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# Factors influencing return rate and marine residence duration in sea trout populations in Central Norway

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## Abstract

Brown trout (*Salmo trutta*) display extensive plasticity in marine migratory behaviours, with marine migrations considered to be an adaptive strategy which enables sea trout to maximize growth and reproductive potential. However, marine migrations are not without associated costs, including threats posed by ever-increasing salmon lice (*Lepeophtheirus salmonis*) infestations. In the present study, we used passive integrated transponder technology to characterize variability in sea trout migration behaviour amongst three catchments situated in a region of intensive salmon farming in central Norway. Specifically, we investigate how lice infestation, out-migration date and body size alter sea trout return rate and marine residence duration during the first out-migration to sea from each catchment. Distinct catchment-specific differences in sea trout out-migration size and the number of cohorts were observed, but larger body size did not guarantee the successful return of migrating trout. The marine residence duration of individuals that successfully returned to freshwater was positively correlated with lice infestation risk, suggesting for these individuals the lethal infestation threshold had not been reached. Our results also suggest that sea trout populations from lotic-dominated catchments are potentially at greater risk from size-related threats to their survival encountered during their marine migrations than sea trout from lentic-dominated catchments. The variability in sea trout migratory behaviour amongst catchments observed here emphasizes the challenges fisheries managers face when deciding the best actions to take to protect the anadromous portion of brown trout populations.

KEYWORDS
anadromous, brown trout, Norway, out-migration, salmon lice

## 1 | INTRODUCTION

Brown trout (*Salmo trutta* L.) are a facultative anadromous fish species with a resident form residing in freshwater throughout its lifecycle and an anadromous form (hereafter sea trout) that migrates to brackish or marine environments before returning to freshwater to spawn (Ferguson *et al.*, 2019; Klemetsen *et al.*, 2003; Nevoux *et al.*, 2019). Sea trout display extensive plasticity in marine migratory behaviours, including timing of out-migration, marine residence duration, frequency and migration distance (Eldøy *et al.*, 2015; Thorstad *et al.*, 2016). Marine migrations are considered to be an adaptive strategy enabling individuals to maximize foraging opportunities, and thus growth and reproductive potential (Gross *et al.*, 1988; Lucas & Baras, 2001). Increasingly, migration is also recognized amongst fish to be a mechanism enabling juveniles to escape the population regulatory influences of parasites associated with adult fish (*e.g.*, Krkošek *et al.*, 2006; Poulin *et al.*, 2012).

Marine migrations are, however, not without associated costs for individuals. The smoltification process itself, whereby fish undergo physiological processes enabling them to tolerate high salinity environments, is energetically demanding (Hoar, 1988; Høgåsen, 1998). Migrating sea trout smolts may also experience mortality during both the passage to sea (0.19% per km, Aarestrup *et al.*, 2014; 0.93%–2.08% per day, Aldvén *et al.*, 2015) and from exposure to marine predators, especially during the initial days after entry to coastal environments (Dieperink *et al.*, 2001; Koed *et al.*, 2006). For sea trout that successfully overcome these threats, survival is still dependent on the ability to locate profitable marine foraging resources and to escape the regulatory effects of a raft of new marine parasites that they are exposed to (Davidsen *et al.*, 2017; Unger & Palm, 2016). Acquisition of the parasitic copepod *Lepeophtheirus salmonis* Krøyer 1837 in particular is considered to have detrimentally affected sea trout populations (Thorstad *et al.*, 2015). Despite *L. salmonis* being a native parasite of anadromous salmonids, including sea trout, Atlantic salmon (*Salmo salar* L.) and Arctic charr (*Salvelinus alpinus* L.), increased host availability in the form of farmed Atlantic salmon has transformed this relatively common, albeit benign parasite (mean *L. salmonis* infection intensity (lice per infected fish) 4.7–8.0, prevalence 80%–100%; Rikardsen, 2004; Schram *et al.*, 1998) into a highly pathogenic species in regions of intensive salmon farming [*e.g.*, mean (maximum) *L. salmonis* infection intensity 40 (689), prevalence 27%–100%; Serra-Llinares *et al.*, 2014].

Sea trout are potentially exposed to the *L. salmonis* infective stage (copepodid) throughout their marine residence, with the availability of *L. salmonis* being largely regulated by both density-dependent host availability (Penston & Davies, 2009; Torrissen *et al.*, 2013) and temperature-dependent development rates (Groner *et al.*, 2014; Stien *et al.*, 2005). Out-migration timing has the potential to alter exposure to *L. salmonis*, such that early spring migrants may initially experience lower *L. salmonis* infestations than individuals out-migrating during late spring/early summer (Nilsen *et al.*, 2019). However, salmon farm production cycles may shift seasonal peaks in *L. salmonis* infestations by modifying the availability of the most abundant *L. salmonis* host. Migration behaviour may also modify *L. salmonis* infestations on sea trout. For instance, individuals which migrate to areas without salmon farms, those that make brief returns to fresh or brackish water and/or individuals with shorter overall marine residence durations may benefit from lower exposure to *L. salmonis* infective stages (Diserud *et al.*, 2020; Serra-Llinares *et al.*, 2020). Low salinity waters reduce the survival of *L. salmonis* (Andrews & Horsberg, 2020; Bricknell *et al.*, 2006), in addition to reducing the effects of lice-induced osmotic stress to infected trout (Birkeland & Jakobsen, 1997; Wells *et al.*, 2007). Host size may also influence the effects of *L. salmonis* infestations, with greater lice-induced mortality expected for relatively small first-time migrants than larger veteran migrants (Halttunen *et al.*, 2018).

In the present study we used passive integrated transponder (PIT) technology to describe the variability in migration behaviour amongst three sea trout populations in central Norway. Specifically, we investigate the combined influences of *L. salmonis* infestation, out-migration date and fish size on (i) the likelihood of sea trout up-migrating to freshwater during the same year as out-migration and (ii) the marine residence duration during their first out-migration.

## 2 | MATERIALS AND METHODS

### 2.1 | Study locations

Sea trout migration behaviour was assessed from three central Norwegian catchments (Fremstad, Sylte and Vatne; Figure 1) connected to coastal fjords with varying salmon farming intensity. The Fremstad catchment (area 27.6 km$^2$, drainage 29.3 mill m$^3$ y$^{-1}$, 63°37′N, 9°38′E) is located in the outer region of Trondheimsfjorden (Trøndelag; Figure 1a), immediately beyond the limits of the designated 'national salmon fjord' in which commercial Atlantic salmon production is prohibited (Anonymous, 2006). The catchment consists of two lakes, Storvatnet [2.92 km$^2$, depth 16 m, 6 m above sea level (masl)] and Litlvatnet (0.47 km$^2$, depth 3 m, 5 masl), which are connected by the river Fremstadelva (0.8 km). The river Heggaelva (1 km) connects Litlvatnet to Trondheimsfjord. Approximately 8 km of the catchment is accessible to anadromous fish, including the streams Musdalselva and Vollaelva above Storvatnet.

The Sylte catchment (area 49.1 km$^2$, drainage 93.2 mill m$^3$ y$^{-1}$, 62°50′N, 7°12′E) is located at the head of Frænfjorden (Møre og Romsdal; Figure 1b). The catchment consists of two river branches, Rødalselva and Moaelva, which join to form the river Sylteelva ~1.4 km above Frænfjorden. A total of 18 km of the river catchment is accessible to anadromous fish.

The Vatne catchment (area 31.9 km$^2$, drainage 64.9 mill m$^3$ y$^{-1}$, 62°33′N, 6°36′E) is located at the head of Vatnefjorden, an 8 km long side arm of Midtfjorden/Romsdalsfjorden (Møre og Romsdal; Figure 1c). The catchment consists of two anadromous river stretches (Oselva 0.4 km, Storelva 4 km) separated by lake Vatnevatnet (0.9 km$^2$, depth 31 m, 9 masl). Three concrete weirs/fish ladders were installed in the lower Oselva in 1980 to improve upstream fish passage through a 35 m section of low waterfalls and bare rock, which previously created a migration barrier during low flow periods.

### 2.2 | Fish capture and tagging

Trout were captured over a 3 to 4-year period between 2015–2019 in the rivers Fremstadelva (Fremstad) and Oselva (Vatne) by fyke net, and by a combination of fyke nets and electrofishing in Sylteelva (Sylte; Figure 1c). Unbaited fyke nets (wing length 7.5–10.0 m,

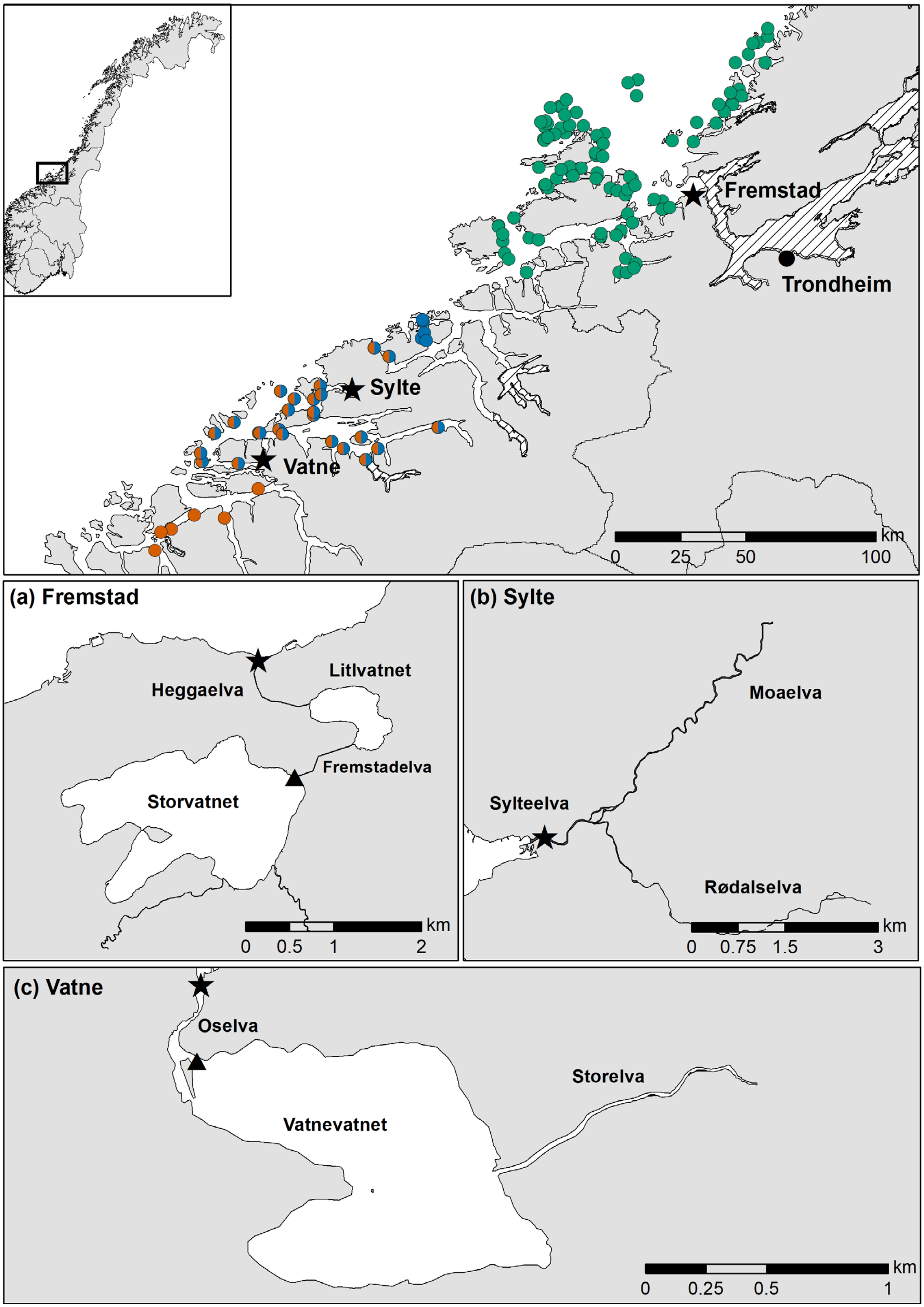

**FIGURE 1** Map of (a) Fremstad, (b) Sylte and (c) Vatne study catchments and their associated fjord systems (Trondheimsfjorden, Malmefjorden/Frænfjorden and Vatnefjorden–Midtfjorden/Romsdalsfjorden) in central Norway. Tagging and antenna locations are indicated by triangles and stars respectively, with salmon farms in an 80 km nautical radius of the study catchment indicated by filled circles (Fremstad = green, Sylte = blue, Vatne = orange). National salmon fjord areas are indicated by diagonal lines

stretched mesh size 20 mm) were deployed late April–early May in Fremstad and Vatne catchments (expected initiation of out-migration period) and inspected once per day. Fish captured with electrofishing were tagged <1 h after capture. All fish >100 mm total length ($L_T$) were tagged after being anesthetized with benzocaine (Benzoak vet, 200 mg/ml, 15–20 ml/100 l water dilution) or isoeugenol (AQUI-S, 540 mg/ml, 1.9–2.6 ml/100 l water dilution) and weighed (g). Anesthetized fish were scanned to determine whether they were untagged or a previously tagged individual, with the former then fitted with a unique 12.5 mm PIT tag (Biomark HPT full duplex 134 kHz) inserted into the body cavity using a Biomark MK25 implant gun preloaded with sterile tags (APT 12 or HPT 12). All anesthetized fish were transferred into a 10 l bucket containing river water to monitor initial recovery from the anaesthetic. Fish were then transferred into 90 l perforated recovery cages placed in the river and were maintained overnight before being released immediately downstream of the capture site. Low capture/tagging-induced mortality was observed during the period prior to release (0.12%–1.92%, $n = 2–7$ fish per catchment per year).

## 2.3 | Tracking of tagged fish

Fish movements were detected using stationary bottom radio frequency identification (RFID; Biomark, Boise, Idaho, USA) full-duplex antennas spanning the entire width of each river directly upstream of the highest tidal mark [catchment (river), width and distance from outlet: Fremstad(Heggaelva) 5, 50 m; Sylte(Sylteelva) 12, 800 m; Vatne(Oselva) 20, 50 m; Figure 1]. PIT-antenna systems in Heggaelva and Sylteelva consisted of two parallel strings of antennas approximately 4 m apart, whereas Oselva was equipped with two single-string antennas located on each side of a divide in the river, one spanning across the lower weir in the river and the other across the water outlet underneath an old mill (Figure 1c). Mean annual water depth at antennas in all catchments was ~45 cm, with antennas having a detection range of at least 75 cm. Antennas were set to record each unique tag up to 10 times per second.

## 2.4 | Ethical statement

The care and use of experimental animals complied with Norwegian Animal Research Authority (NARA) animal welfare laws, guidelines and policies as approved by the local responsible laboratory animal science specialist under the surveillance of the NARA and registered by the Authority (2015/31657–1, 10.02.15; 2015/31657–2, 10.03.15; 2015/111338–3, 16.06.15; 16/267674–1, 09.02.17; 18/14225–1, 13.03.18).

## 2.5 | Defining timing of out-migration and return

To investigate the influence of total length and body condition on sea trout migration behaviour, our study focused on individuals which out- and up-migrated the same year in which they were tagged and measured. The following catchment-specific criteria was used to define the observed migration behaviour.

Fremstad and Sylte sea trout were defined as out-migrating if first detected on the upper then the lower antenna, and *vice versa* for up-migrating. Data for individuals detected on multiple occasions were manually inspected if the migration direction could not be determined from this criteria, with direction assignment based on the known migration direction before or after the specific detection event. For example, if the direction of the first of two separate detection events was unknown, but the second detection was an up-migration, then the first detection was defined as an out-migration. Furthermore, 37 (11%) and 46 (10%) individuals from Fremstad and Sylte, respectively, were detected on a single event on the upper or lower antenna only. These fish were assumed to be out-migrating as their detections between 22 April and 16 June correspond to the expected sea trout smolt out-migration period in central Norway (median 23 May, range 2 April to 25 June; H.H. Berntsen, personal observation; L'Abée-Lund & Vøllestad, 2017).

Out-migrating Fremstad and Sylte sea trout generally displayed one of three behaviours: (a) individuals with a single out-migration event that did not return the same year; (b) out-migrating individuals which returned and overwintered in the freshwater catchment; and (c) out-migrating individuals that returned, but did not overwinter in the catchment (Table 1). Individuals in the two latter groups (Fremstad $n = 140$, Sylte $n = 115$) displayed highly variable migration behaviour in terms of out- and up-migration frequency (Fremstad 1–10, Sylte 1–9 events per fish) and marine residence duration per migration event (Fremstad 1 min to 205.6 days, Sylte 1 min to 208.4 days). In Fremstad, 35% of registered marine stays (76 of 226 registrations for 44 of 140 fish) were less than 1 day (mean ± S.D., 4.5 ± 4 h), whereas in Sylte marine stays of less than 1 day contributed 23.4% (8 ± 6.2 h, 40 of 171 registrations for 27 of 115 fish). These short marine migrations typically occurred either before final out-migration to the sea or after a marine stay of >7 days, and likely represent an acclimatization period to or from sea water for out- and up-migrating individuals, respectively.

In the present study we define an individual as having a marine stay when more than 1 day (>24 h) was spent downstream of the antenna. For all returning sea trout, the time of first out-migration was defined as the out-migration event prior to a marine stay of ≥1 day, with 7.9% (11 of 140) and 4.3% (5 of 115) of Fremstad and Sylte sea trout, respectively, having brief marine stays of <1 day before out-migrating.

For Vatne, the migration direction of sea trout detected by the single antenna system was assigned based on the known sea trout out-migration period (Fremstad 21 April to 17 October, Sylte 21 April to 20 October) and duration at the antenna during a detection event (first–last detection at antenna: Fremstad mean 1.2 h, Sylte 0.2 h), with >90% of all out-migrations occurring before 1 July in both catchments. Thus, Vatne sea trout were defined as out-migrating if (a) they were first detected between 1 April and 1 July, and (b) the detection event duration was <1.2 h, with the last detection time determined to

**TABLE 1** Summary of capture and out-migration period, length and migration behaviour of sea trout (*Salmo trutta*) during the same year of capture from the Fremstad, Sylte and Vatne catchments, central Norway

| Catchment | Year | Capture date | *N* tagged | *N* out-migrating | Total length (mm) ± s.d. (range) | Median (range) out-migration date | *N* returning | Median (range) return date | *N* fw over-wintering | *N* sea over-wintering | Mean ± s.d. (range) marine residence time (days) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Fremstad | 2016 | 3 May–18 May | 335 | 154 | 304.3 ± 43.0 (205–510) | 14 May (6 May–25 June) | 54 | 14 Aug (25 May–9 Dec) | 52 (4) | 2 (1) | 92.1 ± 37.1 (10.4–205.6) |
| | 2017 | 18 Apr–8 May | 249 | 135 | 318.6 ± 68.1 (210–570) | 8 May (21 Apr–7 Jul) | 59 | 26 June (26 Apr–14 Oct) | 50 (4) | 9 (3) | 71.7 ± 47.5 (1.1–160.9) |
| | 2018 | 30 Apr–16 May | 153 | 45 | 245.3 ± 43.9 (121–359) | 20 May (4 May–30 June) | 16 | 29 June (22 May–13 Nov) | 14 (3) | 2 | 101.2 ± 48.9 (1.2–170.6) |
| Sylte | 2017 | 20 Apr–16 May | 774 | 356 | 157.9 ± 30.2 (111–260) | 11 May (21 Apr–24 Jul) | 75 | 19 Sep (8 May–16 Nov) | 60 (6) | 15 (6) | 120.4 ± 46.6 (1.2–208.4) |
| | 2018 | 16 Apr–31 May | 105 | 69 | 145.2 ± 21.8 (123–228) | 26 May (18 Apr–22 June) | 30 | 29 Sep (27 May–30 Oct) | 24 (3) | 6 (2) | 117.2 ± 39.6 (10.7–170.7) |
| | 2019 | 9 Apr–23 May | 207 | 152 | 145.9 ± 20.6 (118–254) | 21 May (10 Apr–1 Jul) | 23 | 18 Aug (15 Apr–24 Oct) | 12 (5) | 11 (3) | 67.4 ± 57.5 (2.1–156.3) |
| Vatne | 2015 | 4 May–7 May | 81 | 51 | 234.4 ± 45.7 (121–351) | 9 May (4 May–3 Jul) | 33 | 3 July (5 June–1 Oct) | - | - | 75.3 ± 38.5 (24.6–147.7) |
| | 2016 | 2 May–15 May | 480 | 313 | 213.3 ± 45.6 (139–385) | 13 May (2 May–24 Jul) | 172 | 18 July (2 June–11 Dec) | - | - | 69.2 ± 43.2 (15.2–221.5) |
| | 2018 | 28 Apr–21 May | 730 | 486 | 194.8 ± 51.6 (131–450) | 19 May (28 Apr–19 Jul) | 250 | 22 June (2 June–31 Oct) | - | - | 72.6 ± 33.5 (6.7–170.4) |
| | 2019 | 24 Apr–19 May | 746 | 505 | 220.9 ± 47.3 (125–460) | 3 May (25 Apr–2 Jul) | 273 | 13 June (1 June–5 Nov) | - | - | 52.8 ± 38.2 (9.3–188.7) |

*Note*. Nonreturning and nonover-wintering includes individuals that returned the year after capture or were never detected after out-migration. Numbers in parenthesis for fish overwintering in freshwater (fw) or at sea is the number of individuals performing multiple sea migrations with a duration of more than 1 day during the same year as capture and tagging. Over-wintering locality could not be determined for Vatne sea trout.

be the time of out-migration. The first detection made after the defined time of out-migration was assumed to represent up-migration. Individuals which made their first out-migration after 1 July or up-migrated between 1 April and 1 July were manually inspected to assign the migration direction based on the above criteria.

Overall, 65.7% (2535 of 3860) of tagged fish were detected at the PIT-antennas on the same year as tagged. Based on the outlined criteria, migration behaviour could not be assigned for 255 individuals, which were excluded from further analysis. An additional seven individuals which up-migrated less than 5 min after out-migration were excluded from both Fremstad and Sylte. In total 2266 fish were included in this study (Table 1).

**TABLE 2** Number, mean distance and production capacity of salmon farms in an 80 km radius from the outlet river of each study catchment (see Figure 1 for salmon farm locations)

| Catchment | Number of farms | Mean distance (km) from river outlet (range) | Mean production capacity (tonnes) |
|---|---|---|---|
| Fremstad | 91 | 49.3 (10.9–76.0) | 4141.2 |
| Sylte | 31 | 46.4 (12.5–72.0) | 3196.0 |
| Vatne | 32 | 41.0 (10.2–79.7) | 3327.6 |

## 2.6 | Estimation of lice infestation risk during marine residence

We estimated the mean lice infestation risk for each individual sea trout during their marine residence as a function of the weekly adult female *L. salmonis* abundance and farm production capacity (BarentsWatch, 2020; Equation 1). Only salmon farms in a 80 km radius of each river outlet (*n* farms: 91 Fremstad, 31 Sylte, 32 Vatne; Table 2) were included to account for the maximum migration distance for sea trout (Flaten *et al*., 2016; Thorstad *et al*., 2016). However, as sea trout commonly migrate <4 km from their origin rivers (Berg & Berg, 1987; Berg & Jonsson, 1990; Eldøy *et al*., 2015; Flaten *et al*., 2016), lice infestation risk was further modified by distance to river outlet. An overlap of >80% in salmon farms was noted between Sylte and Vatne, whereas salmon farms in the vicinity of Fremstad did not overlap with the other catchments (Figure 1).

$$\sum_{i=1}^{N} \frac{(n_i * K_i)}{N * D_i} \tag{1}$$

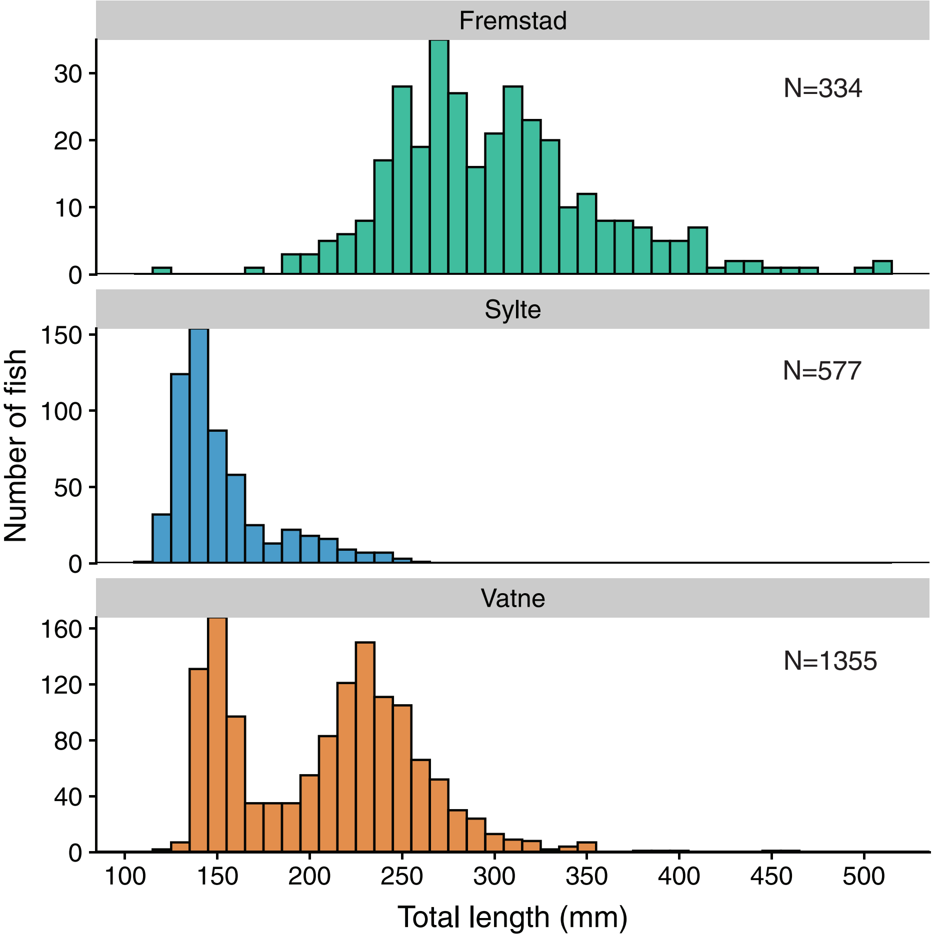

**FIGURE 2** Length distribution of PIT-tagged sea trout (*Salmo trutta*) that out-migrated from the Fremstad, Sylte and Vatne catchments. Note that scales on *y* axis differ for each catchment

In Equation 1 $n$ is the number of reported adult female *L. salmonis* for farm $i$, $K$ is the production capacity of farm $i$, $N$ is the total number of farms in the defined area and $D$ is the distance from farm $i$ to the river outlet in kilometres.

For individuals with marine residence durations of <7 days, the lice infestation risk was assigned to zero based on the development time for newly attached copepodids to pathogenic pre-mature adults capable of inducing sea trout behaviour alterations (Stien *et al*., 2005).

## 2.7 | Statistical analysis

All statistical analyses were conducted in R v. 3.6.3 (R Core Team, 2020). To avoid autocorrelation between total length ($L_T$) and body condition (Fulton's $K$), the residual condition [log ($K$) ~ log($L_T$)] was calculated following Flaten *et al*. (2016). Continuous variables (out-migration date, total length, lice infestation risk) were centred on the mean and scaled by two standard deviations (Gelman, 2008). Model fit of linear models, that is, heteroscedasticity and normality, were inspected from residual plots. Contrast analyses were constructed for all models listed below to determine where differences between catchments occurred.

### 2.7.1 | Return rate

Preliminary analysis for each catchment separately showed no difference in return rate probability between years in Fremstad and Vatne (both $P > 0.1$), and only a significantly higher return probability in 2018 than in 2017 and 2019 at Sylte ($P < 0.001$; Table 1). However, since all catchments were not sampled on the same years, statistical comparisons between years across catchments were not made. We fitted a generalized linear mixed effects model with a binomial family and year as a random factor to determine the influence of catchment, total length and out-migration date on whether or not (1/0) out-migrating sea trout were redetected (up-migrating) at the antenna on the same year as the fish were tagged. This dataset did not distinguish between individuals remaining in freshwater from those returning to sea after the up-migration event. Initial data inspection revealed negative correlation between total length and out-migration date in all catchments ($P = 0.006$ in Fremstad, $P < 0.001$ in Sylte and Vatne) with bigger fish migrating earlier in the season than smaller fish (Figure 3). The interaction term between total length and out-migration date was therefore not included in the model.

### 2.7.2 | Marine residence duration

Separate linear mixed effects models with year as random factor were fitted for each catchment to assess the influence of total length, out-migration date, residual condition and lice infestation risk on the marine residence duration of sea trout. Initial data inspection revealed non-independence amongst explanatory variables. In all catchments, out-migration date was influenced by total length, with larger fish migrating earlier than smaller fish ($P = 0.06$ Fremstad, $P < 0.001$ Sylte, Vatne). Furthermore, the estimated lice infestation risk is a function of both marine residence duration and out-migration date (see Supporting Information Figure S1). Thus to account for nonindependence of these explanatory variables, models include the main effects only, with the exception of the total length and residual condition interaction term. The marine residence duration for Fremstad and Sylte sea trout included the total time at sea for individuals with more than one marine migration, whereas the duration of the first marine migration only was assessed for Vatne as the single antenna design did not allow for directional detection after first return to the antenna. Furthermore, Vatne sea trout up-migration (return) and marine residence time displayed a bimodal distribution (Supporting Information Figure S2), with few detections being made between day of year 200 and 225 (late July to early August). This pattern was consistent across all years and is likely to be related to a period of low precipitation resulting in low river water levels which restrict up-migration of fish (P. Naalsund, personal communication, November 2020; NVE, 2020). We therefore analysed the marine residence duration for Vatne sea trout returning to the river before ($n = 464$) and after ($n = 259$) day of year 212 separately. Residual condition was excluded from the Fremstad and Sylte models due to the absence of weight measurements for 23% of the out-migrating sea

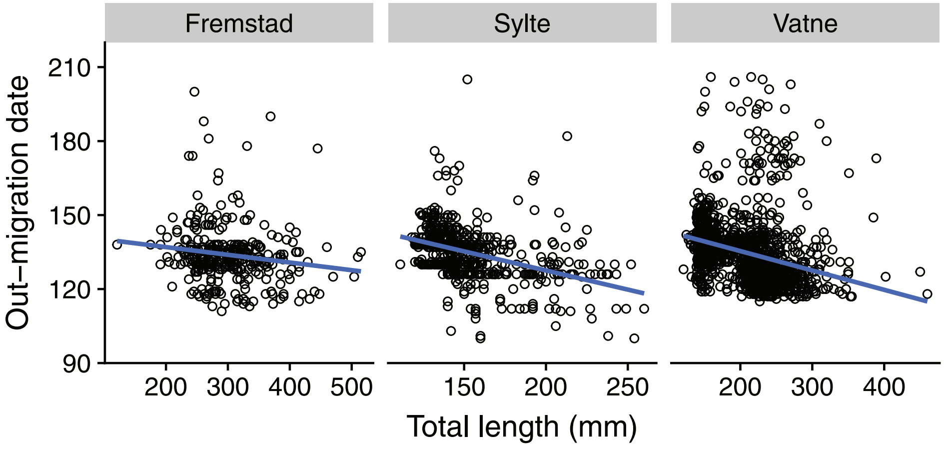

**FIGURE 3** Relationship between total length (mm) and out-migration date (day of year) of sea trout (*Salmo trutta*) from Fremstad, Sylte and Vatne catchments. Note that scales on the $x$ axis differ for each catchment. Linear regression ($y = axe + b$): Fremstad ($N = 334$), $-0.031{*}x + 143.2$, $P = 0.006$, $R^2 = 0.02$; Sylte ($N = 577$), $-0.15{*}x + 158.5$, $P < 0.001$, $R^2 = 0.15$; Vatne ($N = 1355$), $-0.08{*}x + 151.5$, $P < 0.001$, $R^2 = 0.08$

trout population in Fremstad and absence of weight measurements for all fish in Sylte in 2019.

## 3 | RESULTS

Of the 3860 individuals tagged across all three study catchments, a higher proportion of tagged fish were observed to out-migrate from Vatne (66.5%, 1355 of 2037 fish; Table 1) in comparison to Fremstad (45.3%, 334 of 737 fish) and Sylte (53.1%, 577 of 1086 fish). Sea trout populations displayed distinctly different size cohorts of out-migrating individuals, with a single predominantly small (<170 mm $L_T$) or large (>230 mm $L_T$) cohort at Sylte and Fremstad, respectively, whereas the Vatne sea trout population comprised two size cohorts (<180 and >180 mm $L_T$; Figure 2). Although the median out-migration date was similar between catchments (Fremstad 13 May, Sylte and Vatne 12 May; Table 1 and Supporting Information Figure S1), a general pattern of larger fish out-migrating earlier in the season than smaller fish was observed (Figure 3).

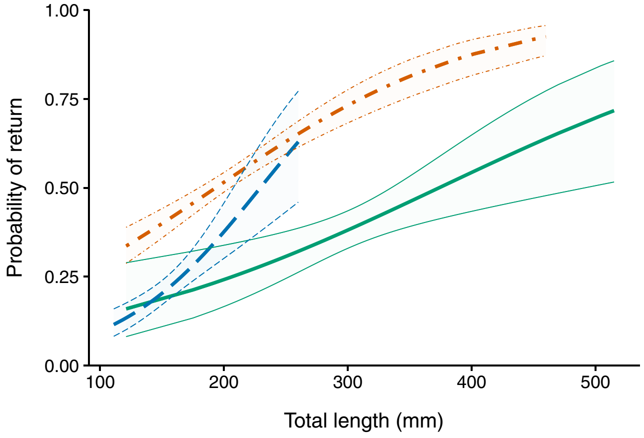

**FIGURE 4** Influence of total length (cm) on the probability of out-migrating sea trout (*Salmo trutta*) returning to the Fremstad, Sylte and Vatne catchments during the same year. Lines are parameter estimates and 95% confidence intervals. (——) Fremstad; (-----) Sylte; (-·-·-) Vatne

### 3.1 | Return rate

Sea trout return rate was highest in Vatne, with 53.7% of out-migrating individuals observed to up-migrate during the same year, whereas 38.5% and 24.8% of sea trout returned to Fremstad and Sylte catchments, respectively (Table 1). Few individuals were observed to over-winter at sea before their first return to freshwater (Fremstad 1.2%, Sylte 5.8%, Vatne 1.9%) and no sea trout from Fremstad or Vatne returned after more than one marine over-winter period (maximum marine residence 451 and 444 days, respectively) or more than two marine over-winter periods from Sylte (maximum marine residence 905 days). The likelihood that out-migrating sea trout would return during the same year increased as a function of increasing total fish length for all catchments (Figure 4 and Table 3). However, the total length required to attain a 50% probability of returning for Fremstad sea trout was twice the length of Vatne sea trout (>380 mm *vs.* >190 mm $L_T$). For Sylte sea trout, which were generally smaller than out-

**TABLE 3** Influence of catchment, out-migration date and total length on the return rate of sea trout (*Salmo trutta*) during the same year of out-migration

| Base catchment | Variable | Estimate | S.E. | *z* value | *P* |
|---|---|---|---|---|---|
| Fremstad | Intercept | −1.07 | 0.23 | −4.63 | <0.001 |
| | **Sylte** | 0.80 | 0.31 | 2.58 | **0.010** |
| | **Vatne** | 1.21 | 0.24 | 5.15 | **<0.001** |
| | **Total length** | 0.86 | 0.27 | 3.20 | **0.001** |
| | Out-migration date | −0.23 | 0.20 | −1.15 | 0.250 |
| | **Sylte * Total length** | 1.52 | 0.53 | 2.9 | **0.003** |
| | Vatne * Total length | 0.46 | 0.31 | 1.49 | 0.140 |
| | Sylte * Out-migration date | 0.47 | 0.29 | 1.70 | 0.095 |
| | Vatne * Out-migration date | 0.40 | 0.24 | 1.66 | 0.096 |
| Sylte | Intercept | −0.27 | 0.21 | −1.24 | 0.214 |
| | **Fremstad** | −0.80 | 0.31 | −2.58 | **0.010** |
| | Vatne | 0.41 | 0.23 | 1.82 | 0.068 |
| | **Total length** | 2.38 | 0.47 | 4.39 | **<0.001** |
| | Out-migration date | 0.25 | 0.21 | 1.19 | 0.233 |
| | **Fremstad * Total length** | −1.53 | 0.53 | −2.90 | **0.004** |
| | **Vatne * Total length** | −1.06 | 0.48 | −2.20 | **0.028** |
| | Fremstad * Out-migration date | −0.47 | 0.29 | −1.70 | 0.095 |
| | Vatne * Out-migration date | −0.08 | 0.25 | −0.32 | 0.747 |

*Note*. Estimates are reported for mean centred continuous variables. Statistically significant effects ($\alpha = 0.05$) are in bold.

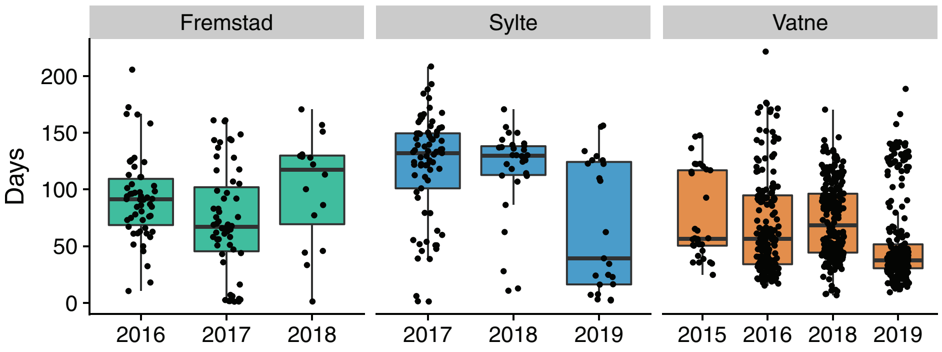

**FIGURE 5** Variation in marine residence duration during the same year as tagging for sea trout (*Salmo trutta*) from the Fremstad, Sylte and Vatne catchments

**TABLE 4** Influence of total length, residual condition, out-migration date and lice infestation risk on marine residence duration of sea trout (*Salmo trutta*) from the Fremstad, Sylte and Vatne catchments

| Catchment | | Estimate | S.E. | d.f. | *t* | *P* |
|---|---|---|---|---|---|---|
| **Fremstad** | Intercept | 88.91 | 20.63 | 1.97 | 4.31 | 0.051 |
| | Total length | 9.11 | 5.21 | 120.12 | 1.75 | 0.083 |
| | Out-migration date | −5.03 | 5.523 | 120.13 | −0.91 | 0.364 |
| | **Lice infestation risk** | 105.39 | 7.542 | 120.99 | 13.96 | **<0.001** |
| **Sylte** | Intercept | 105.77 | 38.55 | 1.95 | 2.73 | 0.114 |
| | Total length | 5.97 | 7.18 | 120.94 | 0.83 | 0.407 |
| | **Out-migration date** | −34.19 | 7.29 | 120.75 | −4.68 | **0.011** |
| | **Lice infestation risk** | 76.06 | 8.99 | 121.91 | 8.46 | **<0.001** |
| **Vatne a)** | Intercept | 50.44 | 11.2 | 2.99 | 4.51 | 0.021 |
| | **Total length** | −2.94 | 0.89 | 456.05 | −3.32 | **<0.001** |
| | Residual condition | −5.10 | 5.46 | 456.06 | −0.94 | 0.351 |
| | **Out-migration date** | −33.91 | 1.39 | 458.01 | −24.46 | **<0.001** |
| | **Lice infestation risk** | 45.59 | 2.79 | 458.99 | 16.35 | **<0.001** |
| | Length x condition | 6.47 | 7.20 | 455.01 | 0.90 | 0.371 |
| **b)** | Intercept | 102.13 | 8.57 | 2.8 | 11.92 | 0.002 |
| | **Total length** | −11.51 | 2.88 | 253.18 | −4.01 | **<0.001** |
| | Residual condition | 36.74 | 19.42 | 252.03 | 1.89 | 0.059 |
| | **Out-migration date** | −56.95 | 3.31 | 186.75 | −17.19 | **<0.001** |
| | **Lice infestation risk** | 43.48 | 6.59 | 127.73 | 6.59 | **<0.001** |
| | Length x condition | 35.49 | 44.46 | 251.34 | 0.80 | 0.420 |

*Note*. Vatne (a) and (b) represent fish returning to the river before and after a low flow period restricting access to the antenna (day of year 212). Note that estimates are reported for mean centred continuous variables. Statistically significant effects ($\alpha = 0.05$) are in bold.

migrating individuals from the other catchments, the probability of return for most individuals was less than 50%. Out-migration date did not influence sea trout return rate to the studied catchments.

A proportion of sea trout returning to Fremstad (11.6%, $n = 15$ fish) and Sylte catchments (14.2%, $n = 18$ fish) were observed to temporarily suspend their marine residence by re-entering freshwater habitats above the antennas before returning to the sea. For the majority of individuals, this behaviour consisted of a single entry of 45 min to 23 days (Fremstad) or 3 min to 5 days (Sylte). In Fremstad, two sea trout were observed to make repeated ($n = 2$ and 4) temporary entrances into freshwater, with mean durations of 23 and 17 days. In Sylte, three sea trout made three temporary re-entries into freshwater, with mean durations of 3, 3.5 h and 3 days. This behaviour could not be evaluated for Vatne sea trout due to the absence of a directional antenna system.

## 3.2 | Marine residence duration and lice infestation risk

Marine residence time varied between years in all catchments, and on average Sylte sea trout spent 101.7 days (range 1.2–208.4) at sea per year, whereas Fremstad sea trout spent just 83.9 days (range 1.0–205.6; Table 1 and Figure 5). Vatne sea trout spent an average of 40.6 days (range 6.7–87.8) before and 107.2 days (range 15.2–221.5)

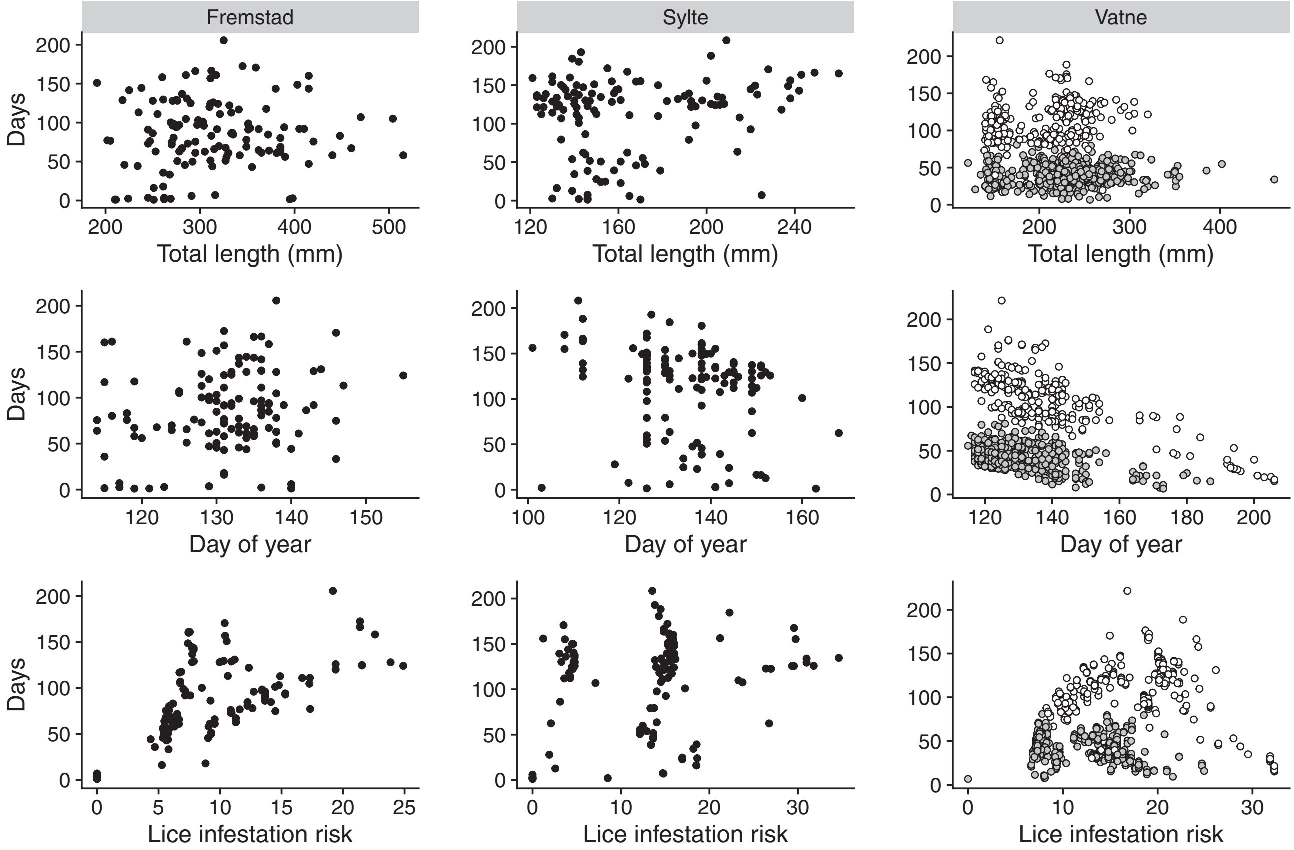

**FIGURE 6** Relationship between total length (mm), out-migration date (day of year) and lice infestation risk and sea trout (*Salmo trutta*) marine residence duration (days) in Fremstad (left panel), Sylte (middle panel) and Vatne (right panel). Grey and white circles for Vatne represent fish returning before and after the low flow period (day of year 212) respectively

after the low water period, with 80% of the latter cohort of sea trout observed to up-migrate in the 48 days following the low water period (day of year 212; Table 1 and Supporting Information Figure S2). Corrected for between-year variation, out-migration date negatively influenced the marine residence duration of Sylte and Vatne sea trout, and total length negatively influenced only the marine residence duration of Vatne sea trout. Neither body condition (residual condition) nor its interaction with total length (Vatne only) were observed to influence sea trout marine residence duration (Table 4). The marine residence duration of all trout populations was positively correlated with lice infestation risk (Table 4 and Figure 6), with trout which spent a longer time at sea experiencing a higher risk of lice infestation.

## 4 | DISCUSSION

Our study demonstrates that although the out-migration timing of sea trout populations from three central Norwegian catchments may be similar, both the duration of their first marine residence and the likelihood that they will successfully return to freshwater differs. Furthermore, we found that sea trout populations from a limited geographic region may display distinct catchment-specific differences in the size distribution ($L_T$) and number of cohorts of out-migrating individuals. Our results show that the majority of Fremstad sea trout undergo their first marine migration when larger than 230 mm $L_T$, whilst Sylte sea trout seldom out-migrate when greater than 170 mm $L_T$. However, as the highest rate of return for any study catchment was observed for Vatne sea trout, a population comprising two out-migrating size cohorts, our study suggests that a larger body size does not completely safeguard the successful return of out-migrating individuals as demonstrated by Fremstad sea trout. Additionally, our study demonstrates that two sea trout populations (Vatne and Sylte) may display distinctly different return rates despite a >80% overlap in nearby salmon farms and associated lice infestation risk.

The duration of sea trout marine migrations is thought to be linked to the relative fitness benefits experienced by each individual in their respective habitats (Thorstad *et al*., 2016). In general, our study finds an inverse relationship between body length and marine residence duration, with predominantly large Fremstad sea trout spending on average the least amount of time at sea compared to the generally small Sylte sea trout (83.9 *vs*. 101.7 days). However, amongst individuals in a specific catchment, only Vatne sea trout were observed to display differences in marine migration duration with regard to body length. Surprisingly, we did not observe body condition in combination with body length to alter marine residence duration in sea trout as reported elsewhere (*e.g*., Flaten *et al*., 2016). Although body condition may be an important driver determining if and when an individual will out-migrate (Archer *et al*., 2019; Peiman *et al*., 2017), foraging in energetically rich marine environments enables sea trout to rapidly alter their body condition (Berg & Jonsson, 1990; Rikardsen *et al*., 2006) and potentially results in body condition estimates from out-migrating individuals having little bearing on marine residence durations.

Distinct intercatchment differences in the body length of out-migrating individuals are evident in this study and may reflect the limited capacity for growth and development of young trout in lotic-dominated catchments such as Sylte. Our results also suggest that sea trout populations from lotic-dominated catchments are potentially at greater risk from size-related threats to their survival encountered during their marine migrations. Contrasts between Fremstad and Vatne also suggests that differences in the size classes of out-migrating sea trout may also be present in lentic-dominated catchments, though it remains unknown as to whether properties of these two freshwater catchments and/or their associated marine habitats have driven such differences. For instance, the relatively large, shallow, highly productive lakes of the Fremstad catchment may provide profitable foraging resources enabling trout to grow larger and/or delay out-migration. Alternatively, the presence of larger out-migrating sea trout from this catchment may reflect a prolonged size-related selection pressure driven by salmon lice infestations (Eldøy *et al*., 2020) and/or predatory fish and mammals associated with the relatively open coastal waters of the outer Trondheimsfjord. In contrast, the presence of two size cohorts of out-migrating Vatne sea trout demonstrates that a range of out-migration sizes remains a viable life history strategy for sea trout from this catchment. Whether selection pressures from increased salmon lice infestations will eventually cause a shift in out-migration size to a single large size class (Eldøy *et al*., 2020) or shorter marine migrations to avoid being unable to escape rising salmon lice infestations which coincide with summertime low river level periods is yet to be seen.

The three studied sea trout populations in central Norway catchments were all situated in areas of intensive salmon farming with high, but variable, salmon lice infestation levels between July and October (BarentsWatch, 2020; Supporting Information Figure S1). Further variation in encounters between sea trout and infective lice stages originating from farms may be driven, amongst other factors, by water currents capable of transporting salmon lice considerable distances from their source (Asplin *et al*., 2014), in combination with the week of out-migration (Supporting information Figure S2) and the specific localities that sea trout migrate to. When sea trout and lice distributions overlap, reduced return rates may result from a combination of the direct effects of lice-induced sea trout mortality and the indirect effects of lice-induced vulnerability to predators. Intuitively, marine residence duration can only be assessed for the 'winners' of marine migrations (*i.e*., returning fish) being those individuals that were either exposed to sublethal lice infestations or were able to return to freshwater before succumbing to the direct or indirect effects of lice infestations.

Our study found limited evidence of sea trout shortening or temporarily suspending their marine residence by re-entering freshwater habitats before returning to the sea (Birkeland & Jakobsen, 1997; Serra-Llinares *et al*., 2020). In contrast, brief marine stays (<1 day) immediately prior to or after a marine stay of longer than 7 days occurred more frequently. However, the timing of brief marine stays suggests that this behaviour may be linked to an acclimation period associated with transitioning between freshwater and marine environments (Finstad & Ugedal, 1998; Ugedal *et al*., 1998). Of the 33 sea trout which temporarily suspended their marine residence, only three individuals remained in freshwater for more than the minimum duration observed to induce a reduction in pre−/adult salmon lice burdens in *S. salar* (>3 h; reviewed in Wright *et al*., 2016). It should be noted, however, that freshwater survival of attached salmon lice shows considerable variation between salmonid hosts and between salmon lice life stages (Connors *et al*., 2008; Finstad *et al*., 1995; Sievers *et al*., 2019), with sea trout-specific estimates of salmon lice survival in freshwater currently unavailable. Furthermore, given the infrequency that temporary suspension of marine residence was observed in this study, this provides further support that lice infestations attained by sea trout that successfully up-migrated had not reached a level to invoke such behaviour. This does not imply that salmon lice did not affect the survival of the sea trout populations, since marine residence duration could only be estimated for individuals which successfully up-migrate and not for those individuals that may have experienced lethal lice infestations, nor from individuals that may have deloused in brackish waters below the antennas or in neighbouring streams. Although direct assessments of lice infestations acquired by sea trout during their marine migrations are invaluable for improving our understanding of how lice may impact sea trout populations, it must be taken into account that even when lice infestation pressures are similar, like those observed for Vatne and Sylte (Supporting Information Figure S1), catchment-specific differences in sea trout migration patterns and life history strategies may alter sea trout–lice interactions (Birnie-Gauvin *et al*., 2019).

To advance our understanding of the effects of various stressors on the survival of the sea trout it is important to place the migratory group into context of the whole trout population in the catchment. For instance, the potential impacts of lice-induced mortality to a given trout population are likely to be considerably stronger in populations comprising mostly anadromous sea trout in comparison to populations comprising mostly resident individuals. Whilst the relative proportions of anadromous and resident trout in the three study catchments are unknown, it is likely that a greater proportion of the lotic Sylte trout population are migratory compared to the other lentic catchments. Our study also suggests that lentic-dominated catchments may be able to partially buffer the detrimental effects of salmon lice on the survival of sea trout by providing a refuge for trout to attain larger sizes before out-migrating, though smaller out-migrating individuals may be lost from the population as a consequence. However, as the collapse of Ireland's Burrishoole sea trout population reminds us (Poole *et al*., 2006), lentic-dominated catchments may not be capable of safe-guarding all sea trout populations.

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## CONTRIBUTIONS

Original study concept by B.F., M.B. and T.F.N. Data generation by B.F., M.B. and H.H.B. Data analysis by H.H.B. and R.A.P. Interpretation of results by R.A.P., H.H.B. and T.F.N. Manuscript writing led by R.A.P. and H.H.B. with contributions from all authors. Funding obtained by B.F. and T.F.N.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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