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Sea trout adapt their migratory behaviour in response to high salmon lice concentrations

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Abstract

Sea trout face growth–mortality trade-offs when entering the sea to feed. Salmon lice epizootics resulting from aquaculture have shifted these trade-offs, as salmon lice might both increase mortality and reduce growth of sea trout. We studied mortality and behavioural adaptations of wild sea trout in a large-scale experiment with acoustic telemetry in an aquaculture intensive area that was fallowed (emptied of fish) synchronically biannually, creating large variations in salmon lice concentrations. We tagged 310 wild sea trout during 3 years, and gave half of the individuals a prophylaxis against further salmon lice infestation. There was no difference in survival among years or between treatments. In years of high infestation pressure, however, sea trout remained closer to the river outlet, used freshwater (FW) habitats for longer periods and returned earlier to the river than in the low infestation year. This indicates that sea trout adapt their migratory behaviour by actively choosing FW refuges from salmon lice to escape from immediate mortality risk. Nevertheless, simulations show that these adaptations can lead to lost growth opportunities. Reduced growth can increase long-term mortality of sea trout due to prolonged exposure to size-dependent predation risk, lead to lower fecundity and, ultimately, reduce the likelihood of sea migration.

KEYWORDS
bet-hedging, *Lepeophtheirus salmonis*, parasite, *Salmo trutta*, host, salmon farming

1 | INTRODUCTION

In a variable and unpredictable environment, individuals that can adapt their behaviour to current conditions have a greater chance to maximize their long-term fitness (bet-hedging theory, e.g., Philippi & Seger, 1989). One of these adaptable behaviours for salmonids is migrating between sea feeding and freshwater (FW) spawning areas. Sea migration has evolved in salmonids as an evolutionary strategy to increase growth due to better feeding opportunities at sea compared to FW (Gross, 1987). Even though sea migration both delays maturation and lowers an individual's survival probability through increased predation risk and infestation risk by parasites and pathogens, it typically results in a much larger body size and greater reproductive success for the surviving individuals (Fleming & Reynolds, 2004; Roff, 2002; Stearns, 1992). This behaviour, however, will persist only if the benefits exceed the costs (Sandlund & Jonsson, 2016; Werner & Gilliam, 1984). The expansion of industrial aquaculture in coastal and near-shore areas has increased the intensity and unpredictability of epizootics of salmon lice (*Lepeophtheirus salmonis* K.) (Finstad & Bjørn 2011; Thorstad

et al., 2015). These salmon lice epizootics can reduce growth and increase mortality risk for sea migrating salmonids (Costello, 2009; Fjørtoft, Borgstrøm, & Skaala, 2014; Wells et al., 2006, 2007), thereby increasing the costs of sea migration.

The increased mortality risk due to salmon lice epizootics may be due to a combination of physiological stress, secondary infections reducing fish growth and/or altered predator avoidance behaviour, all of which could increase predation risk (Bjørn & Finstad, 1997, 1998; Peacock, Krkošek, Bateman, & Lewis, 2015; Wells et al., 2006, 2007) . Growth may be reduced through physiological stress, reduced swimming and foraging capacity and therefore lost feeding opportunities (Birkeland & Jakobsen, 1997; Dawson, 1998; Godwin, Dill, Reynolds, & Krkosek, 2015; Shephard, MacIntyre, & Gargan, 2016). Because salmon lice do not tolerate low salinities for extended periods (Heuch, 1995; Wright, Oppedal, & Dempster, 2016), coastal migrating salmonids like sea trout (*Salmo trutta* L.) can actively reduce or get rid of a salmon lice infestation by seeking FW (Birkeland & Jakobsen, 1997; Gjelland et al., 2014; Wells et al., 2007). Nevertheless, spending time in the estuary or returning to a river has a cost of reduced foraging opportunity and efficiency (Birkeland, 1996). Considering that sea trout have an enormous growth potential at sea during their feeding migrations (Fjørtoft et al., 2014; Jensen, Finstad, Fiske, & Saksgård, 2016; Jonsson & Jonsson, 2011) and that survival increases with size (e.g., Jørgensen & Fiksen, 2010; Peterson & Wroblewski, 1984), even small modifications on migratory and feeding behaviour caused by salmon lice might therefore lead to large individual differences in growth and survival, and thereby also in reproductive potential (Birkeland, 1996; Fjørtoft et al., 2014; Wells et al., 2007).

Here, we studied how salmon lice infestation affects the survival and migration behaviour of acoustically tagged wild sea trout in a large-scale field experiment over three consecutive years in an aquaculture intensive area in western Norway. As a result of a synchronized fallowing regime shared by all companies operating in the study area, all farmed fish (lice hosts) were removed from the site for varying periods, every second year. As a consequence, we anticipated that this would result in an alternating pattern of "high–low–high" lice infestation pressure in the study fjord during the three study years. We tested whether in years of high infestation pressure, fish treated with a prophylaxis (emamectin benzoate/substance EX) against further salmon lice infestations would have higher survival and/or more extensive migrations compared to untreated fish. In addition, we simulated sea trout growth based on different migratory scenarios to assess growth effects of sea trout behavioural adaptations in response to salmon lice infestations.

## 2 | MATERIAL AND METHODS

2.1 | The study area

The study took place in Etnefjord (59.65°N, 5.88°E, length = 8.1 km, max. depth >150 m), a small side-fjord in the outer part of the largest and most aquaculture intensive fjord system in Norway, Hardangerfjord (Figure 1a, total standing stock of ~94,000 t farmed salmon on 31 December 2016; Directorate of Fisheries). Etnefjord is a protected area in which no fish farming activities are allowed, but there are active farming sites as close as 8 km from the fjord mouth (Figure 1a). Therefore, due to the potential spread of infective salmon lice copepodites with water currents, lice infestation pressure inside Etnefjord can be expected to depend strongly on the production regime in the outer part of Hardangerfjord (Asplin et al., 2014; Johnsen, Fiksen, Sandvik, & Asplin, 2014; Serra-Llinares et al., 2014; Serra-Llinares et al., 2016). During the study period, salmon farming in Hardangerfjord was synchronously fallowed biannually, that is, all fish farms in a fallowing zone were emptied for fish for at least a month (March) every second spring. Thus, adjacent farms to the study area were in full production in 2012 and 2014, and fallowed in 2013, which was sufficient to reduce lice infestation pressure (see Results). We seized the opportunity offered by the biannual low and high salmon lice infestation pressure at the study area to perform a large-scale field experiment.

Etne River (Figure 1b) is the only large river discharging into the Etnefjord, but several small streams also enter the fjord and may be important to the sea trout in the area. The Etne River summer temperatures (June 1–August 31) in 2012–2014 ranged between 8.4 and 23.0°C, the summer of 2012 being the coolest (mean 13.5°C) and 2014 the warmest (mean 16.7°C, Figure S1 [figures marked with S found in supporting information]). The river discharge in the same period ranged between 2.8 and 27.5 m^3/s, with largest discharge in 2012 (mean 9.9 m^3/s) and lowest discharge in 2014 (mean 7.1 m^3/s; Figure S1, data provided by the Norwegian Water Resources and Energy Directorate). For fjord water temperature and salinity, four data loggers (DST tags, Star-Oddi, Iceland) were deployed in 2013–2014 (recordings at 10-min intervals at 0.5 and 1.5 m depths, see Figure 1b for locations). The sea summer temperatures for 2013 and 2014 in the inner part of the fjord at 1.5 m depth (see Figure 1b for location, Figure S2 for data) ranged between 12.7 and 23.6°C (mean 16.3°C for 2013 and 18.8°C for 2014). Salinities in the same location ranged between 9.8 and 28.9 g/L (mean 21.7 g/L for 2013 and 16.8 g/L for 2014). Temporal variability in both temperature and salinity was observed, with rapid temperature decreases of ~5°C and salinity increases of ~10 g/L occurring over 2 days on several occasions (July 28–30 in 2013 and July 3–5 and August 10–12 in 2014). Rapid decreases in temperature and increases in salinity can be caused by vertical mixing or water exchange processes where water from the outer fjord is transported into the inner part of the fjord (Asplin et al., 2014; Johnsen et al., 2014).

2.2 | Quantification of infestation pressure

In total, 3,546 wild sea trout were sampled in specially designed traps [see Table 1 for details on monitored fish, and for details about capture method, see Barlaup et al. (2013) and Arechavala-Lopez, Berg, Uglem, Bjørn, and Finstad (2016)]. For all years, trout were trapped on a daily basis between mid-May to late June (weeks 20–27), at 0.5–2 and 6–7 km from the Etne River outlet (Figure 1b). Before releasing a fish, we recorded its fork length and weight to the closest mm and g, respectively, and counted its lice burden by copepod life stage groupings (copepodite, chalimus 1 and 2, preadult, adult female and adult male). Throughout the manuscript, we use the terms abundance
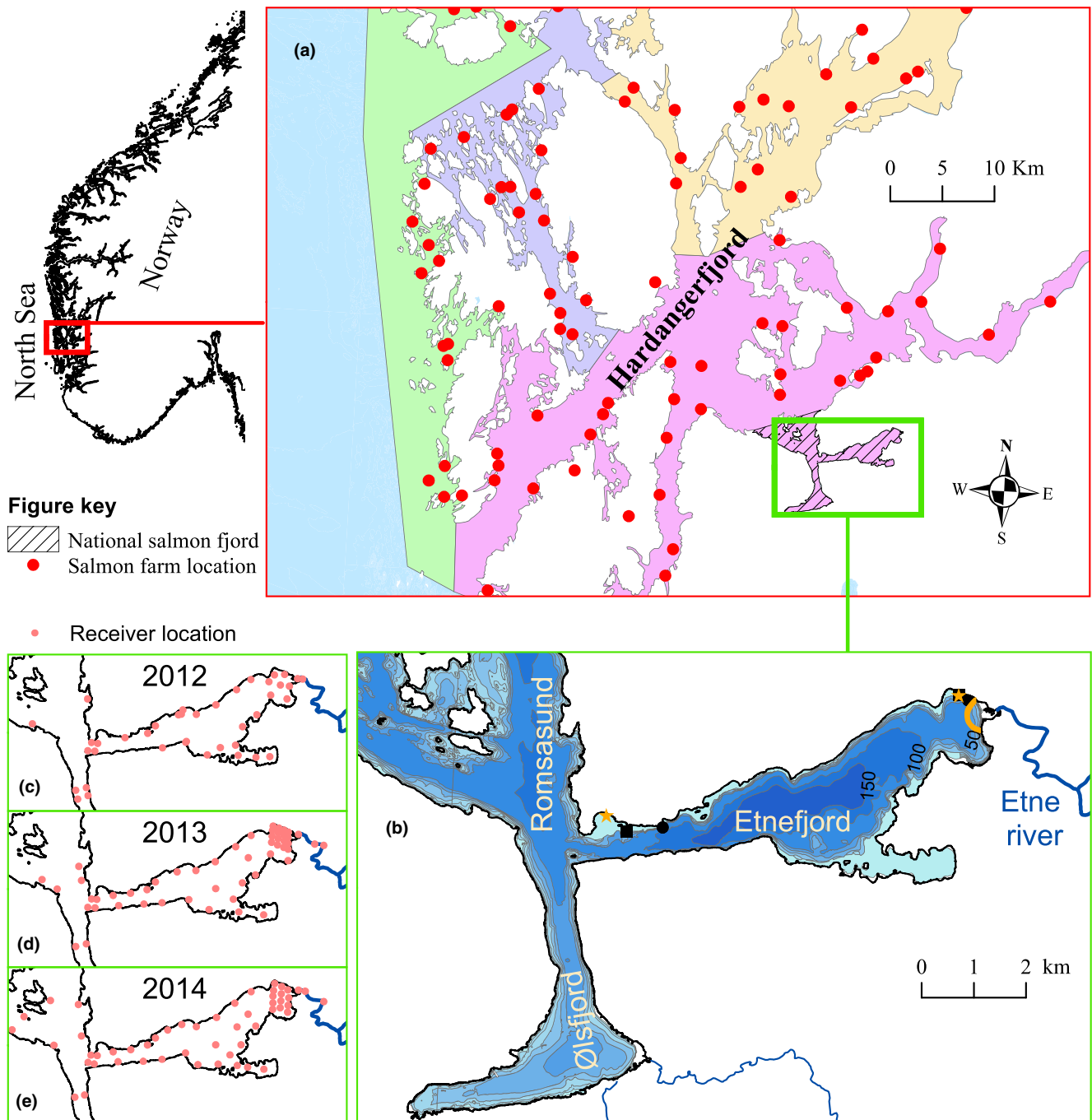
FIGURE 1 Study area and design: (a) study area (rastered), with synchronized fallowing zones marked in different colours, aquaculture sites marked with red dots, (b) Etnefjord and adjoining Ølsfjord and Romsasund, the positions of fish traps are marked with yellow stars, and salinity and temperature recorders with black dots (2013) and squares (2014), the delousing zone at the river outlet marked with an orange half-circle (note the overlap of some of the symbols), and (c–e) acoustic receiver deployment sites in 2012–2014

(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 infestation.

2.3 | Tagging and treatment of fish

Subsamples of the caught fish were tagged with acoustic transmitters each year. In total, over 3 years of study, 310 wild sea trout

(see Table 1 for details) were caught, tagged and released back into the fjord during May/June (weeks 20–25). Each fish was implanted with an individual ultrasonic transmitter (Vemco Inc.) into the body cavity following the general procedures described in Finstad, Økland, Thorstad, Bjørn, and McKinley (2005) and Hedger et al. (2011). In 2012, fish were tagged with V9P-6L acoustic tags (estimated tag life = 123 days, depth sensor with 22-cm resolution, and minimum, mean and maximum signal intervals were 60,

TABLE 1 The number, mean ± SD length and mass, prevalence and mean ± SD intensity of (a) salmon lice of all sampled and (b) tagged wild sea trout in Etnefjord in 2012–2014 (Big = V9P-6L, Small = V8-4L, acoustic tags, Vemco Inc., Canada)

Year	Tag	n	Length (mm)	Mass (g)	Prevalence (%)	Mean intensity
(a)						
2012	–	569	190.3 ± 67.6	105.2 ± 229.8	72	73.8 ± 102.7
2013	–	1,014	158.8 ± 34.9	49.9 ± 93.9	47	13.9 ± 19.5
2014	–	1,539	176.1 ± 52.2	78.6 ± 170.1	52	24.1 ± 49.9
(b)						
2012	Big	30	262.2 ± 28.9	190.5 ± 64.7	100	43.1 ± 63.4
2013	Big	100	295.5 ± 63.9	302.5 ± 190.3	47	14.7 ± 22.1
	Small	30	177.9 ± 16.9	60.8 ± 15.3		
2014	Big	120	262.8 ± 58.4	213.6 ± 189.9	74	21.5 ± 33.2
	Small	30	195.2 ± 10.3	80.5 ± 14.1		

100 and 140 s, respectively, hereafter called big tags). In 2013 and 2014, smaller fish (150 mm < fork length < 220 mm) were tagged with V8-4L transmitters (estimated tag life = 157 days, no depth sensor, and minimum, mean and maximum signal intervals were 80, 115 and 150 s, respectively, hereafter called small tags), while bigger fish (fork length > 220 mm) were tagged with a V9P-6L tag with a slightly different programming than the previous year (estimated tag life = 139 days, depth sensor with 22-cm resolution, and minimum, mean and maximum signal intervals were 80, 115 and 150 s, respectively, hereafter called big tags). The bigger fish (fork length > 220 mm) were also tagged externally with individually numbered T-bars and the smaller fish (fork length <220 mm) were fin-clipped for visual recognition in case of recapture.

Each year, half of the acoustically tagged fish were treated with a prophylaxis. In 2012, the fish were treated with emamectin benzoate (EB), and in 2013–2014 with substance EX bath treatment (subEX; Pharmaq, Norway). The prophylaxes differ in their mechanism: EB is a neural toxin and kills all attached lice (Burka, Fast, & Revie, 2012; Glover, Samuelsen, Skilbrei, Boxaspen, & Lunestad, 2010), whereas subEX is a chitin synthesis inhibitor and therefore inhibits moulting to the next stage (Skilbrei, Espedal, Nilsen, Garcia, & Glover, 2015). The prophylaxes also differed in the administration procedure: EB was injected directly into the body cavity right after tag implantation at a dosage of 400 μg EB/kg fish (Glover et al., 2010), whereas subEX was administered by bathing the fish in a 2 mg/L solution for 30 min in a 50-L aerated tank. The assumed duration of the protection from EB was 9 weeks (Glover et al., 2010), whereas subEX protects the fish against lice infestation development for up to 16 weeks (Skilbrei et al., 2015). Treatment with subEX is considered less stressful for the fish than EB, but the treatments with dose and administration as in our study are comparable in efficiency for both sensitive and less sensitive strains of salmon lice (Skilbrei et al., 2015). Results were not affected by these different treatments because excluding 2012 from the analyses gave similar results.

2.4 | Tracking of fish

A total of 41–65 acoustic receivers (VR2W, Vemco Inc, Canada) were deployed at sea each year with slightly varying positioning among years in Etnefjord and the neighbouring Ølsfjord and Romsasund (Figure 1c–e). Three additional receivers were deployed along the Etne River to monitor potential returns to FW. Different mooring systems (surface and submerged floats) were used for the deployment of the acoustic receivers at sea depending on the depth. The receivers were attached to the mooring systems at depths ranging between 5 and 52 m. Five sentinel tags were used to provide information about receiver detection efficiency (Vemco V16, average transmission interval 15 min). The receiver coverage was denser near the Etne River outlet than in most of the fjord to ensure a high probability of detecting migration back to the river outlet, and double arrays in the outer fjord ensured detecting migration out of the fjord. The detection rate of sentinel tags in much of Etnefjord was lower during the day than at night, but no diurnal pattern was observed in detection rates elsewhere. Consistency of transmitter detections was evaluated by plotting each detection as a function of time and the distance from the receiver to the river outlet, according to an acceptance criterion of maximum 2, 4 or 12 hr between successive detections of the tag at the same receiver. Acceptance criterion of 4 hr in the dense coverage area close to the river outlet, and 12 hr in the rest of the fjord, ensured that false detections were discarded while keeping the number of discarded true detections low. In total, 19,469 of 10,753,189 detections (0.18%) were discarded.

2.5 | Fate assessment of tagged fish

Individual acoustic detection patterns were examined to identify individual fates. As the big tags with a depth sensor recorded a vertical signature, it allowed a more detailed categorization of fates than the small tags without a depth sensor. The fate of each individual was categorized working backwards from the last observation (Figure S3). The individuals were categorized as: (i) River run, if the final detections were within the Etne River (this category is likely

underestimated if fish entered other rivers that were not surveyed); (ii) Emigrated, if the final detections were on the outer receivers in Romsasund; (iii) Alive in the sea, if detections indicated normal swimming activity (normal vertical and horizontal movements) within the fjord at the time of removal of the receiver array; (iv) Dead, if considered dead or lost to predation (sub-categories 4.1 Predation by fish or mammal, 4.2 Predation by fish and 4.3 Dead, only for big tags); and (v) Unknown, if tag detections disappeared within the study area during the study period, without a vertical signature that could be attributed to the other main categories (sub-categories 5.1 Tag loss or predation by an animal behaving similarly as sea trout, 5.2 Fishing, 5.3 Unknown, tag observed stationary, and 5.4 Unknown, tag disappeared; Figure S3). Predation was indicated by a diving pattern that was inconsistent with sea trout vertical swimming behaviour (Gjelland et al., 2014), usually including a sudden change to greater depths, followed by the tag becoming stationary within a few days, thereby indicating that the tag had gone through the digestive system of the predator and had thereafter been dropped to the bottom. Tag loss was indicated by an immediate change from normal vertical swimming activity to a sudden and permanent increase in transmitter depth, followed by the tag becoming stationary within a couple of minutes (three fish whose fates were classified as Tag loss were confirmed by later recapture of the fish). The final individual sea trout record was defined as the last transmitter detection before a predation or tag loss event, or as the last detection record in the study period for all other fish. Transmitter detections after this time were removed from the individual detection data before further analyses of sea trout behaviour and mortality.

All fish that were predated, dead, stationary or disappeared within 48 hr after tagging (n = 13) were removed from analyses, as their mortality could be considered as delayed tagging effects. One fish with an immediate and clear tag malfunction was also removed. As a result, a total of 238 big tags and 58 small tags were used in the analyses. Due to the different fate categorizations between big and small tags, we used different subsets for different analyses, depending on the question.

2.6 | Analyses

All statistical analyses were conducted using the open-source R language for statistical computing and graphics (R Development Core Team 2013).

2.6.1 | Infestation pressure on all sampled fish

To evaluate how lice abundance varied among years, we modelled the lice abundance, intensity and prevalence on all sampled fish (n = 3,716) fitting a generalized linear mixed model (GLMM) using the "glmer" function of the "lme4" package of R (Bates, Maechler, Bolker, & Walker, 2015). For abundance and intensity, we fitted a model with a poisson family and a log link, whereas for prevalence we fitted a model with a binomial family with a logit link. For all three models, we fitted year, catch locality (inner fjord [0.5–2 km] vs. outer fjord [6–7 km]) and their interaction as fixed factors and

week number as a random intercept. Global effects of factors were assessed with the "ANOVA" function of the "car" package based on type II Wald chi-squared tests (Fox & Weisberg, 2011).

2.6.2 | Survival of tagged fish

Because the categories Dead and Predated could only be assessed from tags with a vertical signature, only individuals tagged with big tags (n = 238) were used in the survival analysis. To assess whether the survival differed between treatment and between years of high and low infestation levels, we fitted a Cox proportional hazards regression model with the "survival" package (Therneau, 2016). In the model, the individuals that we could not categorize as Dead at the end of the study were identified as being right-censored. For these censored individuals, the time of death is known to be larger than the last time observed alive, so the time at censoring is used to indicate the survival of an individual prior to censoring and an unknown fate after censoring. By censoring, we could use all the information on the individuals until censored and avoid any bias that could occur when analyses are based only on complete cases (Moore, 2016). Here, individuals were categorized as "dead" if considered dead or lost to predation (fates 4.1, 4.2, 4.3), or as "survived" if alive (fates 1 and 3, i.e., alive at sea or entered the river) at the last observation time. The remaining fates (2, 5.1, 5.2, 5.3, 5.4; Figure S3) were considered as missing data (NAs). The individuals categorized as "dead" were given a status of 1, and those categorized either as "survived" or with missing data were given a status of 0, that is, indicating they were right-censored, using either the last observation, or the last observation when they could be classified as a live trout at the censoring time point. In other words, survival time was the number of days until the fish died (status 1), or the number of days the fish was observed alive at sea/in the river (status 0), with the maximum time being when the study ended.

In this survival analysis, we were interested in assessing the influence of the factors "treatment" and "year". We used years as a contrast between high (years 2012 and 2014) and low (2013) years of lice infestation (see Results on infestation pressure for analyses supporting this classification). To control for individual differences among fish at the time of tagging, we included as covariates tagging time (log of week number to meet the proportional hazards assumption), catch locality (inner/outer fjord) and individual variables at the time of tagging, that is, fork length, body condition index (residuals of the log of mass regressed on the log of length) and relative infestation intensity (number of lice/body mass). We verified that the model met the proportional hazards assumption with the "cox.zph" function of the survival package. The influence of each covariate was assessed with an analysis of deviance table using a sequential ANOVA, that is, the influences of the covariates were included in the analysis first to account for their influence before assessing the effect of the two variables of interest (treatment and year). All variables were centred to allow interpretation of main effects independently of interactions (Schielzeth, 2010). In addition, all continuous variables were standardized to provide parameter estimates that

allowed comparing the magnitude of the effects and hence the importance of each variable (Schielzeth, 2010). Because the models included categorical variables, we used two standard deviations to standardize the continuous variables, therefore permitting comparisons between categorical and continuous variables (Gelman, 2008; Schielzeth, 2010).

Then, we analysed survival in more detail by comparing the frequency of the specific fates between treatments and among years among all tagged fish (small and big, $n = 296$). We used the "Cross-Table" function of the R package "gmodels" (Warnes, Bolker, Lumley, & Johnson, 2015) to perform a contingency table evaluating the independence of the factors "treatment" and "year" across the different fates. Some of the fates had to be pooled due to <5 observations in a cell: these were Dead and Predated (4.1, 4.2, 4.3) and Emigrated and Unknown (2, 5.1, 5.2, 5.3, 5.4).

2.6.3 | Migratory behaviour of tagged fish

For each tracked fish, we measured four behavioural traits relating to migration between sea and FW: the timing of river entry, hourly distance to the river mouth, the proportion of time spent in delousing areas (river or <300 m from the river outlet, see below) and the global migration pattern (movement to and from the delousing areas). All tags ($n = 296$) were used in analysis of timing of last river entry, whereas only big tags (with vertical signature, $n = 238$) were included in the analysis of the distance to river mouth and the proportion of time spent in delousing.

The timing of last river entry was defined as the last time the fish entered the river and stayed there until the end of the study. The influence of treatment and year on the timing of river entry (i.e., time until river entry) was analysed with a right-censored Cox proportional hazards regression model including the same covariates and standardization method as for the survival analysis. The only difference with the survival analysis was the status given to individuals: individuals were given a status of 1 at the time of entry in the river (fate 1), and individuals that were still at sea at their last observation (fate 3) where right-censored and given a status of 0. The remaining fates (2, 4.1, 4.2, 4.3, 5.1, 5.2, 5.3, 5.4) were considered as NAs, and therefore, the time of last observation at sea was used and categorized as right-censored with a status of 0. In other words, survival time is the number of days the fish was observed at sea until the fish entered the river (status 1), or the number of days at sea until its status became unknown or the study ended (status 0). The variable treatment and year showed departure from the proportional hazards assumption tested with the "cox.zph" function, showing a time dependency. Analysis of the Schoenfeld residuals showed a threshold at 100 days, and hence, we used the "survSplit" function in the survival package to make a stratified analysis before and after 100 days (strata). Therefore, the model included an interaction between treatment and strata, and between year and strata. These interactions test for a difference in the proportional hazard before and after 100 days for these two variables, and thereby allow accounting for this difference.

To compute hourly distance from the individual fish to the river mouth, hourly mean positions of each fish were calculated using the weighted centre of activity (CA) method (Simpfendorfer, Heupel, & Hueter, 2002). Distances were assigned as negative for fish upstream of the river mouth (i.e., river run) and positive for fish in the sea. We used a linear model to assess the influence of year (high vs. low infestation levels) and treatment, as well as standardized covariates (catch locality, length, condition and infection intensity at tagging), on the average distance a fish spent from the river mouth, that is, the global average of the hourly mean distances for each fish as the response variable. The global average was used in order to avoid serious autocorrelation in model residuals. To normalize the model residuals, we used a square root transformation, adding the minimum recorded distance (i.e., −1,500) to all values to avoid NAs produced by negative distance values. As for the survival analysis, all variables were centred and standardized and the influence of each covariate was assessed with an analysis of deviance table using a sequential ANOVA.

Sea trout in or close to the river mouth may experience very low salinities and therefore high lice mortality, especially for newly infested lice (Birkeland & Jakobsen, 1997; Wright et al., 2016). Hence, we classified all hourly mean positions with distance <300 m from the middle of the river outlet (Figure 1) as being in a delousing area, and the positions with distance ≥300 m from the river outlet as being in a marine area. The area was chosen conservatively based on constantly low salinities due to proximity to river mouth combined with low depth. Nevertheless, results were not sensitive to this choice as using <600 m as a cut-off leads to similar results. We then calculated for each week the proportion of time each fish spent in the delousing area (i.e., the number of hours spent in delousing areas divided by the total number of hours in the week). We used a GLMM from the binomial family with a logit link to assess the influence of treatment and year (high vs. low infestation levels), as well as standardized covariates (catch locality, length, condition and infection intensity at tagging), on the weekly proportion of time spent in the delousing areas. To account for the nonlinear change with weeks, we also included as a covariate week number, and its interaction with year, which we modelled with a piecewise polynomial of degree 5 (R package "splines"), with the best degree selected based on likelihood ratio tests. Individual identity was used as a random intercept. Again, all variables were centred and standardized and the influence of each covariate was assessed with an analysis of deviance table using a sequential ANOVA.

In addition, 95% bootstrap confidence intervals for arithmetic mean proportions of individual yearly proportions were calculated for comparison of yearly means. Nonparametric bootstrapping was performed with the R package "boot," 10,000 runs, and bca-type confidence intervals (Canty & Ripley, 2017). Bootstrapped 95% confidence intervals were also calculated for weekly arithmetic mean proportions regardless of catch locality and treatment, for comparison with the weekly mean lice intensity on sampled fish. Weekly mean lice intensities with confidence intervals were obtained using the "predictInterval" function in the "merTools" R package (Knowles & Frederick, 2016) with the poisson GLMM on lice count data. The relationship between weekly mean proportions of time spent in

delousing areas and the mean lice intensities on sampled fish were assessed by a linear model, with the proportion of time as response variable in relation with mean intensity (log-transformed) and study year as a fixed factor. To look for a potential lagged response to the mean lice intensities, mean proportion of time spent delousing was also compared to the mean lice intensities 1 and 2 weeks earlier.

To evaluate differences in the global migration patterns among years, we divided individual movements to and from delousing areas into two categories: delousing periods and marine migration periods. The first individual marine migration period was from release until the first mean hourly position within the delousing area. A new individual marine migration period was not assigned until the fish was observed for at least 24 consecutive hours outside the delousing area. If a fish moved more frequently in and out of the delousing area, it would be assigned as one delousing period. A new marine migration period lasted until the next mean hourly position within the delousing area. Hence, a marine migration period lasted for at least 24 hr by this definition, whereas a delousing period could be shorter. We used an ANOVA to compare the length of the delousing periods (restricting the data to a maximum of the three-first delousing periods for each individual and the marine migration periods among years (with sixth-root-transformed period length in order to normalize the model residuals). The length of the marine migration period between the release and first delousing was not considered as we did not know when this started.

2.6.4 | Growth simulations

To evaluate the influence of the time spent in FW on growth, we simulated growth for different variations of FW forays using formulae defining the standardized specific growth rate Ω as follows (Ostrovsky, 1995):

$$\Omega = 100 * (M_2^b - M_1^b)/b * (t_2 - t_1) \qquad (1)$$

where M_1 and M_2 are the fish weight (g) at time t_1 and t_2, that is, the beginning and the end of the time period, and b is an allometric weight exponent. We therefore obtained the simulated end-weight (M_2) according to:

$$M_2 = ([(\Omega/100) * (b * (t_2 - t_1))] + M_1^b)^{(1/b)} \qquad (2)$$

where Ω was set to 8.5% per day at sea (Jensen et al., 2016) and -1.9% per day in FW (calculated from data in Birkeland, 1996), and b set to 0.31 according to Elliott, Hurley, and Fryer (1995). The length of the idealized marine migration was set to May 15 to August 15 (93 days), based on Thorstad et al. (2016).

3 | RESULTS

3.1 | Infestation pressure

Salmon lice abundance on all the sampled trout increased with time in all years (Figure S4 upper panel, variance of week as a random intercept = 1.7), and varied significantly between years and locality (year: $\chi^2 = 38{,}943.4$, $df = 2$, $p < .001$; locality: $\chi^2 = 512.7$, $df = 1$, $p < .001$; year × locality: $\chi^2 = 1{,}024.2$, $df = 2$, $p < .001$). The lice intensity and prevalence were lower in the fallowed year of 2013 (hereafter referred to as low) than in the full production years of 2012 and 2014 (hereafter referred to as high), and the prevalence was higher in the outer catch location than in the inner catch location (Figure S5a,b) (lice intensity—year: $\chi^2 = 30{,}719.9$, $df = 2$, $p < .001$; locality: $\chi^2 = 13.6$, $df = 1$, $p < .001$; year × locality: $\chi^2 = 117.0$, $df = 2$, $p < .001$; prevalence—year: $\chi^2 = 207.1$, $df = 2$, $p < .001$; locality: $\chi^2 = 263.8$, $df = 1$, $p < .001$; year × locality: $\chi^2 = 23.4$, $df = 2$, $p < .001$). The infestation also developed later in the low year, than in high production years (Figure S4) upper panel.
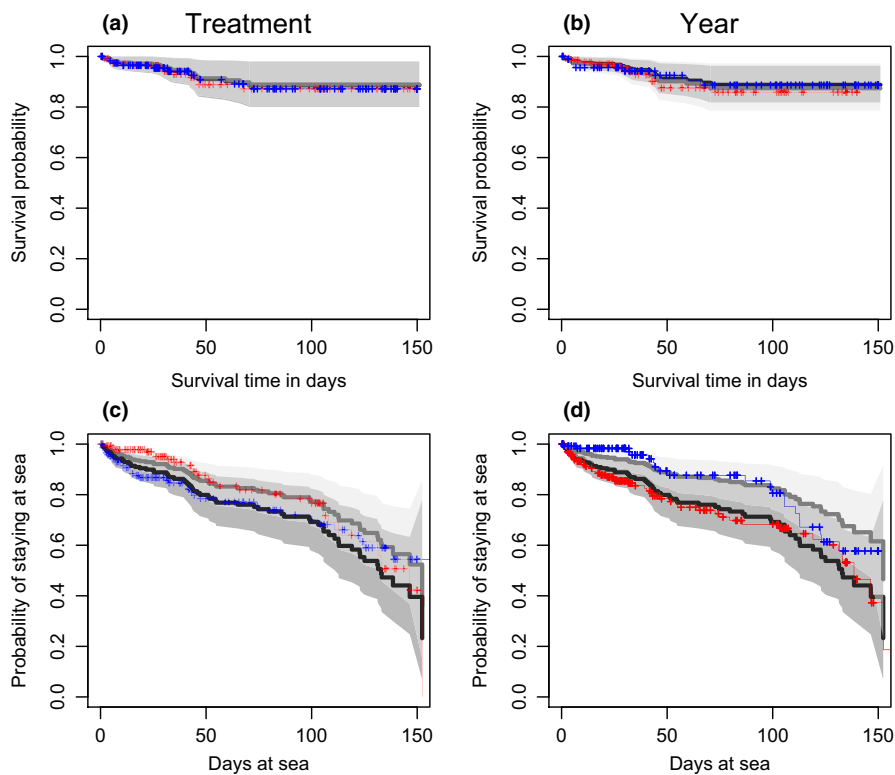
3.2 | Survival

Survival of tagged trout did not differ between treatments or years of high and low infestation pressure (Figure 2a–b, Table 2). The treated trout survived on average ($\pm SD$) 63 ± 47 days, and their untreated counterparts survived on average 66 ± 48 days from tagging. The survival time was shorter in the high years (2012 = mean 55 ± 36 and 2014 = mean 60 ± 47 days from tagging), compared with the low year (2013 = mean 72 ± 51 days from tagging), but this contrast between high and low years was not significant (Table 2). Among the covariates, body length was the only important predictor for survival time, with larger trout having a higher probability of surviving longer than smaller trout (Table 2).

With respect to the specific fates of tagged sea trout, a total of 112 (38%) were either alive at sea or had returned to the river at the end of the three study years, and only 21 (7%) ended up categorized as either Dead or Predated. A large group of fish 163 (55%) were categorized as Emigrated and Unknown (Table 3a, Figure S3). Fates of fish did not differ between treatment groups, neither when all fish were pooled (Table 3a) nor when considering only the group of fish marked with the largest model tag (Table 3b). Fates differed among the years when all fish were pooled (Table 3a), but this difference was driven by the small fish as there was no difference among the years when considering the fish tagged with the largest model tag only (Table 3b).

3.3 | Migratory behaviour

Prophylaxis treatments did not affect the timing of river entry of tagged fish (treated 57 ± 49 vs. untreated 58 ± 47 days), but timing of river entry differed between high and low infestation years (Figure 2c–d, Table 2). The tagged trout returned to the river later in the low year (2013 = mean 60 ± 48 days at sea from tagging) than in the high years (2012 = mean 53 ± 36 and 2014 = mean 56 ± 50 days at sea from tagging). There was a tendency for the fish tagged at the outer part of the fjord to stay in the sea longer than the ones tagged at the inner part (Table 2). The two interactions with strata (Table 2) confirmed the difference in proportional hazard before and after 100 days, particularly for treatment effect.

FIGURE 2 Observed (coloured lines) and predicted (black and dark grey lines, with grey polygons illustrating 95% confidence intervals) survival curves for tagged sea trout survival (a,b) and the probability of staying at sea (c,d), contrasting treatment (a, c; red = untreated, blue = treated) and years (b,d; red = high infestation [2012 and 2014], blue = low infestation [2013]). The crosses mark each censoring time that is not also a death time

This threshold is also confirmed by the crossing of the survival curves at day 100 based on the raw data (i.e., red and blue lines in Figure 2c,d).

Overall, the fish spent more time in the delousing areas in the high years compared with the low year, particularly in late season (Figures 3a, S4 lower panel), and fish caught and released at the inner catch locality spent more time in delousing areas than fish caught and released at the outer catch locality (Figure 3a, Table 4). The average fish distance to the river outlet differed slightly between treatments, but the greatest difference was observed among years, with sea trout staying about 1 km closer to the river outlet in high infestation years as compared with the low infestation year (Figure 3b, Table 5). Among covariates, catch locality affected the average distance to the river outlet, with fish released at the outer locality staying on average 2 km further from the river outlet as compared with fish released at the inner locality (Table 5). In addition, bigger fish in better condition stayed on average further out compared with smaller fish in poorer condition (Table 5).

Weekly mean proportion of time spent delousing was positively correlated to weekly mean lice intensity on all sampled trout (Figure 4a, intensity: $F_{1,11} = 5.7$, $p = .04$, year: $F_{2,11} = 4.3$, $p = .04$, intensity × year: $F_{2,11} = 0.9$, $p = .4$, adjusted $r^2 = .41$). More variation was explained when comparing mean proportions to the mean intensities 2 weeks before (Figure 4b, intensity: $F_{1,11} = 17.0$, $p = .001$, year: $F_{2,11} = 21.1$, $p < .001$, intensity × year: $F_{2,11} = 0.8$, $p = .5$, adjusted $r^2 = .76$), and the model results for a 1-week difference were intermediate between these two.

Although the mean length of the delousing periods was slightly shorter in the low year than in the high years, these differences were not significant (Figure 5, $F = 0.59$, $p = .3$, $df = 2$, adjusted $r^2 = 0$). The length of the marine periods, however, varied among years, with slightly longer marine migration periods in the low year than in the high years (Figure 5, $F = 6.2$, $p = .002$, $df = 2$, adjusted $r^2 = .04$).

3.4 | Growth simulations

Simulating different scenarios for a typical sea trout post-smolt (mean size in Etne River 40 g, pers. comm. Ø. Skaala) feeding in the sea for the full ideal sea migration period of May 15 to August 15, the sea trout had the potential to increase their weight by 165 g (end-weight 254 g). A 2-week delousing stay in FW would reduce this growth potential by 24%, a 4-week stay by 43% and a 6-week stay by 59%, resulting in end-weights of 194 g, 144 g and 104 g, respectively (Figure 6).

4 | DISCUSSION

The salmon lice infestation pressure for wild sea trout in Etnefjord differed among the years as anticipated from the fallowing regime. We observed clear behavioural responses in sea trout migration duration, range and time spent in delousing habitats among the years. The sea trout migrated further out and spent more time in the fjord in the low infestation pressure (fallowed) year than in high

TABLE 2 ANOVA table of deviance for the sequential[a] effects of week number, locality, length, condition, intensity of salmon lice infestation at the time of tagging, treatment (control vs. treated) and year (low vs. high) on (a) survival and (b) time spent at sea before returning to the river. For the time spent at sea analysis, time at sea was stratified (strata: before and after 100 days) to model the time dependency for the variable treatment and year, and hence meet the proportional hazards assumption

Variables[a]	Coef $\pm$ SE	LogLik	Chisq	df	Pr(>Chisq)
(a)					
NULL model		−106.5			
Log (week)	−0.7 $\pm$ 2.6	−106.5	0.04	1	.8
Locality (outer)	−0.8 $\pm$ 0.5	−105.5	2.1	1	.1
Length	−1.3 $\pm$ 0.7	−102.9	5.1	1	.02
Condition	0.4 $\pm$ 2.2	−102.9	0.02	1	.9
Intensity	0.5 $\pm$ 0.8	−102.7	0.3	1	.6
Treated	−0.03 $\pm$ 0.5	−102.7	0.001	1	1.0
Year (low)	0.1 $\pm$ 0.5	−102.7	0.06	1	.8
(b)					
NULL model		−318.43			
Week	0.04 $\pm$ 0.1	−317.6	1.7	1	.2
Locality (outer)	−0.4 $\pm$ 0.3	−315.7	3.7	1	.06
Length	0.4 $\pm$ 0.2	−315.0	1.5	1	.2
Condition	−1.9 $\pm$ 1.3	−314.4	1.1	1	.3
Intensity	0.6 $\pm$ 0.5	−313.9	1.2	1	.3
Treated	0.7 $\pm$ 0.3	−313.4	0.96	1	.3
Year (low)	−0.9 $\pm$ 0.3	−310.3	5.6	1	.02
Treated $\times$ strata	−1.5 $\pm$ 0.6	−308.0	5.2	1	.02
Year (low) $\times$ strata	1.0 $\pm$ 0.6	−306.6	2.7	1	.1

NULL model, baseline hazard without no covariates. Coef, regression coefficient, SE, standard error, LogLik, log likelihood, Chisq, model chi-squared, df, degrees of freedom, Pr(>Chisq), probability.
[a]Effects of variables were assessed sequentially in the ANOVA in the order they are presented.

TABLE 3 Contingency table and Pearson's chi-squared tests on fates (first row: n, second row: % (in italics), df: degrees of freedom) between treatments and among years on (a) all tagged fish pooled (n = 296) and (b) big tags fish only (n = 238)

	Treatment		Year			Row
Fate	Yes	No	2012	2013	2014	total[a]
(a)						
At sea	23	22	7	20	18	45
	8	*7*	*2*	*7*	*6*	
River run	31	36	10	20	37	67
	11	*12*	*3*	*7*	*13*	
Dead or Predated	11	10	5	8	8	21
	4	*3*	*2*	*3*	*3*	
Unknown	84	79	8	76	79	163
	28	*27*	*3*	*26*	*27*	
Column total	149	147	30	124	142	296
	50	*50*	*10*	*42*	*48*	
Chi-squared (df, p-value)	0.58 (3, .9)		16.1 (6, .01)			
(b)						
At sea	23	20	7	20	16	43
	10	*8*	*3*	*8*	*7*	
Dead or Predated	11	10	5	8	8	21
	5	*4*	*2*	*3*	*3*	
River run	27	32	10	20	29	59
	11	*13*	*4*	*8*	*12*	
Unknown	60	55	8	47	60	115
	25	*23*	*3*	*20*	*25*	
Column total	121	117	30	95	113	238
	51	*49*	*13*	*40*	*47*	
Chi-square (df, p-value)	0.83 (3, .8)		9.31 (6, .2)			

[a]The row total is the same for the contingency table contrasting treatments on the left and that contrasting years on the right. Note: categories Dead or Predated and year 2012 includes only big tags.

infestation pressure (full production) years. Despite the interannual differences in infestation pressure and our treating half of the fish against salmon lice infestation, we observed no difference in survival, either among the years or between the treatment group and their controls. This suggests that sea trout might compensate for direct mortality from salmon lice (lethal infestation) by adapting their behaviour and that treatment is unlikely to affect this behaviour. However, there might still be mortality consequences due to the changed behaviours on the long run; reduced growth resulting from reduced feeding time in periods with high salmon lice infestation pressure will extend the time the fish are vulnerable to size-dependent predation.

We found many different indications of a correlation between salmon lice infestation pressure and fish behaviour. Between years, fish spent more time in the river and estuary and returned earlier in years of high infestation pressure (2012 and 2014) compared to the low infestation pressure year (2013). There was also a strong within-

year correlation between salmon lice infestation pressure and time spent in delousing areas by the tracked fish, corroborating the interpretation of the between-year results. That being said, hydrography might act in concert with the infestation pressure to either subdue or exacerbate a behavioural effect. For example, both salmon lice development rate and sea trout metabolism have been shown to speed up with temperature (Elliott & Hurley, 2000; Shephard et al., 2016). Increased development rate of the salmon louse can intensify associated physiological stress for the host, but on the other hand, high temperatures also mediate faster host growth and the benefits of marine foraging. The seawater temperatures during the present study were mostly within ranges for optimum growth for brown trout, and rarely above the range where temperature may get stressful (Elliott & Hurley, 2000). Moreover, river temperatures were generally higher than sea temperature, and river temperature in 2013
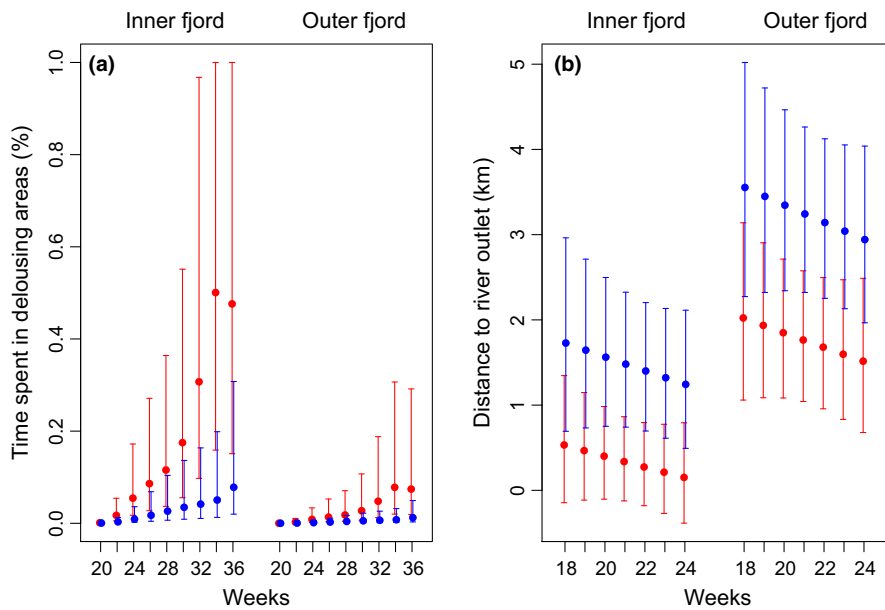
FIGURE 3 Changes throughout the summer (week number) in the percentage of time spent in delousing areas (a) and the distance (km) to river outlet (b) for tagged sea trout, contrasting locality (inner and outer fjord) and years (red = high infestation [2012 and 2014], blue = low infestation [2013]). Bars represent means and 95% confidence intervals predicted from the models based on the mean value for all covariates

TABLE 4 ANOVA table of deviance for the sequential[a] effects of week, catch locality, length, condition, intensity of salmon lice infestation at the time of tagging, treatment (control vs. treated) and year (high vs. low) on the time spent in delousing areas

Variables[a]	Estimate ± SE	F[c]	numdf	dendf	Pr (>F)
Intercept	−7.6 ± 0.6	−12.7			
Week[b]		4,698	5	2,506	<.001
1	2.7 ± 0.1				
2	4.4 ± 0.1				
3	4.4 ± 0.1				
4	6.8 ± 0.1				
5	5.3 ± 0.1				
Locality (outer)	−1.9 ± 0.7	8.2	1	214	.01
Length	−0.1 ± 0.7	1.4	1	214	.2
Condition	−0.1 ± 0.6	0.3	1	214	.6
Intensity	−0.4 ± 0.7	0.1	1	214	.7
Treated	0.9 ± 0.6	1.7	1	214	.2
Year (low)	−1.1 ± 0.8	4.8	1	214	.03
Year (low) × Week[b]		851	5	2,506	<.001
1	−0.4 ± 0.2				
2	−1.0 ± 0.1				
3	0.5 ± 0.1				
4	−2.5 ± 0.1				
5	0.2 ± 0.1				

SE, standard error; numdf, degrees of freedom numerator; dendf, degrees of freedom denominator; Pr(>F), probability.
[a]Effects of variables were assessed sequentially in the ANOVA in the order they are presented.
[b]Parameters presented (1–5) are the five coefficients of the spline for the week effect.
[c]z-value for intercept.

TABLE 5 ANOVA table of deviance for the sequential[a] effects of week, catch locality, length, condition, intensity of salmon lice infestation at the time of tagging, treatment (control vs. treated) and year (high vs. low) on the average tagged fish distance to the river outlet

Variables[a]	Estimate ± SE	F[b]	df	Pr(>F)
Intercept	63.5 ± 18.5	3.4		
Week	−0.7 ± 0.9	0.9	1	.4
Locality (outer)	14.3 ± 3.3	20.8	1	<.001
Length	−0.2 ± 3.6	3.1	1	.08
Condition	4.2 ± 3.3	3.9	1	.049
Intensity	5.9 ± 4.0	0.1	1	.8
Treated	−5.1 ± 3.3	2.6	1	.1
Year (low)	11.7 ± 3.8	9.7	1	.002

SE, standard error; df, degrees of freedom; Pr(>F), probability.
[a]Effects of variables were assessed sequentially in the ANOVA in the order they are presented.
[b]t-value for intercept.

was intermediate to that of 2012 and 2014. Thus, if temperature was the driver of the proportion of FW visits or exits, we should have expected gradients from low to high or the opposite, and not high–low–high FW use as we observed. The findings of the present study concur with findings by Birkeland and Jakobsen (1997) who found experimentally lice-infested sea trout returning to the estuarine area earlier compared to controls. Birkeland and Jakobsen (1997) explained this premature return to brackish water by the osmoregulatory failure based on blood chemistry.

The similar survival between the treatment groups found in the present study is in contrast to previous findings reporting higher survival among treated salmon and sea trout (Krkošek et al., 2013; Skaala, Kålås, & Borgstrøm, 2014; Skilbrei et al., 2013; Vollset et al., 2016). These studies, however, exposed non-infested fish to salmon

FIGURE 4 (a) Weekly proportion of time spent in delousing areas for tagged sea trout as a function of the mean lice intensity on all sampled sea trout in the corresponding week each study year. (b) Weekly proportion of time spent in delousing areas for tagged sea trout as a function of the mean lice intensity on all sampled sea trout sampled 2 weeks earlier the same study years. Lines indicate linear model smoothers for each year separately
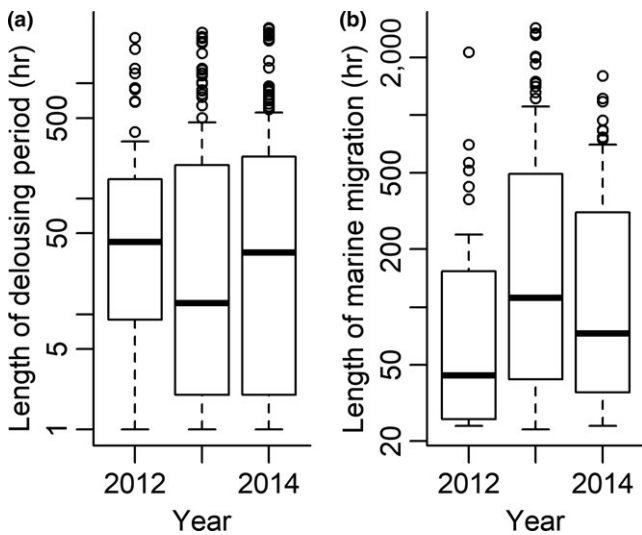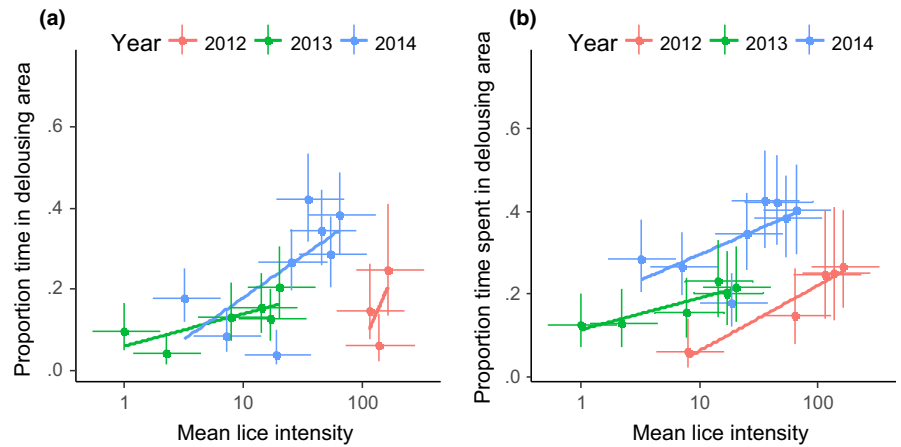

FIGURE 5 Length of (a) the three-first delousing periods and (b) the three-first marine migration periods for tagged sea trout after the first visit to the delousing area at the river outlet. Note the log scale

lice at the start of the experiment, whereas in our study the fish had already acquired significant amounts of salmon lice at the start of the experiment. The fish in our study had a mean infestation level of 0.08 lice/g at study's start, close to the 0.1 lice/g threshold for

physiological impact (Wagner, Fast, & Johnson, 2008), and therefore, they may have been negatively affected before the treatment had any effect on the attached salmon lice. In addition, the treatments used in this study do not protect the fish from being infested, and being infected might be a very powerful cue to seek refuge, regardless of treatment, especially as it is easiest to get rid of a recent infestation in FW. The copepodite stage that lasts ca. 5 days on Atlantic salmon at 10 degrees (Johnson, 2006) dies within 15–60 min in full FW (salinity <1 g/L), whereas more advanced stages can take up to 8 days to die (Wright et al., 2016). In addition, motile stages cause considerably more damage and osmoregulatory problems for the fish (Heuch et al., 2005). This might induce for frequent FW forays for rapid delousing before lice development and severe lice damage. For example, Birkeland and Jakobsen (1997) observed FW return of heavily infected sea trout within 4 days of sea entry, and sea re-entry of the same after 20 hr of successful delousing. These frequent FW forays might additionally mask for the treatment effect, as the fish would be able to rid themselves of recent infestations regardless of treatment.

Shorter migration duration and range, interspersed with FW stays for delousing, can have a high energetic cost for sea trout both in lost growth opportunities and in negative growth. For example, Birkeland (1996) found a median decrease of 23.5% in body mass among sea trout recovering from a severe louse attack, after spending a median of 37.5 days in FW before sea re-entry. Based on our
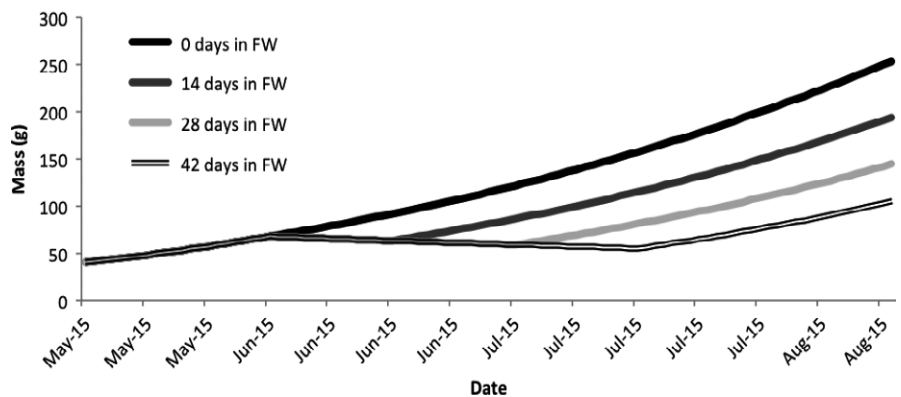
FIGURE 6 Sea trout simulated growth curves for different lengths of freshwater (FW) stays during an ideal sea migration period between May 15 and August 15

simulated growth calculations, trout spending time in FW during the feeding season could lose considerable proportions of their potential growth. This type of delousing behaviour would explain the 20%–40% summer growth reduction that Fjørtoft et al. (2014) calculated from Etne River sea trout scales between a baseline period of little sea cage salmon farming in 1976–1982, and the intensive salmon farming of 2000–2007. In addition to losing growth opportunities due to delousing behaviour, the fish also grow less at sea when infested (Godwin, Dill, Krkosek, Price, & Reynolds, 2017; Shephard et al., 2016). Growth is a particularly important component of fitness for juveniles, because it both expands their prey size range and reduces predation risk (Sogard, 1997). In addition, fish mature at an older age if growth rate is reduced (Jonsson, Jonsson, & Finstad, 2013; Stearns, 1992; Vollset, Barlaup, Skoglund, Normann, & Skilbrei, 2014), which might further increase indirect mortality due to salmon lice by prolonging the time the fish is vulnerable to gape-limited predators (Mittelbach & Persson, 1998). Finally, reduced growth has also direct consequences for fecundity, which is directly dependent on size. Therefore, reduced growth might have significant population-regulating effects in the long run, and might ultimately reduce or eliminate the propensity for anadromy in the affected population. For example, Sandlund and Jonsson (2016) found that the migration trait in a trout population was lost after only 10 generations due to reduced habitat quality, rendering the cost of the migration greater than the benefit.

Based on earlier studies (Gjelland et al., 2014; Godwin et al., 2015; Skaala et al., 2014; Vollset et al., 2016) , we expected to see higher predation and other mortality in the untreated group and in the high infestation years. In addition to trout adapting their behaviour to infestation pressure as discussed above, the results of this study might be also partly explained by both the high individual variability in behaviour among the tagged trout, and relatively large emigrated and unknown fate groups, that led to relatively small-sized remaining fate groups. Therefore, despite a large original sample size, we ended up with low statistical power to detect potential mortality differences. Nevertheless, in accordance with earlier findings (Dieperink, Pedersen, & Pedersen, 2001; Middlemas, Stewart, Mackay, & Armstrong, 2009), we observed higher mortality among the small fish. This finding is in contrast with the risk estimation index for salmon lice proposed by Taranger et al. (2012, 2015) that takes into account the weight of the fish and the amount of lice relative to weight, but expects 5% mortality among trout <150 g and 20% mortality among trout >150 g. We observed higher mortality for small trout (20% mortality among trout <150 g) and lower mortality for large trout (13% mortality among trout >150 g). Our observations differ from the calculated estimates, most likely because much of the data foundation for the mortality estimates in Taranger et al. (2012) are based on available laboratory studies, and therefore do not either account for predation or allow for adaptive behaviour. Predation is an important mortality factor for fish compromised by parasites, and this is even worse for small fish that are vulnerable to predation in the first place (Dieperink et al., 2001; Krkošek et al., 2011; Peacock et al., 2015). Even though the observed mortality for small fish in the present study is higher than expected from laboratory studies, it is likely to still be an underestimate of the total sea migration mortality. Sea migration mortality may be expected to be highest during the first 14 days after sea entrance (Dieperink et al., 2001; Middlemas et al., 2009), and we tagged sea trout post-smolt that had been to sea for an unknown period. Also, we tagged relatively large trout and tracked the sea trout for a relatively short time (over one summer as opposed to over a lifetime). Because sea trout have a high salmon lice infestation pressure in intensive salmon sea cage culture regions due to their near-shore marine migration behaviour, the combined effects of direct mortality and indirect mortality could be expected to be significant, given a sufficient sample size over time.

4.1 | Implications to management

Despite being vulnerable to being infested repeatedly with salmon lice, sea trout can compensate for direct mortality from salmon lice by adapting their behaviour. This adaptive behaviour can complicate attempts to predict mortality from a given lice burden on a wild sea trout at a given time. The fact that sea trout seek out estuaries in years of high infestation pressure highlights the importance of these refuges for sea trout, especially in areas of high lice infestation pressure. Finally, estimating growth loss from shortened sea migration is paramount in order to assess potential population effects of sea louse for sea trout, as both fecundity and indirect mortality are directly coupled to the size of the fish.

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