Sigve Nistad Arntzen

# Factors Influencing Sea Trout (*Salmo trutta*) Migration Dynamics in Western Norway

**Master's thesis**

**NTNU**
Kunnskap for en bedre verden

Sigve Nistad Arntzen

# Factors Influencing Sea Trout (*Salmo trutta*) Migration Dynamics in Western Norway

Master's thesis in Ocean Resources
Supervisor: Bengt Finstad
Co-supervisor: Rachel Paterson, Ingebrigt Uglem
May 2022

Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

**NTNU**
Kunnskap for en bedre verden

# Acknowledgements

# Abstract

Anadromous brown trout or sea trout (*Salmo trutta*) perform marine migrations to maximize their growth due to better feeding opportunities in the marine habitat. Since the duration of marine stay and time of migration are influenced by a combination of genetics and environmental variation, these life-history traits show considerably intra- and interpopulation variation. Moreover, the precise timing of upstream migration is controlled by environmental cues, such as water flow and temperature. However, the most critical environmental factors seem to be site-specific, and it is therefore important to investigate a large variety of catchments to better understand sea trout migration dynamics.

The present study aimed to investigate the factors influencing marine residence duration and timing of upstream migration of sea trout in the Vatne catchment, Møre og Romsdal, western Norway. This was done by PIT-tagging and measuring biological characteristics of 226 downstream migrating sea trout during spring 2021. The date and time of downstream and upstream migrations were registered by PIT-antennas installed in the outlet of the river. Environmental factors were monitored by sensors in the river (water flow and temperature), in sea (water temperature, depth and salinity) and on land (light intensity). Statistical analyses were used to determine any potential influence of biological and environmental factors on marine residence duration and timing of upstream migration.

The results indicate that marine residence duration is influenced by several factors. A positive correlation between time at sea and total length was found. Additionally, the marine stay was longer for individuals entering the sea early in the season, and for individuals in a poorer body condition. Moreover, in general, a longer marine stay was associated with a higher exposure to salmon lice (*Lepeophtheirus salmonis*), and late migrants experienced a higher infestation risk compared to early migrants. Change in water flow was the most important environmental factor controlling upstream migration, as increasing water flow initiated migration at all water flows. This study emphasizes the complexity of sea trout migration dynamics, making it challenging to design efficient and general conservation and management practices.

# Sammendrag

Anadrom brunørret eller sjøørret (*Salmo trutta*) vandrer til sjøen for å maksimere dens vekst på grunn av bedre næringstilgang i marine habitater. Hvor lenge fisken er i sjøen og tidspunktet for vandring er påvirket av en kombinasjon av genetikk og miljøvariasjoner. Det er dermed store forskjeller i disse livshistorietrekkene, både innad og mellom populasjoner. Den mer presise timingen av oppstrøms migrasjon kontrolleres av de lokale miljøforholdene, slik som vannføring og vanntemperatur. Hva som er de viktigste miljøfaktorene ser ut til å være stedsavhengig, og det er dermed viktig å undersøke ulike vassdrag, slik at kunnskapen om sjøørret sin vandringsatferd blir så god som mulig.

Dette studiet hadde som mål å undersøke hvilke faktorer som påvirket lengden på sjøopphold og tidspunktet for oppstrøms vandring hos sjøørret i Vatnevassdraget, lokalisert i Møre og Romsdal, Vestlandet. Dette ble gjort ved å PIT-merke og måle biologiske karakteristikker av 226 ut-migrerende sjøørreter i løpet av våren 2021. Dato og tid for hver nedstrøms og oppstrøms vandring ble registrert av to PIT-antenner i utløpet av elva. Miljøparametere ble målt ved bruk av sensorer i elva (vanntemperatur og vannføring), i sjøen (vanntemperatur, dybde og salinitet) og på land (lysintensitet). Statistiske analyser ble utført for å vurdere hvordan lengden på sjøopphold og tidspunktet for oppstrøms vandring ble påvirket av miljøfaktorer og biologiske faktorer.

Resultatene tyder på at den marine oppholdstiden blir påvirket av ulike faktorer. En positiv korrelasjon mellom oppholdstid og fiskens lengde ble funnet. I tillegg var den marine oppholdstiden lengre for individer som vandret til sjøen tidlig og for individer med en lav kondisjonsfaktor. Generelt var et lengre sjøopphold forbundet med en høyere risiko for infestasjon av lakselus (*Lepeophtheirus salmonis*), og sene migranter hadde en høyere risiko for lakseluspåslag enn tidlige migranter. Endring i vannføring ble funnet til å være den viktigste miljøfaktoren som kontrollerer oppstrøms vandring, da økende vannføring trigget vandring på alle vannstander. Dette studiet viser kompleksiteten i sjøørret sin vandringsdynamikk, noe som gjør det utfordrende å lage effektive og generelle forvaltningstiltak.

# Table of content

# 1 Introduction

Migration is a biological phenomenon found in all major branches of the animal kingdom (Dingle & Drake, 2007). The diversity of migration is vast, from an individual's movements over a few millimetres, to seasonal movements of whole populations over long distances. In common for all migratory activity is the movements between two well-defined habitats on a temporally predictable basis (e.g., daily, seasonal or once-a-lifetime migration) (Brönmark et al., 2014). The migration process is controlled by both genetics (i.e., ultimate cues) and by phenotypic response to experienced conditions (i.e., proximate cues) (Ferguson, 2006; Jonsson & Jonsson, 2011). As mobile organisms are able to exploit various habitats during their life, they are expected to migrate to the most profitable habitat (Werner & Gilliam, 1984). This is often referred to as the habitat where the ratio of mortality rate over growth rate is minimized. The organisms' ultimate goal of migration is to maximize their individual fitness (Brönmark et al., 2014).

Migration of fish between fresh water and the sea is a strategy named diadromy, and species that undertake such migrations are called diadromous (Brönmark et al., 2014). The term is further divided into anadromous fish, fish migrating to sea for feeding and return to fresh water for spawning, and catadromous fish, fish migrating to fresh water for feeding and return to sea for spawning (Jonsson & Jonsson, 2011). Brown trout (*Salmo trutta*) is a facultative anadromous species, and populations with access to the sea can perform seaward migrations (Klemetsen et al., 2003). These are known as sea trout. The main benefit of marine migrations is better feeding opportunities, resulting in higher growth rates, larger size-at-age, and higher fecundity (Hendry, 2004). Fish can also migrate to avoid unfavourable conditions such as icing-up of streams and low water flow (Jonsson & Jonsson, 2011). However, this life-history strategy may also involve disadvantages for the sea trout. First, osmotic and ionic regulation in cold seawater is difficult for salmonids (Finstad et al., 1988). Second, the abundance of predators is often higher at sea (Koed et al., 2006). Third, sea trout will be exposed to parasites from both the freshwater and the marine environment, such as salmon lice (*Lepeophtheirus salmonis*)(Boxaspen, 2006). Finally, the energetic investment necessary during migration may be high (Thorstad et al., 2016).

Sea trout show considerable variation in time of migration, duration of the marine stay, and migration distance. Individuals generally make seaward migrations in spring or early summer. Sea trout can undertake short visits to either fresh and/or brackish water throughout their marine stay (Chernitsky et al., 1995; Jensen & Rikardsen, 2012). Some individuals return to fresh water and spawn after only one summer at sea, usually in autumn (Aarestrup et al., 2015). Others can spend winter at sea and even have a marine residence time of several years (Jensen & Rikardsen, 2012). Several studies have found a robust relationship between duration of marine stay and date of downstream migration, with longer marine stays for early migrating individuals (e.g., Jensen et al., 2022; Paterson et al., 2021). Fish age and length have also been shown to be positively correlated with the duration of marine stay (Eldøy et al., 2015). Conversely, stressors in the marine habitat such as high temperature, unfavourable feeding opportunities, and parasites can cause salmonids to return earlier than expected (Hodgson & Quinn, 2002). This behaviour, often referred to as premature return, has been observed as a response to infestations with salmon lice (e.g., Bjørn et al., 2001; Halttunen et al., 2018; Serra-Llinares et al., 2020). By premature returning to fresh water, sea trout can mitigate physiological stress and

regain osmotic balance (Serra-Llinares et al., 2020). Additionally, salmon lice have a low tolerance to low levels of salinity and will die if the fish remains in fresh water. However, the probable cost of the premature return is reduced fish growth, and hence fecundity, due to reduced feeding opportunities (Birkeland, 1996; Thorstad et al., 2015). The majority of sea trout remain in coastal areas close to their home river (< 80 km) (Thorstad et al., 2016). However, individuals have been observed > 300km away from their river of origin (Okumus et al., 2006).

Changes in photoperiod is a major proximate factor indicating the season of migration of fish (Smith, 2012). However, the precise seasonal timing of upstream migration is controlled by environmental cues, that is the local conditions a sea trout meets when returning to the river (Jonsson & Jonsson, 2011). Individuals who experience unfavourable migratory conditions in the river mouth may prolong their marine stay. The two most cited abiotic factors controlling the upstream migration of salmonids are water flow and river temperature (Jonsson & Jonsson, 2011). Both high water flow and increasing water flow facilitate upstream migration (Klemetsen et al., 2003). High discharge may shelter ascending fish from predators, since turbidity, bubbles, and surface turbulence make it more difficult for visual predators (Abrahams & Kattenfeld, 1997; Tetzlaff et al., 2005). This is especially important in smaller streams where ascending fish are more vulnerable to predation (Jonsson & Jonsson, 2011). However, higher water flow increases the fish's energetic costs (Enders et al., 2005), and too high flow may temporarily stop the upstream migration (Jonsson et al., 2007). Since sea trout are poikilothermic, migratory costs increase with increasing water temperature (Enders et al., 2005). Long freshwater migrations are both stressful and energy demanding and will be even more stressful during periods of higher river temperatures (Jonsson & Jonsson, 2011). Swimming performance is also lower at high temperatures due to low oxygen saturation in the water (Salinger & Anderson, 2006). Conversely, the ability to pass waterfalls is reduced at lower temperatures (Jonsson & Jonsson, 2011). Consequently, the optimal temperature for upstream migration might be a trade-off between migratory costs and the performance to pass obstacles and avoid predators.

During the day, sea trout may choose to initiate upstream migration during periods that minimize vulnerability to predators and/or facilitate the homing migration. Migration during darker periods (i.e., nocturnal migration) may be one strategy to minimize vulnerability to predators, as light intensity determines the risk of being preyed on (Lucas & Baras, 2008; Smith & Smith, 1997). This hypothesis is supported by studies where nocturnal conditions are preferred in periods of low water flow and in smaller streams (Bendall et al., 2005; Potter, 1988; Smith & Smith, 1997). In larger rivers and areas with midnight sun, upstream migration takes place during both day and at night (Karppinen et al., 2004; Smith & Smith, 1997). The effect of tides on upstream migration of salmonids is less clear and varies among catchments. In most catchments, salmonids ascend during every stage of the tidal cycle (e.g., Erkinaro et al., 1999; Lilja & Romakkaniemi, 2003; Smith & Smith, 1997). However, some tidal stages seem to be more preferred than others. A study conducted in river Tanaelva observed the highest number of upstream migrating Atlantic salmon (*Salmo salar*) at high tide (Smith & Smith, 1997). At high tide, rivers are more accessible for the fish, and it might also minimize the vulnerability to predators (Jonsson & Jonsson, 2011). Ebbing tide (falling sea level) is also seen as a preferable stage, as the effect of river flow usually increases in the estuaries (Lilja & Romakkaniemi, 2003), which might provide salmonids with olfactory cues facilitating the homing process (Priede et al., 1988; Smith & Smith, 1997).

This study aimed to extend our knowledge on factors regulating the marine migration of sea trout by investigating two important life-history traits in the Vatne catchment, Møre og Romsdal, western Norway. In the first part of the study, I investigated the marine residence duration and how it is influenced by abiotic and biotic factors. Then I explored the upstream migration pattern and uncovered the most important environmental cues influencing the timing of upstream migration on a seasonal and daily basis. The present study aimed to test three hypotheses:

1. Sea trout's marine residence duration is influenced by a combination of abiotic and biotic factors and is positively correlated with a) length of the fish and b) lice infestation risk, and negatively correlated with c) out-migration date and d) condition factor.

2. During the season, sea trout prefer to initiate upstream migration during periods of increased water discharge, at high water flow and at moderate temperatures.

3. During the day, sea trout prefer to initiate upstream migration during darker periods and at high and ebbing tide, as these periods might reduce the predation risk and provide returning sea trout with olfactory cues.

# 2 Materials and methods

## 2.1 Study area

The present study was conducted from April to October 2021 in the Vatne catchment (area 31.9 km$^2$, drainage 64.9 mills m$^3$ y$^{-1}$, 62°33'N, 6°36'E) in Møre og Romsdal, western Norway (Figure 1). The catchment consists of two anadromous river stretches separated by lake Vatnevatnet (0.90 km$^2$, depth 31 m, 9 masl). River Oselva is 400 m long and connects Vatnevatnet to the head of Vatnefjorden. Here, a fish ladder of 35 m is installed to improve the passage of salmonids under low water levels (Figure 2). A larger pool with brackish water is located downstream of the river outlet. From Vatnevatnet, residing salmonids can migrate up into river Storelva (4 km). Both Oselva and Storelva are used as spawning areas and nursery habitats for brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). European eel (*Anguilla anguilla*) and three-spined stickleback (*Gasterosteus aculeatus*) are also present in the catchment.

Vatnefjorden is an 8 km long sidearm of Romsdalsfjorden, located in the outermost part of the fjord system. The largest river in the area is Oselva, but smaller rivers and creeks drain into the fjord. No aquaculture sites are found within Vatnefjorden. However, Romsdalsfjorden is an intensive salmon farming area, and several locations are found just outside Vatnefjorden.
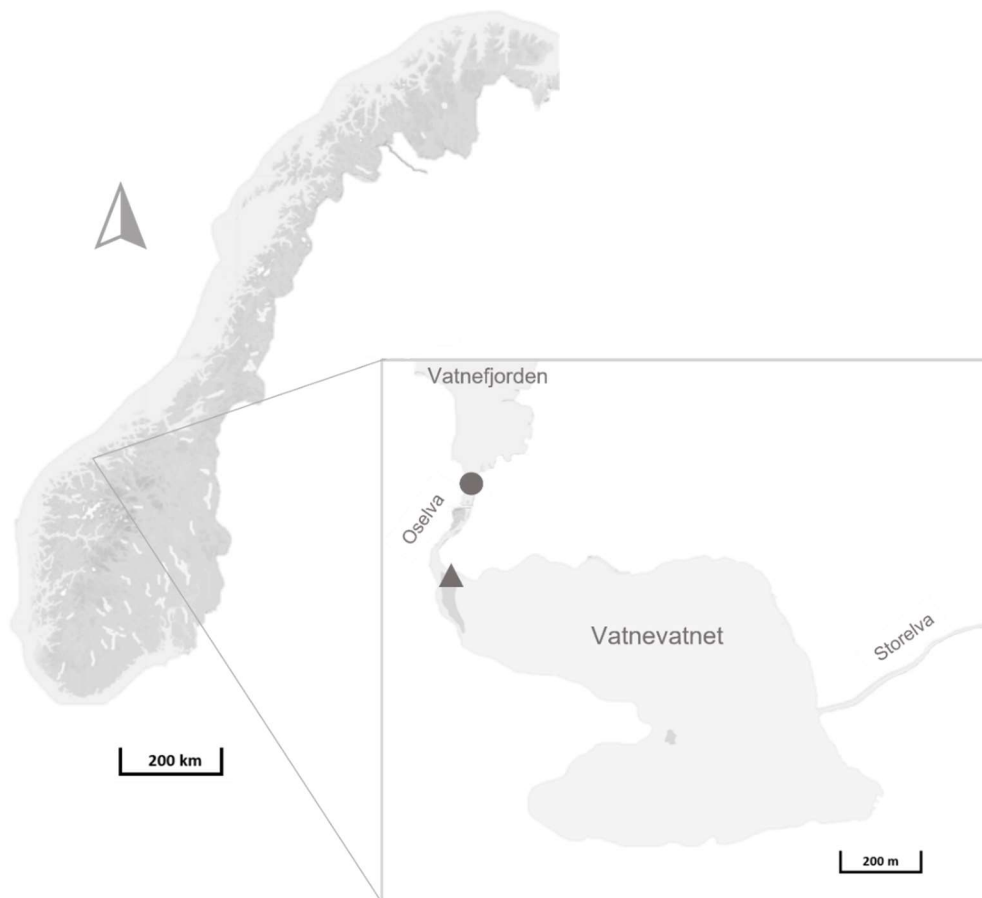


**Figure 1:** Map of the Vatne catchment (62°33'N, 6°36'E). The fyke net is marked as a triangle and PIT-antennas as a circle. The map is modified after www.norgeskart.no.

**Figure 2:** [A] The fish ladder located in the lower part of Oselva. [B] The two river outlets and PIT-antennas, marked with arrows. Photos: Sigve Nistad Arntzen.

## 2.2 Fish capture and tagging

Downstream migrating sea trout were captured in a fyke net at the outlet of Vatnevatnet between 24 April and 14 June 2021 (Figure 3). Only individuals that migrated to sea and returned within the same year were included in this study (n = 226; average ± SD total length ($L_T$) = 221 ± 55 mm; range = 139 - 374 mm; average ± SD weight = 93 ± 65 g; range = 19 – 376 g). The fyke net (wing length 7.5 – 10.0 m, mesh size 20 mm) spanned the entire river width. It was inspected once per day. Captured fish were collected in a 60 L bucket and transported by boat to shore. Here, a knotless handheld net was used to transfer the fish to a 10 L bucket containing benzocaine (Benzoak vet, 200 mg/ml diluted by 15-20 mL/100 L water). The fish were kept in the solution for three to four minutes, and sedation was determined based on opercular beat rate and tail root pinch reflex. When anaesthetized, weight (g) and total body length ($L_T$, i.e., snout tip to the tip of the caudal fin) of the fish were measured. Prior to tagging, the fish were scanned with Biomark 601 Handheld Reader to determine whether they were previously tagged or not. Untagged individuals > 120 mm total length ($L_T$) were tagged with a unique 12.5 mm Passive Integrated Transponder tag (PIT-tag; Biomark HPT full-duplex 134 kHz) injected into the right side of the body cavity (Figure 3). The tag was inserted using a Biomark MK25 implant gun. After tagging, the fish were transferred to a 60 L holding tank in the river to observe recovery. After regaining normal behaviour, the fish were released downstream of the fyke net. All capture, sampling and tagging were done in accordance with the regulations set by the Norwegian Food and Safety Authority (permission no. 22993). All tagging personnel had undergone proper training and had passed NINA's course in Laboratory Animal Science.

**Figure 3:** [A] The fyke net in the outlet of Vatnevatnet. [B] The tagging procedure. The PIT-tag was injected into the right side of the body cavity. Photos: Sigve Nistad Arntzen.

## 2.3 Tracking of tagged fish

Tracking of PIT-tagged sea trout was done using stationary bottom radio frequency identification full-duplex antennas (RFID; Biomark, Boise, Idaho, US). Two antennas were installed in Oselva, as the river separates into two outlets. The mean annual water depth at the antennas was approximately 45 cm, and the detection range of the antennas was at least 75 cm. Antennas were set to record each unique tag up to ten times per second. When tagged sea trout passed the antenna, a unique PIT-tag ID, date and time were recorded and saved by the reader box. The data were retrieved online using Biomark Tag Manager Software.

## 2.4 Recording of environmental parameters

Water temperature (°C), water depth (m), and salinity (ppt) were measured at different locations in the study area by data loggers (DST centi-TD and DST CT, Star-Oddi Ltd., Reykjavik, Iceland) between 18 June and 3 October 2021. All sensors were inspected frequently throughout the study period. The data were retrieved using SeaStar software version 8.90 provided by Star – Oddi systems (Star-Oddi Ltd., Reykjavik, Iceland).

In Oselva, water temperature and depth were measured using DST centi-TD with an interval of 15 minutes. The data logger was put in a self-made protective housing. The logger was anchored to a stone and placed in the first deeper pool upstream of the fish ladder.

6

Sea temperature and sea salinity were measured using DST CT with an interval of 15 minutes. The sensors were placed 50 m away from the river outlet of Oselva (62°33'28N, 6°36'42E). The sensors were attached to a mooring system at 0.5 m, 1 m and 1.5 m depth to monitor temperature and salinity gradients (Figure 4). Additionally, a DST centi-TD was attached to the anchor at the seafloor to monitor the sea level every 15 minutes.

Light intensity (lx) was measured every 15 minutes using HOBO MX2202 waterproof temperature/light level logger (Onset Computer Corporation, Bourne, US). The logger was installed horizontally on land, close to the catchment. The data were retrieved online using HOBOmobile (Onset Computer Corporation, Bourne, US).
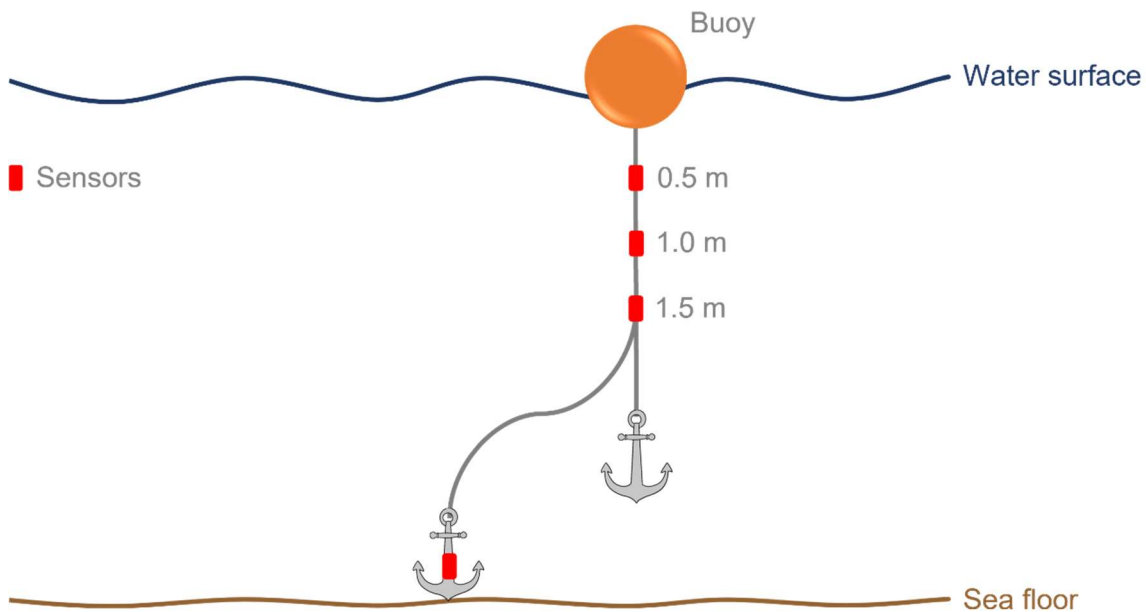


**Figure 4:** Overview of the sensors (red rectangles) in the sea. Three DST CT measured temperature and salinity at 0.5 m, 1 m and 1.5 m depths. A DST centi-TD at the seafloor measured the sea level. Figure made by Sofie Uttian Alstad and Sigve Nistad Arntzen.

## 2.5 Estimation of water flow

Measurement errors of the water depth in Oselva were observed when analyzing the data. The DST centi-TD measurements of the water depth were based on the pressure, and the river was most likely too shallow to produce precise data. Consequently, the water flow in the outlet of Engsetvatn (< 3 km away from Oselva, https://sildre.nve.no/Station/101.1.0) was used as an estimate of the water flow in Oselva. When comparing the water flow in the outlet of Engsetvatn with the available data from Oselva, a similar flow pattern was observed.

## 2.6 Estimation of salmon lice infection pressure

Estimations of salmon lice infection pressure were provided by The Institute of Marine Research (IMR). IMR has developed a national operational model that estimates numbers of infective salmon lice larvae with high resolution in both time and space (Sandvik et al., 2020). In the model, numbers of newly hatched salmon lice larvae are calculated based on

the reported total number of fish, adult female lice, and temperature by all active salmon farms in Norway. The salmon lice particle tracking model includes both hydrodynamics and lice behaviour, making it possible to estimate the distribution of lice with local variations along the fjord axis (Myksvoll et al., 2018; Sandvik et al., 2020). The data provided by IMR was daily numbers of copepodites per square meter in the study area (sea trout's habitat use was set to max 20 km from Oselva) throughout the study period.

## 2.7 Data analyses

### 2.7.1 Defining timing of downstream migration, upstream migration and marine stay

This study focused on individuals that entered the sea and returned within the same year. The Vatne catchment consists of only a single antenna system, which makes it difficult to assess the direction of fish movements. The direction of migration was therefore based on known sea trout out-migration period and duration at the antenna during a detection event. Criteria were retrieved from an earlier study in the area (Paterson et al., 2021). Here, sea trout were defined as out-migrated if they were first detected between 1 April and 1 July, and the detection event duration was < 1.2 h (repeated registrations), with the last detection time determined to be the time of out-migration. The first detection made after the defined time of out-migration was assumed to represent upstream migration. Individuals which made their first out-migration after 1 July or returned between 1 April and 1 July were manually inspected to assign the migration direction based on the above criteria.

Since it is only possible to determine the direction of the first and the second registration on the antenna (downstream and upstream migration), it is important to note that the registered upstream migration event represents an individual's first return to the river. Some individuals could have returned to sea after a re-visit in the river and made a final return later in the season.

Individuals were defined to have a marine stay when more than one day was spent downstream of the antenna.

### 2.7.2 Calculation of body condition factor

Fulton's condition factor (K-factor) is calculated from the relationship between a fish's weight and length and reflects an individual's condition. The formula used was (Fulton, 1904):

$$K = \frac{Weight\ (g)}{Total\ body\ length\ (cm)^3} \times 100 \qquad \text{equation 1}$$

## 2.8 Data filtration and statistical analyses

All data filtration and statistical analyses were performed using R version 4.0.2 (R Core Team, 2020) and RStudio version 1.4.1717 (RStudio Team, 2020). The statistical significance level was set to $\alpha = 0.05$. All figures used to present the results were made using the ggplot2 package (Wickham, 2016) in RStudio.

Analysis of the raw data identified five individuals with unusual low/high condition factor, most likely due to data entry error. These fish were therefore excluded from all analyses.

### 2.8.1 Factors influencing the marine residence duration

The influence of total fish length ($L_T$), condition factor (K), date of out-migration (i.e., day of the year) and lice infestation risk on the marine residence duration was investigated using a parametric regression model. A linear model (LM) was chosen as this was suggested to best fit the data. Since body length is included in the calculation of condition factor, the residual values from the linear model $\log (K) \sim \log (L_T)$ were used to avoid autocorrelation between the two variables (Flaten et al., 2016). The lice infestation risk was defined and calculated as the total copepodites exposure for each individual throughout the marine stay. The lice infestation risk was set to zero for sea trout with marine stay less than eight days because of the development time from copepodites to pathogenic pre-mature adult (Stien et al., 2005). Linearity and independence were inspected from basic data visualization, and homoscedasticity and normality were inspected from residual plots.

To be able to compare the effects of the different variables, all predictors were standardized and centered on the mean using the "scale" function in base RStudio. Multicollinearity between the predictors was tested using the "check_collinearity" function in the "performance" RStudio package (Lüdecke, 2021). Variance inflation factors (VIF) was used as a measure and found to be sufficient low ($< 1.5$) in all predictors included in the model.

Model selection was conducted using the "dredge" function in the RStudio package "MuMIn" (Barton, 2020). Corrected Akaike information criteria (AICc) was used to compare the different candidate models and to identify the ones that best fit the data, that is the one that explains the greatest amount of variation using the fewest possible explanatory variables (Anderson et al., 2001). AICc is a correction to the AIC and is found to perform better when the sample size to parameter ratio is $< 40$ (Hurvich & Tsai, 1989). ΔAICc is the difference in AICc score between the model with lowest AICc score (best fit) and the model it is compared to. All models ΔAICc $< 2$ were considered in the top model set (Burnham & Anderson, 2004).

Conditional model averaging was applied on the top model set to calculate the average of each parameter coefficient from the models where the parameter coefficient was included. The ggeffects package (Lüdecke, 2018) in Rstudio was used to estimate the average marginal effect for any significant variables in the model.

## 2.8.2 Factors influencing the timing of upstream migration during the season

To investigate the variation in timing of upstream migration on a seasonal basis, the number of sea trout performing upstream migration each day (count) was used as a response variable. A series of factors that are suggested to influence the timing of upstream migration were tested (daily means): river water flow, change in water flow (with respect to the day before), sea temperature, sea salinity and change in river temperature (with respect to the day before). A negative binomial regression model was used to account for over-dispersed count data. The actual river temperature was excluded as a predictor because of its collinearity with sea temperature. Sea temperature in the estuary was therefore assumed to be a better predictor of the experienced water temperature by a returning sea trout. However, the river temperature was accounted for through the predictor "change in river temperature". Linearity and independence were inspected from basic data visualization, and homoscedasticity and normality were inspected from residual plots.

All predictors were standardized and centered on the mean in the same way as the first analysis (see 2.8.1). Multicollinearity was found to be sufficient low (VIF < 4.35) for all predictors included in the model. Model selection and conditional model averaging were conducted with the same criteria as the first analysis (see 2.8.1).

The temperature and salinity sensors were deployed on 18 June 2021 and environmental data before this day is therefore missing. This analysis was therefore performed on individuals performing upstream migration between 18 June and 3 October 2021 (n = 162).

## 2.8.3 Factors influencing the timing of upstream migration during the day

To investigate how the tidal cycle and light intensity influenced the timing of upstream migration during the day, two different analyses were conducted. To evaluate the effect of tidal stages, the water level was matched with the corresponding hour of each fish registration at the antenna. Number of minutes from high tide for each registration was converted to degrees with high tide at 0° and 360° and low tide at 180°. The circular data were plotted and tested with Rayleigh's test of uniformity, using the "r.test" function in RStudio package "CircStats" (Lund & Agostinelli, 2018). Rayleigh's test of uniformity is a test for significant unimodal orientation. In this study, a significant unimodal orientation would mean that the data have a significant clustering of registrations in one part of the tidal cycle.

To test whether upstream migration tended to occur during specific light regimes, the light intensity was treated as a categorical variable. The light intensity was divided into four different categories based on a combination of definitions (American Meteorological Society, 2012a, 2012b, 2012c; Engineering ToolBox, 2004; Schlyter, 2017). The following categories were used: daylight, dimmed light, twilight conditions and night conditions (Table 1). Since the available hours in each light category differed, a Chi-Square goodness of fit test was used to compare the observed distribution with the expected distribution (distributed number of sea trout in each light category given that the fish returned at random light intensities). The test was performed using the "chisq.test" function in RStudio, with a null hypothesis stating that it is no significant variation between the observed and expected distribution.

Both the depth sensor and the light sensor were deployed on 18 June 2021. These tests were therefore performed on individuals performing upstream migration between 18 June and 3 October 2021 (n = 162).

# 3 Results

## 3.1 Recorded environmental parameters

### 3.1.1 Sea temperature and salinity

Sea temperature and salinity at 0.5 m, 1 m and 1.5 m depth showed minor variations throughout the study period. The measurements done at 1 m depth were therefore used for the analyses (Figure 5). Water temperatures in the inner part of Vatnefjorden increased progressively from June to August, except for a cold period in middle of July, and thereafter declined throughout the season. The water was relatively saline during the season (mean 29.6 ppt ± 2.1 ppt). A few days throughout the study period the salinity was as low as 6 ppt. This decline in salinity was likely due to a combination of heavy rainfall and increased water discharge in the river.
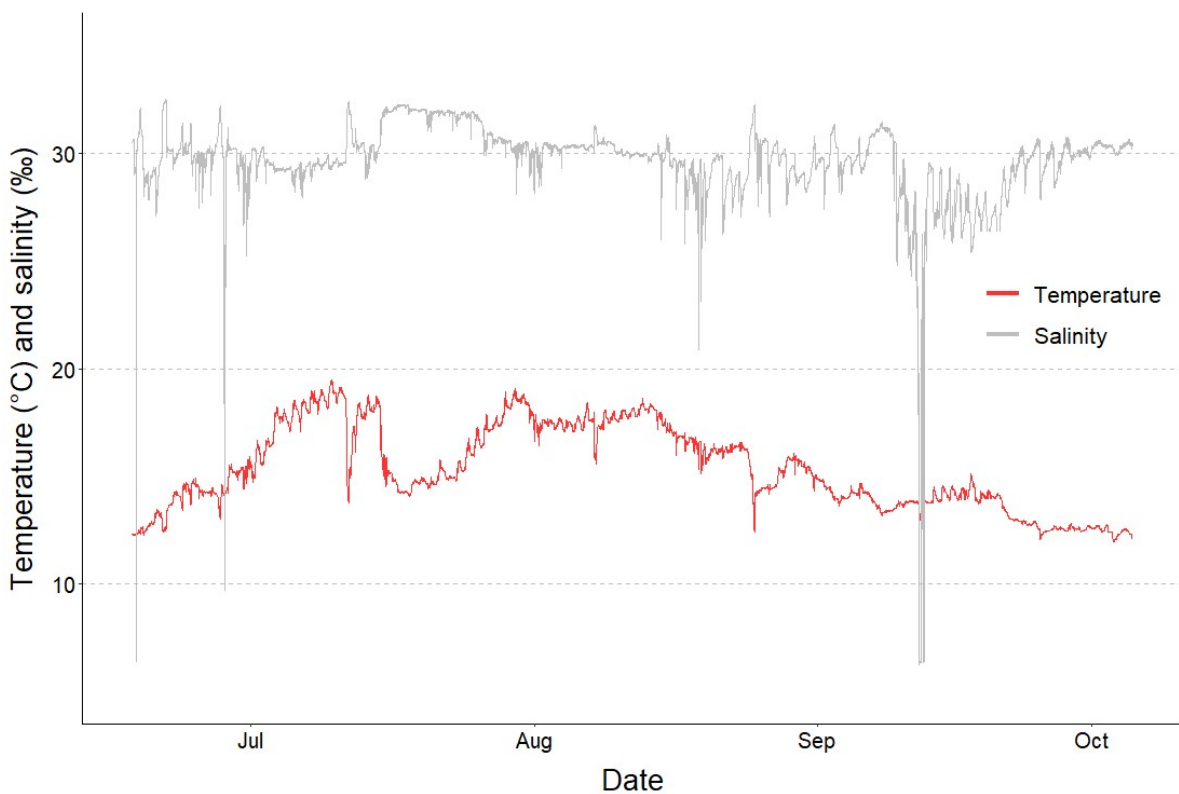


**Figure 5:** Water temperature and salinity at 1 m depth in the inner part of Vatnefjorden in the period 18 June to 3 October 2021.

### 3.1.2 River temperature and water flow

Water flow measurements in the outlet of Engsetvatn between 18 June and 3 October 2021 showed a minimum flow of 0.1 $m^3$/s and a maximum flow of 2.8 $m^3$/s (Figure 6). It was a decline in water flow from the start of the study period until the middle of August. Heavy rainfall in late August and September resulted in increased water flow, with two distinct peaks in September.

The water temperature in Oselva showed a minimum temperature of 11.2 °C and a maximum temperature of 20.5 °C (Figure 6). The water temperature increased steadily towards the middle of July and thereafter declined throughout the season.
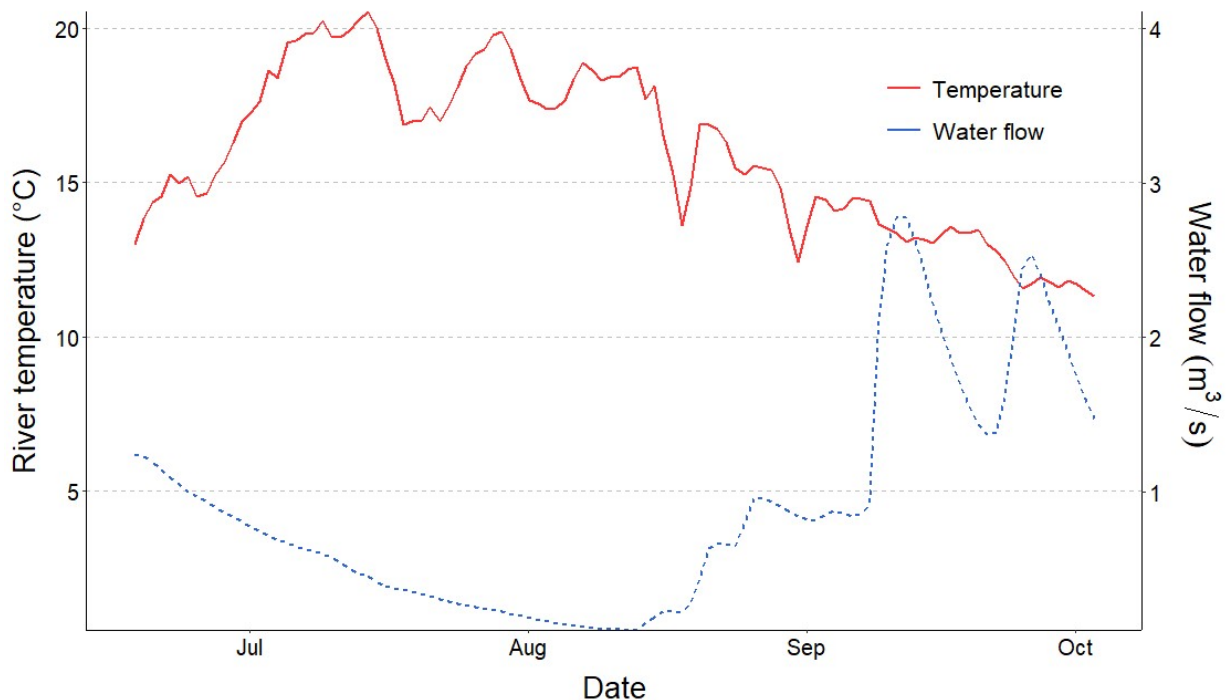


**Figure 6:** Water temperature in Oselva and water flow in the outlet of Engsetvatn in the period 18 June to 3 October 2021. Water flow was retrieved from https://sildre.nve.no/Station/101.1.0.

### 3.1.3 Light intensity

Light intensity measurements varied from 0 lux to 118 825 lux in the period 18 June to 3 October 2021 (Figure 7). Weekly light intensity increased towards July before it decreased throughout the season. When conducting the analysis, light intensity data was treated as a categorical variable (see 2.8.3). Light intensity categories, light intensity and the corresponding conditions and times are given in Table 1.
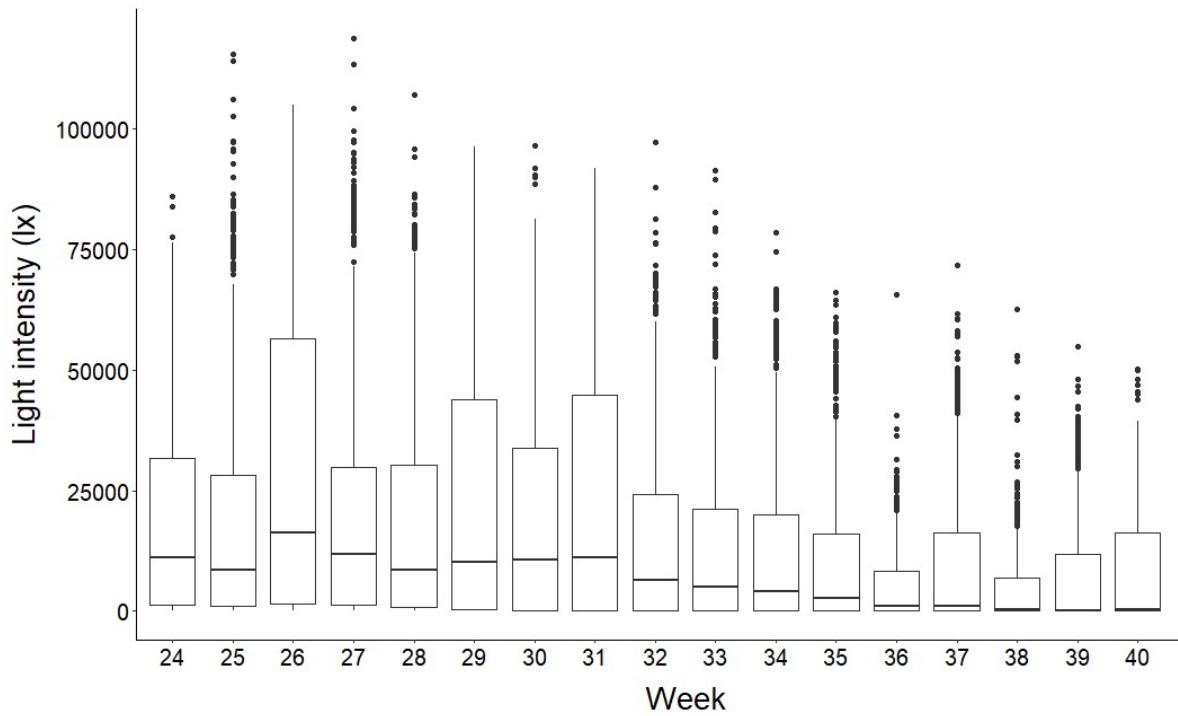
**Figure 7:** Box and whiskers plot of the light intensity (lux) during the study period. Weekly light intensity increased towards July before it decreased throughout the season.

**Table 1:** Light intensity categories and the corresponding light intensity (lux), condition and time. Light intensity categories were based on different definitions (American Meteorological Society, 2012a, 2012b, 2012c; Engineering ToolBox, 2004; Schlyter, 2017).

| Light intensity category | Light intensity (lux) | Condition | Corresponding time in a) June/July and b) Aug/Sept |
|---|---|---|---|
| Daylight | > 10752 | Full daylight Direct sunlight | a) 07 – 20.00 b) 09 – 18.00 |
| Dimmed light | > 585 & ≤ 10752 | A very cloudy day or evening/morning | a) 20 – 23.00 and 04 - 07:00 b) 18 – 21:00 and 06 – 09:00 |
| Twilight condition | > 1 & ≤ 585 | Civil twilight or late evening/early morning | a) 23 – 04:00 b) 21 – 23:00 and 04 – 06:00 |
| Night condition | ≤ 1 | Nautical/astronomical or night. | a) Never or 01 – 03:00 b) 23 – 04:00 |

## 3.1.4 Tidal cycle

The sea level in Vatnefjorden varied with 198 cm between maximum high tide and minimum low tide during the study period. Spring tide was observed every two weeks (Figure 8 for illustration of the tidal cycle).
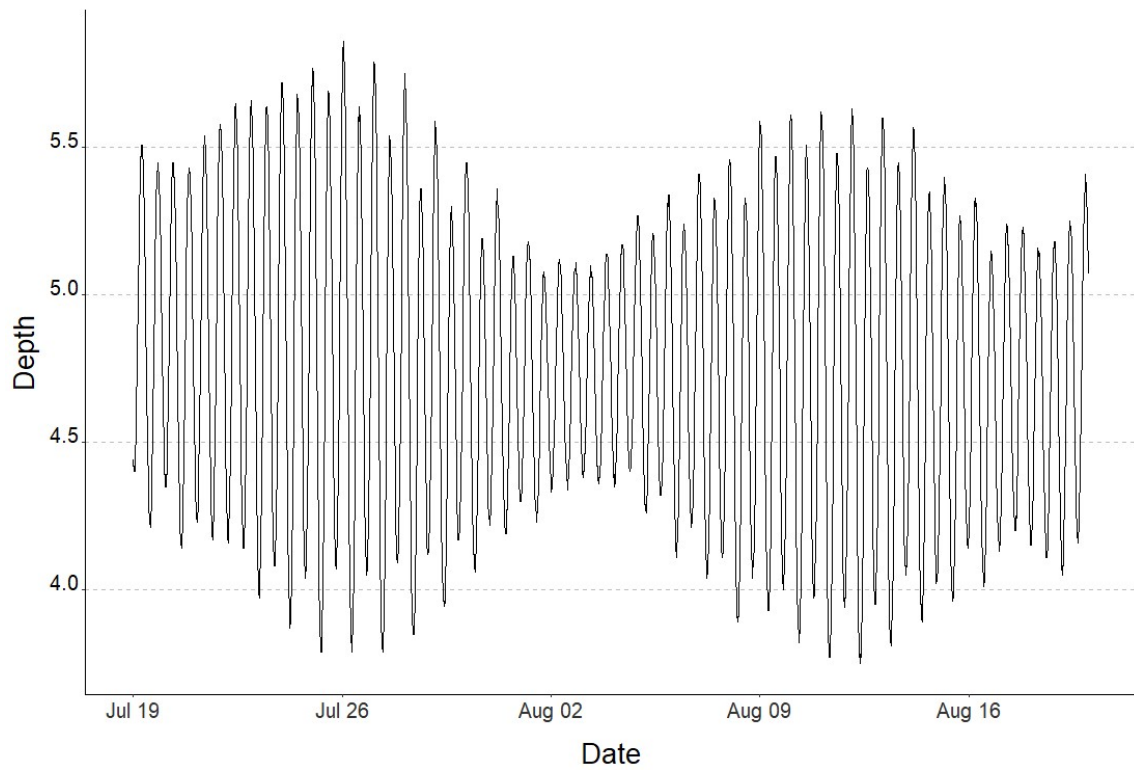


**Figure 8:** Variation in sea level in Vatnefjorden with changing tide. A period of one month (19 July to 19 August 2021) is highlighted for illustration purposes.

### 3.1.5 Estimated salmon lice concentration

The salmon lice concentration in Vatnefjorden was estimated to be low until the middle of June when it started to increase steadily (Figure 9). Two distinct peaks of salmon lice concentration were estimated, one in the first part of July and another in the middle of August. Thereafter the concentration declined throughout the season.
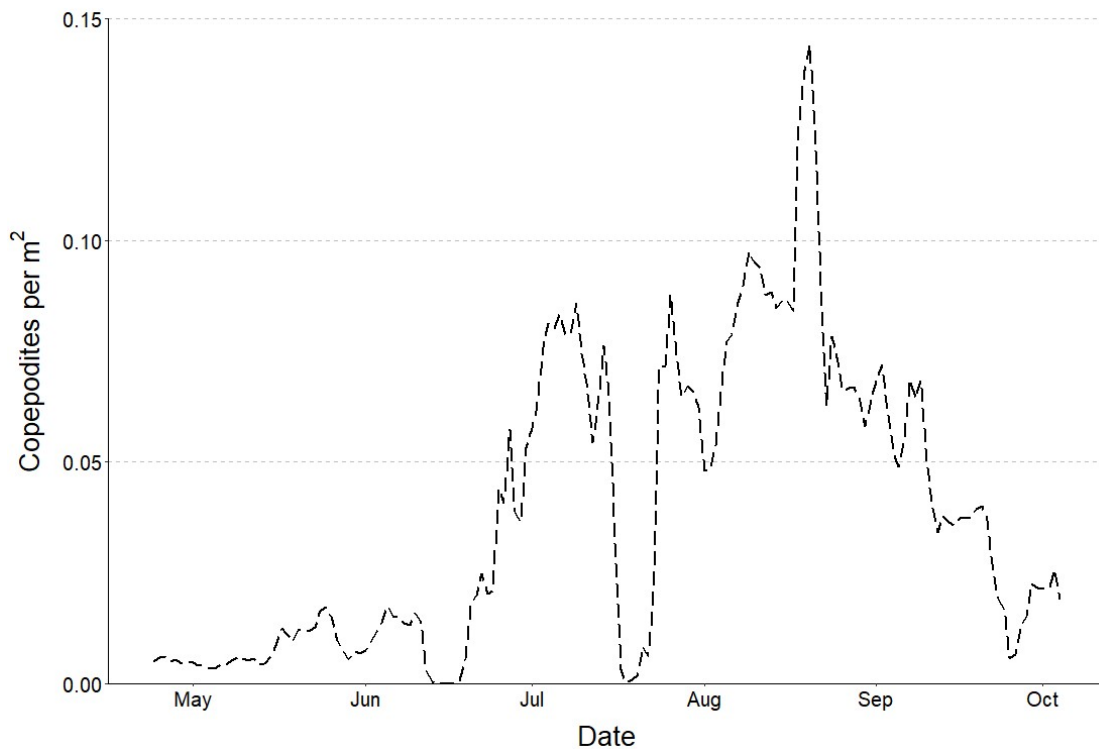


**Figure 9:** Estimated salmon lice level (copepodites per $m^2$) in Vatnefjorden between 24 April and 3 October 2021 (first downstream and last upstream migration).

## 3.2 Migration timing

A total of 226 PIT-tagged sea trout were registered to enter sea and return in the study period between 24 April and 3 October 2021 (Figure 10). Sea trout migrated to sea over a long time period, but most frequently during the first part of May, with a median date of 11 May. Mean marine residence duration was 66.2 days ± 45.4 days. The upstream migration showed a bimodal distribution with no detections being made between 11 June and 26 June. Highest frequency of upstream migrations was in middle of August and the first part of September, with a median date of 15 August.

16
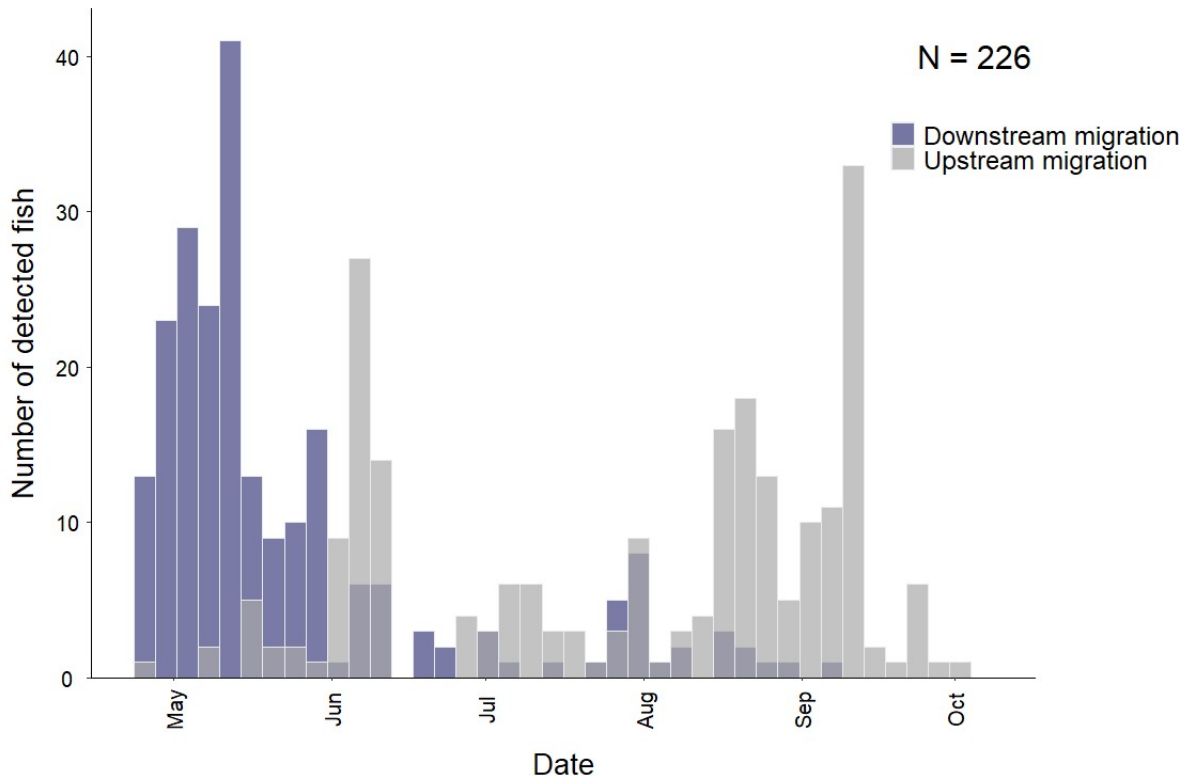
**Figure 10:** The histogram shows how downstream and upstream migrations in Oselva were distributed throughout the season.

## 3.3 Factors influencing the marine residence duration

There were two equally well fitted regression models exploring the number of days spent at sea (Δ AICc < 2, Table 2). The first model included all predictors: out-migration date, total body length, residual condition, lice infestation risk and the interaction term total body length x residual condition. The second model included the same predictors except for the interaction term.

The estimates from the conditional model averaging (Table 3) indicated that larger fish spent more time at sea compared to smaller individuals, and that sea trout which spent a longer time at sea had a higher risk of lice infestation. Moreover, the results suggested that early migrants and individuals with a lower condition factor spent more time at sea compared to late migrants and individuals with a high condition factor. The interaction between total body length and residual condition seemed to have limited effect on duration of marine stay, as the 95 % confidence interval included zero. The relationships between marine residence duration and each significant predictor are given in Figure 11.

17

**Table 2:** The three top-ranked models sorted by corrected Akaike information criterion (AICc), with difference in AICc from the best model (ΔAICc), model weight (AIC$_W$) and degrees of freedom (d.f.). Response variable is marine residence duration. (OD) is out-migration date, (TL) total body length, (RC) residual condition, and (LR) lice infestation risk.

| Model tested | AICc | ΔAICc | AIC$_W$ | d.f. |
|---|---|---|---|---|
| [OD] + [TL] + [RC] + [LR] + [TL] x [RC] | 1616.7 | 0.00 | 0.476 | 7 |
| [OD] + [TL] + [RC] + [LR] | 1616.7 | 0.07 | 0.459 | 6 |
| [OD] + [TL] + [LR] | 1620.7 | 4.01 | 0.064 | 5 |

**Table 3:** Standardized coefficient of model predictors for marine residence duration after model conditional averaging the two best regression models (ΔAICc < 2, Table 2), including standard error (SE), z value and 95 % confidence interval.

| Predictor | Estimate | SE | z value | 95% CI |
|---|---|---|---|---|
| Intercept | 66.53 | 1.866 | 35.46 | 65.42 to 67.65 |
| Lice infestation risk | 40.41 | 0.596 | 67.41 | 39.23 to 41.58 |
| Total body length | 3.539 | 0.694 | 5.099 | 2.179 to 4.899 |
| Residual condition | -1.311 | 0.597 | 2.183 | -2.488 to -0.134 |
| Length x condition | -0.728 | 0.496 | 1.460 | -1.701 to 0.249 |
| Out-migration date | -10.21 | 0.703 | 14.45 | -31.68 to -23.65 |



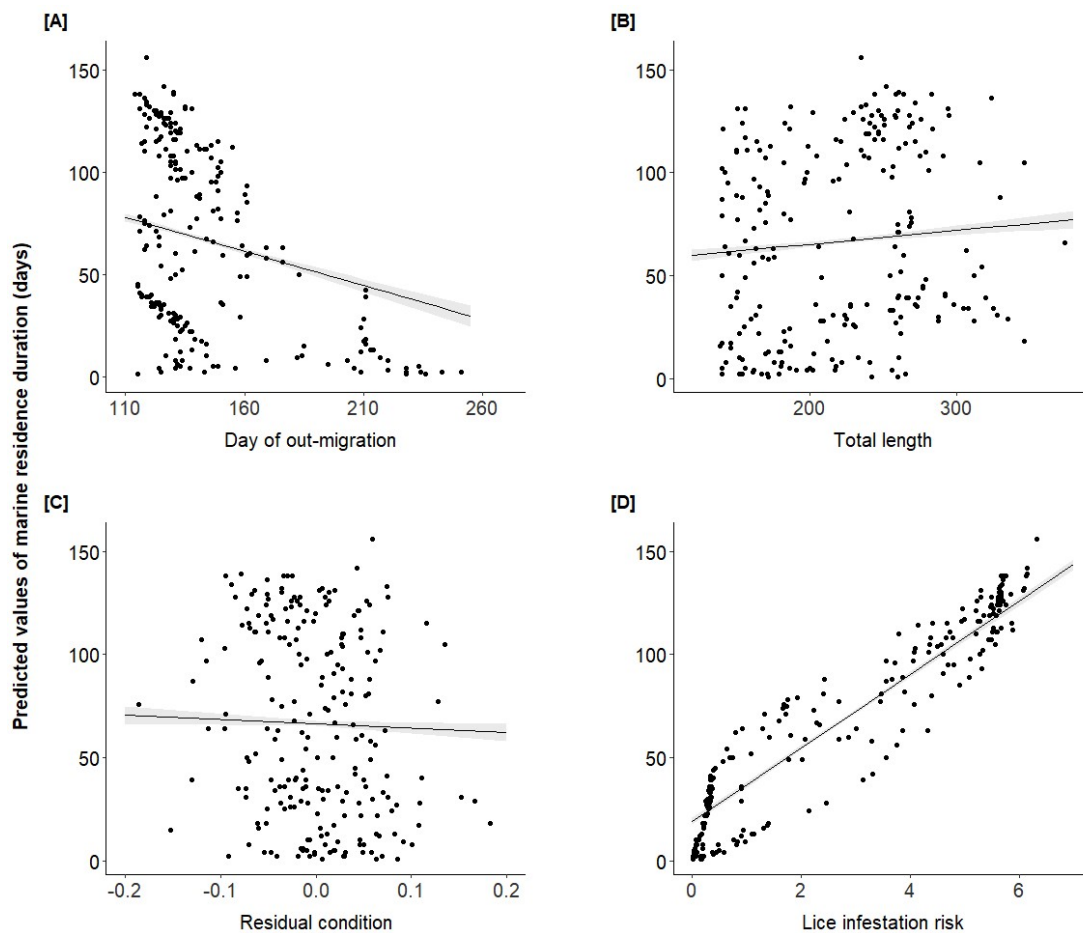**Figure 11:** The relationships between marine residence time and the significant predictors. The regression line is the predictive values for the marginal effect of [A] day of out-migration ($R^2$ = 0.23), [B] total body length ($R^2$ = 0.026), [C] residual condition ($R^2$ = 0.033), and [D] lice infestation risk ($R^2$ = 0.89). Confidence intervals (95%, shaded area) are displayed around the regression line (solid line).

## 3.4 Factors influencing the timing of upstream migration during the season

There were six equally well fitted regression models exploring the numbers of sea trout performing upstream migration each day (Δ AICc < 2, Table 4). The models indicated that marine residence duration was influenced by all predictors included (i.e., water flow, change in water flow, sea temperature, change in river temperature and sea salinity). Change in water flow was found to be the most important factor initiating upstream migration of sea trout, being included in all six candidate models. The estimates from the conditional model averaging (Table 5) indicated that an increasing water flow stimulated upstream migration of sea trout. The actual water flow, sea temperature, change in river temperature and sea salinity seemed to have limited effect on the timing of upstream migration, as the 95 % confidence intervals included zero (Table 5).

**Table 4:** The six top-ranked models sorted by corrected Akaike information criterion (AICc), with difference in AICc from the best model (ΔAICc), model weight (AIC$_W$) and degrees of freedom (d.f.). Response variable is number of upstream migrating sea trout each day. An extensive model selection table including all tested models with weight is found in Appendix A.

| Model tested | AICc | ΔAICc | AIC$_W$ | d.f. |
|---|---|---|---|---|
| Delta water flow + Sea temperature | 339.1 | 0.00 | 0.187 | 4 |
| Delta water flow | 339.6 | 0.47 | 0.148 | 3 |
| Delta water flow + Water flow + Sea salinity | 339.7 | 0.54 | 0.142 | 5 |
| Delta water flow + Water flow | 339.9 | 0.75 | 0.128 | 4 |
| Delta water flow + Sea temperature + Sea salinity | 340.7 | 1.55 | 0.087 | 5 |
| Delta water flow + Sea temperature + Delta river temperature | 341.0 | 1.86 | 0.072 | 5 |

**Table 5:** Standardized coefficient of model predictors for number of upstream migrating sea trout each day after model conditional averaging the six best regression models (Δ AICc < 2, Table 4), including standard error (SE), z value and 95 % confidence interval.

| Predictor | Estimate | SE | z value | 95 % CI |
|---|---|---|---|---|
| Intercept | 0.185 | 0.125 | 1.461 | -0.0629 to 0.431 |
| Delta water flow | 0.631 | 0.102 | 6.135 | 0.430 to 0.832 |
| Sea temperature | 0.212 | 0.125 | 1.670 | -0.0373 to 0.460 |
| Delta river temperature | 0.060 | 0.119 | 0.499 | -0.176 to 0.296 |
| Sea salinity | -0.184 | 0.141 | 1.288 | -0.464 to 0.0960 |
| Water flow | -0.243 | 0.159 | 1.510 | -0.558 to 0.072 |

The two days with the most fish performing upstream migration (n = 13 and n = 14) were the two days with strongest increase in water flow during the season (Figure 12). However, a higher number of sea trout were also observed to perform upstream migration in relation to smaller increases in water flow, such as the first increase in water flow in the middle of August. Additionally, sea trout were observed to perform upstream migration at all water flows throughout the season.
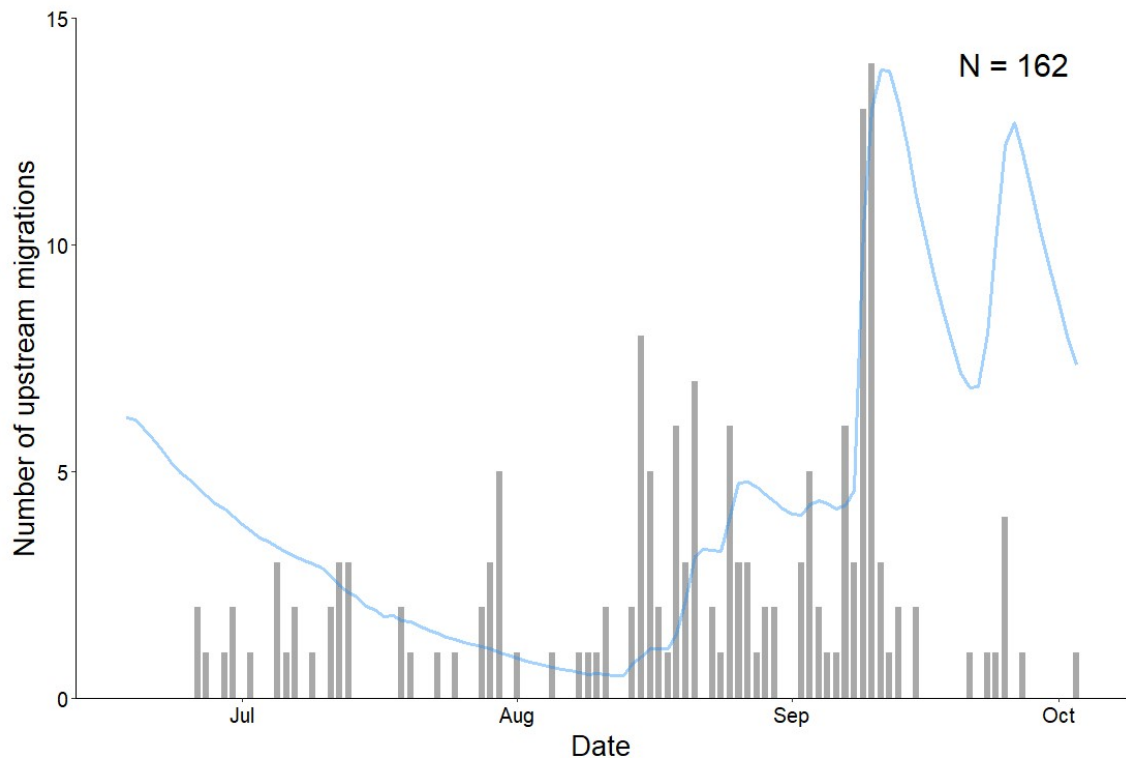
**Figure 12:** Number of sea trout performing upstream migrations each day in relation to the estimated water flow (solid line).

## 3.5 Factors influencing the timing of upstream migration during the day

The observed upstream migration pattern within different light intensity categories was significantly different from what was expected, given the available hours within each light category ($\chi^2 = 10.1$, $p < 0.05$). Throughout the whole study period, sea trout preferred to initiate upstream migration during periods of dimmed light (Table 6 and Figure 13), which corresponded to evenings and mornings (Table 1). The three other light categories had fewer observations than expected. There was no significant correlation between total length of the fish and light category ($\chi^2 = 4.8$, $p > 0.05$).

**Table 6:** Number and proportion of registrations and available hours in each light intensity category during the study period.

| Light category | Registrations (n) | Hours in study period (h) | Registrations per hour (n) | Proportion of registration per hour |
|---|---|---|---|---|
| Daylight | 60 | 1019 | 0.0589 | ~ 24 % |
| Dimmed light | 59 | 665 | 0.0887 | ~ 36 % |
| Twilight | 18 | 357 | 0.0504 | ~ 21 % |
| Night | 25 | 551 | 0.0454 | ~ 19 % |
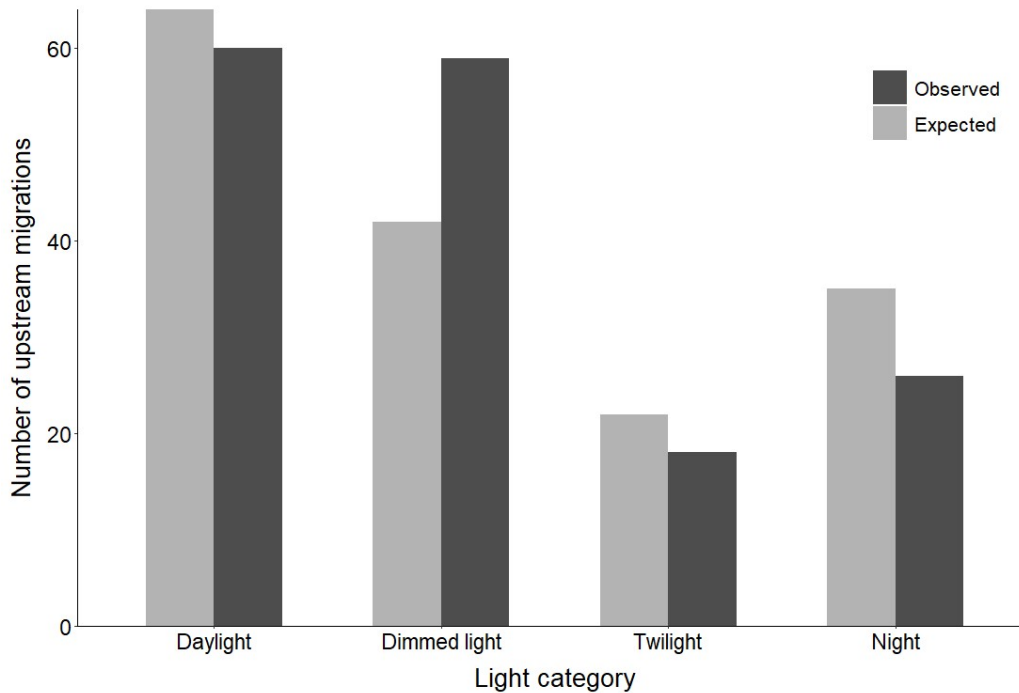
**Figure 13:** Observed and expected number of upstream migrations distributed in the different light categories. The expected value represents the distributed number of sea trout given that the sea trout returned at random light intensities (accounted for differences in available hours within each category).

Sea trout were observed to initiate upstream migration during all stages of the tidal cycle, but a significant clustering of registrations was found at ebbing tide (Figure 14, Rayleigh's test of uniformity, $p <0.001$). As much as 46 % of the returning sea trout initiated upstream migration during ebbing tide. The other proportions of registrations were 21 % during high tide (maximum high tide ± 1 h), 18 % during low tide (minimum low tide ± 1 h) and 15 % during rising tide.
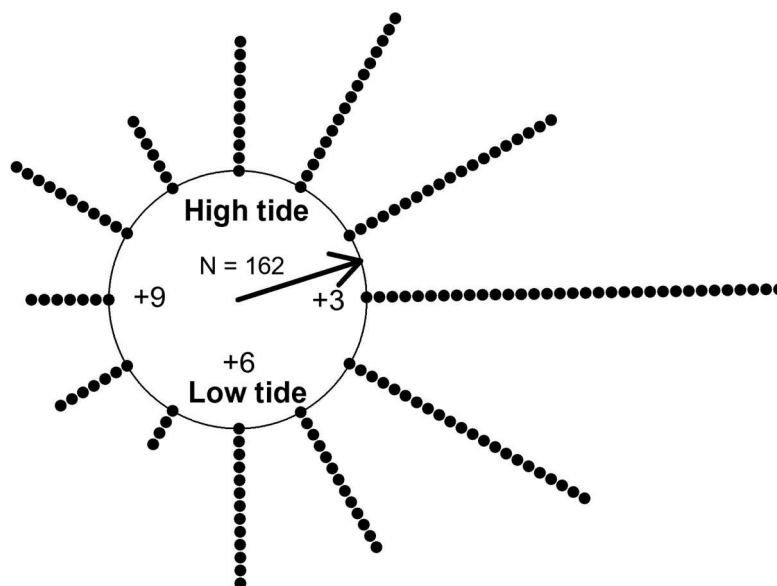


**Figure 14:** Timing of upstream migration in relation to the tidal cycle. Number of minutes from high tide for each registration was converted to degrees with high tide at 0° and 360° and low tide at 180° (+6 h). Each black dot is a registration of upstream migration. The arrow indicates the mean tidal stage of upstream migration (ebbing tide, 2.4 h after high tide).

# 4 Discussion

## 4.1 Factors influencing the marine residence duration

The first part of the study investigated the marine residence duration, and how this life-history trait is influenced by several factors. A strong correlation between time spent at sea and date of out-migration was found, with early migrants spending longer time at sea compared to late migrants. This finding aligns with the hypothesis and previous studies conducted in geographically distinct areas such as northern Norway (Jensen et al., 2022), central Norway (Eldøy et al., 2015), and western Norway (Paterson et al., 2021). The duration of marine migrations is thought to be controlled by the relative fitness benefits associated with different habitats (Thorstad et al., 2016). The results from this study may indicate that the fitness gained by monopolizing the best spawning sites (Dahl et al., 2004) exceeds the benefits of prolonged feeding in the sea, tipping the cost vs. benefit trade-off in favour of return to the river, also for late migrants. Generally, sea trout's consumption rate varies throughout the season being highest in early summer and lowest during autumn and early winter (Thorstad et al., 2016). Consequently, the advantages of autumn feeding in the marine habitat may be reduced. However, the results predicted only ten days reduced marine stay for late migrants (entering sea in late May) compared to early migrants (entering sea in late April). In terms of fitness, the benefits gained by ten days of prolonged feeding might be low. Hence, a significant reduction in fitness due to reduced marine stay may only be the case for fish that for some reason migrate to sea late in the summer. Since the study period ended on 3 October, the marine residence time of late migrants might be underestimated as only the late migrants with a short marine stay were included.

Sea trout were found to display differences in duration of marine migrations with regard to body length, where longer fish spent longer time at sea compared to smaller ones. In general, the effect of body length on marine residence duration is less clear and shows intercatchment differences. Some studies agree with the present results (e.g., Eldøy et al., 2015; Flaten et al., 2016), while studies in other catchments have observed an inverse relationship between body length and marine residence duration (Paterson et al., 2021). Larger fish have a higher swimming speed and endurance time compared to smaller individuals (Ojanguren & Brana, 2003). This, in combination with better seawater tolerance and higher sensory capability are suggested to result in larger fish being less susceptible to predation (Dieperink et al., 2001). Consequently, extended marine stay might be more favourable for larger individuals as the main cost (i.e mortality rate) is reduced. However, the effect of length on marine residence duration should be interpreted with caution, as a high variation is displayed (low $R^2$ value). The study included individuals with small variations in body length, and an inclusion of different size classes is needed to evaluate the effect of length further. Additionally, the effect size was relatively small, for instance, an individual with a length of 320 mm had only ten days longer predicted marine stay compared to an individual of 180 mm. Consequently, the effect of length on individual fitness may only be significant in combination with other factors, such as increased predation pressure for smaller individuals (Davidsen et al., 2013).

Sea trout with a lower condition factor when migrating to sea were observed to have a longer marine stay compared to individuals with a higher condition factor. This observation is in accordance with the hypothesis and several studies, such as a newly published paper by Eldøy et al. (2021). Marine migration is believed to provide better feeding opportunities as marine habitats have a higher productivity than freshwater habitats (Gross et al., 1988). However, marine migrations are associated with higher energetic costs, a greater abundance of predators and a higher risk of infestation of parasites (Thorstad et al., 2016). In line with the study by Eldøy et al. (2021), the present results indicate that sea trout with a poorer body condition might adopt a riskier migration strategy with longer marine stays to regain a sufficient body condition before spawning season. While blood plasma triglycerides have been observed to change in response to food intake over a short time (Congleton & Wagner, 2006), body condition results from the balance between energy intake and expenditure over time frames of weeks or months (Eldøy et al., 2021). Consequently, individuals in a poor condition when entering sea may use a significant amount of time to regain normal condition. For females, the strategy of prolonged feeding to regain a good condition might be driven by the strong relationship between body size and reproductive success (Jonsson & Jonsson, 1993). Larger females are also more likely to acquire better spawning sites (Jonsson & Jonsson, 1993). The importance of body size is reduced for males but may be important in terms of male-male interactions during the spawning (Jacob et al., 2007). However, the effect of condition factor on marine residence duration should be interpreted with caution due to high variation in the data (low $R^2$ value).

The results of the present study show intrapopulation variation in lice infestation risk due to differences in life strategies and migration patterns. As hypothesized, a correlation between marine residence duration and lice infestation risk was found, with sea trout spending more time at sea experiencing a higher risk of lice infestation. However, this relationship was not true for all fish groups as the salmon lice concentration varied throughout the season. The concentration of copepodites peaked through late summer, resulting in late migrants being more exposed to salmon lice larvae compared to early migrants. For example, late migrants spending only 50 days at sea were observed to experience the same lice infestation risk as early migrants spending more than 100 days at sea. Hence, timing of migration is an important life-history trait that may affect individuals' fitness, as lice infestations may lead to mortality or indirect effects, such as lice-induced vulnerability to predators (Paterson et al., 2021). Anadromy evolves in response to the total budget of costs and benefits associated with marine migrations versus freshwater residency (Ferguson et al., 2016). Changes in these budgets through alterations of environmental conditions can therefore result in population shifts in life-history strategy. Increased lice-induced mortality may shift the selective balance in favour of earlier seaward migration or a freshwater resident life history, as these strategies reduce the lice infestation risk (Ferguson et al., 2016; Thorstad et al., 2016). Moreover, the timing of both salmon lice blooms and seaward migrations of sea trout will be influenced by climate changes, but not necessarily in a synchronized manner (Bøhn et al., 2020). A possible consequence is a mismatch scenario between timing of marine migrations and optimal conditions, with an unknown outcome.

The research method in the present study made it challenging to assess lice-induced effects on sea trout. One of the problems with PIT-technology is that marine residence duration can only be assessed for individuals returning to the river. Sea trout that get lost at sea because of lice-induced mortality, predation etc. are excluded. Moreover, estimated lice infestation risk on an individual level by models may be inaccurate, as the distribution of

lice among individuals is typically skewed (Serra-Llinares et al., 2020). An alternative approach is lice counting of recaptured PIT-tagged sea trout in the fjord.

## 4.2 Factors influencing timing of upstream migration during the season

This study revealed an environmental influence on the precise timing of upstream migration. Change in water flow was found to be the critical environmental factor controlling upstream migration, as increasing discharge triggered upstream migration of sea trout at all water flows. There are several possible reasons for why increasing water flow initiates upstream migration. First, increasing discharge may be an important factor for providing returning sea trout with olfactory cues which facilitates the homing process (reviewed by Jonsson, 1991). Moreover, increasing water discharge is generally correlated with turbidity (Banks, 1969). High turbidity is reported to reduce the antipredator behaviour of fish (Abrahams & Kattenfeld, 1997), which might trigger upstream migration. However, the effect of discharge on turbidity is site-specific (Davies-Colley & Smith, 2001), and an inclusion of turbidity measurements is needed to evaluate the relationship between turbidity and upstream migration further.

No significant effect of the actual water flow on timing of upstream migration was unexpected, as a positive correlation between these variables is reported in small rivers elsewhere (e.g., Jonsson & Jonsson, 2002; Svendsen et al., 2004). Increasing water flow was observed to initiate migration at all water flows, indicating that the water flow did not reach levels where upstream migration was totally impeded. This may be a consequence of the fish ladder installed in the catchment. The fish ladder consists of several pools which might provide a more stable flow regime compared to rivers without anthropogenic impacts (Dahl et al., 2004). Consequently, important environmental factors in rivers with fishways may be site-specific and different from those affecting natural rivers (Thorstad et al., 2008). Moreover, Svendsen et al. (2004) observed that adult sea trout did not initiate upstream migration during periods of low discharge when periods with high discharge occurred frequently. In the present study, the flow pattern was the opposite, meaning high water flow rarely occurred. Consequently, sea trout might have to use the opportunity to perform upstream migration during periods of increasing water flow because the opportunities for improved conditions later in the season may be bad or uncertain. Moreover, Jonsson et al. (2007) suggested that smaller fish are less dependent on high water level compared to larger individuals. This study included individuals with an average weight of 93 g, a size class that is suggested to be less susceptible to predators during periods of low water flow (Davidsen et al., 2013). This may be another reason for the lack of flow response. It should be noted that measurements of water flow were retrieved from the outlet of Engsetvatn and used as an estimation of the water flow in Oselva. Even though Engsetvatn is located less than 3 km from the Vatne catchment and was suggested to fit the water flow in Oselva well, variations may occur as the catchments vary in physical features.

Throughout the study period, no significant effects of sea temperature nor change in river temperature on timing of upstream migration were observed. This was unexpected as temperature is often ranked as the second most important factor controlling upstream migration of salmonids (reviewed by Banks, 1969 and Jonsson, 1991). The optimal temperature for upstream migration might be a trade-off between migratory costs (Enders et al., 2005) and performance to pass obstacles (Jonsson & Jonsson, 2011), both increasing at higher temperatures. However, energetic costs of migrations vary with

distance and elevation of the migration (Brönmark et al., 2014). The migration distance in the Vatne catchment is short and the elevation low. The spawning migration may therefore be less stressful and energy demanding than migration in larger catchments. Moreover, after the installation of the fish ladder, the river stretch does not include any waterfalls that require a high performance by the ascending sea trout. These physical features of the Vatne catchment may be an explanation for why sea trout do not need to rely on an optimal temperature but can perform upstream migrations over a wide temperature range.

The importance of performing upstream migration during periods of increasing water discharge could have mitigated the effects of water temperature. As mentioned above, rising water flow was only observed a few days throughout the season and was often followed by a decline the next day. Performing upstream migration during these intervals may be critical, as the opportunities for increasing discharge later in the season are uncertain. Hence, sea trout cannot take the risk of waiting for both optimal water temperature and increasing water flow. This hypothesis is supported by studies suggesting that the effect of temperature is different in larger systems, as discharge is not a constraining factor (Jonsson et al., 2007). Moreover, it is possible that water temperatures must reach a high or low threshold before an effect is observed. Ojanguren and Brañta (2000) reported that 90 % of brown trout's swimming speed was sustained at temperatures between 12.2 °C and 19.9 °C., which may indicate that the temperature range in this study (11.2 °C - 20.5 °C) was too narrow to detect any temperature effect.

The number of sea trout performing upstream migration each day was determined to be the most sufficient response variable in this study. However, some challenges may arise when relating fish counts to environmental factors. One of the main weaknesses is the lack of information on how many fish that are present downstream of the antenna (Trépanier et al., 1996). A higher number of detected fish may not necessarily correspond to more optimal conditions but might be a result of an increased abundance of fish downstream of the antenna for other reasons. On the contrary, favourable conditions might be provided on days with few available fish downstream of the antenna, as they are somewhere else (e.g., at sea or in the river). Consequently, few detections are made, and regression models will underestimate the effect of environmental stimuli (Trépanier et al., 1996). Another method for studying upstream migration patterns is fish telemetry using radio and acoustic transmitters which allows for more detailed information about migration patterns of individual fish (Thorstad et al., 2008). However, limitations of telemetry studies are low sample sizes and costs. A cheaper alternative that was considered in the present study is snorkelling or use of underwater cameras in the outlets and/or estuaries in combination with PIT-technology. This technique can provide estimates of fish abundance downstream of the antenna, information useful for studying upstream migration patterns.

It is possible that other factors, not included in this study, may influence the precise timing of upstream migration. Since there is a limit to the number of independent variables that can be included in a global model, the selection of environmental factors was based on two criteria. First, the factor had to be frequently reported as important in the literature. Moreover, it had to be possible to measure it passively throughout the study period. Examples of other potential environmental factors considered, but not included in this study, were general weather pattern, wind direction and dissolved oxygen. Future studies on upstream migration dynamics should consider a wide set of potential predictors, including both inter-annual and intra-annual variations.

## 4.3 Factors influencing timing of upstream migration during the day

This study revealed a preference for upstream migration at ebbing tide, an observation in accordance with the hypothesis and several studies where river entry of salmonids has been monitored at the tidal limit (e.g., Karppinen et al., 2004; Smith & Smith, 1997). During ebbing tide, the strength of seaward currents increases, which may increase fresh water supply to the estuaries (Lewis, 1990). This might provide returning sea trout with olfactory cues that facilitates the homing migration (Smith & Smith, 1997). Additionally, during periods of low water flow and low tide, the pool downstream of the river outlet was almost enclosed. This may have forced the sea trout to make a decision about returning to the sea or enter the river at falling tides. The influence of tides on timing of upstream migration varies between catchments and is affected by river size, physical features of the estuaries and where the fish counter is located (Karppinen et al., 2004; Smith & Smith, 1997). The effects of ebbing tide may be greater in rivers with generally low water flow, such as Oselva, compared to larger rivers, as salmonids approaching larger rivers do not need ebb tide to recognise the outflowing fresh water from the home river (Davidsen et al., 2013). It is difficult to assess the effects of ebbing tides in the estuaries without measuring the water transport. Future studies should consider measuring the water transport in estuaries in relation to the tides to get more knowledge about how the tides might influence sea trout in these areas.

Sea trout preferred upstream migration during periods of dimmed light, a light category corresponding to late evenings and early mornings. This finding is in accordance with the hypothesis and studies conducted in other rivers in southern latitudes of Norway (e.g., Jonsson & Jonsson, 2011; Karppinen et al., 2004; Smith & Smith, 1997). Nocturnal migration is likely an antipredator strategy (Bendall et al., 2005), because light intensity determines the risk of being preyed upon by visual predators (Lucas & Baras, 2008). No other piscivorous fish species than salmonids are present in the Vatne catchment, but European herring gull (*Larus argentatus*) and otter (*Lutra lutra*) were observed in the outlet of the river. Individuals of European herring gull were often sitting on the concrete of the fish ladder, likely scouting for potential prey entering the river. Both European herring gull and otter are potential predators for salmonids (Carss et al., 1990; Dieperink et al., 2002), which may explain why sea trout preferred migration during darker periods. Moreover, Banks (1969) suggested that there may be a trade-off between the need for light to see how to pass obstacles and the reduced predation pressure during darker periods. This hypothesis is in line with the present findings, indicating that sea trout preferred dimmed light instead of total darkness (i.e., night conditions).

The advantages of upstream migration during darker periods may vary with fish size and river discharge (Davidsen et al., 2013; Potter, 1988). Upstream migration during darker periods may be more important for smaller individuals compared to adult salmonids, as smaller fish experience a higher predation risk (Davidsen et al., 2013). The present study included individuals with an average weight of 93 g, thus the potential high predation pressure may be a reason for the observed preference for darker conditions. Moreover, Potter (1988) observed that Atlantic salmon entered the river at daylight during periods of high discharge. High discharge is, as mentioned, correlated with turbidity, which suppresses light penetration (Lloyd et al., 1987). However, during the present study, high discharge was rarely observed, and the turbidity was likely low. This could explain why sea trout in the Vatne catchment had to rely on darker conditions than what Potter (1988) observed in his study.

## 4.4 Conservation perspective

The results of the present study highlight the complexity of sea trout migration behaviour. Sea trout are influenced by human impacts in both the sea and freshwater because of their anadromous lifestyle. Consequently, sea trout are especially vulnerable to alterations of natural conditions. Knowledge of factors influencing sea trout migration dynamics is crucial to assess sea trout's vulnerability to anthropogenic impacts and to make reliable predictions of the consequences. This study has emphasized the importance of timing, as salmon lice infection pressure depends on both sea trout's migration timing and the timing of lice blooms. A better understanding of migration timing and timing of lice blooms is therefore important to improve management strategies in the future (Bøhn et al., 2020). Moreover, the present findings have shown how environmental cues may control upstream migration of sea trout. These cues act as signals and indicate favourable migratory conditions (Jonsson & Jonsson, 2009). However, the adapted cues might get lost due to direct human impacts (e.g., regulation of rivers), or alteration of natural conditions through climate change (Jonsson & Jonsson, 2009; Thorstad et al., 2008). Future management may therefore need to adapt to new conditions to mitigate the influence of human impacts. The results indicate that increasing water flow was an important factor triggering upstream migration. Consequently, regulated rivers should consider mimicking the natural conditions, for instance use of artificial freshets (Thorstad et al., 2008). Without efficient management practices, may increased marine mortality and reduced growth of sea trout because of altered environmental conditions result in populations where freshwater residency is favoured over anadromy as the optimal life-history strategy (Thorstad et al., 2016).

# 5 Conclusion

The present study has demonstrated that two important life-history traits of sea trout, marine residence duration and timing of migration, are influenced by abiotic and biotic factors. Consequently, the study supports the assumption that these life-history traits may show considerably intra and interpopulation variation. The results suggest that marine residence duration of Vatne sea trout is negatively correlated with date of out-migration and condition factor. These findings are in accordance with the hypothesis that marine residence duration is a trade-off between costs and benefits associated with different habitats at different times. Moreover, a positive correlation between length of the fish and marine residence duration was found. The study has also shown the importance of timing of marine migrations, as late migrants may experience a higher salmon lice infestation risk compared to early migrants. A possible consequence may be a selection against earlier out-migration or a freshwater resident life strategy.

Moreover, the findings in the study indicate that precise timing of upstream migration is controlled by environmental factors, both on a seasonal and daily basis. The results suggest that increasing water flow is the most important factor initiating upstream migration in the Vatne catchment, as it seems to act as a trigger during periods of both high and low water flow. Surprisingly, no significant effect of the actual water flow nor water temperature was found. This may be because of the low frequency of high water flow throughout the study period. The sea trout might have to use the opportunity to perform upstream migrations during periods of increased water flow, as the opportunities for improved conditions later in the season may be bad or uncertain. This could have mitigated the effects of actual water flow and temperature. During the day, sea trout preferred to initiate upstream migration during periods of dimmed light and at ebbing tide. This might be a strategy to minimize the predation risk and to take advantages of olfactory cues when entering small rivers.

Sea trout are exposed to anthropogenic impacts in both freshwater and the marine habitat because of their anadromous lifestyle. Alterations of the natural conditions may influence the migration dynamics of sea trout, as marine residence duration and timing of migration are affected by abiotic and biotic factors. Over the last decades, sea trout populations in many countries have suffered stock declines (Harris & Milner, 2008). Knowledge about factors influencing migration pattern of sea trout is essential for effective conservation of populations, and to evaluate their vulnerability to anthropogenic impacts.

# References

Aarestrup, K., Baktoft, H., Thorstad, E. B., Svendsen, J. C., Höjesjö, J. & Koed, A. (2015). Survival and progression rates of anadromous brown trout kelts *Salmo trutta* during downstream migration in freshwater and at sea. *Marine Ecology Progress Series, 535*, 185-195. https://doi.org/10.3354/meps11407

Abrahams, M. V. & Kattenfeld, M. G. (1997). The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology, 40*(3), 169-174. https://doi.org/10.1007/s002650050330

American Meteorological Society (2012a). Astronomical twilight. https://glossary.ametsoc.org/wiki/Astronomical_twilight

American Meteorological Society (2012b). Civil twilight. https://glossary.ametsoc.org/wiki/Civil_twilight

American Meteorological Society (2012c). Nautical twilight. https://glossary.ametsoc.org/wiki/Nautical_twilight

Anderson, D. R., Link, W. A., Johnson, D. H. & Burnham, K. P. (2001). Suggestions for presenting the results of data analyses. *The Journal of Wildlife Management, 65*(3), 373-378. https://doi.org/10.2307/3803088

Banks, J. (1969). A review of the literature on the upstream migration of adult salmonids. *Journal of Fish Biology, 1*(2), 85-136. https://doi.org/10.1111/j.1095-8649.1969.tb03847.x

Barton, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bendall, B., Moore, A. & Quayle, V. (2005). The post-spawning movements of migratory brown trout *Salmo trutta* L. *Journal of Fish Biology, 67*(3), 809-822. https://doi.org/10.1111/j.0022-1112.2005.00786.x

Birkeland, K. (1996). Consequences of premature return by sea trout (*Salmo trutta*) infested with the salmon louse (*Lepeophtheirus salmonis* Krøyer): migration, growth, and mortality. *Canadian Journal of Fisheries and Aquatic Sciences, 53*(12), 2808-2813. https://doi.org/10.1139/f96-231

Bjørn, P., Finstad, B. & Kristoffersen, R. (2001). Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. *Aquaculture Research, 32*(12), 947-962. https://doi.org/10.1046/j.1365-2109.2001.00627.x

Boxaspen, K. (2006). A review of the biology and genetics of sea lice. *ICES Journal of Marine Science, 63*(7), 1304-1316. https://doi.org/10.1016/j.icesjms.2006.04.017

Brönmark, C., Hulthén, K., Nilsson, P., Skov, C., Hansson, L.-A., Brodersen, J. & Chapman, B. (2014). There and back again: migration in freshwater fishes. *Canadian Journal of Zoology, 92*(6), 467-479. https://doi.org/10.1139/cjz-2012-0277

Burnham, K. P. & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research, 33*(2), 261-304. https://doi.org/10.1177/0049124104268644

Bøhn, T., Gjelland, K. Ø., Serra-Llinares, R. M., Finstad, B., Primicerio, R., Nilsen, R., Karlsen, Ø., Sandvik, A.D., Skilbrei, O.T., Elvik, K. M. S., Skaala, Ø. & Bjørn, P.A. (2020). Timing is everything: survival of Atlantic salmon Salmo salar postsmolts during events of high salmon lice densities. *Journal of Applied Ecology, 57*(6), 1149-1160. https://doi.org/10.1111/1365-2664.13612

Carss, D., Kruuk, H. & Conroy, J. (1990). Predation on adult Atlantic salmon, *Salmo salar* L., by otters, *Lutra lutra* (L.), within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology, 37*(6), 935-944. https://doi.org/10.1111/j.1095-8649.1990.tb03597.x

Chernitsky, A. G., Zabruskov, G. V., Ermolaev, V. V. & Shkurko, D. S. (1995). Life history of trout, *Salmo trutta* L., in the Varsina River estuary, (The Barents Sea). *Nordic Journal of Freshwater Research, 71*, 183-189.

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology, 5*(2), 159-170. https://doi.org/10.1093/beheco/5.2.159

Congleton, J. & Wagner, T. (2006). Blood-chemistry indicators of nutritional status in juvenile salmonids. *Journal of Fish Biology, 69*(2), 473-490. https://doi.org/10.1111/j.1095-8649.2006.01114.x

Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Löf, A. & Ragnarsson, B. (2004). The timing of spawning migration: implications of environmental variation, life history, and sex. *Canadian Journal of Zoology, 82*(12), 1864-1870. https://doi.org/10.1139/z04-184

Davidsen, J. G., Rikardsen, A. H., Thorstad, E. B., Halttunen, E., Mitamura, H., Præbel, K., Skardhamar, J. & Næsje, T. F. (2013). Homing behaviour of Atlantic salmon (*Salmo salar*) during final phase of marine migration and river entry. *Canadian Journal of Fisheries and Aquatic Sciences, 70*(5), 794-802. http://doi.org/10.1139/cjfas-2012-0352

Davies-Colley, R. & Smith, D. (2001). Turbidity suspeni)ed sediment, and water clarity: a review. *Journal of the American Water Resources Association, 37*(5), 1085-1101. https://doi.org/10.1111/j.1752-1688.2001.tb03624.x

Dieperink, C., Bak, B., Pedersen, L. F., Pedersen, M. I. & Pedersen, S. (2002). Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology, 61*(3), 848-852. https://doi.org/10.1111/j.1095-8649.2002.tb00917.x

Dieperink, C., Pedersen, S. & Pedersen, M. I. (2001). Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts. *Ecology of Freshwater Fish, 10*(3), 177-183. https://doi.org/10.1034/j.1600-0633.2001.100307.x

Dingle, H. & Drake, V. A. (2007). What is migration? *Bioscience, 57*(2), 113-121. https://doi.org/10.1641/B570206

Eldøy, S. H., Bordeleau, X., Lawrence, M., Thorstad, E. B., Finstad, A. G., Whoriskey, F. G., Crossin, G.T., Cooke, S.J, Aarestrup, K., Rønning, L., Sjursen, A.D. & Davidsen, J.G. (2021). The effects of nutritional state, sex and body size on the marine migration behaviour of sea trout. *Marine Ecology Progress Series, 665*, 185-200. https://doi.org/10.3354/meps13670

Eldøy, S. H., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Aarestrup, K., Næsje, T. F., Rønning, L., Sjursen, A.D., Rikardsen, A.H. & Arnekleiv, J. V. (2015). Marine migration and habitat use of anadromous brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences, 72*(9), 1366-1378. https://doi.org/10.1139/cjfas-2014-0560

Eldøy, S. H., Davidsen, J. G., Thorstad, E. B., Whoriskey, F. G., Aarestrup, K., Næsje, T., Rønning, L., Sjursen, A.D. & Arnekleiv, J. V. (2017). Marine depth use of sea trout *Salmo trutta* in fjord areas of central Norway. *Journal of Fish Biology, 91*(5), 1268-1283. https://doi.org/10.1111/jfb.13463

Enders, E. C., Boisclair, D. & Roy, A. G. (2005). A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences, 62*(5), 1079-1089. https://doi.org/10.1139/f05-007

Engineering ToolBox (2004). Illuminance - Recommended Light Level. https://www.engineeringtoolbox.com/light-level-rooms-d_708.html

Erkinaro, J., Økland, F., Moen, K., Niemelä, E. & Rahiala, M. (1999). Return migration of Atlantic salmon in the River Tana: the role of environmental factors. *Journal of Fish Biology, 55*(3), 506-516. https://doi.org/10.1111/j.1095-8649.1999.tb00695.x

Ferguson, A. (2006). Genetics of sea trout, with particular reference to Britain and Ireland. In: Harris, G. & Milner, N. (Eds.) *Sea trout: Biology, Conservation and Management*, pp. 157-182. Oxford: Blackwell.

Ferguson, A., Reed, T. E., McGinnity, P. & Prodöhl, P. A. (2016). Anadromy in brown trout (*Salmo trutta*): a review of the relative roles of genes and environmental factors and the implications for management and conservation. In: Harris, G.

(Ed), *Sea Trout: Science and Management,* pp. 1-40. Leicestershire, England: Matador Publishing Etd.

Finstad, B., Sandvik, A. D., Ugedal, O., Vollset, K., Karlsen, Ø., Davidsen, J. G., Sægrov, H. & Lennox, R. J. (2021). Development of a risk assessment for sea trout in coastal areas exploited for aquaculture. *Aquaculture Environment Interactions, 13*, 133-144. https://doi.org/10.3354/aei00391

Finstad, B., Staurnes, M. & Reite, O. B. (1988). Effect of low temperature on sea-water tolerance in rainbow trout, *Salmo gairdneri*. *Aquaculture, 72*(3-4), 319-328. https://doi.org/10.1016/0044-8486(88)90220-7

Flaten, A. C., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Rønning, L., Sjursen, A. D., Rikardsen, J.V. & Arnekleiv, J. V. (2016). The first months at sea: Marine migration and habitat use of sea trout *Salmo trutta* post-smolts. *Journal of Fish Biology, 89*(3), 1624-1640. https://doi.org/10.1111/jfb.13065

Fulton, T. W. (1904). The rate of growth of fishes. *Fisheries Board of Scotland Annual Report, 22*, 141-241.

Gross, M. R., Coleman, R. M. & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science, 239*(4845), 1291-1293. http://doi.org/10.1126/science.239.4845.1291

Halttunen, E., Gjelland, K. Ø., Hamel, S., Serra-Llinares, R. M., Nilsen, R., Arechavala-Lopez, P., Skardhamar, J., Johnsen, I.A., Asplin, L., Karlsen, Ø., Bjørn., P-A. & Finstad, B. (2018). Sea trout adapt their migratory behaviour in response to high salmon lice concentrations. *Journal of Fish Diseases, 41*(6), 953-967. https://doi.org/10.1111/jfd.12749

Harris, G. & Milner, N. (2008). *Sea trout: Biology, Conservation and Management*. Oxford: Blackwell Pubslishing.

Hendry, A. P. , Bohlin, T., Jonsson, B. & Berg, O.K. (2004). To sea or not to sea? Anadromy versus non-anadromy in salmonids. *Evolution Illuminated: Salmon and Their Relatives,* pp. 92-125. New York: Oxford University Press.

Hodgson, S. & Quinn, T. P. (2002). The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. *Canadian Journal of Zoology, 80*(3), 542-555. https://doi.org/10.1139/z02-030

Hurvich, C. M. & Tsai, C-L. (1989). Regression and time series model selection in small samples. *Biometrika, 76*(2), 297-307. https://doi.org/10.1093/biomet/76.2.297

Jacob, A., Nusslé, S., Britschgi, A., Evanno, G., Müller, R. & Wedekind, C. (2007). Male dominance linked to size and age, but not to'good genes' in brown trout (*Salmo trutta*). *BMC Evolutionary Biology, 7*(1), 1-9. https://doi.org/10.1186/1471-2148-7-207

Jensen, A. J., Diserud, O. H., Finstad, B., Fiske, P. & Thorstad, E. B. (2022). Early-season brown trout (*Salmo trutta*) migrants grow and survive better at sea. *Journal of Fish Biology*. https://doi.org/10.1111/jfb.15052

Jensen, J. & Rikardsen, A. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *Journal of Fish Biology, 81*(2), 735-749. https://doi.org/10.1111/j.1095-8649.2012.03343.x

Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries, 3*(4), 348-365. https://doi.org/10.1007/BF00043384

Jonsson, B. & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology, 75*(10), 2381-2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic salmon and Brown Trout: Habitat as a Template for Life Histories*. pp. 247 – 307. Amsterdam, Netherlands: Springer.

Jonsson, B., Jonsson, N. & Hansen, L. (2007). Factors affecting river entry of adult Atlantic salmon in a small river. *Journal of Fish Biology, 71*(4), 943-956. https://doi.org/10.1111/j.1095-8649.2007.01555.x

Jonsson, N. (1991). Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater research, 66*, 20-35.

Jonsson, N. & Jonsson, B. (1998). Body composition and energy allocation in life-history stages of brown trout. *Journal of Fish Biology, 53*(6), 1306-1316. https://doi.org/10.1111/j.1095-8649.1998.tb00250.x

Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshwater Biology, 47*(8), 1391-1401. https://doi.org/10.1046/j.1365-2427.2002.00873.x

Karppinen, P., Erkinaro, J., Niemelä, E., Moen, K. & Økland, F. (2004). Return migration of one-sea-winter Atlantic salmon in the River Tana. *Journal of Fish Biology, 64*(5), 1179-1192. https://doi.org/10.1111/j.0022-1112.2004.00380.x

Klemetsen, A., Amundsen, P. A., Dempson, J., Jonsson, B., Jonsson, N., O'connell, M. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr S*alvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish, 12*(1), 1-59. https://doi.org/10.1034/j.1600-0633.2003.00010.x

Koed, A., Baktoft, H. & Bak, B. D. (2006). Causes of mortality of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts in a restored river and its estuary. *River Research and Applications, 22*(1), 69-78. https://doi.org/10.1002/rra.894

Lewis, R. (1990). The nature of outflows from the north-east estuaries. *Hydrobiologia, 195*(1), 1-11. https://doi.org/10.1007/BF00026809

Lilja, J. & Romakkaniemi, A. (2003). Early-season river entry of adult Atlantic salmon: its dependency on environmental factors. *Journal of Fish Biology, 62*(1), 41-50. https://doi.org/10.1046/j.1095-8649.2003.00005.x

Lloyd, D. S., Koenings, J. P. & Laperriere, J. D. (1987). Effects of turbidity in fresh waters of Alaska. *North American Journal of Fisheries Management, 7*(1), 18-33. https://doi.org/10.1577/1548-8659(1987)7%3C18:EOTIFW%3E2.0.CO;2

Lucas, M. & Baras, E. (2008). *Migration of Freshwater Fishes*, p. 25. Oxford: Blackwell Science.

Lund, U. & Agostinelli, C. (2018). CircStats: Circular Statistics, from "Topics in Circular Statistics" (2001). R package version 0.2-6. https://CRAN.Rproject.org/package=CircStats

Lüdecke, D. (2018). ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. (Version 26). *Journal of Open Source Software*. https://doi.org/10.21105/joss.00772

Lüdecke, D. (2021). Performance: An R Package for Assessment, Comparison and Testing of Stastical Models. *Journal of Open Source Software*, 6(60), 3139. https://doi.org/10.21105/joss.03139

Myksvoll, M. S., Sandvik, A. D., Albretsen, J., Asplin, L., Johnsen, I. A., Karlsen, Ø., Kristensen, N. M., Melsom, A., Skardhamar, J. & Ådlandsvik, B. (2018). Evaluation of a national operational salmon lice monitoring system—From physics to fish. *PLOS ONE, 13*(7). https://doi.org/10.1371/journal.pone.0209949

Ojanguren, A. & Brana, F. (2003). Effects of size and morphology on swimming performance in juvenile brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish, 12*(4), 241-246. https://doi.org/10.1046/j.1600-0633.2003.00016.x

Ojanguren, A. & Brañta, F. (2000). Thermal dependence of swimming endurance in juvenile brown trout. *Journal of Fish Biology, 56*(6), 1342-1347. https://doi.org/10.1111/j.1095-8649.2000.tb02147.x

Okumus, I., Kurtoglu, I. & Atasaral, S. (2006). General overview of Turkish sea trout (*Salmo trutta* L.) populations. *Sea trout: Biology, Conservation and Management*, 115-127. https://doi.org/10.1002/9780470996027.ch9

Paterson, R. A., Berntsen, H. H., Næsje, T. F., Berg, M. & Finstad, B. (2021). Factors influencing return rate and marine residence duration in sea trout populations in Central Norway. *Journal of Fish Biology*, *99*(3), 875 -877. https://doi.org/10.1111/jfb.14770

Potter, E. (1988). Movements of Atlantic salmon, *Salmo salar* L., in an estuary in south-west England. *Journal of Fish Biology, 33*, 153-159. https://doi.org/10.1111/j.1095-8649.1988.tb05569.x

Priede, I. G., Solbé, J. d. L., Nott, J., O'Grady, K. & Cragg-Hine, D. (1988). Behaviour of adult Atlantic salmon, *Salmo salar* L., in the estuary of the River Ribble in relation to variations in dissolved oxygen and tidal flow. *Journal of Fish Biology, 33*, 133-139. https://doi.org/10.1111/j.1095-8649.1988.tb05567.x

Quinn, T. P., Unwin, M. J. & Kinnison, M. T. (2000). Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution, 54*(4), 1372-1385. https://doi.org/10.1111/j.0014-3820.2000.tb00569.x

R Core Team. (2020). R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

RStudio Team. (2020). RStudio: Integrated Development for R. : RStudio, PBC, Boston. http://www.rstudio.com/

Rustadbakken, A., L'Abée-Lund, J. H., Arnekleiv, J. V. & Kraabøl, M. (2004). Reproductive migration of brown trout in a small Norwegian river studied by telemetry. *Journal of Fish Biology, 64*(1), 2-15. https://doi.org/10.1111/j.1095-8649.2004.00275.x

Salinger, D. H. & Anderson, J. J. (2006). Effects of water temperature and flow on adult salmon migration swim speed and delay. *Transactions of the American Fisheries Society, 135*(1), 188-199. https://doi.org/10.1577/T04-181.1

Sandvik, A. D., Johnsen, I. A., Myksvoll, M. S., Sævik, P. N. & Skogen, M. D. (2020). Prediction of the salmon lice infestation pressure in a Norwegian fjord. *ICES Journal of Marine Science, 77*(2), 746-756. https://doi.org/10.1093/icesjms/fsz256

Schlyter, P. (2017). *How bright are natural light sources?* Radiometry and photometry in astronomy. http://stjarnhimlen.se/comp/radfaq.html#10

Serra-Llinares, R. M., Bøhn, T., Karlsen, Ø., Nilsen, R., Freitas, C., Albretsen, J., Haraldstad, T., Thorstad, E.B., Elvik, K.M.S. & Bjørn, P. A. (2020). Impacts of salmon lice on mortality, marine migration distance and premature return in sea trout. *Marine Ecology Progress Series, 635*, 151-168. https://doi.org/10.3354/meps13199

Smith, I. & Smith, G. (1997). Tidal and diel timing of river entry by adult Atlantic salmon returning to the Aberdeenshire Dee, Scotland. *Journal of Fish Biology, 50*(3), 463-474. https://doi.org/10.1111/j.1095-8649.1997.tb01942.x

Smith, R. J. F. (2012). *The control of fish migration*. pp. 5-64. Berlin: Springer-Verlag.

Stien, A., Bjørn, P. A., Heuch, P. A. & Elston, D. A. (2005). Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. *Marine Ecology Progress Series, 290*, 263-275. http://doi.org/10.3354/meps290263

Svendsen, J. C., Koed, A. & Aarestrup, K. (2004). Factors influencing the spawning migration of female anadromous brown trout. *Journal of Fish Biology, 64*(2), 528-540. https://doi.org/10.1111/j.0022-1112.2004.00319.x

Tetzlaff, D., Soulsby, C., Youngson, A., Gibbins, C., Bacon, P., Malcolm, I. & Langan, S. (2005). Variability in stream discharge and temperature: a preliminary assessment of the implications for juvenile and spawning Atlantic salmon. *Hydrology and Earth System Sciences, 9*(3), 193-208. https://doi.org/10.5194/hess-9-193-2005

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., Kålås, S., Berg, M. & Finstad, B. (2015). Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta* a literature review. *Aquaculture Environment Interactions, 7*(2), 91-113. http://doi.org/10.3354/aei00142

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., Kålås, S., Berg, M. & Finstad, B. (2016). Marine life of the sea trout. *Marine Biology, 163*(3), 47. https://doi.org/10.1007/s00227-016-2820-3

Thorstad, E. B., Økland, F., Aarestrup, K. & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human

impacts. *Reviews in Fish Biology and Fisheries, 18*(4), 345-371. https://doi.org/10.1007/s11160-007-9076-4

Trépanier, S., Rodriguez, M. & Magnan, P. (1996). Spawning migrations in landlocked Atlantic salmon: time series modelling of river discharge and water temperature effects. *Journal of Fish Biology, 48*(5), 925-936. https://doi.org/10.1111/j.1095-8649.1996.tb01487.x

Werner, E. E. & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics, 15*(1), 393-425. https://doi.org/10.1146/annurev.es.15.110184.002141

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. New York: Springer-Verlag. https://ggplot2.tidyverse.org

# Appendix A

**Table A1:** All models tested with weight sorted by corrected Akaike information criterion (AICc), with difference in AICc from the best model (ΔAICc), model weight (AIC$_W$) and degrees of freedom (d.f.). Response variable is marine residence duration.

| Model tested | AICc | ΔAICc | AIC$_W$ | d.f. |
|---|---|---|---|---|
| Delta water flow + sea temperature | 339.1 | 0.00 | 0.187 | 4 |
| Delta water flow | 339.6 | 0.47 | 0.148 | 3 |
| Delta water flow + water flow + sea salinity | 339.7 | 0.54 | 0.142 | 5 |
| Delta water flow + water flow | 339.9 | 0.75 | 0.128 | 4 |
| Delta water flow + sea temperature + sea salinity | 340.7 | 1.55 | 0.087 | 5 |
| Delta water flow + sea temperature + delta river temperature | 341.0 | 1.86 | 0.072 | 5 |
| Delta water flow + water flow + sea temperature | 341.2 | 2.10 | 0.0055 | 5 |
| Delta water flow + sea salinity | 341.4 | 2.29 | 0.050 | 4 |
| Delta water flow + delta river temperature | 341.5 | 2.35 | 0.048 | 4 |
| Delta water flow + water flow + delta river temperature + sea salinity | 341.6 | 2.50 | 0.045 | 6 |
| Delta water flow + water flow + sea temperature + sea salinity | 341.8 | 2.68 | 0.041 | 6 |
| Delta water flow + water flow + delta river temperature | 341.8 | 2.70 | 0.041 | 5 |
| Delta water flow + sea temperature + delta river temperature + sea salinity | 342.6 | 3.48 | 0.028 | 6 |
| Delta water flow + water flow + sea temperature + delta river temperature | 343.2 | 4.06 | 0.021 | 6 |
| Delta water flow + delta river temperature + sea salinity | 343.4 | 4.19 | 0.019 | 5 |
| Delta water flow + water flow + sea temperature + delta river temperature + sea salinity | 343.8 | 4.67 | 0.015 | 7 |