



RESEARCH ARTICLE

Salmon-lice as a potential threat to anadromous Arctic charr populations

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Abstract

Salmon-lice have the potential to change the behaviour and growth of their salmonid host species. Here, the baseline infection levels of salmon-lice of post-smolts ($n = 815$) and veteran migrants ($n = 875$) of sea-run Arctic charr (*Salvelinus alpinus* Linnaeus, 1758) were monitored over two successive years in a sub-Arctic Norwegian fjord without farming of salmonids. All Arctic charr were collected after the sea-migration period from a trap placed in the river, ascending to their overwintering freshwater habitat (Lake Laksvatn). The sea-lice infection showed a stable infection across the 2 years while increasing through the migration period and with the size of the wild sea-run Arctic charr. The prevalence of sea-lice infection was intermediate to high, and the intensities of sea-lice infections observed were generally modest, although some individuals had high infections. The relatively high infection of salmon-lice highlights the potential detrimental effects these parasites can have at both the individual and population level of such endangered sub-Arctic life-history strategies. A comparative study should be performed in fjords with aquaculture activity as focal points for salmon-lice, to investigate the impact farming have on sea-run Arctic charr populations.

KEYWORDS

Lepeophtheirus sp, post-smolt, prevalence, *Salvelinus alpinus*, veteran migrants

1 | INTRODUCTION

Sea-lice have for a long time been regarded as a threat to wild anadromous salmonids (Wagner et al., 2008) and have received attention as a potential cause of decreasing populations of sea-run salmonid fishes at northern latitudes in the most recent years (Forseth et al., 2017). Increasing aquaculture production has elevated the exposure of local wild salmonid populations to salmon-lice (Sandvik

et al., 2020; Serra-Llinares et al., 2014). Sea-lice are now regarded as a main cause of the collapse in many sea-trout (*Salmo trutta* Linnaeus, 1758) populations as the trout primarily migrate inside the fjords or inshore areas (Thorstad et al., 2015) where the highest density of salmon farms is located and act as focal points for lice larvae (e.g. Bøhn et al., 2020; Murray & Moriarty, 2021). Other sea-migratory species like Arctic charr (*Salvelinus alpinus* Linnaeus, 1758) hardly or ever leave coastal nearshore waters (Atencio et al., 2021;

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Klemetsen, Amundsen, et al., 2003; Moore et al., 2016) and therefore could potentially be severely affected by sea-lice as seen in sea-trout. The knowledge of infection pressure of sea-lice on anadromous Arctic charr is almost nonexistent (but see Bjørn et al., 2007; Bjørn & Finstad, 2002; Karbowski et al., 2019). Here, we report the first baseline salmon-lice infection level of post-smolts and veteran migrants' sea-run Arctic charr over two successive years from a sub-arctic Norwegian fjord without any fish farming and mandatory catch reports for the local fishermen.

Arctic charr is known to be the most cold water-adapted freshwater species (Elliott & Elliott, 2010). A review of field data from numerous European lakes suggests Arctic charr to be one of the species most affected by climate warming (Jeppesen et al., 2012; Svenning et al., 2022). As Arctic charr anadromous behaviour is only observed at high latitudes (Klemetsen, Amundsen, et al., 2003) and given the sensitivity of Arctic aquatic ecosystems (Hoegh-Guldberg & Bruno, 2010; Post et al., 2019), the anadromous life-history strategy in Arctic charr is increasingly vulnerable with ongoing climate change. Besides the vulnerable freshwater nursery environment, anadromous life-history renders salmonids more susceptible to potential negative effects of shifting temperatures, prey resources and competitors (Morrissey-McCaffrey et al., 2019) also in sub-Arctic fjord environments (e.g. Davidsen et al., 2017; Hodgson et al., 2020; Svenning et al., 2022).

An anadromous lifestyle depends on access to energy-rich marine resources (Gross et al., 1988), and the energetic gain must balance the migration costs such as altered competition, predation and parasitism (Chapman et al., 2012). Indeed, migration costs can be great as Arctic charr post-smolts in a population may exhibit high mortality (up to ~70%) during their first sea migration (Rikardsen et al., 1997). Parasites acquired through marine migration (e.g. through foraging) could be one cause of elevated mortality, but the infection knowledge of endogenous trophically transmitted parasites of sea-run charr is generally low (but see Bouillon & Dempson, 1989; Due & Curtis, 1995; Knudsen et al., 2011). Increased parasite exposure (e.g. to salmon-lice) is strongly associated with changes in fjord temperatures (Hoegh-Guldberg & Bruno, 2010) that may optimize lice development and thus become a crucial factor reducing the migratory benefit and drive these unique sea-run Arctic charr populations towards extinction.

Salmon-lice infecting salmonids in northern Norway consist of the host-specific *Lepeophtheirus salmonis salmonis* (Krøyer, 1837) and species from the host generalist genera *Caligus* spp. (see review by Hemmingsen et al., 2020). The development of sea-lice, thereby their recruitment output, is highly temperature dependent (e.g. Hamre et al., 2019). The exposure of sea-lice seems to be relatively similar across sea-trout and anadromous Arctic charr from northern Norwegian fjords (Bjørn et al., 2007; Bjørn & Finstad, 2002). As Arctic charr stays in the sea for only a short time (25–40 days; Atencio et al., 2021; Rikardsen et al., 1997) compared with other native salmonids (sea-trout and Atlantic salmon (*Salmo salar* Linnaeus, 1758)), and overwinter in a freshwater environment (but see Jensen & Rikardsen, 2012), the source community of salmon-lice must mainly be these other native salmonids and marine fishes inhabiting

the fjord. For instance, Atlantic cod (*Gadus morhua* Linnaeus, 1758), herring (*Clupea harengus* Linnaeus, 1758) and lumpfish (*Cyclopterus lumpus* Linnaeus, 1758) are known to be infected by *Caligus* spp. (e.g. Øines et al., 2006; Øines & Heuch, 2007).

High infestation levels of *L. salmonis* decrease the specific growth rates (SGR), increase the osmoregulatory impairment and mortality rates compared with uninfected control groups of Arctic charr post-smolts from laboratory experiments (Fjellidal et al., 2019; Tveiten et al., 2010). Moreover, osmoregulatory problems caused by salmon-lice can force sea-trout infected post-smolts to return prematurely to brackish water (e.g. Thorstad et al., 2015; Wells et al., 2007) or cause behaviour alterations while in the marine environment (Gjelland et al., 2014). Similar effects could also appear in Arctic charr post-smolts and possibly show even more severe effects than co-occurring sea-trout as Arctic charr have smaller and fewer scales and thus are less morphologically protected from salmon-lice infections. Additionally, wounds from salmon-lice can make Arctic charr highly vulnerable to secondary infections (i.e. pathogenic bacteria, fungus) when returning to their freshwater overwintering habitats (e.g. Llewellyn et al., 2017). Therefore, anadromous Arctic charr may be more severely impacted by salmon-lice than other co-occurring native salmonids in northern Norway.

The aim of this two-year study was to establish a baseline infection level of salmon-lice for Arctic charr captured promptly after their sea migration in a sub-arctic marine ecosystem without salmonid farming. We first hypothesized that a high proportion of the sea-migratory Arctic charr is infected by salmon-lice. We secondly hypothesized that there is a high stability of salmon-lice infection between studied years. Thirdly, we hypothesized that veteran migrants had higher infections (prevalence and abundance) than first-year migrants (post-smolts). Last, we hypothesized a generally higher infection for the latest homecoming fish.

2 | MATERIAL AND METHODS

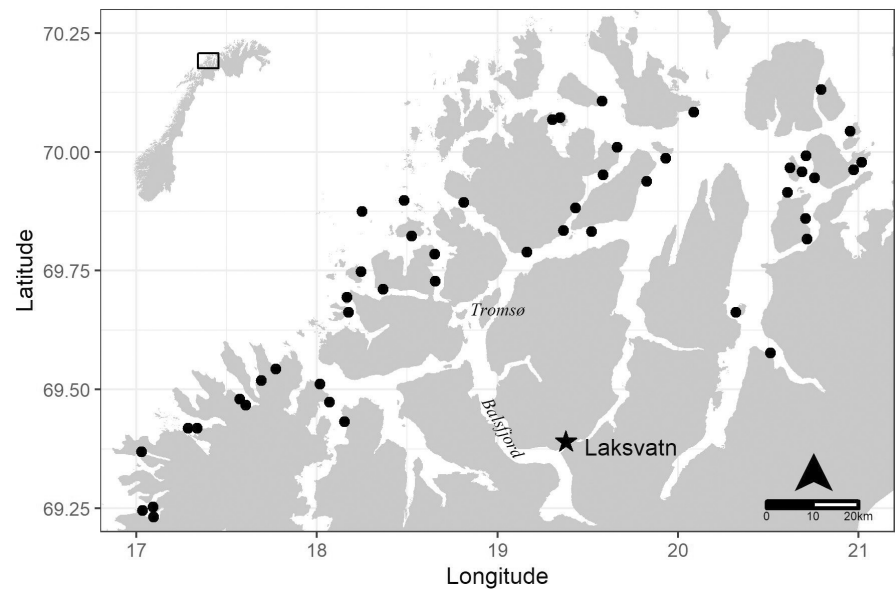
2.1 | Sampling site

The study was carried out in the outlet of the subarctic Lake Laksvatn (69°22'35"N, 19°22'00"E) in Balsfjord, northern Norway during the summers of 2020 and 2021 (Figure 1). Laksvatn is a relatively shallow lake with an average and maximum depth of 6 and 15 m, respectively. The lake drains via river Buktelva (600 m long) to the 57 km long Balsfjorden where salmon farms are prohibited. This lake is mainly inhabited by a population of anadromous Arctic charr, but the lake also holds sea-trout and sporadically Atlantic salmon (Svenning et al., 2013).

2.2 | Arctic charr sampling

In total, 1690 Arctic charr (mean size: 366.2 mm ± 79.5 SD, range: 215–670 mm) were collected in a trap placed 200 m upstream from

FIGURE 1 Map of Laksvatn (star) in Balsfjord with the location of all fish farms (circles) in the area. Inset map of Norway on the top left-hand corner indicates the extent of the main map within the rectangle. Balsfjord and city of Tromsø are indicated in italics. Data on the location of fish farms are public and retrieved from the Norwegian Directorate of Fisheries while the map data are open access and were retrieved from GeoNorge



the river outlet (post marine migration), from June to August 2020 and 2021. Arctic charr was anaesthetized with benzocaine (Gontijo et al., 2003) to reduce the fish's stress during its manipulation. All Arctic charr were measured for total length (LT in mm) from the tip of the snout to the tip of the longest lobe of the caudal fin without compressing the lobes along the midline and weighed (mass in g). The care and use of experimental animals complied with Norwegian animal welfare laws, guidelines and policies as approved by the County Governor of Troms and Finnmark, permit reference number 2020/14374.

2.3 | Salmon-lice infection

To reduce sedation and handling of the fish, which cause the unnatural source of stress, the lice infections were registered only on one side (left side) (Gharbi et al., 2015) when measuring (length, weight) the sedated fish. Moreover, the species and developmental stage of the lice were not determined during the field sampling to further reduce handling time thus stress. The number of salmon-lice was registered by counting live lice on the body and fins along with the number of lice bite marks (dark scars or lesions on the skin, presumably from lice lost after entering freshwater, see Figure S1; Finstad, 1993; Johnson et al., 1996; Krkošek et al., 2011). Sampling was performed in association with local citizen participants who were not tasked with the counting of lice and lice bite marks. Therefore, only a subset of the fish caught during the entirety of the sampling season has complete data on lice and bite marks and these are used in this manuscript.

2.4 | Statistical analyses

All statistical analyses were performed in R (R Core Team, 2021) using the R studio interface (RStudio Team, 2019). Data exploration

highly dependent on data visualizing methods was performed prior to data analysis (Zuur et al., 2009, 2010).

For the analyses, it was necessary to separate first-time migrants (smolts) and second (or more) year migrants (veterans). A total of 60 individuals marked behind the dorsal fins using Floy marks (floytags.com) in 2020 were also recorded in 2021. From these individuals, we can estimate the size expected from a returning veteran, while smaller individuals were noted as post-smolts. The average size of known veterans in 2021 (i.e. marked in 2020 and recaptured in 2021) was 422(±78) mm and 822(±494) g, thus we expect post-smolts to be smaller than these upon return from their first sea migration. To further determine the size threshold for classifying a fish as a smolt or veteran we analysed histograms of size classes. We expect a bi-modal to multi-modal distribution with the smolts being represented in the smallest mode. In both years, 2020 and 2021, the first mode and the second mode met at 350 mm (see Figure S2). This suggests that first-year smolts would be less than 350 mm in length when returning to the lake after their first year at sea. We therefore set the threshold to 350 mm as the maximum size for a returning post-smolt. This resulted in 875 individuals being classified as veterans and 815 individuals as post-smolts.

To assess the stability of the prevalence of lice infections and bites a logistic model was built for both variables using the generalized linear model (GLM) command from the stats package (R Core Team, 2021). Data exploration suggested that an interaction term between post-smolt status and year should be included for both models in addition to the year and post-smolt status of the variables. This model also allowed us to compare infections between post-smolts and veterans.

The stability of the intensity of lice infection (i.e. average lice/bites per individual Arctic charr) between years was tested using a model including the year and migrant status (post-smolt vs. veteran) as covariates using the pscl package (Jackman, 2020). With this model, it was also possible to test the third hypothesis by comparing veterans and

post-smolts. Due to the nature of the count data, and with the high prevalence of 0 counts for lice, a zero-inflated Poisson distribution and negative binomial were compared as potential suitable distributions using a likelihood ratio test (Zuur et al., 2009). Due to the overdispersion of the data, the zero-inflated negative binomial was selected as most suitable for use in the analysis. The zero-inflated negative binomial model is composed of two parts, one assessing the non-zero count data and one assessing the probability of the zeros being true vs. false zeros through a logistic model (Zuur et al., 2009). The zero portion of the zero-inflated model included a term for the intercept and one for smolt status as we expect potentially different behaviours in the sea based on size (i.e. smolt status). The same model variables were used to determine the stability in the intensity of lice bites.

The variation in infection intensity over the period of the entire migration was tested using a zero-inflated negative binomial model with the *pscl* package (Jackman, 2020). The factors included in the model were the week of the year nested within the year and the post-smolt status including an interaction between the terms. The portion of the model accounting for the zeros included a term for the intercept and one for the post-smolt status. The same model was used for the variation in lice bite marks over the period of the return migration.

3 | RESULTS

In the summer of 2020, 1125 Arctic charr were recorded in the trap while 1518 individuals were recorded in the upstream migration in 2021. The dataset was reduced to include only individuals where counts of lice and bite marks, including counts of absence, were noted by trained personnel. A total of 1690 individuals were used in the study of which 832 were sampled in 2020 and 858 in the 2021 field season. The fish size ranged from 215 mm to 670 mm and from 92 g to 3210 g in 2020 and 2021 combined (Table 1).

3.1 | Hypothesis 1—High proportion of lice infection in charr

Out of the 1690 individuals used in this study, 954 individuals had lice or lice bite marks. Of those, 702 individuals were infected with at least one salmon louse and 649 were recorded to have lice bite marks with 397 of those individuals having both lice and bite marks (Figure 2 and Figure 3). The number of lice recorded on a single fish ranged from 0 to 30 in 2020 and from 0 to 24 in 2021. As this is recorded on only a single side of the fish, an individual fish could theoretically have an infection double from that recorded here (Gharbi

et al., 2015). Lice bites recorded on a single fish ranged from 0 to 226 and from 0 to 53 in 2020 and 2021, respectively.

3.2 | Hypothesis 2—Stability of lice infection in charr through time

In 2020, out of the 832 Arctic charr 283 (29%) individuals had recorded lice infections and 261 (31%) had evidence of lice bites. In 2021, 419 of 858 (49%) Arctic charr had lice infections and 388 (45%) had lice bites. The prevalence of lice infection and lice bites was variable between 2020 and 2021 with 2021 having a higher occurrence of fish with lice infection and lice bites (lice 1.2, $p < .001$; bites 1.7 $p < .001$). We determined that there was no change in the abundance or mean number of lice per fish, between 2020 and 2021 (estimate -0.03 , $p = .76$). The abundance of lice bites per Arctic charr also did not change from 2020 to 2021 (estimate -0.11 , $p = .51$). The zero part of the model for the lice data indicated an insignificant intercept (estimate -8.48 , $p = .70$) and that smolt status did not influence the occurrence of lice (6.08, $p = .79$) while for the lice bite model the zero part of the model had an insignificant intercept (estimate -0.82 , $p = .06$) and showed a higher probability of bite occurrence for veterans (estimate 0.83, $p = .02$).

3.3 | Hypothesis 3—Veterans have higher infections

Veteran migrants have a higher prevalence of lice infections than do first-year migrants (estimate 1.07, $p < .001$; Figure 2). The prevalence of lice bites is also higher in veterans than post-smolts (estimate 1.08 $p < .001$; Figure 3). The interaction term between year and post-smolt status was significant and suggests that the abundance of lice and bites was lower than expected in veterans in 2021 relative to 2020 (lice -1.06 $p < .001$, bites -2.06 , $p < .001$; Figure 2 and Figure 3). Individuals classified as veterans had a higher abundance of lice infections per fish than did post-smolts (estimate 0.98, $p < .001$; Figure 2). The abundance of lice bites was also higher in veterans than in first-time migrant Arctic charr (estimate 1.24, $p < .001$; Figure 3).

3.4 | Hypothesis 4—Higher infection in last homecoming fish

Veterans were determined to have a generally higher infection rate than first-year smolts (estimate 10.40, $p < .001$). The intensity of lice

Year	N	Length (mm)	Weight (g)	Lice \pm s.d.	Lice bite marks \pm s.d.
2020	832	374 \pm 90	577 \pm 423	1.4 \pm 3.4	2.6 \pm 9.6
2021	858	359 \pm 67	508 \pm 342	1.2 \pm 2.1	1.5 \pm 2.8

TABLE 1 Metadata on Arctic charr used in the study with mean and standard deviation of the mean

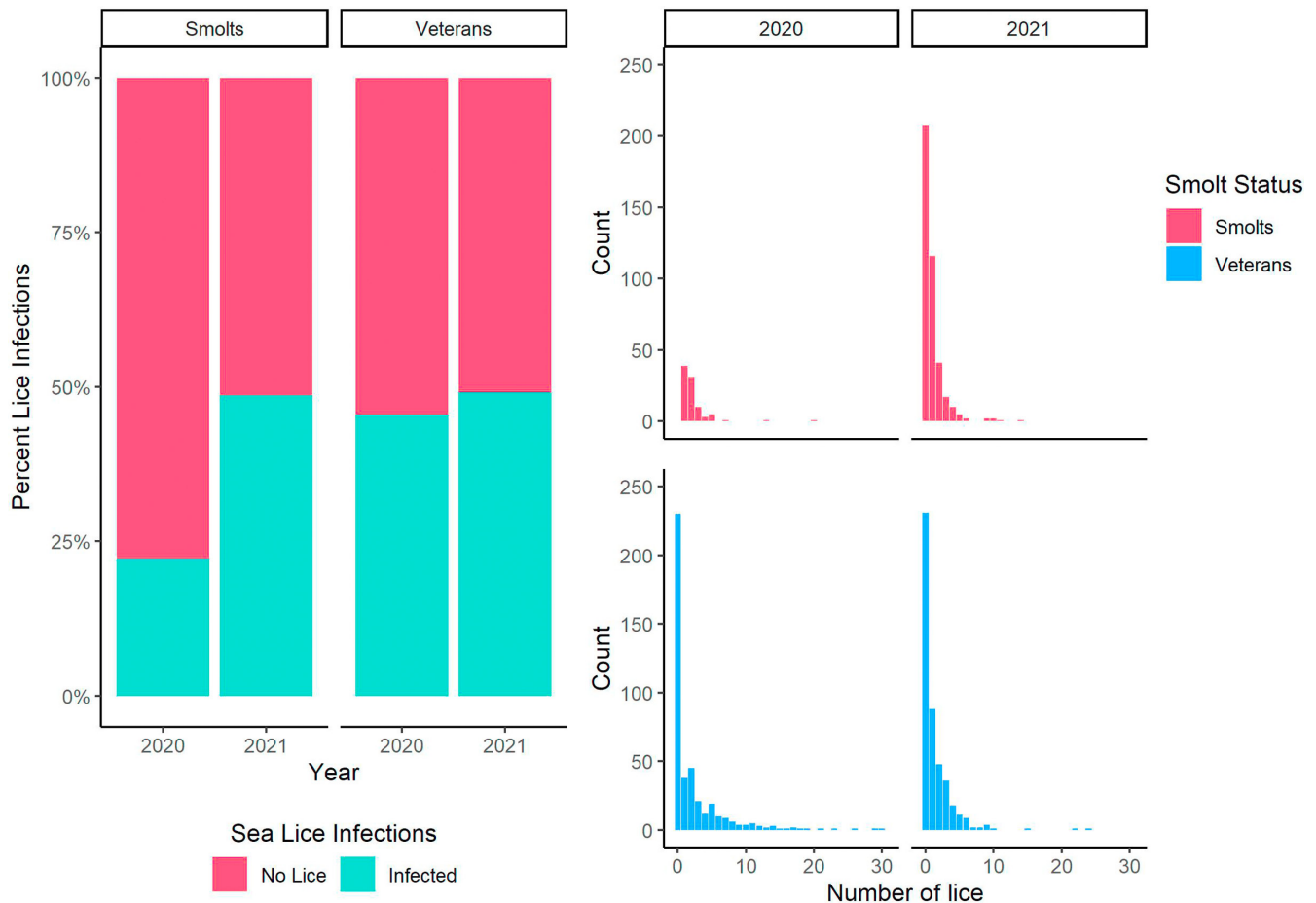


FIGURE 2 Percent of sampled post-smolts and veteran migrant Arctic charr with and without lice infections and the intensity (number of lice) for each individual in 2020 and 2021 sampling. Note the break in the y axis

infection increased over the return migration period in 2020 (estimate 0.13, $p = .015$) and 2021 (0.16, $p = .005$) (Figure 4). The interaction between post-smolt status and week (nested within the year) informs that the abundance of lice on veterans is not as pronounced as it is for post-smolts in 2020 (estimate -0.29 , $p < .001$) and 2021 (estimate -0.34 , $p < .001$) (Figure 4). For the zero-inflated part of the model the intercept was insignificant (estimate -8.01 , $p = .85$) as was the effect of post-smolt status therefore there is no difference between veterans and post-smolts in the probability of being infected (estimate 6.51, $p = .88$).

The abundance of lice bite marks increased over the return migration season in both 2020 and 2021 (respectively, estimate 0.31, $p < .001$; estimate 0.36, $p < .001$) (Figure 5). Veterans have an overall higher abundance of lice bite marks relative to post-smolts (estimate 8.83, $p < .001$). The increase in bite marks over the migration period was not as severe for veterans in 2020 (estimate -0.19 , $p = .018$) and in 2021 (estimate -0.28 , $p < .001$) relative to post-smolts in both years (Figure 5). This model has a significant intercept (-2.07 , $p = .004$) and effect of post-smolt status (estimate 2.07, $p = .002$) where veterans have a higher probability of having at least one bite mark.

4 | DISCUSSION

This study shows a stable infection of sea-lice between consecutive years, within season and across the size of the wild sea-run Arctic charr. The prevalence of infections was intermediate to high, and the intensities of sea-lice infections observed on sea-run Arctic charr were generally low and below the estimated thresholds for negative population impacts of their hosts (Bjørn et al., 2001; Fjellidal et al., 2019). As there are no aquaculture farms located nearby (ca. 60km to the nearest; Figure 1) that could promote the sea-lice infestation, we consider the overall infection pressure to be medium for this vulnerable sea-migratory population of Arctic charr (Bjørn et al., 2001; Karbowski et al., 2019).

Most of the sea migratory Arctic charr were infected with salmon-lice, which has also been shown in other studies (Bjørn et al., 2001). The infection level of salmon-lice reported here are clearly minimum infestations as the small juvenile infection stages could have been missed in our counts, as well as only one side of the fish was registered as a standardized method. The high prevalence of salmon-lice suggests that most individuals registered in the fish trap have been to sea and been feeding on marine prey for some time. Indeed, from

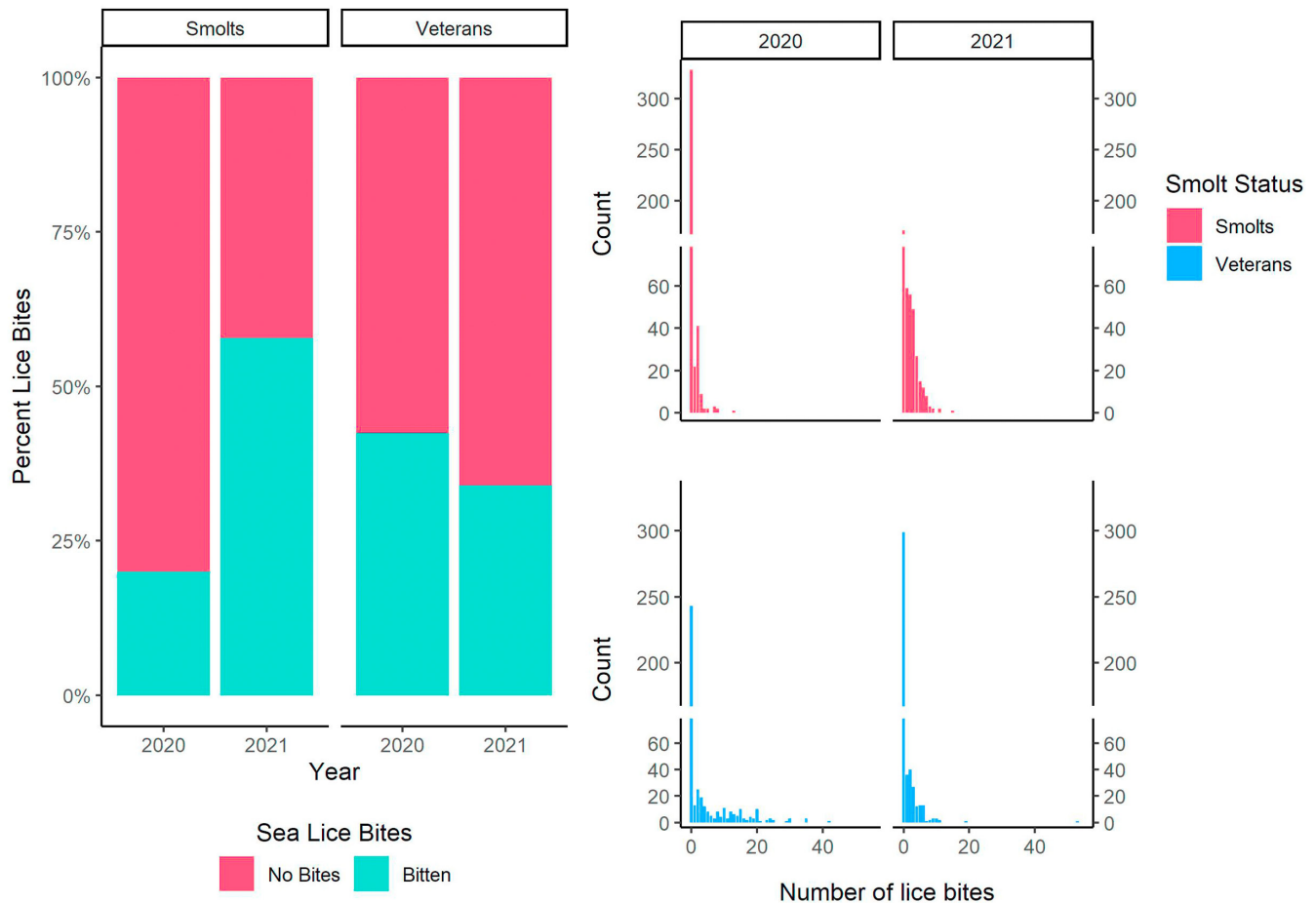


FIGURE 3 Percent of sampled post-smolts and veteran migrant Arctic charr with and without lice bite marks and the intensity (number of lice bites) for each individual in 2020 and 2021 sampling. Note that one value, 226, is not shown in the histogram of lice bites in 2020, also note the break in the y axis

a limited number ($n = 30$) of first-time migrants, the potential sea-run Arctic charr also had a high prevalence of parasites transmitted from marine molluscs (i.e. 90% of fish infected by *Cryptocotyle lingua*; Rochat unpublished data) and have been feeding on marine (i.e. crustacean, fish) prey (Opheim, 2022). The larval trematodes of the genus *Cryptocotyle* are commonly found to infect anadromous Arctic charr (Kristoffersen, 1994) and other marine fishes such as Atlantic cod (Hemmingsen & MacKenzie, 2001). A preliminary study on the present Arctic charr population of Laksvatn indicates a sea residency time of a mean 53 days for veteran migrants and 48 days for first-time migrants (Opheim, 2022; Figure S3, Figure S4). Other studies from northern Norway suggest that anadromous Arctic charr stays in the sea for 33–35 days (Jensen et al., 2020), while first-year migrants only stay for about 22–32 days (Atencio et al., 2021; Strøm et al., 2022). A short sea residence time will constrain the possibility to aggregate directly transmitted parasites (i.e. salmon-lice and *Cryptocotyle* sp.). On the other hand, the prevalence and abundance data of salmon-lice were similar across the two successive years, suggesting stable transmission patterns within the present fjord system without salmonid aquaculture farms. Such consistent patterns are also found in sea-trout studies although there could also be year-to-year fluctuations (Serra-Llinares et al., 2014).

The relatively high prevalence and the intensity data suggest that this fjord without aquaculture activity has a relatively high baseline salmon-lice infection compared with wild salmonids (i.e. sea-trout and Arctic charr) from other sub-Arctic fjords with low aquaculture activity (Serra-Llinares et al., 2014). There are observations that the infection pressure is even higher in other northern fjords without aquaculture activity (Bjørn et al., 2001). This indicates that the infection pressure on Arctic charr from local populations of native salmonids like sea-trout and Atlantic salmon is relatively high. Sea-trout and Atlantic salmon stay in marine waters longer (Jensen et al., 2020) and in general migrate longer distances (Atencio et al., 2021; Rikardsen et al., 2003) compared with the sea-run Arctic charr population that overwinters in the present watercourse (Laksvatn) and whose first-time migrants remain near their natal river while at sea (max range 45 km; Nordli, 2021). Also, returning adult salmon may have relatively high infections with adult egg-bearing sea-lice picked up in different open sea areas (Krkošek et al., 2007). Thus, other sea-run Arctic charr populations with a potentially high infection pressure of salmon-lice from nearby salmon aquaculture farms may suffer even stronger negative effects from lice infestation (Bjørn & Finstad, 2002; Costello, 2009) than the present population from Laksvatn.

FIGURE 4 Number of lice recorded on a weekly scale for each individual post-smolt (red) and veteran migrant (blue) Arctic charr during the 2020 (left) and 2021 (right) return migration (top) and Arctic charr length (bottom)

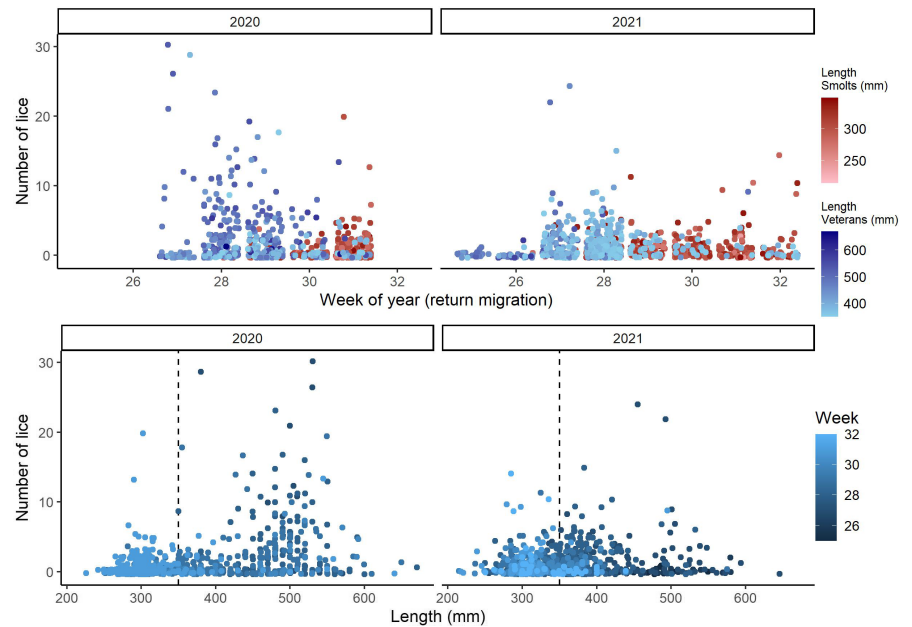


FIGURE 5 Number of lice bite marks recorded on a weekly scale for each individual post-smolt (red) and veteran migrant (blue) Arctic charr during the 2020 (left) and 2021 (right) return migration (top) and Arctic charr length (bottom)



Larger individuals have a somewhat higher prevalence and abundance than smaller fish (i.e. first-time migrants). Veteran migrants may have a higher infection for several reasons. First, they migrate earlier and return earlier than smolts (Rikardsen et al., 1997), so they could encounter a different infection pressure from other wild salmonids (sea-trout and Atlantic salmon). Veterans also migrate longer distances in the estuary/fjord (Atencio et al., 2021) and thereby could pick up infections over a broader area. Also, bigger fish have a larger surface area that has been shown to be important for the intrapopulation size of directly transmitted crustacean parasites of Arctic charr (Henriksen et al., 2022). Larger individuals (here veterans) will generally tolerate a higher parasite load than smolts. As post-smolts in general have much higher natural mortality than veteran migrants (Rikardsen et al., 1997), they will also suffer most from parasite-induced mortality, and some

post-smolts with high infection intensities will constantly be removed from the population during their first sea-migratory period. Finally, the foraging and habitat choice, such as time at sea and preference for nearshore habitat will affect salmon-lice infection in wild Arctic charr and sea-trout (Simmons et al., 2019; Strøm et al., 2022). The shorter sea residency time and smaller surface area could explain the lower infection of the first-time migrants relative to veteran migrants.

There were higher sea-lice infections in the latest returning sea-run Arctic charr. The development rate of the salmon louse *L. salmonis* is greatly influenced by seawater temperature (e.g. Hamre et al., 2019), and the infection pressure may increase with a relatively small change in sea temperature (Sandvik et al., 2021). Female lice may become adults at 21 days post-infection at sea temperatures of about 15°C (Hamre et al., 2019). The sea temperature in

Balsfjord (fjord connected to Laksvatn) during the summer season was between 12 and 16°C and thus perfect for sea-lice development. As the veteran migrants descend to the sea earlier than the smolts, veteran migrants could develop mature female lice within their time spent at sea, which then poses an infection pressure on the out-migrating smolts before the veterans' return to the freshwater habitat. This could promote a higher infection pressure late in the season in addition to the higher occurrence of other native Atlantic salmon and sea-trout in this fjord system. The sea residency of Arctic charr post-smolts could also be shortened from this infection pressure through a premature return to the freshwater (e.g. Thorstad et al., 2015; Wells et al., 2007) as osmotic stress could be a problem for some of the highly infected individuals. Thus, the highest infection pressure most likely originates from sea-trout that may stay in the same sea habitat as Arctic charr as they have a longer migratory period (Atencio et al., 2021) and may also stay in the estuary during the colder winter periods (Thorstad et al., 2016). There are several sea-trout populations in this fjord system and could be the main reason for the relatively high infection level in the sea-run Arctic charr population of Laksvatn with other fish species in the fjord also contributing to the infection pressure from the non-host-specific *Caligus* spp. (Boxshall, 1974; Heuch et al., 2007). Additionally, sea-run Arctic charr will also accumulate high infection of other trophically transmitted parasites during their foraging migration (Bouillon & Dempson, 1989; Desdevises et al., 1999; Dick & Belosevic, 1981; Due & Curtis, 1995; Knudsen et al., 2011). The total parasite load acquired during sea migration could therefore represent an extra cost that presumably will affect the smallest first-year migrants most; however, there is not much information about the total parasite burden of salmonid post-smolts in sub-Arctic fjords (but see, Bristow et al., 1996; Holst et al., 1993; Knudsen et al., 2005).

4.1 | Conservation & management

The anadromous behaviour of Arctic charr is a threatened life-history strategy with predicted global warming and other anthropogenic-induced stressors in high latitudes area (Svenning et al., 2022). The anadromous individuals from Laksvatn appeared to grow well, as most returning post-smolts had a size of up to 330 mm and veteran migrants reaching sizes of >400 mm as seen in other northern populations (Davidsen et al., 2020; Dempson & Green, 1985; Johnson, 1980; Klemetsen, Amundsen, et al., 2003; Rikardsen et al., 2003). Several individuals were vomiting marine crustaceans (*Gammarus* spp.) and sand lance (*Ammodytes* spp.) during handling (H. Jensen personal observation). In other studies, these prey groups appear to be vital for sea-migrating Arctic charr in both sub-Arctic Norway and Greenland (e.g. Davidsen et al., 2020; Grønvik & Klemetsen, 1987; Knudsen et al., 2011). The potential productive feeding environments in the fjord and estuary outside Laksvatn are reflected by a normal to high condition (mean ~1.2) factor for both first-year and veteran migrants. This indicates that

salmon-lice infecting Arctic charr together with other potential internal parasites accumulated from foraging during their sea-migration period (Knudsen et al., 2011), could have relatively low negative impacts on individual Arctic charr and thereby may have minor consequences for the population. However, a recent Arctic charr study stated that even low infection levels of salmon-lice may induce severe loss in growth opportunity and thereby have important fitness consequences (Strøm et al., 2022). Therefore, even the intermediate infection levels of salmon-lice observed in the present study may have important negative impacts at the population level with the synchronous effects of other anthropogenic stressors in the near future.

Arctic charr is a cold water-adapted fish (Klemetsen, Knudsen, et al., 2003) strongly tied to growth opportunities (Siikavuopio et al., 2010). The present Arctic charr populations return, after extensive feeding at sea, to the freshwater mainly during the warm water month of July where they overwinter in Laksvatn (max depth 16 m). Arctic charr in Laksvatn, as for similar populations in shallow lakes and riverine sea-migrating populations living at the southern edge of their distributions (e.g. Jeppesen et al., 2012; Malmquist et al., 2009; Murdoch & Power, 2013; Winfield et al., 2010), may be more affected by global warming as the buffer of cold water available in the lake during summer and early autumn is limited. Additionally, by being exposed to a potentially warmer climate in the future, Arctic charr in sub-Arctic areas in lakes will most likely experience higher resource competition from coexisting species such as e.g. brown trout (e.g. Eloranta et al., 2011; Eloranta et al., 2013; Finstad & Hein, 2012; Hayden et al., 2013) that seem more warm water-adapted (e.g. Elliott & Elliott, 2010). In lakes in the same geographic region, the fish community structure is under drastic change with a decrease in cold water-adapted fish species (Svenning et al., 2022), while anadromous Arctic charr populations are further affected by increasing marine temperatures (Sandvik et al., 2021). Thus, the prolonged sea-lice infection potentially limited by lower marine temperatures in the sub-Arctic will likely intensify the potential threats in the future. The Arctic charr and especially their anadromous populations may therefore be affected both directly (e.g. increasing temperature) and indirectly (e.g. altered resource competition) by global warming. Thus, being infected by different parasite taxa (e.g. salmon louse *L. salmonis*) could be a factor increasing the stress and thereby costs while reducing the benefits of a delicate life-history strategy pushing the populations to extinction and/or reduce the utilization of the anadromous life-history strategy. Sub-Arctic fjords are generally less risky for salmon-lice infections in Arctic charr in some former studies (Bjørn et al., 2007; Serra-Llinares et al., 2014) mainly because they have a short stay in salt water and low infection pressure in fjords with low aquaculture activity. Thus, the local infection pressure of salmon-lice, e.g. salmonid aquaculture farms, may be a factor that is important to monitor in the future especially with a changing climate bringing forward increasing unknowns and stressors.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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