Inferring time at sea from scale circuli: implications for the interpretation of salmon lice distributions on sea trout

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ABSTRACT: Infestations with the ectoparasite salmon louse *Lepeophtheirus salmonis* are considered one of the main stressors for wild salmonids in farm-intensive areas. In Norway, lice infestations on sea trout *Salmo trutta* are monitored annually at fixed stations distributed along the coast, providing management authorities with an empirical basis to evaluate the potential parasite transmission between farmed and wild salmonids and to evaluate the effect of different management strategies. However, the representativeness of these data is debated, as information on where and for how long the fish have been at sea before capture is rarely available. In this study, we used scale circulus counts to determine marine residency time for sea trout postsmolts caught in Hardangerfjord, a farm-intensive area in western Norway, and show how this information can be used for a better interpretation of lice infestations reported by surveillance programs. By analyzing scales from individuals of known marine residency time (n = 48), we established a periodicity of circulus deposition over the first summer at sea of approximately 8 d per circulus [95% CI: 7.6−8.4 d]. Next, we applied zero-altered ('hurdle') statistical models to show how marine residency time, inferred from scale circuli, significantly affected both the probability and intensity of infestation with salmon lice among wild sea trout postsmolts of unknown migration timing (n = 321). Importantly, incorporating circulus counts as a proxy for time at sea significantly improved model likelihood, highlighting the importance of incorporating supporting data on individual sea trout migration traits into salmon lice surveillance programs to improve our understanding of the observed distributions.

KEY WORDS: Salmon lice · Sea trout · Circulus formation rate · Scales · Marine residency

1. INTRODUCTION

Since its start in the late 1960s, Atlantic salmon *Salmo salar* aquaculture has grown to become an important industry worldwide, currently playing an important role in global food production. Norway pioneered this industry, with the first commercial farm established in 1969, and is at present the world's largest producer of farmed Atlantic salmon, accounting for approximately 50% of global production. From its beginning, the industry has been accompanied by environmental concerns including the genetic interaction between farmed escapees and wild conspecifics, the use of antibiotics and other chemicals, the discharge of waste and excess feed into the ocean and the spread of diseases and parasites to wild fish (Taranger et al. 2015). Particularly, the spread of the parasitic salmon louse *Lepeophtheirus salmonis* from farmed to wild salmonids rapidly became a major issue for the management of sustainable salmon farm-

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ing in Norway and elsewhere (Brandal & Egidius 1977, Torrissen et al. 2013).

Salmon lice are marine ectoparasitic caligid copepods that occur naturally in marine areas in the northern hemisphere (Kabata 1979), where they live as specialized parasites of salmonid fishes. The spread of salmon lice occurs during the pelagic free-living nauplii and copepodid stages, as they drift with water currents. Once they reach the copepodid stage, lice are dependent on finding a suitable host to complete their life cycle. Salmon lice feed on the skin, mucus and blood of the host fish, exposing the fish's tissue to the seawater, which disturbs the osmotic balance and increases susceptibility to bacterial and fungal infection (Jónsdóttir et al. 1992). This entails further costs for the host, including osmoregulatory problems and physiological stress responses, reduced swimming performance, reduced fitness and, in the worst case, physiological breakdown and death of the host fish (Grimnes & Jakobsen 1996, Bjørn & Finstad 1997, Fjelldal et al. 2019). Salmon lice have historically been observed parasitizing wild salmonids in low numbers (Thorstad et al. 2015). However, after the establishment of salmon aquaculture in open-net pens at sea, unprecedented lice abundances started to be reported in areas with intensive salmon farming in Norway, Ireland and Scotland. These lice epidemics were attributed mainly to the spread of salmon lice from aquaculture sites (Heuch & Mo 2001, Dempster et al. 2021), and monitoring lice infestations on both farmed and wild salmonids rapidly became a key priority.

The Norwegian salmon lice surveillance program was established in 1992 and has since collected an extensive dataset comprising documentation of salmon lice on wild Atlantic salmon, brown trout *Salmo trutta* and Arctic char *Salvelinus alpinus* in the marine environment along the Norwegian coast, providing management authorities with an empirical basis to evaluate the potential parasite transmission between farmed and wild salmonids and to evaluate the effect of different management strategies. The main methods of data collection include trawling surveys of salmon postsmolts with specially modified pelagic trawls (Holst & McDonald 2000, Johnsen et al. 2020) and sampling sea trout and Arctic char in littoral areas using gill nets or fyke nets (Serra-Llinares et al. 2014, Helland et al. 2015, Bøhn et al. 2022). Salmon lice numbers on sea trout and Arctic char are often used to assess local lice infestation pressures and to identify local trends or changes over time (Middlemas et al. 2013, Serra-Llinares et al. 2014, Helland et al. 2015, Shephard et al. 2016, Bøhn et al. 2022). These species are good indicators of the local sea lice infestation

pressure because they spend their seawater feeding period inside the fjords or along the coast, usually within close range of their native rivers (Lyse et al. 1998, Eldøy et al. 2015, Flaten et al. 2016). However, interpretation of lice distribution from catch samples is not straightforward. Salmon louse abundances on wild fish typically display 0-inflated negative binomial distributions, where few hosts carry high parasite loads while most others harbor few or none (Helland et al. 2015, Serra-Llinares et al. 2016). Although there are many factors contributing to this heterogeneity, part of the variation may be explained by the spatial and temporal variation in the distribution of infective lice stages in the environment (Salama et al. 2013, Johnsen et al. 2016, Skarðhamar et al. 2018) combined with variation in the behavior of individual hosts. While the development of coupled hydrodynamic—biological models has recently increased our understanding of how infective lice larvae are dispersed in space and time (Murray & Gillibrand 2006, Asplin et al. 2020) and lice densities can now be modelled across Norway at a high spatio-temporal resolution, information on where and for how long the fish have been at sea before capture is rarely available. Sea trout display a high plasticity in migratory tactics, and previous studies have revealed a large variation in migration timing, migration duration and migration distance, both within and among populations (Berg & Berg 1987, Flaten et al. 2016, Aldvén & Davidsen 2017). Moreover, salmon lice can induce behavioral changes in their host fish, such as inducing the host's return to brackish or fresh water to restore osmotic balance and rid themselves of lice (Birkeland & Jakobsen 1997, Serra-Llinares et al. 2020, Strøm et al. 2022). Consequently, catch samples will be composed of different sub-groups of fish with individual differences in migration timing and marine habitat use and thus having experienced different lice exposures. Identifying these unique spatio-temporal groups is paramount in understanding how the observed lice distributions are generated. This is especially important when monitoring data is to be used for comparison against model-based predictions (Sandvik et al. 2016, Sandvik et al. 2020).

The main goal in the present study was to test whether scale circulus counts could be used as a simple and nonlethal method for estimating marine residency time for sea trout postsmolts captured during the national surveillance program and to investigate how circulus counts relate to the observed lice distribution on the fish. Fish scales have been used for over a century for age determination and retrospective individual growth analyses of teleosts, particularly sal-

monids (Dahl 1910, Nall 1930). Such analyses have usually focused on estimating age and growth rates associated with annual increments. With recent advances in microscopy and digital image processing, it is now possible to capture high-resolution scale images, allowing the analysis of scale growth at sub-annual time scales. As fish increase in length, circuli are deposited at the scale margin (Wootton 1998). The rate of circulus formation is not constant in time, but a function of physical and nonphysical factors such as temperature, food, light, genetic factors, and physiological factors (Bilton 1975). However, deposition times have been shown to stay relatively consistent during the same growth period and under similar environmental conditions for various salmonid species (Friedland & Haas 1996, Wells et al. 2003). For post-smolts, this opens up the possibility of estimating marine residency time upon capture based on the number of circuli deposited after the freshwater—marine transition, which is easily identifiable on scales.

Here, we first investigated the periodicity of circulus deposition on sea trout postsmolts by analyzing scales from recaptured individuals with known marine residency time. Thereafter, we used this information to estimate marine residency time for sea trout postsmolts of unknown migration timing based on the number of circuli deposited after the freshwater—marine transition. Finally, we combined this information to assess how the observed lice burdens related to the number of marine circuli (as a proxy for time at sea). More specifically, we hypothesize that (1) circulus formation rate is stable within a season and a geographic area, meaning that direct counting of circuli can be used to estimate timing of sea-entry for sea trout postsmolts and (2) lice burdens are positively correlated with circulus counts (given it is proven as a valid proxy for timing of sea-entry). The study is based on data collected in Etnefjord and the Etne River, in the outer parts of Hardangerfjord, western Norway.

2. MATERIALS AND METHODS

2.1. Study area and data collection

The Etne River is located on the southwestern coast of Norway (59.673° N, 5.934° E) and drains into Etnefjord, a small side arm of the Hardangerfjord system (Fig. 1). The river system has self-sustaining populations of Atlantic salmon and anadromous brown trout, with a total river length available for anadromous salmonids of 13 km, including tributaries. The outer and central regions of the Hardangerfjord system, where

Etnefjord is located, hold one of the world's densest concentrations of farmed salmonid fish (Skaala et al. 2014a, Sandvik et al. 2020), and high lice infestations have frequently been reported on wild salmonids in the area (Skaala et al. 2014b, Halttunen et al. 2018).

The Etne River is equipped with a full-coverage upstream fish migration trap (from here on referred to as the main trap) situated in the lower reach of the river, approximately 500 m from the river mouth, using the resistance board weir system (Skaala et al. 2015). Just above the main trap, a smolt trap covering approximately 3/4 of the river width enables the capture of out-migrating smolts during their natural downstream migration. The main trap is operative from early April to mid-November, when it gets dismantled for the winter. The smolt trap is only operated during the main migration window for trout and salmon, typically from the middle of April until the end of May. All salmonid fish entering either of the traps are identified to species and measured (weight and length). A few scales are collected from all fish above the lateral line between the dorsal and adipose fins, and a micro-clip is taken from the tip of the adipose fin for genotyping before the fish is released back into the river above (returning individuals) or below (smolts) the trap. In addition, out-migrating smolts are tagged using 12/13 mm PIT-tags before release.

Salmon lice levels on sea trout have been monitored in Etnefjord for the last 15 yr as part of the national salmon lice surveillance program. Fish are captured using fyke nets and anesthetized (benzocaine 30—40 mg l^{-1}) prior to lice counting. Lice counts are performed by trained personnel with the fish submerged in a white plastic tub (5—10 l) and using a strong headlamp (>500 lumen). The following 6 lice stages are recorded: copepodite, chalimus 1, chalimus 2, pre-adult, adult male and adult female. All fish are additionally measured (length and weight), tagged with passive integrated transponder (PIT) tags and sampled (scales and tissue, as specified above) before being released back to the sea following recovery from anaesthesia.

In this study we use the standard terms abundance (number of lice on all sampled fish), prevalence (proportion of infested fish among sampled fish) and intensity (number of lice found on infested fish) when discussing salmon lice infestations.

2.2. Scale reading

Prior to analysis, scales samples were photographed (Nikon DS Fi3) under a stereomicroscope (Nikon SMZ 1500). For each fish, 3—4 scales were
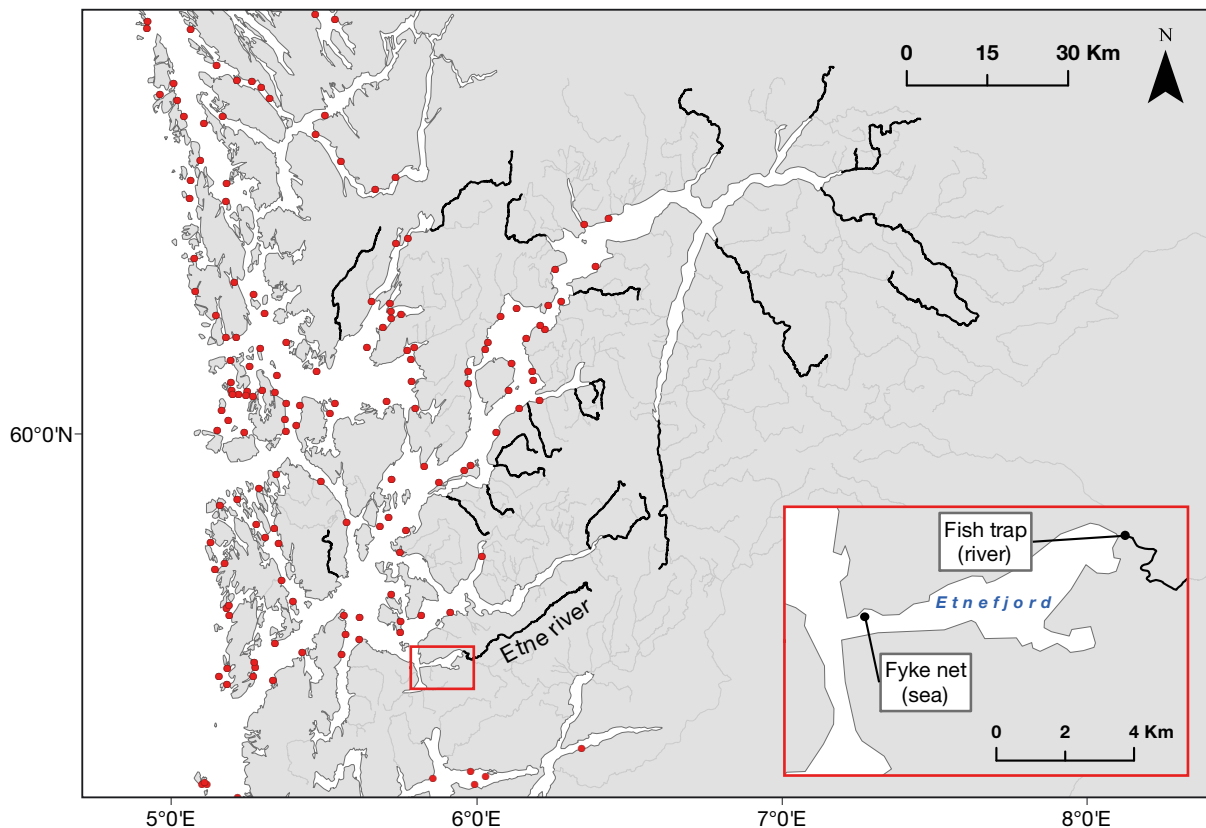
Fig. 1. Study area, showing Hardangerfjord, Etnefjord (inset) and the Etne River. All main rivers in the area sustaining sea trout populations are shown as thick black lines. Red dots show the location of salmon farms

examined under the microscope and the best one was selected for photographing. All magnifications were calibrated in the Nikon Elements Documentation program, and further analyses were performed on calibrated photographs.

First, the transition between freshwater and the sea was identified by a marked increase in circulus spacing. Scale growth serves as a proxy for somatic growth (Dahl 1910). Typically, the growth rate of brown trout in freshwater is lower than in a marine environment (Klemetsen et al. 2003). Therefore, an increase in the intercirculi spacing on scales is a reliable indicator of the point at which an individual migrates to the sea. However, pinpointing the exact transition zone between freshwater and marine growth in the scales can be challenging and often a subjective task. To minimize bias, we enlisted a single experienced reader for this task. Subsequently, circulus counts during the first marine growth period were conducted along the middle axis of the scale. Only fully set circuli were counted; those located at the outermost tip of the scale were counted as half circuli. No information on time at sea or lice numbers on individual fish was available for the reader.

2.3. Statistical analyses

Two datasets were used for analysis. Dataset 1 was used to investigate circulus formation rate on sea trout scales during the marine growth season. As circulus formation rate is not constant in time and differences between different ages have been shown (Wells et al. 2003), we restricted this analysis to include only first-time migrants (postsmolts). Dataset 1 included scales samples from sea trout postsmolts for which migration timing was known (i.e. individuals captured and tagged in the smolt trap) as well as postsmolts of unknown migration timing but from which scales had been collected at different times during the same marine growth period. To ensure a sufficient number of samples, Dataset 1 included samples from the years 2019—2022 (n = 48). The number of circuli deposited after the freshwater—marine transition or between 22 sequential scale readings was modeled as a function of marine residency time using linear regression. Scale circulus formation rate has been found to be positively correlated with growth rate in several salmon species (Pearson 1966, Bilton & Robins 1971a, Fisher & Pearcy 2005), and thus we included

mass-specific growth rate (*SGR*) in the model. *SGR* was calculated as $100 \times (\log(w_{t1}) - \log(w_{t0}))/t$, where w_{t0} and w_{t1} are the weight of the fish at first observation and at recapture, respectively, and *t* is the number of days between observations. To account for interannual differences in environmental conditions, *year* was also included as a covariate in the model. The full model was specified as follows:

$$Circuli \sim \alpha + \beta_1 \, SGR + \beta_2 \, days + \beta_3 \, year + \beta_4 \, days \times year \quad (1)$$

where $\Delta Circuli$ (number of circuli deposited) is the response variable and *SGR*, *days* (number of days at sea between circulus counts), *year* and the interaction term *days × year* are the explanatory variables. After fitting the full model, model selection was performed by sequential removal of non-significant terms and the best fit model was used for parameter estimation.

Dataset 2 was used to investigate the correlation between observed lice burdens on sea trout postsmolts and scale circulus counts and included all trout postsmolt captured in Etnefjord in 2021 (n = 321). We used negative binomial 'hurdle' models (also called zero-altered negative binomial models, ZANB) (Zuur et al. 2009) to model the variation in lice numbers while accounting for both overdispersion and an excess of zero counts. Hurdle models include 2 processes: (1) a binomial probability model accounts for the distribution of zero counts (those with nonzero counts having crossed a hurdle), and (2) a count model for the positive counts, conditioned on the zero model. Our full model included the same set of covariates on both the binomial and the count component of the model, and was specified as follows:

$$Lice_i \sim \text{ZANB}(\mu_i, \pi_i, k)$$
$$E(Lice_i) = \frac{1 - \pi_i}{1 - P_0} \times \mu_i$$
$$\text{where } P_0 = \left(\frac{k}{\mu_{ij} - k}\right)^k \quad (2)$$
$$\log(\mu_i) = yearday + flength + circuli$$
$$\text{logit}(\pi_i) = yearday + flength + circuli$$

where *E* denotes the mean of the model, $Lice_i$ is the number of lice (all stages) for the *i*th observation, P_0 represents the probability that the outcome is zero under the negative binomial distribution, *k* is the dispersion parameter (the number of successes in a sequence of Bernoulli trials), *yearday* is the capture date expressed as year-day, *flength* is the fork length of the fish in mm and *circuli* is the number of scale cir-

culi deposited after the freshwater—marine transition. There are 22 components in the model: a binary Bernoulli part for lice presence or absence, with the mean π_i and a logistic link, and a negative binomial part for positive values of lice, with the mean μ_i and a log link.

After fitting the full model, model selection was performed by sequential removal of non-significant terms for each component of the full model using the likelihood ratio test to compare nested models (Zuur et al. 2009). The best fit model was used for parameter estimation. All hurdle models were fitted using the *pscl* R-package (Jackman et al. 2015). Model validation was performed by plotting the Pearson residuals from the ZANB model vs. fitted values, each covariate in the model, and each covariate not in the model. The percentage of zeros obtained by simulating data using the ZANB model was compared with the percentage of zeros in the original data set. A comparison was also made between the sum of squared Pearson residuals for simulated and original data, and between maximum values of simulated and original data. There is currently no tool available to quantify the R^2 of a ZANB model. Instead, we calculated the likelihood-ratio based pseudo-R^2 using the *r.squaredLR* function in the *MuMIn* R-package (Barton & Barton 2015). Unlike ordinary least square-R^2, likelihood-based pseudo-R^2s do not represent the proportion of explained variance but rather the improvement in model likelihood over a null model.

All statistical analyses were performed using R software (www.r-project.org) version 4.0.2.

3. RESULTS

3.1. Circulus formation rate

Linear regression analyses (Dataset 1) showed a strong correlation between the number of circuli deposited ($\Delta Circuli$) and the number of days between counts ($p < 0.001$; $R^2 = 0.88$; Fig. 2). No significant effect was detected for *SGR* ($p = 0.53$), the interaction term *days × year* ($p = 0.10$), or *year* ($p = 0.09$) on the number of circuli deposited. Cir-

Table 1. Results from the best fit linear regression model on circulus formation rate for first-time migrant sea trout

	Estimate	SE	*t*	Pr $(>|t|)$
Intercept	−0.103	0.309	−0.332	0.741
Days	0.125	0.007	18.524	<0.0001

culus formation rate during the first summer at sea was estimated to be approximately 8 d circulus^{-1} (95% CI: 7.6–8.4 d) (Table 1, Fig. 2). Visual inspection of the residuals showed no significant departure from linearity.

3.2. Circulus counts as a proxy for marine residency time at capture

A total of 240 trout smolts (mean ± SD total length: 135 ± 9 mm; fork length not available) were captured and tagged in the Etne River during the smolt run in 2021, with a median migration date of May 14th (Week 19; Fig. 3). During the following weeks, 321 postsmolts were captured in fyke nets at sea (mean ± SD total length: 161 ± 22 mm; mean ± SD fork length: 153 ± 21 mm; Table 2). For these, scale circulus counts after the freshwater-marine transition ranged from 0 to 10 (Fig. 4). There was a large variation in the number of circuli during the whole period, with a tendency towards a higher number of circuli on fish captured later in the season (Table 2, Fig. 4).

Using scale circulus counts, and assuming a circulus formation rate of 8 d circulus^{-1} (see Section 3.1), we back-calculated the estimated migration time for all captured postsmolts. There was a strong agreement between observed and estimated migration curves, with a difference in median migration date of 3 d (Fig. 3). This indicates that postsmolts captured at sea are a representative sample of the population in terms of migration timing.
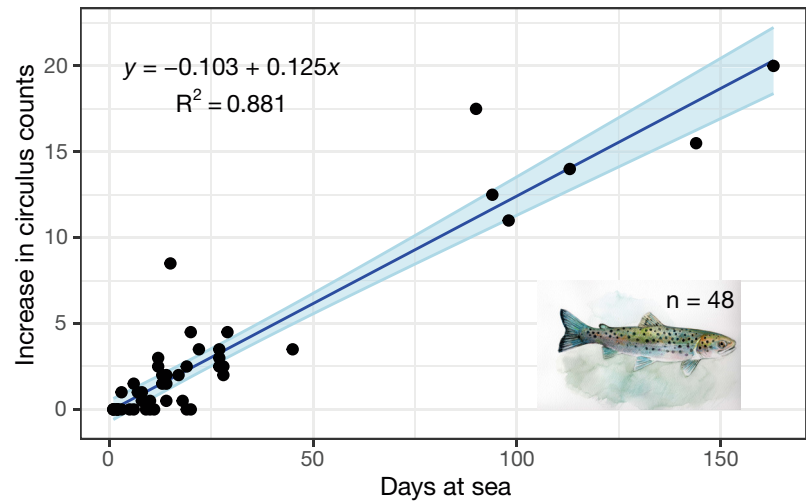

Fig. 2. Estimated circulus formation rate for sea trout postsmolts (n = 48). Days at sea: number of days after migration from freshwater or between sequential samplings
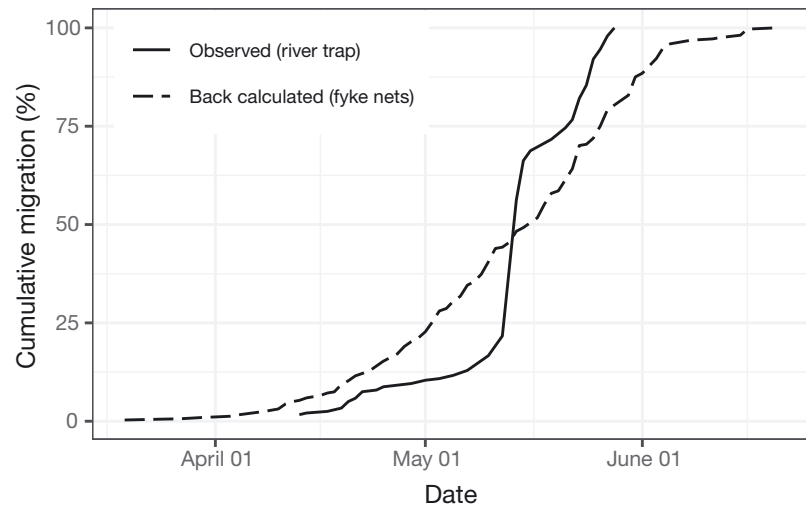

Fig. 3. Migration curve for sea trout smolts in Etne River, as inferred from catches in the down-migration river trap (solid line) and back-calculated based on scale circulus counts for postmolts captured in fyke nets at sea (dashed line)

Table 2. Salmon lice infestation on sea trout postsmolts captured in Etnefjord in fyke nets in 2021 during the Norwegian salmon lice surveillance program

| Week	n	Fork length (mm) (mean ± SD)	Weight (g) (mean ± SD)	N circuli (mean ± SD)	Lice prevalence [95% CI]	Median lice intensity [95% CI]	Min. lice intensity	Max. lice intensity
21	37	167 ± 25	51 ± 32	3.9 ± 1.9	86 [72–94]	6 [4–15]	1	49
22	137	152 ± 19	36 ± 15	2.5 ± 1.9	50 [42–59]	2 [1–3]	1	70
23	13	150 ± 23	36 ± 16	2.3 ± 1.8	54 [29–77]	1 [1–34]	1	34
24	94	147 ± 17	34 ± 17	3.3 ± 1.7	51 [41–61]	4 [2–7]	1	33
25	24	161 ± 32	50 ± 35	6.1 ± 1.7	100 [86–100]	44 [7–54]	1	122
26	10	151 ± 16	40 ± 15	6.3 ± 2.8	80 [49–94]	45 [4–203]	4	203
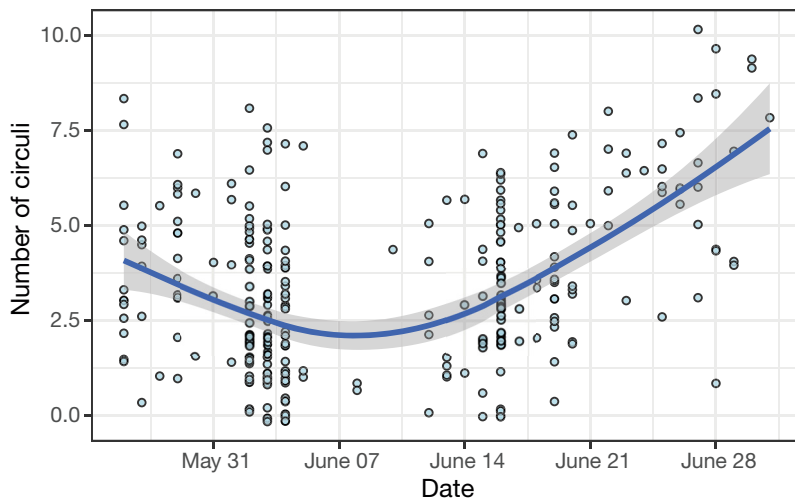
Fig. 4. Scale circulus counts on sea trout postsmolts captured in Etnefjord (Norway) in 2021. A LOESS (locally estimated scatterplot smoothing) curve (solid line) and associated 95% confidence interval (shaded area) have been added to highlight the non-linear trend in the data. Note that small random variations (jitter) have been added on the y-axis to reduce overplotting and improve visualization (circulus counts are never below zero)

more lice (binary part of the ZANB model) (Table 3, Fig. 5a). The effect of fish size became less pronounced as the number of scale circuli increased. No significant effect of capture date (*yearday*) was detected on this part of the model (likelihood ratio test, p = 0.934). For infested individuals (zero-truncated component of the ZANB model), model results identified a positive effect of *circuli*, *flength* and *yearday* on the intensity of the infestation (Table 3, Fig. 5b). Predicted frequencies with the ZANB model corresponded well to the observed frequencies, and the calculated likelihood-based pseudo-R^2 was 0.36. In comparison, exclusion of the covariate *circuli* in the ZANB model resulted in a likelihood-based pseudo-R^2 of 0.23.

3.3. Lice infestations as a function of biological and migratory traits

Salmon lice were found on 60% of the captured postsmolts, with prevalence ranging from 50 to 100% during the 6 wk sampling period (Table 2). Median intensity remained relatively low (1−6 lice fish^{-1}) during the first 4 wk, but increased in Weeks 25−26 to around 44 lice fish^{-1}. Approximately 70% of the lice were attached stages.

Results from the ZANB model showed a positive effect of both circulus counts (*circuli*) and fish length (*flength*) on the probability of having one or

Table 3. Parameter values for the underlying binomial (presence/absence of lice) and zero-truncated negative binomial (positive values of lice) models from the ZANB model (n = 321). *p < 0.05, **p < 0.01, ***p < 0.001

	Estimate	SE	z	Pr (>$|z|$)
Zero hurdle model coefficients (binomial with logit link)				
Intercept	−6.732	2.862	−2.352	0.019*
circuli	0.343	0.071	4.837	<0.001***
flength	0.041	0.008	4.948	<0.001***
yearday	−0.001	0.015	−0.083	0.934
Count model coefficients (truncated negbin with log link)				
Intercept	−9.985	1.986	−5.026	<0.001***
circuli	0.341	0.062	5.501	<0.001***
flength	0.025	0.006	4.582	<0.001***
yearday	0.039	0.010	3.977	<0.001***

4. DISCUSSION

In the present study, we propose a simple and non-lethal method for estimating marine residency time for sea trout postsmolts from catch samples by counting of scale circuli, and show how this information can be used to improve our interpretation of observed lice infestations from surveillance programs. By analyzing scales from individuals of known marine residency time, we showed a fairly constant periodicity of circulus deposition over the first summer at sea, with a frequency of slightly over 1 wk per circulus. Thereafter, we showed how sea trout postmolt caught within days of each other at the same sampling station had spent different lengths of time at sea (inferred from circulus counts) prior to capture, and how this significantly affected both the probability and intensity of infestation with salmon lice. Importantly, incorporating this information significantly improved model likelihood and thus our ability to explain the observed lice distributions.

The assumption that scale circuli are deposited in a time-dependent manner is well established in principle for many fish species (Wootton 1998). However, the rate of circulus deposition is not necessarily constant over the life history of a fish. In salmonids, deposition rates have been shown to be correlated to growth rate. Typically, fish tend to deposit circuli at a faster rate during periods of rapid growth, while the deposition rate may decrease during slower growth
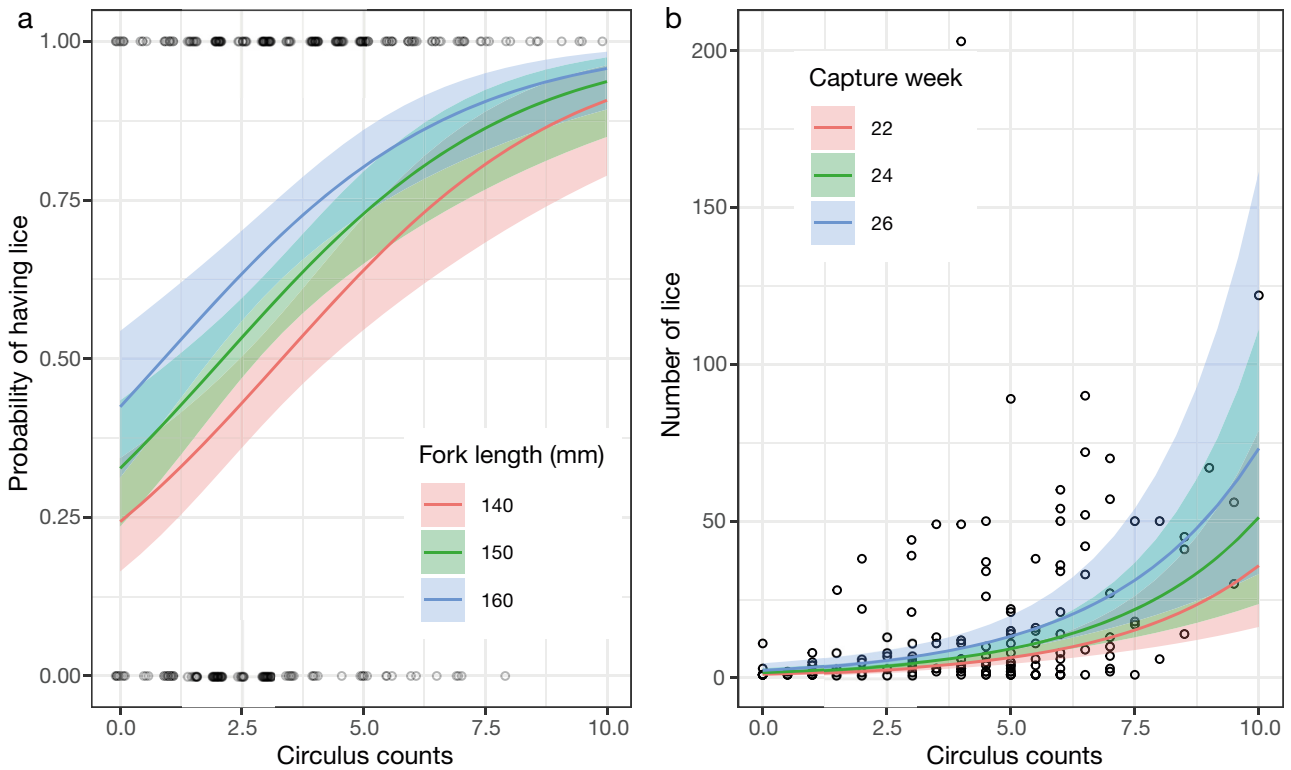
Fig. 5. Results from the ZANB model—(a) binomial component, (b) count component—investigating the correlation between observed lice burdens on sea trout postsmolts and scale circulus counts (proxy for time at sea). Points show observations; solid lines and shaded areas represent model results. (b) Results are shown for individuals of average size (159 mm, mean of individuals with one or more lice) and *yearday* has been converted to calendar week to improve visualization

periods (Haraldstad et al. 2016, Walker & Sutton 2016). Other studies have shown differences between different ages, with mean deposition times being longer during the second summer at sea compared to the postsmolt summer (Wells et al. 2003, Haraldstad et al. 2016). Nonetheless, circulus formation rates have been shown to remain relatively constant during the same growth period and under similar environmental conditions across different salmonid species. For Atlantic salmon postsmolts, multiple studies report deposition times of approximately one week per circulus during spring and summer, decreasing to approximately 1 circulus nearly every 2 wk during autumn and winter (Friedland & Reddin 2000, Friedland et al. 2005, Hubley et al. 2008). Similar deposition times have been estimated for coho *Oncorhynchus kisutch* (Fisher & Pearcy 2005) and pink *Oncorhynchus gorbuscha* salmon (Courtney et al. 2000) during their first growth season. While there are limited studies on circulus formation rate for sea trout, Frier & Rasmussen (2020) reported a consistent periodicity of circulus deposition for sea trout postsmolt captured in the northern part of Denmark during the years 1994–1996, with all values being close to 1 circulus week^{-1} and exhibiting little variation between individuals. These findings are consistent with our study's results, albeit with a slightly slower estimated deposition rate here, averaging approximately 8 ± 0.4 d circulus^{-1}. Differences in deposition times between populations and geographical areas are anticipated, attributed to physical and non-physical factors such as temperature, food, light, genetic factors, and physiological factors, all known to influence circulus deposition rates (Bilton & Robins 1971b, Bilton 1975). Thus, studies investigating circulus formation rate under different environmental conditions and in different geographical areas are needed before results can be extrapolated to other locations. Importantly, results from this study indicate some independence between growth and circulus deposition within the range of growth rates analyzed, supporting the hypothesis that deposition times are relatively consistent at a sub-seasonal scale for individuals of similar size and age and sharing the same geographical area.

Given a fairly constant circulus formation rate, scale reading emerges as a suitable method to estimate the time of sea entry for sea trout postsmolts

from catch samples. Although most sea trout smolts typically migrate downriver to the sea in spring or early summer (Thorstad et al. 2016), migration can occur during all months of the year (Went 1962, Jonsson & Jonsson 2002, Birnie-Gauvin et al. 2019). Also, the duration of the spring smolt migration can span over many weeks, being highly variable among different sea trout stocks and within years. For example, in a river in northern Norway, the mean duration of the smolt run was 118 d over a 22 yr period, whereas the mean duration of the middle 50% of the smolt run was 69 d (Jensen et al. 2012). In river Guddal, in the middle part of Hardangerfjord, the spring smolt migration for trout has been documented to last on average 10 wk, with values oscillating between 7 and 15 wk over an 18 yr period (Harvey et al. 2020). In the present study, scale circulus counts on postsmolts captured in the surveillance program ranged from 0 to 10 circuli throughout the sampling period, with an average span of 7.5 circuli between the lowest and highest count within any given week. These results confirm that catches at any point are composed of individuals that have migrated to sea at different times, often with a time difference of as much as 1 to 2 mo. There was a high degree of agreement between the reconstructed migration curve and observations from the smolt trap, suggesting that fish sampled at sea were representative of the underlying population in terms of migration timing.

As anticipated, both the number of circuli in the marine zone as well as body length were positively correlated with the probability and intensity of lice infestations. Salmon louse infestation levels have been previously shown to increase with the size of the fish (Jaworski & Holm 1992, Helland et al. 2015, Vollset et al. 2017). This may be because bigger fish have a larger body surface area available for colonization by sea lice (Jaworski & Holm 1992), or increased size may be linked to swimming speed and consequently affect the encounter rate with lice (Samsing et al. 2015). Nonetheless, the effect of body size gradually became less important as the number of circuli increased, indicating that time at sea (i.e. accumulated lice exposure) is a better predictor of lice infestations over time than fish size. As the season progressed, infested fish accumulated gradually more lice per unit of time. This could be anticipated, as salmon lice infestation pressure fluctuates seasonally with temperature and is typically lowest in spring and progressively increases during the summer (Schram et al. 1998, Jansen et al. 2012, Sandvik et al. 2021). Interestingly, date of capture significantly affected the number of lice on infested

fish but not the likelihood of infestation. This suggests that infestation pressure was consistently high throughout the sampling period and that infestation was possible at any given time. In such a scenario, marine residency time of the host fish appears to be the primary factor influencing the likelihood of infestation.

Inferring marine residency time based on scale reading offers both advantages and challenges. On the one hand, scales are relatively easy to collect, store, and with training and practice, read, making this approach well suited for large-scale monitoring programs. On the other hand, as with all age determination methods, the accuracy of scale pattern interpretation reflects the reader's training and experience (McNicol & MacLellan 2010, Harris 2020), rendering it inherently subjective. Since the accuracy of the method strongly relies on accurately identifying the transition from freshwater to the marine environment in the scale, future studies should consider employing chemical analysis (i.e. calcium strontium ratios) for this purpose instead of relying solely on a scale reader's judgments based on experience (Wells et al. 2000, Hutchinson & Trueman 2006). The choice of scalimetric method (i.e. number of scales per individual and number of readers) may also affect the results. Here, one scale per fish was read once by a single reader. Although reading multiple scales from each individual can enhance reading precision (Haraldstad et al. 2016), it has been shown that readers and scales contribute minimally to interindividual variance, suggesting that inferences are robust to intraorganism biological variation and thus the addition of extra scales or readers may be an inefficient use of sampling resources (Aulus-Giacosa et al. 2019). Moreover, collecting multiple scales from live fish may elevate the risk of infections and diseases once the fish are released back into their natural environment. Thus, considerations on whether inference accuracy or animal welfare should be prioritized will depend on the goals of the study. Lastly, lice infestations can negatively affect the growth and condition of sea trout, due to adverse stress responses and dehydration (Bjørn & Finstad 1997, Wagner et al. 2008) reduced feeding activity (Dawson 1998, Wells et al. 2006, 2007) or as a consequence of lice-induced behavioral changes such as the premature return to freshwater or brackish areas near the river mouth (Birkeland & Jakobsen 1997, Serra-Llinares et al. 2020). How this affects circulus deposition rates and the speed at which these effects become evident remains unclear and warrants further research.

A still unresolved issue which could further improve our ability to predict and understand the rates of sea lice infestation on wild sea trout is where the captured fish originates from. Whilst most sea trout typically remain in near-coastal areas close to their river of origin (Berg & Berg 1987, Lyse et al. 1998, Flaten et al. 2016), some individuals may perform long distance migrations from their natal watercourse (Pratten & Shearer 1983, Flaten et al. 2016). Thus, catch samples may consist of individuals from mixed populations with different migration histories and potentially different susceptibility and immune response to lice (Glover et al. 2003). One way to disentangle the different populations composing a sample is to apply mixed stock assessment using population genetic tools, where fish captured in a mixed fishery are assigned back to river or region of origin using a genetic baseline of populations from the area of interest. This method has been used in various salmonid fisheries to identify the underlying population assembly and distribution of stocks in a mixed fishery (Svenning et al. 2019, Beacham et al. 2022, Deeg et al. 2022) and have also been used to infer migration timing (Harvey et al. 2019). This method has also been used to reveal the stock components of sea trout fisheries in Finland (Koljonen et al. 2014) and along the British North Sea coast (Bekkevold et al. 2021). While genetic studies on sea trout in Norway exist (Knutsen et al. 2001), studies using mixed stock analysis on sea trout caught in the fjords are rare. One reason for this is that the precision and strength of the method is strongly dependent on the robustness and representativeness of the baseline samples it is built upon. With at least 1251 watersheds producing sea trout in Norway, establishing dependable genetic baselines at a national level is both resource-intensive and time-consuming. Fostering collaboration and facilitating the exchange of genetic data among national institutions is therefore strongly advocated.

Previous attempts at predicting lice infestations on sea trout as a function of biotic and abiotic factors using both statistical (Serra-Llinares et al. 2014, Helland et al. 2015, Serra-Llinares et al. 2016, Vollset et al. 2018) and hydrodynamic lice dispersal models (Bøhn et al. 2022) have been hampered by a large variation around estimated values. Given the highly skewed nature of lice distributions, combined with a high natural stochasticity, it is unrealistic to expect precise predictions for lice infestations on wild fish. However, results from our study illustrate how a proper understanding of the spatio-temporal aspects of migration in the population sampled can significantly reduce the associated uncertainty, enhancing predictive accuracy. We conclude that the collection and inclusion of additional supporting data on individual sea trout migration traits can bring added value to salmon lice surveillance programs by helping disentangle the different spatio-temporal groups that constitute a catch sample. This is essential to ensure the precise interpretation of surveillance data and to develop more accurate prediction tools, ultimately contributing to the implementation of sound management strategies for sea trout.

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