individual growth, which in turn may reduce fecundity and impose significant long-term population effects (Halttunen *et al.*, 2018; Finstad *et al.*, 2021).

Among the salmonids with an anadromous life history, Arctic char *Salvelinus alpinus* is especially well adapted to live in cold waters, with anadromous populations present in Arctic Canada, Greenland, subarctic regions of Norway and Russia, and the Svalbard Archipelago (Jørgensen and Johnsen, 2014). Anadromous Arctic char typically enter the marine environment in early summer and reside in the marine environment for 30–60 d before returning to fresh water for overwintering (Berg and Berg, 1993; Jensen *et al.*, 2020). Although the number of juvenile migrations may vary both within and among populations, Arctic char commonly reach maturation 2–4 years after entering the marine environment as post-smolts
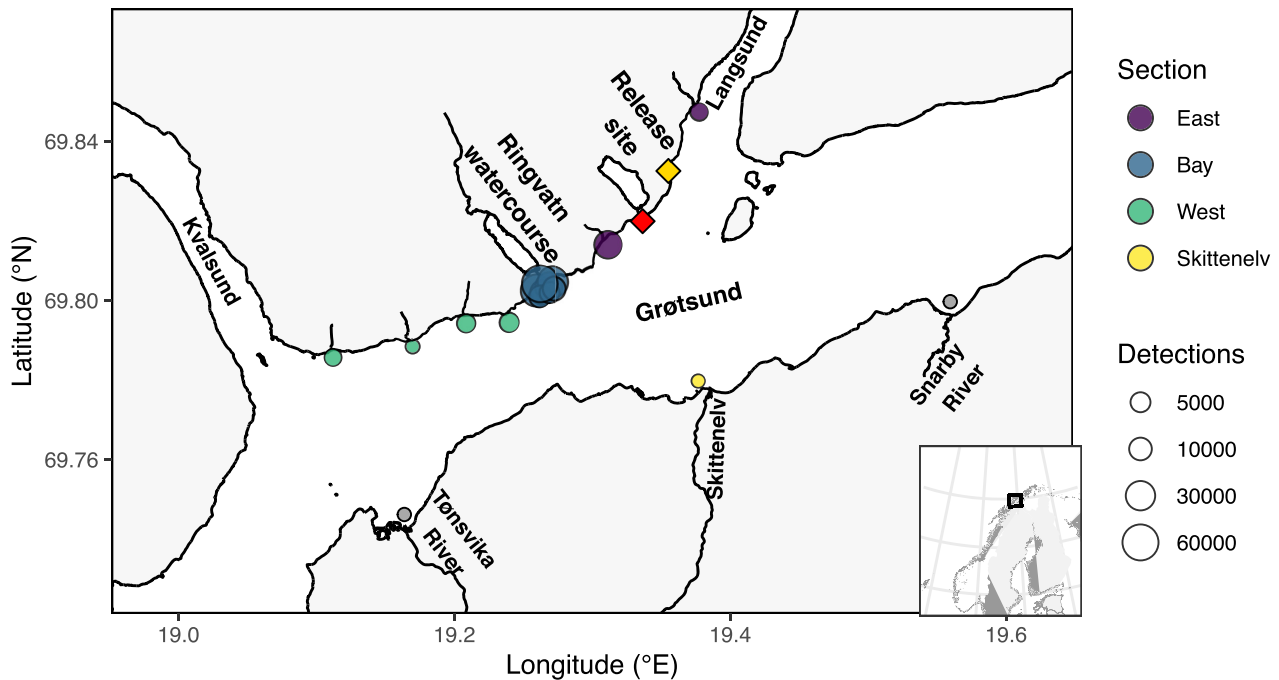
Figure 1. Map of the Ringvatn watercourse and the surrounding marine area. Points show the positions of the acoustic receivers, with number of detections and section coded by size and colour. Yellow diamond denotes the release site. Receivers with no detections are shown in grey and the receiver lost is denoted by a red diamond. Inserted map depicts the position of the Ringvatn watercourse (black square) in Fennoscandia.

(Jensen *et al.*, 2020). During the marine migration, Arctic char primarily utilize near shore habitats within 30 km of their origin, with individuals typically residing in estuary and marine waters close to their natal watercourse (Spares *et al.*, 2015; Atencio *et al.*, 2021).

In Norway, most anadromous populations of Arctic char are found above 65°N (Nordeng, 1983; Jørgensen and Johnsen, 2014). Compared to more southern parts of the Norwegian coast, these high-latitude areas contain a lower density of Atlantic salmon farms and lower sea temperatures, which are less favourable for the development and infectivity of salmon lice (Samsing *et al.*, 2016; Dalvin *et al.*, 2020). This means that the salmon louse spill over from aquaculture to wild salmonids is generally lower at high latitudes (Anon, 2019; Johnsen *et al.*, 2021). However, the expected northward expansion of the Norwegian aquaculture industry (Vollset *et al.*, 2020) and the predicted sea temperature rise in the North Atlantic (Alexander *et al.*, 2018), suggest that Arctic char's exposure to salmon lice will increase substantially in the future.

Here, we investigate the impacts of salmon lice on the marine migration of anadromous Arctic char, by experimentally infesting fish along a continuum of salmon louse burdens and study their behaviour using acoustic telemetry. The study was conducted in an area of northern Norway (69.8057°N 19.2601°E) with a very low salmon louse infestation pressure to minimize the risk of additional infestations. A novel part of our study was that we counted the number of salmon lice on each individual fish post-handling. Hence, we were able to measure and test dose-dependent effects with greater accuracy compared to previous studies on sea trout, where parasite burdens have been group based and inferred from louse counts on either observational data (Halttunen *et al.*, 2018) or reference fish (Serra-Llinares *et al.*, 2020). Although little is known of the effect of salmon lice on the marine migration of Arctic

char, laboratory studies have indicated that physiological responses are triggered at very low parasite burdens (Tveiten *et al.*, 2010; Fjelldal *et al.*, 2019). Based on this, and evidence from *in-situ* experiments on wild sea trout (Serra-Llinares *et al.*, 2018, 2020), we expected that salmon lice will impact the marine survival, marine feeding time, and marine habitat use of anadromous Arctic char. Explicitly, we hypothesize that dose-dependent responses are present and that infested fish will display a reduce likelihood of returning to their native watercourse (H1), spend less time in the marine environment (H2), and reside closer to their home river while at sea (H3).

Material and methods

The handling of experimental animals complied with Norwegian animal welfare laws, guidelines, and policies. The project was approved by the Norwegian Food Safety Authority (permit FOTS ID 23011).

Study area

The study took place in the Ringvatn watercourse (69.8057°N 19.2601°E) and the surrounding marine area from June to October 2021 (Figure 1). The watercourse is located on the southern side of the island of Ringvassøya, which is separated from the Norwegian mainland by the Grøtsund strait, and from the islands of Kvaløya and Reinøya by the Kvalsund and Langsund strait, respectively (Figure 1). The marine areas surrounding the Ringvatn watercourse have a very low density of salmon lice (http://www.hi.no/forskning/marine-dat a-forskningsdata/lakseluskart/html/lakseluskart.html) and in 2021 only two commercial Atlantic salmon farms were operating in Grøtsund, Kvalsund, and Langsund combined (https://portal.fiskeridir.no/portal/apps/webappviewer/index.html?id = 87d862c458774397a8466b148e3dd147).

Table 1. Overview of the anadromous Arctic char included in the infestation experiment.

Treatment	N	N_{OBS}	N_{STA}	N_{RET}	N_{RET2}	N_{UNK}	LF (mm)	Weight (g)	K- factor	Lice	Lice g^{-1}
Control	10	9	1	8	–	–	267 ± 23	164 ± 41	0.85 ± 0.04	–	–
Low	20	20	–	16	–	4	266 ± 19	155 ± 35	0.81 ± 0.04	11 ± 5	0.08 ± 0.04
High	20	19	–	13	1	5	261 ± 25	148 ± 41	0.80 ± 0.08	37 ± 16	0.30 ± 0.24
Total	50	48	1	37	1	9	264 ± 22	154 ± 38	0.82 ± 0.06	–	–

N refers to the number of fish assigned to each group, N_{OBS} refers to the number of fish observed after release, N_{STA} refers to the number of fish for which the tag became stationary, N_{RET} refers to the number of fish that returned to the Ringvatn watercourse, N_{RET2} refers to the number of fish last detected adjacent to other watercourses accessible to anadromous salmonids, and N_{UNK} refers to the number of fish lost in the marine environment. LF (mm), Weight (g), and K-factor denote the mean ± SD FL, weight in g, and condition factor (Fulton's Condition factor K). Lice denotes the mean salmon louse burden (i.e. the number of lice per infested fish) ± SD, and Lice g^{-1} denotes the mean weight-relative salmon louse infestation ± SD per gram fish.

The Ringvatn watercourse has a catchment area of 16 km^2 and consist of a 1-km river stretch that drains into a 0.9-km^2 lake situated 11 m above sea level, and a 0.4-km river which drains from the lake into the sea (Figure 1). A low migration barrier to the lake and the short outlet river makes the watercourse highly suitable for anadromous Arctic char (Kristoffersen, 1994). In addition to Arctic char, the watercourse holds resident and anadromous brown trout, as well as a small population of Atlantic salmon. Arctic char dominates the anadromous catch in the system, with 206 registered catches in 2019 and 2020, compared to 20 sea trout and 14 Atlantic salmon during the same period (www.scantura.no/fangstrapport).

Capture of out-migrating fish, artificial infestation, and tagging

Fish were captured by a non-permanent river trap, consisting of a fyke net tunnel, consecutive funnels, and a cylindrical storage tank (diameter 590, height 975 cm). The trap was connected to two modified resistance weird board side arms that closed the entire river's width. The trap was emptied at least once per day and fish were placed in holding tanks within the river for temporary storage (length 103, width 76, height 74 cm). The trap was operative from 28 May to 7 July, catching a total of 124 Arctic char, 27 brown trout, and 14 Atlantic salmon.

The salmon louse copepodids used for artificial infestation were produced by the Institute of Marine Research in Bergen, according to the procedure described by Hamre et al. (2009). After collection in the lab, copepodids were sent by plane from Bergen to Tromsø, before immediately being transported to the field site.

For the artificial infestation, 50 anadromous Arctic char, with fork lengths (FLs) from 186 to 312 mm (mean ± SD = 264 ± 22 mm) and body weights from 36 to 242 g (mean ± SD = 154 ± 38 mm), were randomly assigned to three transportable 300-L infestation tanks (length 85, width 65, height 55 cm) positioned at the riverbed filled with sea water pumped up from below the halocline (32.4 salinity, 8.3°C). The artificial infestation took place on 29 June, and all fish used in the experiment were captured within 2 d of infestation. After allowing the fish to acclimatize for 1 h, two of the infestation tanks, containing 20 Arctic char each, were treated with 4000 and 12000 salmon louse copepodids, respectively. The third tank, containing ten Arctic char, was sham treated and fish were not expose to salmon lice. During infestation, water circulation was stopped in all three tanks, and the water level kept at ~10 cm for 1 h. Following infestation, the tanks were refilled, and sea water was circulated every 2 h, for ~15 min, to ensure full oxygen saturation. Fish were kept overnight before further handling.

Prior to tagging, fish were transported ~5 km by car in a tank with oxygenated sea water from the Ringvatn watercourse to the release location (Figure 1). The release site was highly suitable for a controlled release and prevented fish from immediately returning to their native watercourse as a response to the handling. The tagging procedure was initiated by immersing fish in an aqueous solution of benzocaine (0.2 ml l^{-1}) for anesthetization. After an anesthetization period of ~3–6 min, a small incision was made on the ventral surface, posterior the pelvic girdle. Through the incision an individually coded acoustic tag (Vemco V7T-4x-69 kHz, length 21, diameter 7 mm, weight in water 0.9, weight in air 1.8 g), with no environmental sensors (e.g. pressure, temperature) was inserted. The incision was subsequently closed using a single silk suture (4/0 Ethicon). The entire tagging procedure lasted ~2–3 min. While the fish were gradually awakening from the anaesthetics, the number of attached salmon louse copepodids were counted in accordance with the protocols in the NALO-surveillance program (Bøhn et al., 2021). For fish from the control group, a sham count was conducted to ensure equal treatment of infestation groups. Total treatment time from start of anesthetization until release was ~10 min. In all steps of the process, we aimed to minimize the stress imposed on the fish to ensure natural behaviour and limit loss of copepodids. This meant that no scales samples were taken, and the life history stage of the fish remained unanswered. However, based on the FLs of the Arctic char (186–312 mm), we assumed that they were either first- or second-time migrants (Berg and Berg, 1993; Jensen et al., 2020). The entire tagging procedure was conducted on 30 June, 1 d after the artificial infestation.

For the exposed fish, the number of successfully attached salmon louse copepodids ranged from 4 to 57 (mean ± SD = 24 ± 17), which corresponded to weight-relative infestations ranging from 0.02 to 1.17 lice g^{-1} fish (mean ± SD = 0.19 ± 0.20 lice g^{-1} fish) (Table 1, Figure 2). Out of the 16000 copepodids used in the experiment, 975 attached to the fish, giving an infestation efficiency of 6.1%.

Receiver deployment

A total of 22 acoustic receivers (Vemco VR2W-69 kHz and VR2Tx-69 kHz) were deployed to quantify the migration of Arctic char from the Ringvatn watercourse (Figure 1). This included 19 receivers deployed in the marine environment and three receivers deployed in fresh water. The receivers deployed in fresh water included one receiver positioned in the lower part of the river and two within the lake. Of the 19 receivers deployed at sea, 16 were positioned on the northern side of Grøtsund and three were deployed on the strait's southern side (Figure 1). The receivers positioned in adjacency to Ringvassøya included a high density of receivers (n = 9)
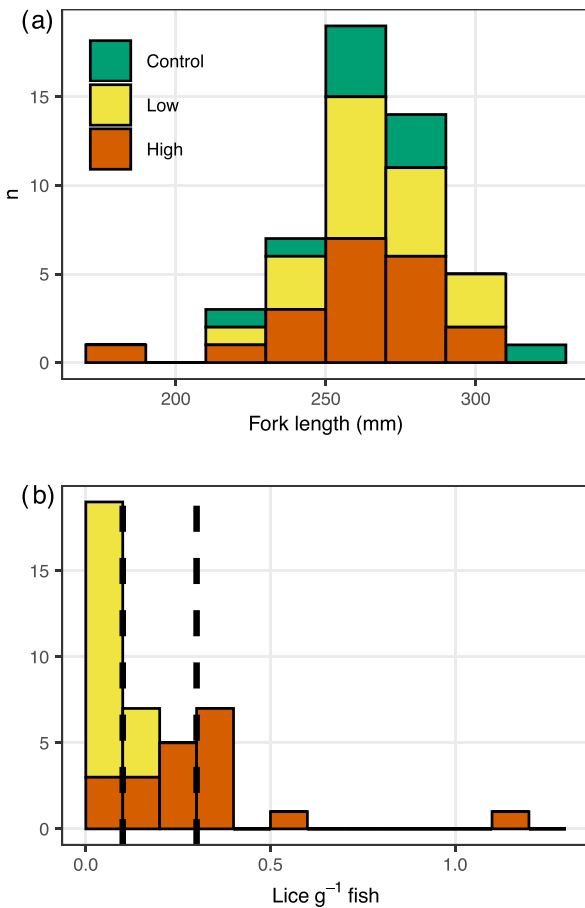
Figure 2. (a) Size distribution of anadromous Arctic charr included in the infestation experiment (n = 50) and (b) the weight-relative infestation (lice g^{-1} fish) for fish artificially infested with salmon lice copepodids (n = 40), colour coded by treatment group. Vertical stippled lines refer to infestation levels assumed to impact anadromous salmonids (0.1 lice g^{-1} fish) and cause severe health effects (0.3 lice g^{-1} fish) (Taranger *et al.*, 2015).

in the Ringvatn River bay, as well as receivers positioned strategically along the shoreline to cover the outlets of neighbouring rivers and streams, none of which are accessible to anadromous salmonids (Figure 1). These receivers were categorized based on their position: East section, Bay section, and West section (Figure 1). The three receivers deployed on the southern side of Grøtsund were deployed in the outlets of the Tønsvika River, Skittenelv, and Snarby River (Figure 1). These three rivers are all accessible to anadromous salmonids.

Data filtering
Of the 22 deployed receivers, 21 were successfully retrieved and downloaded, whereas one receiver deployed at sea was lost for unknown reasons (Figure 1). The downloaded data set was filtered manually before analyses were conducted. Only tag numbers corresponding to tags included in the study were evaluated and acoustic noise (*i.e.* tag IDs not included in the study) was removed from the data set without further evaluation. Of the 50 tagged Arctic char, 48 were detected by the acoustic receivers for periods ranging between 1 and 110 d (mean ± SD = 87 ± 42 d). This included a total of 920550 detections, whereof 244797 were in the marine environment.

Fate assessment
The fate of the Arctic char was assessed by examining individual detection plots. Based on their horizontal movements fish were classified as:

1. Stationary: When the tag was detected with regular intervals on a single receiver for a prolonged period lasting until the receiver was retrieved. This was considered indicative of either mortality or tag loss and the final Arctic char detection was defined as the last detection before the tag became stationary.
2. Return: When the fish was last detected within the Ringvatn watercourse.
3. Potential freshwater return: When the fish was last detected at a receiver positioned in the outlet of a river accessible to anadromous salmonids.
4. Unknown: When the fish disappeared before the end of the study.

Data analyses
All statistical analyses were conducted using the R software version 4.1.3.

Return to native watercourse
The impact of salmon lice on the probability of Arctic char to return to fresh water (H1) was investigated using a binomial generalized linear model (*GLM*, logit link function), with weight-relative infestation of salmon lice in lice g^{-1} fish (*Salmon lice*) and Fulton's Condition factor K (*Condition*) as predictor variables (Table 2).

Marine residency times
To investigate if salmon louse burden influenced marine residency times (H2), an accelerated failure-time (*AFT*) model was used (Table 2).

$$\log(\text{Time}_i) = \alpha + \beta_1 \text{Salmonlice}_{i} + \beta_2 \text{Condition}_i \text{Condition}_i + W_i.$$

The *AFT* model is a parametric survival model, where log(Time), denotes the logarithm of the time until an observable event, i.e. freshwater return; α denotes the model's intercept; β_n denote the regression coefficients; *Salmon lice* and *Condition* denote the weight-relative infestation of salmon lice in lice g^{-1} fish and Fulton's condition factor K, which were included as covariates in model; and W denotes the residuals. Like other survival models, the *AFT* model allows for right censoring, thus accounting for fish that were not observed to return to fresh water by the end of the study by censoring them at the time of their last observation. We opted for using this approach, rather than the Cox proportional hazard model that is frequently used for analysing survival-type telemetry data (Halttunen *et al.*, 2018; Serra-Llinares *et al.*, 2020), to ensure a more straightforward interpretation of how the covariates impact the time until the event (i.e. freshwater return) as this is defined as the response variable in the model. An important property of the *AFT* model is that the distribution of the residuals, W_i, must be specified *a priori* (Saikia and Pratim Barman, 2017). We assumed that W_i followed a Weibull distribution, which was verified graphically by comparing the model residuals against the extreme value distribution (Saikia and Pratim Barman, 2017). The fitting and validation of the

Table 2. Overview of statistical models used to describe impacts of salmon louse burden on the marine migration of Arctic char.

Model type	Response variable	Predictor variables	95% CI
GLM	Probability of freshwater return	*Salmon lice* (lice g^{-1} fish)	
		Condition (*K*-factor)	−1.263–23.212
AFT	Marine residency time	*Salmon lice* (lice g^{-1} fish) [†]	−1.58 to −0.67
		Condition (*K*-factor)	
GLM	Proportion of time spent in Bay section	*Salmon lice* (lice g^{-1} fish) [†]	−5.395 to −0.241
		Condition (*K*-factor)	

For the *GLMs*, 95% CI denotes the 95% bootstrap confidence intervals of the regression coefficients included in the most parsimonious models, whereas for the *AFT* model the parametric 95% CI is given. [†] denotes statistically significant predictor variables.

AFT model was done using the *survreg* and *survfit* functions from the *survival* package (Therneau, 2020).

Marine habitat use

To describe overall patterns in habitat use, a daily principal section was calculated for each fish. This metric was estimated by counting the number of times a fish was detected in each section and set to the section where the fish was most frequently observed (Figure 1). Only days when fish were detected were given a principal section.

To test if salmon louse burden influenced time spent near their native watercourse (<800 m) a binomial *GLM* was formalized (logit link function). In the *GLM*, the proportion of days the fish was located in the Bay section (i.e. daily principal section) was investigated, with weight-relative infestation of salmon lice in lice g^{-1} fish (*Salmon lice*) and Fulton's condition factor *K* (*Condition*) as predictor variables (Table 2). To account for overdispersion (i.e. variance > mean) the standard errors were corrected using a dispersion parameter φ.

Model selection and parameter significance

For the binomial *GLM* investigating the probability of Arctic char to return to their native watercourse, and for the *AFT* model investigating the marine residency time, model fit was assessed using the conditional Akaike Information Criterion values (AICc). In the binomial *GLM* investigating the proportion of days spent in the section closest to the native watercourse, the most parsimonious model was set as the model that produced the lowest quasi conditional AIC value (QAICc). AICc and QAICc values were estimated using the *AICc* function and *QAICc* function from the *MuMIn* package (Barton, 2020).

In the *GLMs*, parameter significance was determined by calculating parametric bootstrap *CIs* of the regression coefficients included in the most parsimonious models. The bootstrap procedure was conducted by drawing random samples from the most parsimonious model, with additional noise obtained from the model's residuals, and then fitting these pseudo samples using the same model structure. This sampling process was conducted 5000 times for each of the most parsimonious models, and based on the simulated regression coefficient, 95% *CIs* were estimated using the *bcaboot* function from the *bcaboot* package (Efron and Narasimhan, 2021). Regression parameters were considered significant if the 95% bootstrap *CIs* did not overlap zero.

Power analysis

To determine the effect size required to obtain a significant impact of salmon louse burden on the return probability, given our current sample size (*n* = 50), data was simulated using different *Salmon lice* coefficients. For all *Salmon lice*

coefficients, 5000 interactions were executed, in which fish were assigned a new status (returned or not returned) based on a probability derived from the observed salmon louse burden, the candidate effect size, and random noise derived from the observed model's residuals. Within each iteration, a binomial *GLM* was fitted to the simulated data. The structure of the binomial *GLM* was set to the model that provided the best fit (see Model selection) of all models that included *Salmon lice* as a predictor variable.

Using the same model, a second numerical experiment was conducted to estimate the sample size needed for the observed effect to be significant. Here, the sample was enhanced in increments of 20 fish, and for each sample size 5000 iterations were performed. Within each iteration, four of the pseudo samples were assigned zero salmon lice to represent the control group, while the remaining samples were given a salmon louse burden drawn from a log-normal distribution parameterized based on the weight-relative infestation of the infested fish included in the experiment (μ = -2.062, σ = 0.889). Parametrization of the log-normal distribution was done using the *fitdist* function from the *fitdistrplus* package (Delignette-Muller and Dutang, 2015). Based on these louse burdens, the estimated *Salmon lice* regression coefficient, and random noise derived from the model's residuals, individual probabilities were derived, individual statutes assigned, and a binomial *GLM* fitted. The thresholds required to obtain statistical significance was set as the first effect and sample size to obtain 95% bootstrap *CIs* not overlapping zero.

Results

Of the 50 tagged Arctic char, 48 were detected at sea, whereof 37 returned to the Ringvatn watercourse from 5 July to 6 August, after spending 5–37 d at sea. This corresponded to an overall return rate of 74%. For the non-returning fish, nine were lost at sea (i.e. unknown fate), one was fitted with a transmitter that eventually became stationary at the sea floor, and one individual was last detected in the Skittenelv estuary 21 d after release (Table 1).

Freshwater return

Of the 37 Arctic char returning to the Ringvatn watercourse, two fish (one from each infestation group) resided within the river for short periods (<24 h) before re-entering the marine environment. Both these individuals were last detected within their natal watercourse. All individuals that returned to the Ringvatn watercourse were last observed within the lake.

The percentage of freshwater returns was identical for the control group and the low infestation group, both with 80% (*n* = 8 and *n* = 16, respectively) returning to the Ringvatn watercourse. For the high infestation group, the percentage of

freshwater returns was somewhat lower, with 65% ($n = 13$) of the fish returning. No significant effect was evident of *Salmon lice* and *Condition* (Fulton's condition factor *K*) on Artic char's return probability, despite that the most parsimonious *GLM* (ΔAICc $= -1.00$) included *Condition* as a covariate ($\beta = 10.974$, 95% *CI* $= -1.263$–23.212, Table 2). The model with *Salmon lice* as the single predictor provided the second best fit, with a ΔAICc values of -0.54 compared to the null model.

The power analysis documented that for the effect of salmon louse burden to have a significant impact on the return probability, i.e. the 95% bootstrap *CIs* not overlapping zero, the *Salmon lice* coefficient had to be decreased from initial value of -2.644 (95% *CI* $= -6.539$–1.252) to -4.092 (95% *CI* $= -8.018$ to -0.165). This reflects a change from a 93.4% decrease in the return probability per unit increase in lice g^{-1} fish, to a 98.4% decrease. Furthermore, when increasing the sample size and fitting both the observed and simulated data to the same model (*Salmon lice* $\beta = -2.644$), it was evident that a sample of 110 fish was required for the effect of *Salmon lice* to be significant (95% *CI* $= -5.025$ to -0.262).

Marine residency time

For the 37 Arctic char that returned to the Ringvatn watercourse, a clear difference in marine residency time was evident between the control and treatment groups (Figure 3). Fish from the control group spent between 21 and 37 d in the marine environment (mean $\pm$ *SD* $= 32 \pm 5$ d), with 88% returning after >30 d sea. In contrast, the infested fish resided at sea between 5 and 31 d (mean $\pm$ *SD* $= 22 \pm 6$ d).

The influence of salmon louse burden on time spent in the marine environment was confirmed by the *AFT* model. The most parsimonious *AFT* model (ΔAICc $= -1.92$) included *Salmon lice* as the only predictor variable and documented a significant negative effect of *Salmon lice* on the time until freshwater return ($\beta \pm SE = -1.124 \pm 0.232$, *p*-value $< 10^{-5}$, Table 2). This estimated effect size corresponds to a 68% reduction in marine feeding time per increase in lice g^{-1} fish. No effect of *Condition* was evident (Table 2).

Marine habitat use

While present in the marine environment, the Arctic char were primarily detected close to the Ringvatn watercourse (Figure 1). Overall, 85% of detections occurred at receivers positioned close to their natal river, and of the 993 accumulated days Arctic char were situated in the marine environment, 500 had the Bay section as the principal section. Although a fidelity towards marine habitats adjacent to the Ringvatn watercourse was evident in all treatment groups, the percentage of marine days spent in the Bay section was greater for fish from the control group (mean $\pm$ *SD* $= 78 \pm 26\%$), than for fish from the low (mean $\pm$ *SD* $= 39 \pm 30\%$) and high infestation group (mean $\pm$ *SD* $= 33 \pm 33\%$) (Figure 4). Most fish in the control group were detected near their natal watercourse within few days after release (Figure 4a). In contrast, a substantial proportion of the fish from the infested groups stayed in the East section, near the release point, during the first 10 d after release (Figure 4b and c).

The tendency for fish with lower infestations to display a stronger fidelity towards the Bay section was confirmed by the *GLM*, where a negative relationship between the proportion of days spent in the Bay section and *Salmon lice* was evident
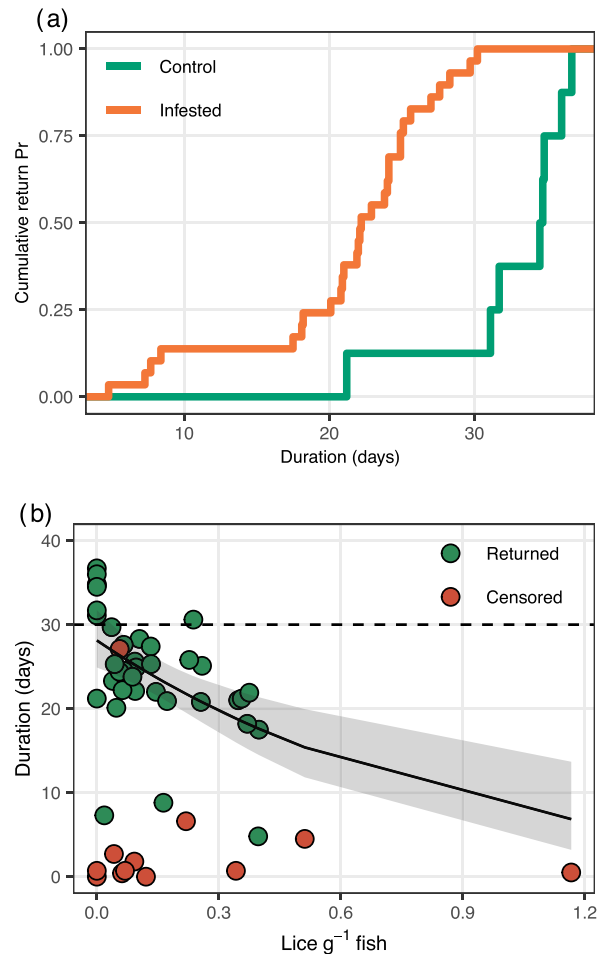

Figure 3. (a) Cumulative probability of return to the Ringvatn watercourse for anadromous Arctic charr infested with salmon lice and the control group. (b) Correlation between the marine feeding time and weigh-relative infestation (lice g^{-1} fish), colour coded by whether fish returned to fresh water or were lost at sea (i.e. censored at the time of last detection). Line depicts the regression line estimated by the accelerated failure-time (*AFT*) model, with shades representing the 99% confidence interval.

($\beta \pm SE = -2.818$, 95% bootstrap *CI* $= -5.395$ to -0.241) in the most parsimonious model (dispersion parameter $\varphi = 8.94$, ΔQAICc $= -0.84$, Table 2). No effect of *Condition* was evident (Table 2).

Discussion

Manipulative field experiments are considered especially valuable for revealing causality in scientific investigations, as they enable hypothesis testing at ecologically realistic scales (Barley and Meeuwig, 2017; Birnie-Gauvin *et al.*, 2020). By experimentally infesting anadromous Arctic char with salmon lice *in situ* at a location with very low infestation pressure and counting the number of lice attached to each fish posthandling, we were able to explicitly test our hypotheses for dose-dependent effects. This has to our knowledge never been done previously when studying the impacts of salmon lice on wild salmonids and refines earlier randomized field experiments, where group-based infestations have been inferred from either observational data or reference fish (Halttunen *et al.*, 2018; Serra-Llinares *et al.*, 2020). Despite a modest
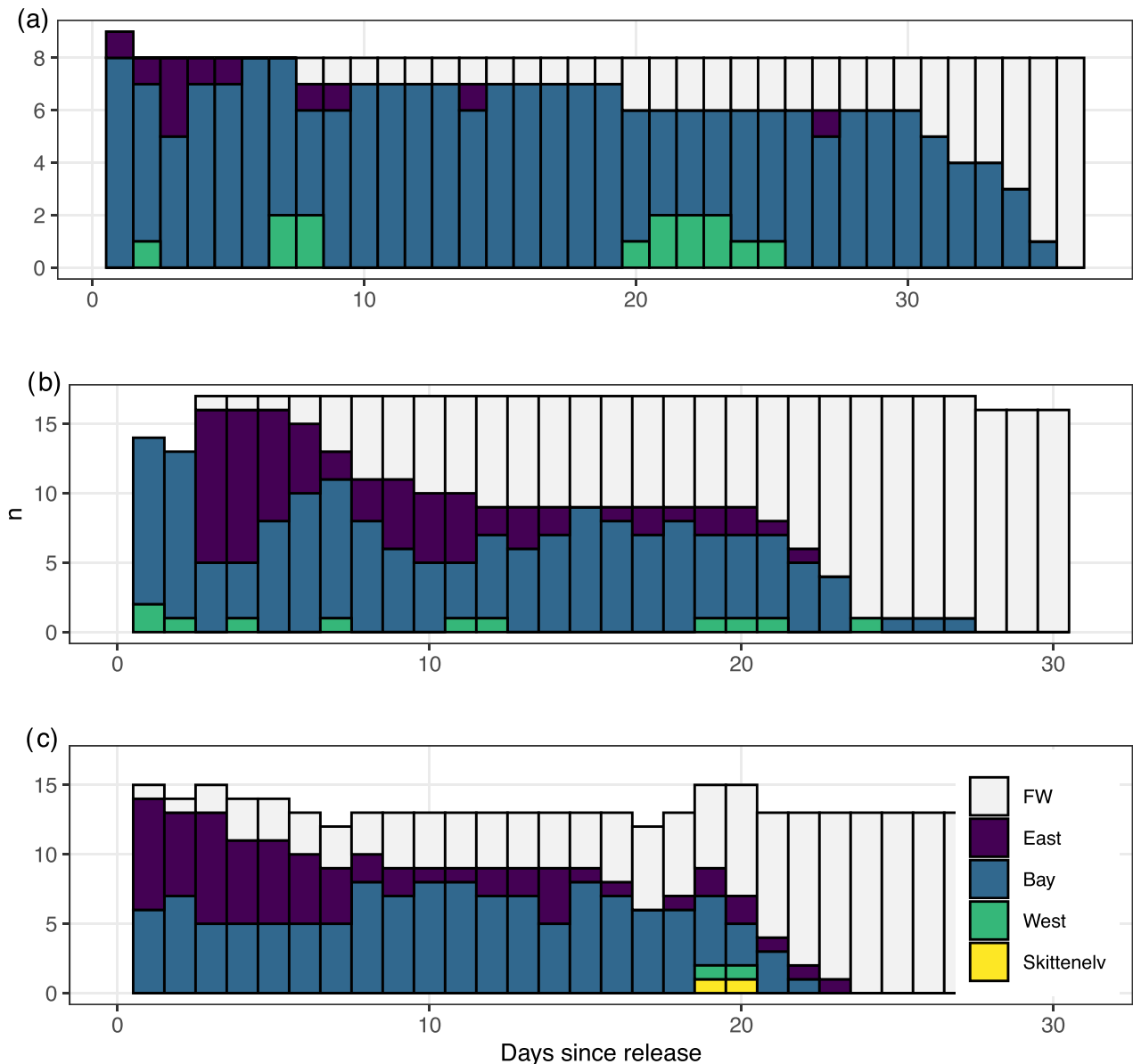
Figure 4. Marine habitat use of Arctic charr, with panels depicting the daily residency (daily principal section) of fish from (a) the control group, (b) the low infestation group, and (c) the high infestation group.

sample size, we demonstrate that salmon louse infestation causes significant changes in the behaviour of anadromous Arctic char, even at low infestation levels (i.e. <0.05 lice g^{-1} fish). In fact, it seemed like the presence of salmon lice initiated a behavioural change, highlighted by infested fish spending less time in the marine environment compared to non-infested individuals. While the observed behavioural changes could be attributed to logistical constraints related to the experimental design, with no replicates of the infestation groups, we argue that the presence of a dose-dependent response on both the marine feeding time and the marine habitat use suggests that the observed effects are representative of the impact of salmon louse infestations on anadromous Arctic char.

Return rate and marine survival

Anadromous Arctic char typically display a strong fidelity to their natal watershed if lentic habitats are available

(Jensen *et al.*, 2015). The presence of a lake within the Ringvatn watercourse, in combination with our study design, which included deployment of acoustic receivers covering all neighbouring rivers, suggest that most of the non-returning fish (26%) had died at sea and that the observed return rate is an appropriate proxy for marine survival. For Arctic char, marine mortality is greatest during the first migration and by using data from a northern Norwegian river spanning a 25-year period, Jensen *et al.* (2019) estimated that the mean marine survival increased from 33.6% in first-time migrants to exceeding 60 and 80% for second- and third-time migrants. Although the life history stage of the Arctic char in the present study was not determined, the size range (186–312 mm) indicates that these fish were either first- or second-time migrants. This suggest that the Arctic char included in the experiment experienced low mortality at sea as the observed survival of 74% exceeds the estimated marine survival for both these life stages in Jensen *et al.* (2019).

When comparing the experimental groups, fish from the high infestation group had a somewhat lower return rate (65%) than fish from the low infestation and control group (both 80%). Despite this, the effect of salmon louse burden on the return rate was not significant (H1). For Arctic charr posts-smolts, a recent laboratory experiment has documented that non-infested fish experienced higher survival compared to individuals parasitized with salmon lice (Fjelldal et al., 2019). While our results may suggest that the marine survival of wild Arctic char is not affected by salmon lice, the lack of a significant correlation between louse burden and return rate should be treated with great caution given the modest sample size. In the power analysis it was evident that to detect an impact of salmon lice on freshwater returns, an increase in either effect or sample size was required. In a series of *in-situ* infestation experiments with wild sea trout, the authors experienced similar challenges and significant louse-induced mortality was only evident at very high parasite burdens (average of 2.4 lice g^{-1} fish) and when data from multiple studies were included (Serra-Llinares et al., 2018, 2020). This indicates that an effect of salmon lice infestation on the marine survival may be difficult to prove in natural populations with limited sample sizes, if not individuals are exposed to very high parasite burdens.

Marine residency time

Facultative anadromous salmonids infested with salmon lice may return prematurely to fresh water to mitigate osmoregulatory stress imposed by salmon lice or for delousing (Birkeland and Jakobsen, 1997). In the present study, it was evident that even Arctic char with low infestations had a marked reduction in the time spent at sea, suggesting that this response was initiated at low parasite burdens. Moreover, fish with higher infestations showed a further dose-dependent reduction in marine feeding times. Hence, we find strong support for our hypothesis that Arctic char reduce the time spent in the marine environment when infested with salmon lice (H2). For Arctic char, the duration of the marine migration correlates with somatic growth and energy allocation (Jensen et al., 2018). By using the regression coefficients estimated from the relationship between somatic mass increase and marine residency time in Jensen et al. (2018), the observed 11-d (33%) reduction in marine feeding time of infested fish would represent a 30-g reduction in somatic growth. The loss of accumulated growth is likely further affected by negative impacts of salmon lice on the somatic growth rates. In a laboratory experiment, Tveiten et al. (2010) documented a significant decrease in growth rate for mature Arctic char with similar louse burden as in the present study (0.07–0.15 lice g^{-1} fish), with a more pronounced decay for those with greater infestations. A similar negative impact was observed in Arctic char post-smolts, where fish experienced negative growth rates at infestations >0.40 lice g^{-1} fish (Fjelldal et al., 2019).

Anadromous Arctic char depend strongly on numerous marine migrations to reach maturation (Jørgensen and Johnsen, 2014; Jensen et al., 2020). If salmon louse infestations persistently reduce the marine growth in Arctic char, individuals will likely delay maturation or mature at a smaller size at the cost of individual fecundity, given their phenotypically plastic maturation schedules (Klemetsen et al., 2003). Furthermore, in mature Arctic char, salmon louse infestations have been documented to reduce the proportion of maturing fish, postpone reproductive development, and decimate the egg quality of spawning females (Tveiten et al., 2010). All these responses will lead to reduced reproductive output and fitness, which ultimately will have negative population consequences.

Marine habitat use

We observed that Arctic char spent most their time in the marine environment close to their natal watercourse. When investigating the impact of salmon lice on the marine habitat use, it was evident that this fidelity was negatively correlated with parasite infestations, and we found no support of our hypothesis that increased salmon louse burdens will increase Arctic char's fidelity to marine habitats close to their home river (H3). In addition to spending a lower proportion of their time at sea close to their native watershed, infested Arctic char displayed a greater tendency to utilize areas close to release point during the initiation phase of the marine migration. While the impact of salmon lice on the marine habitat use of Arctic char has not been documented previously, sea trout have been observed to change their behaviour and display a more restricted migration both in infestation experiments and observational studies (Halttunen et al., 2018; Mohn et al., 2020; Serra-Llinares et al., 2020). The reasons why infested sea trout are attracted to fresh water overlap the mechanism causing premature freshwater returns, i.e. osmoregulatory disturbance and delousing (Bjørn et al., 2001; Wells et al., 2006), and while it is possible that the behavioural deviation observed by the infested fish is related to mitigating stress imposed by salmon lice, this cannot be stated with any certainty. Nevertheless, as the habitat use demonstrated by the control group arguably represents the population's natural behaviour, and salmon louse is the only treatment in our experiment, we suggest that the observed behavioural deviation is caused by the salmon louse infestation. To what extent this behavioural differentiation has any ecological consequences is unknown; however, previous studies on anadromous Arctic char have highlighted the importance of estuaries and bays for marine growth and survival (Spares et al., 2015; Atencio et al., 2021).

Multiple stressors

It is well documented that global climate change can have substantial impacts on anadromous salmonids (Mills et al., 2013; Crozier et al., 2021), and for Arctic char, elevated freshwater temperatures may decrease the overall prevalence of anadromy. This can occur if lentic habitats become sufficiently productive, causing a shift in the benefit of anadromy (Finstad and Hein, 2012), or if climate change favors less coldwater-adapted species as have been suggested to explain the declining catch of anadromous Arctic char in Norway and Iceland over the past decades (Svenning et al., 2021). Less is known on how climate change will impact the marine segment of the Arctic char life cycle, although it has been suggested that Arctic char shift their spatial distribution as a response to temperature, abandoning the inner fjord areas when temperatures reach a certain threshold (Jensen et al., 2014).

Moreover, climate change is likely to elevate the transmission of salmon lice from farmed to wild salmonids (Sandvik et al., 2021). Skern-Mauritzen et al. (2020) found both peak and integrated copepodid infectivity to increase by almost three

times when temperatures were elevated from 5 to 15°C. In addition, higher temperatures reduce the developmental time of salmon lice (Samsing *et al.*, 2016), whereas parasite loss remains limited up to 24°C (Dalvin *et al.*, 2020). If these effects are combined with the expected northward shift of the Norwegian aquaculture industry (Vollset *et al.*, 2020), Arctic char's exposure to salmon lice will increase substantially in the future, which, in turn, may impose severe risks for anadromous populations.

Conclusion

In the summary, we observed a negative impact of salmon louse burden on the marine feeding time of anadromous Arctic char, and that infested fish spent less time near their natal river. The experimentally infested Arctic char altered their marine behaviour at lower infestation levels than what have been assumed to impact salmonids (Taranger *et al.*, 2015) and at much lower levels than what is observed on sea trout along the Norwegian coast (Nilsen *et al.*, 2021). Although we observed no impact of salmon louse burden on the marine survival, the sample size was only sufficient to detect extremely large effects, meaning that small or moderate impacts may have remained undetected. In future studies, researchers should aim for larger sample sizes, with greater ability to detect possible mortality effects, to facilitate a complete understanding of the impacts of salmon louse on anadromous Arctic char. Nevertheless, we argue that results presented here highlight Arctic char's vulnerability to salmon louse infestations and that the observed negative effects of salmon lice on Arctic char behaviour represent a severe loss in growth opportunity. This will likely have a substantial negative impact on anadromous Arctic char, and future research should aim to provide quantitative data on the impacts of salmon lice on individual growth and fecundity to determine demographic population effects and the possible selection against anadromy. For sea trout, measurements of reduced marine living area and reduced marine feeding time have been suggested as sustainability indicators for first-time migrants (Finstad *et al.*, 2021). These sustainability indicators may also prove highly valuable in the conservation of anadromous Arctic char.

Author contributions

PAB, EEB, and TB designed the sampling. JFS, PAB, and TB conceived the idea for the manuscript. BS led the laboratory work with salmon lice. JFS analysed the data. JFS and TB interpreted the data. JFS led the writing of the manuscript, with contribution from TB, PAB, and LK. All authors approved the final version of the manuscript.

Conflict of interest statement

The authors have no conflicts of interest to declare.

Data availability statement

The data underlying this article is available at NMDC—norsk marint datasenter (https://nmdc.no) with the title "Arctic char experimentally infested *in situ* with salmon lice—Ringvatn watercourse 2021".

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