*Fisheries Management and Ecology*

WILEY

Fisheries Management and Ecology

**ARTICLE** OPEN ACCESS

# Impact of Environmental Conditions on the Spawning Migration of Sea Trout (*Salmo trutta* L.) in Two Large, Sub-Arctic River Systems

L. Lähteenmäki[1] | A. Romakkaniemi[2] | R. Huusko[2] | G. Hellström[3] | P. Orell[2] | J. Erkinaro[2] | A. H. Rikardsen[4] | J. Jensen[5] | M. Snickars[1]

[1]Environmental and Marine Biology, Faculty of Science and Engineering, Åbo Akademi University (ÅAU), Åbo, Finland | [2]Natural Resources Institute Finland (Luke), Oulu, Finland | [3]Swedish University of Agricultural Sciences (SLU), Department of Game, Fish, and the Environment, Umeå, Sweden | [4]The Arctic University of Norway (UiT), Department of Arctic and Marine Biology, Tromsø, Norway | [5]Akvaplan Niva, Tromsø, Norway

**Correspondence:** L. Lähteenmäki (linus.lahteenmaki@abo.fi)

**Received:** 11 September 2025 | **Revised:** 25 February 2026 | **Accepted:** 6 March 2026

**Keywords:** anadromy | environmental adaptation | life history | migrations | salmonids | telemetry

## ABSTRACT

The global decline in salmonid stocks has increased the need for knowledge of local adaptations and life history strategies of salmonids. In this study, we used radio-telemetry tracking data from sea trout populations in two large high-latitude rivers to model upstream spawning migration speed of trout in response to prevailing environmental conditions and different stages of the migration. The results indicate that studied populations had similar responses to environmental changes, as trout inhabiting both rivers displayed similar responses to variation in discharge, temperature, and migrated distance covered. Higher discharge and temperature had a positive influence on trout migration speed, as did moderate discharge fluctuations. Migration distance influenced movements, as speed increased as trout moved upstream, while speed decreased late in the migration prior to spawning. These results highlight the adaptability of sea trout populations, underlining the importance of stock-specific information on habitat use and migration strategies for targeted management.

## 1 | Introduction

Salmonid species have endured global declines due to a variety of anthropogenic pressures related to climate change, river alterations and unsustainable fishing practices (e.g., Dadswell et al. 2022; Gargan et al. 2006; Waldman and Quinn 2022). These global declines have increased the need for knowledge of populations adaptations to local conditions, their habitat utilisation, and life history strategies which are important for implementing targeted management, conservation efforts and fisheries regulation. This is especially important considering endangered or threatened migrant populations since their life history includes habitat shifts, exposing individuals to differing habitats, predation pressures and environmental conditions throughout their life cycle (Birnie-Gauvin et al. 2021; Klemetsen et al. 2003; Waldman and Quinn 2022).

Migration strategies of animals can be defined as the outcome of several actions taken during movements between habitats, with each action having different fitness implications (Houston and McNamara 1999; Winkler et al. 2014). Migrations of iteroparous, anadromous salmonids generally include long-distance spatiotemporal movements between freshwater and marine habitats, with species and populations displaying diverse and presumably adaptive strategies in terms of migration timing, overwintering behaviour and choice of spawning periods (Birnie-Gauvin et al. 2023; Jensen and Rikardsen 2012; Jonsson and Jonsson 2011; Klemetsen et al. 2003; Rikardsen et al. 2021). Migration strategies are displayed on a population level, as salmonids predominantly return to spawn in their natal river systems (Nall 1930). All individuals choosing a specific migration strategy do not necessarily share the same migration tactics, which are defined as variations in population response patterns to environmental fluctuations (Rochet 2000; Wootton 1984). Individuals within a population can also display plasticity and interpopulation variation in reaction norms to environmental drivers such as discharge and temperature (e.g., Campbell 1977; Jonsson and Jonsson 2011), leading to individuals expressing differing tactics and behaviours through variable degrees of phenotypic plasticity.

Brown trout (*Salmo trutta* L. 1758) populations show high diversity in terms of life histories (Klemetsen 2013). Some populations are non-migrant, staying resident in freshwater throughout their life cycles, while others are facultative migrants, as part of the population migrates between fluvial areas and more productive habitats such as lakes or the sea (Ferguson et al. 2019; Jonsson and Jonsson 1993). Anadromous brown trout (sea trout) migrate from natal rivers out to sea as smolts and return to freshwater for spawning as mature adults (Jonsson and Jonsson 2002). This life history strategy benefits anadromous individuals by increasing growth potential which is directly linked to fitness benefits (Brönmark et al. 2014; Ferguson et al. 2019; Rikardsen et al. 2004). Migrant populations have developed in various river systems of differing morphologies and geographical locations throughout the species distribution, displaying a wide diversity in life histories and migration strategies (Klemetsen et al. 2003).

Sea age at first spawning varies with latitude as growth opportunities at sea influence timing of maturation and subsequent return migrations of sea trout (Jonsson and L'Abée-Lund 1993; L'Abée-Lund et al. 1989). For example, a study by Jonsson and L'Abée-Lund (1993) reported that sea age at maturation increased with latitude, as 50% of trout from southern populations (between latitudes 54°–58°) reached maturation after 1 year at sea while it took almost 3 years for populations in northern Norway (64°–70°). Mature trout mainly return to the natal rivers for spawning in spring/summer (Elliott 1994; Jonsson 1985) or autumn (Campbell 1977; Klemetsen et al. 2003), while some populations ascend throughout the year for spawning (Jonsson and Jonsson 2011). Spawning takes place in autumn/early winter (Klemetsen et al. 2003), after which spent trout (called kelts) either overwinter in-river or return to sea (Kennedy et al. 2022; Östergren and Rivinoja 2008). Recent studies have reported an alternative migration strategy which involves overwintering in-river prior to migration upstream in the following year, causing the spawning migration to last for up to 2 years (Huusko et al. 2023; Lähteenmäki et al. 2025; Orell et al. 2017). These differences in migration strategies have been proposed to reflect population-specific adaptations to conditions of the natal river systems (Jensen et al. 2015; Jonsson and Jonsson 2009a).

Fish movements in cold climate rivers are impacted by the annual ice-cover (Thellman et al. 2021), which shortens the open water season and restricts migration in winter and early spring. Populations inhabiting cold climate rivers have developed migration strategies and behaviours in response to these seasonal differences in conditions. Seasonal changes in discharge, temperature and photoperiod are important in triggering river ascent in migratory salmonids (Dahl et al. 2004; García-Vega et al. 2022; Jensen et al. 2012). Furthermore, salmonid spawning, the endpoint of upstream migration, is influenced by decreasing temperature in autumn, as embryonic development and time of emergence of juveniles is highly temperature dependent (Crisp 1981; Elliott and Hurley 1998). Adaptations of migration strategies and the behaviour of migrants may reflect the natal river conditions, as migrating salmonids have been reported to alter behaviour during the migration in response to changes in environmental conditions (Jonsson and Jonsson 2002; Lähteenmäki et al. 2023). Furthermore, salmonids have also been observed to alter behaviour in response to spawning periods drawing closer, and as they enter spawning habitats (Finstad et al. 2005; Økland et al. 2001). Swimming performance is also impacted by environmental conditions, as changes in temperature and discharge influence energy expenditure (Booth 1998; Fenkes et al. 2016; Svendsen et al. 2004).

The sea trout life cycle has been extensively studied (Jonsson and Jonsson 2011), but there is limited information available on how environmental conditions impact spawning migration behaviour and strategies of mature sea trout inhabiting large, free-flowing river systems in the subarctic. Based on primary field data from two previous tracking studies (Huusko et al. 2023; Orell et al. 2017), the present study generates exploratory models of the migration patterns and behaviour of sea trout during upstream spawning migrations in two large, high-latitude river systems (the Teno and Tornio River) in the northernmost areas of the species distribution. Sea trout in both systems have been reported to display a 2-year spawning migration strategy, spending almost two calendar years in-river during spawning migrations (Lähteenmäki et al. 2025; Orell et al. 2017), which has not been reported for sea trout populations from other river systems. Previous studies conducted in these rivers have primarily described spawning migration patterns of sea trout (Huusko et al. 2023; Lähteenmäki et al. 2025; Orell et al. 2017); yet these studies have not evaluated how experienced environmental conditions and individual characteristics influence movements during migrations in these large river systems. Furthermore, studies evaluating spatiotemporal movements of sea trout in relation to environmental conditions in large rivers are scarce, especially in cold climates where seasonal variations in temperature are likely to alter movements. The two main aims of the study were therefore to (1) use exploratory models to analyse the effect of observed environmental conditions, individual characteristics and migrated distances on migration speed of sea trout during upstream spawning migration, and to (2) describe migration timing, patterns, and habitat use of mature sea trout during the migration. We expected to observe similar responses to ambient temperature conditions during the open water season, since both river systems are subarctic and have similar seasonal ice conditions. Experienced discharge has been reported to influence upstream movements of salmonids and was therefore expected to be important for the swimming speed of trout in both systems, especially in the Teno which has lower annual discharge than the larger Tornio River. Furthermore, we aimed to evaluate critical habitat use patterns to identify areas where fisheries management measures may be most effective, highlight key migration conditions influencing sea trout movements, and propose corresponding management measures.

## 2 | Materials and Methods

### 2.1 | Study Area

The Teno River (70.5° N, 28.4° E) is a large subarctic border river system, located between Finland and Norway (catchment area of 16,386 km$^2$), draining into the Barents Sea on the northeast coast of Norway (Figure 1, Table 1). The Tornio River (coordinates of estuary: 65.8° N, 24.1° E) is a subarctic border river between Finland and Sweden (catchment area of 40,157 km$^2$), draining into the northern Bothnian Bay in the Baltic Sea, and it is one of the largest free-flowing rivers in Europe (Figure 1, Table 1). Several genetically distinct sea trout populations inhabit both rivers (Palm et al. 2019; Natural Resources Institute Finland, *unpublished*). Both river systems are free-flowing, and catchments are largely pristine. They have relatively little human influence and are also economically and culturally important for the local communities as they host large and diverse populations of Atlantic salmon (*Salmo salar* L. 1758; Erkinaro et al. 2019; Miettinen et al. 2021). The open water season extends between May/June and October/November in both river systems. Seasonal differences in environmental conditions are extreme with major variation in discharge and water temperature (Figures 2 and 3). The mean temperatures

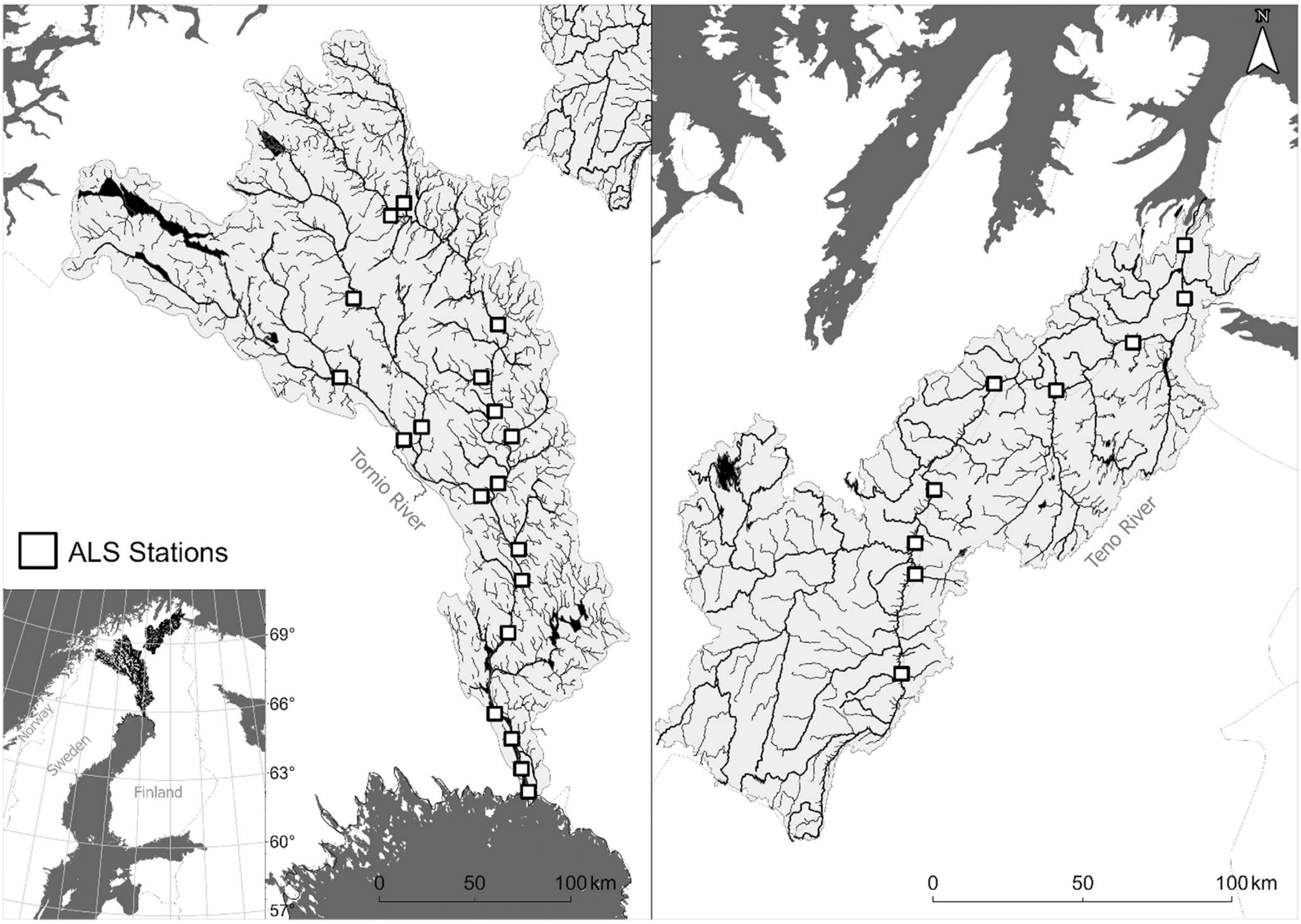

**FIGURE 1** | Map of the studied river systems: Tornio River and Teno River. Placement of automated listening stations (ALS) is shown. Drainage basin data obtained from Länsstyrelserna Geodatakatalogen open database (dataset collected and distributed by Vattenmyndigheterna, SWE), from the Finnish Environmental Institute (SYKE, FI), and from Norges vassdrags- og energidirektorat (NVE, NO).

**TABLE 1** | River characteristics of the study river systems and measured environmental conditions during study periods. River characteristics: Coordinates, and location of the river outlet, drainage area (km$^2$), and river length (km). Environmental conditions: daily discharge (m$^3$ s$^{-1}$) and water temperature (°C).

| River system | Study period | Coordinates | Outlet | Drainage area | River length | m$^3$ s$^{-1}$ | °C |
|---|---|---|---|---|---|---|---|
| *River characteristics* | | | | | | | |
| Teno | 2011–2014 | 70.5° N, 28.4° E | Barents Sea | 16,386 | 350 | 156 (38–1228) | 12.8 (1–20.2) |
| Tornio | 2018–2021 | 65.8° N, 24.1° E | Baltic Sea | 40,157 | 520 | 466 (92–3024) | 14.1 (1–24.4) |

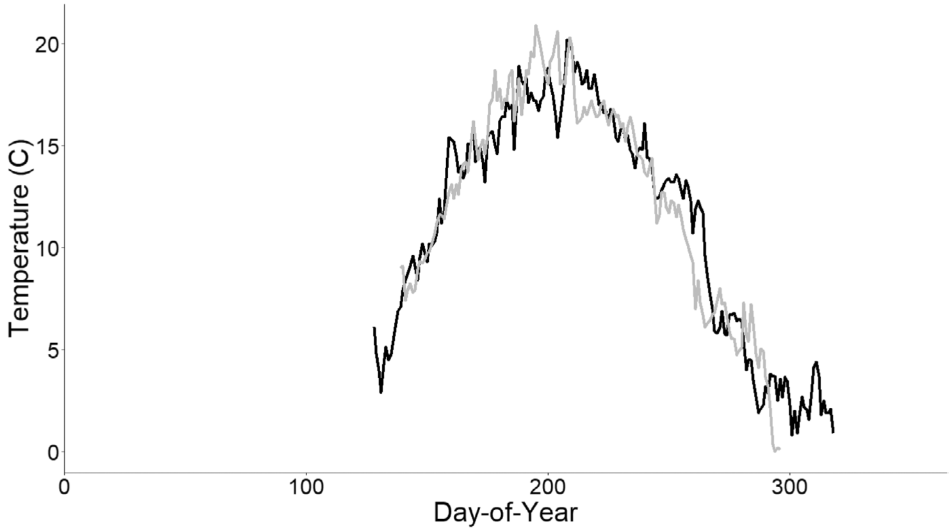

**FIGURE 2** | Median daily water temperature (°C) during the data collection periods (day number) in Teno River (2011–2014, black) and Tornio River (2018–2021, grey). No measurements from the season of ice-cover are included.

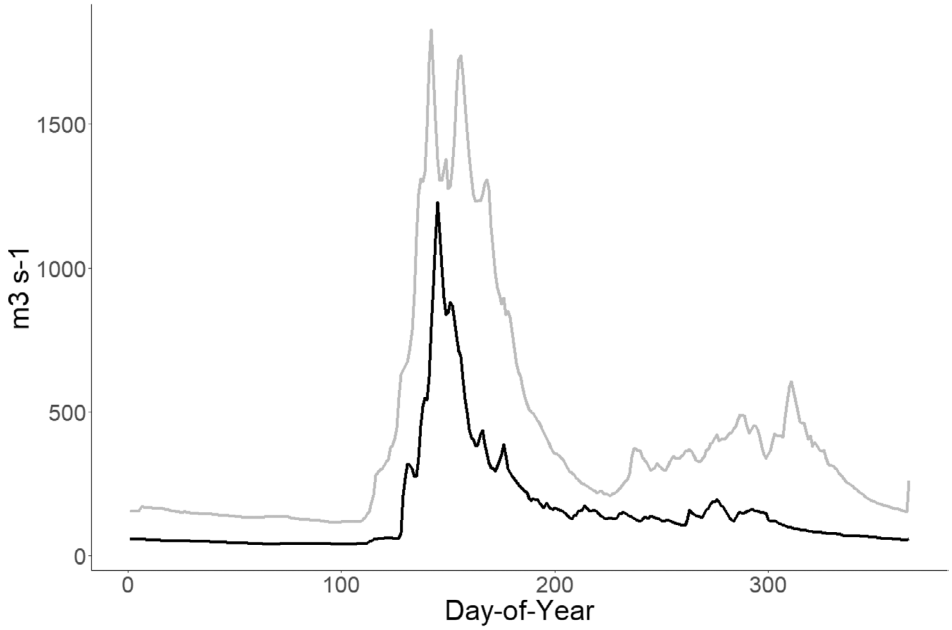

**FIGURE 3** | Median daily river discharges ($m^3$ $s^{-1}$) during the data collection periods (day number) in Teno River (2011–2014, black) and Tornio River (2018–2021, grey).

stay < 1°C during winter months, while temperatures can exceed 20°C during summers. Information about the rivers and tracking data on the sea trout populations are summarised in Tables 1 and 2.

## 2.2 | Fish Capture and Tagging Methods

Data from two radio telemetry tracking studies were gathered for the purpose of analysing sea trout migration behaviour within the two rivers (Teno River: Orell et al. 2017; Tornio River: Huusko et al. 2023; Table 2). Sea trout in both systems were caught using rod and reel in early summer and in late summer/autumn in the lower river reaches of both systems. However, some individuals were also caught as far upstream as > 100 km from sea in both rivers. Each caught individual was visually inspected prior to tagging to ensure that all tagged individuals were in good condition and of suitable size for tagging. The length (total length, cm) and weight (wet mass, g) of trout were measured prior to tagging, and scale samples were taken for age analysis and estimation of previous spawning experience (maiden vs. repeat spawner). Individuals were given anaesthesia (buffered MS-222 solution, < 100 mg/L) before being placed in a custom tagging cradle for the surgical procedure. The radio tags (Advanced Telemetry Systems Inc., models F1580 and F1835 in Teno; Lotek Wireless Inc., model MCFT2-3A in Tornio) were placed in the body cavity through a 20–30 mm longitudinal incision

**TABLE 2** | Characteristics of tracked sea trout: Number of tracked individuals (n), number of observations (n), total length (total length TL, cm), mass (wet mass, kg), age (total age, years), and distance migrated upstream from the sea (km). All measurements given as medians with ranges (min–max).

| River system | Study period | Trout | Obs. (*n*) | TL (cm) | M (kg) | Age | Distance migrated (km) |
|---|---|---|---|---|---|---|---|
| *Trout characteristics* | | | | | | | |
| Teno | 2011–2014 | 22 | 512 | 52 (36–69) | 1.2 (0.5–2.4)[a] | 8 (6–11)[a] | 192 (43–274) |
| Tornio | 2018–2021 | 32 | 373 | 63 (52–85) | 2.5 (1.3–6.5) | 6 (5–11)[a] | 241 (113–343) |

[a] Weight and total age are not available for all tagged trout.

on the ventral skin posterior to the pectoral fins, and the tag antennae were brought through the skin using a hypodermic needle (1.5 × 50 mm/17Gx2) picked caudally to the incision. The incision was closed using monofilament sutures. The tagging took an estimated 2–3 min, whereafter tagged individuals were placed in recovery containers. Once tagged trout had visually recovered from tagging, the trout was released back to the location where it was caught, whereafter tracking of movements commenced.

## 2.3 | Tracking Design

Similar tagging and tracking protocols were used in both studies, tracking sea trout throughout the riverine migration using active and automated tracking arrays, allowing comparison of behaviour between and within the river systems. Tracking was performed using automated listening stations consisting of radio receivers (Models: R4500S (Advanced Telemetry Systems Inc.) in Teno; SRX-DL or SRX800 (Lotek Wireless Inc.) in Tornio) connected to a four-, six-, or nine-elements Yagi-antennae placed strategically in the river systems (Figure 1), which allowed continuous monitoring of sea trout movements upstream. The automated tracking was supplemented with weekly manual tracking by foot and car during the open water season (May–October) and once per month during winter (November–April), allowing tracking of movements in locations between automated stations and in areas outside of their reach. Tracking was also conducted on a few occasions by boat (twice in autumn 2018, and once in 2019 in Tornio) and plane (in autumn of 2012 and 2013 in Teno; in autumn of 2018 and 2021 in Tornio). Tracking was continuous from 27th May 2011 to 15th October 2014 in the Teno and June 1st 2018—December 31st 2021 in Tornio, respectively. Tagged trout included both immature trout that were caught in autumn prior to overwintering and trout caught in spring in freshwater overwintering habitats. In this study, only individuals that were observed to have successfully migrated to a spawning habitat were included in the analysis to ensure comparability of behaviour. Individuals that stayed in the lower river sections or in the estuaries without migrating upstream to potential spawning habitats were thus excluded from the dataset. Information on tagged sea trout age and size was included in the dataset and used to highlight population specific differences (Table 2). The vast majority of tagged individuals (100% in Teno, 91% in Tornio) that were included in the final dataset were tracked from the lower reaches of the river system (< 30 km from sea), while three individuals were tracked from tagging locations further upstream in the Tornio River.

## 2.4 | Environmental Data

To analyse the effect of environmental conditions on the behaviour of trout, river discharge ($m^3\ s^{-1}$) and temperature (°C) data were gathered in the field during the studies (Table 1). Temperature measurements were gathered in the main stem of both rivers (55 km and 20 km from the sea for Teno and Tornio, respectively) throughout the study periods, and these data were further supplemented with river specific environmental data from the Finnish Environmental Institutes (SYKE) environmental database. We used the daily discharge and temperature measurements in these fixed locations as a proxy for river specific variation in environmental and seasonal conditions, due to the vast size of the river systems limiting observation and location specific measurements. Measurements of river discharge (daily $m^3\ s^{-1}$) and temperature (daily °C) at each observation were included and used to calculate the change in the conditions between fish observations (given as a percentage increase/decrease). We used daily averages in discharge and temperature for the analysis since most trout movement observations were made on a daily/weekly basis rather than on a smaller hourly basis, limiting interpretation of small-scale triggers in movements caused by changes in conditions. However, using daily averages allowed modelling of environmental conditions influence on large-scale spatiotemporal upstream movements.

## 2.5 | Radio Telemetry Data Processing

Radio telemetry tracking data from the two river systems included coordinate data for observations of sea trout movements, estimated spawning- and overwintering locations in the river systems as well as time and date of each observation. A total of 22 trout (providing 512 unique observations of trout movements within the river system) were observed to have completed the spawning migration in the Teno River with the median number of observations per trout being 25 observations (SD ± 11.0), while median number of observations for 32 trout (373 observations) in the Tornio River was 13 observations (SD ± 5.8; Table 2). The data was used to evaluate the migration speed of sea trout in relation to observed environmental conditions and measured biological variables. Furthermore, the data was used to evaluate migration tactics used by trout, including habitat use during the migration, choice of overwintering location, timing of upstream movement post-wintering, and migration distance (from sea to spawning habitats). Estimated spawning locations were used as the end destination of the migration. The coordinate data were used to calculate migration distances (migrated km upstream from the sea), movement distance between observations (km) and migrated proportion (%) of the total distance migrated. Time and date of observations were used to calculate elapsed time between observations (days). A migration speed measure (km day$^{-1}$) was calculated for each observation by dividing migrated distance between observations (km) with the elapsed time (days). The migration speed measures provide a measure of spatiotemporal movements of trout, allowing analysis of how actively individuals moved upstream, and comparison of movements of individuals that migrated varying distances to spawning habitats. Furthermore, only the observations made during the open water season were included in the analysis, due to the small spatial movements observed during periods of ice-cover, as trout were mainly stationary in freshwater overwintering habitats and made only minor short-range movements within said habitats. Therefore, the final dataset contained observations between day numbers 100–350 (10 April–16 December). Kolmogorov–Smirnov tests were used to assess whether environmental conditions (i.e., temperature and discharge) in the studied rivers had similar underlying distribution. Migration speed measurements were log transformed prior to analysis, and Wilcoxon rank-sum tests were used to analyse for differences in measured migration speed between the studied populations.

## 2.6 | Data and Statistical Analysis

The migration speed measurements (km day$^{-1}$) were used as the response variable in the river specific migration speed models, while the environmental predictors used in model generation were discharge (m$^3$ s$^{-1}$), temperature at observation (°C), change in discharge between observations (%), change in temperature between observations (absolute value), and proportion of total distance migrated at observation (%). All predictors were log transformed prior to analysis, except for temperature, to reduce skewness of the data. Percentage change (discharge) variable was log (+1) transformed. We included migration year and tagging location (km from sea) as factors to separate potential influence of yearly- and tagging location dependent variation in migration speed. Furthermore, we included the following characteristics to allow assessment of potential influence of individual condition, age, and spawning experience: length-at-tagging (cm), sea age at tagging (years), and previous spawning experience (maiden or repeat spawner). Generalised additive mixed models (GAMM) were used to identify potential drivers of sea trout migration speed in the studied river systems. GAM models are a useful tool for analysing non-normally distributed data and for modelling non-linear relationships between response and predictor variables (Hastie 2017; Hastie and Tibshirani 1990). Furthermore, we developed a mixed model to treat Individual as a random effect to account for pseudo-replication due to repeated measures at the level of individual. The modelling also included potential predictor interactions. GAMM models were generated for both river systems separately, applying the following model:

$$\mathrm{Log}\left(A_m\right) = \mathrm{s}\left(V_i\right) + \mathrm{s}\left(V_j\right) + \ \dots\ + \mathrm{s}\left(V_l\right) \qquad (1)$$

where $A_m$ is the migration speed measurement (km day$^{-1}$), s the spline smoother function, and $V_{i,l}$ the predictor variables. The models were generated with variable exclusions to remove variables that had no significant impact on model results. All models were inspected for normal distribution of the residuals using the DHARMa residual diagnostics package (Hartig 2022), the models were checked for autocorrelation (Durbin Watson test), concurvity between predictors and heterogeneity to ensure that model criteria were met. Concurvity was assessed using mgcv package (version 1.9–1; Wood 2011) diagnostics and considered acceptable where pairwise values were $<0.5$, and smooth-level estimates did not compromise smooth stability. Number of knots (*k*-values) for each variable was estimated using the gam.check-function included in mgcv package. Akaike Information Criterion (AIC) (Burnham and Anderson 2002) values were used to evaluate model fit, and for the choice of the best fitting model. Models that did not meet the criteria were discarded in cases where transformations did not allow model criteria to be met. The validation of the final models was conducted using generalised cross-validation scores (gCV), deviance explained percentage and $R^2$-values. All GAMM models were generated using the mgcv package. We used the predict function in the car package (Fox and Weisberg 2019) to generate predictions from the fitted GAMM models, by increasing predictive variables over the observed range, while keeping other model variables at their means. These predictions allowed calculation of predicted migration speed at varying conditions of the predictive variables, and calculation of confidence intervals. All analyses presented in this study were conducted using R statistical software, R version 4.3.2 (R Core Team 2023).

# 3 | Results

## 3.1 | Migration Characteristics of Studied Sea Trout Populations

Most tagged trout included in this study (57% of tagged trout; 95% of tracked trout in Teno and 28% in Tornio) were observed to have entered freshwater in autumn in the year prior to spawning and were observed to have overwintered in freshwater habitats, prior to migrating upstream to spawning habitats in the following year. The rest of tagged individuals were tagged at in-river overwintering habitats prior to migration upstream (5% in Teno and 72% in Tornio). Most sea trout migrating in the Teno River (Figure 4) chose pre-spawning overwintering habitats further upstream in the river ($\text{Median} \pm \text{SD} = 63.6 \pm 51.2$ km from sea), while overwintering generally occurred in the lower reaches of the Tornio River ($14.9 \pm 75.2$; Figure 4; Figure S1). Movements during winter were limited as tagged trout displayed sedentary holding behaviour in the overwintering habitats. Median water temperatures during overwintering periods were close to 0°C in all tracking years, in both river systems. Both river water temperature conditions (Kolmogorov–Smirnov test, $D = 0.16$, $p < 0.05$; Figure 2) and discharge conditions (Kolmogorov–Smirnov test, $D = 0.53$, $p < 0.0005$; Figure 3) differed significantly between the rivers during the open water season. Tagged sea trout

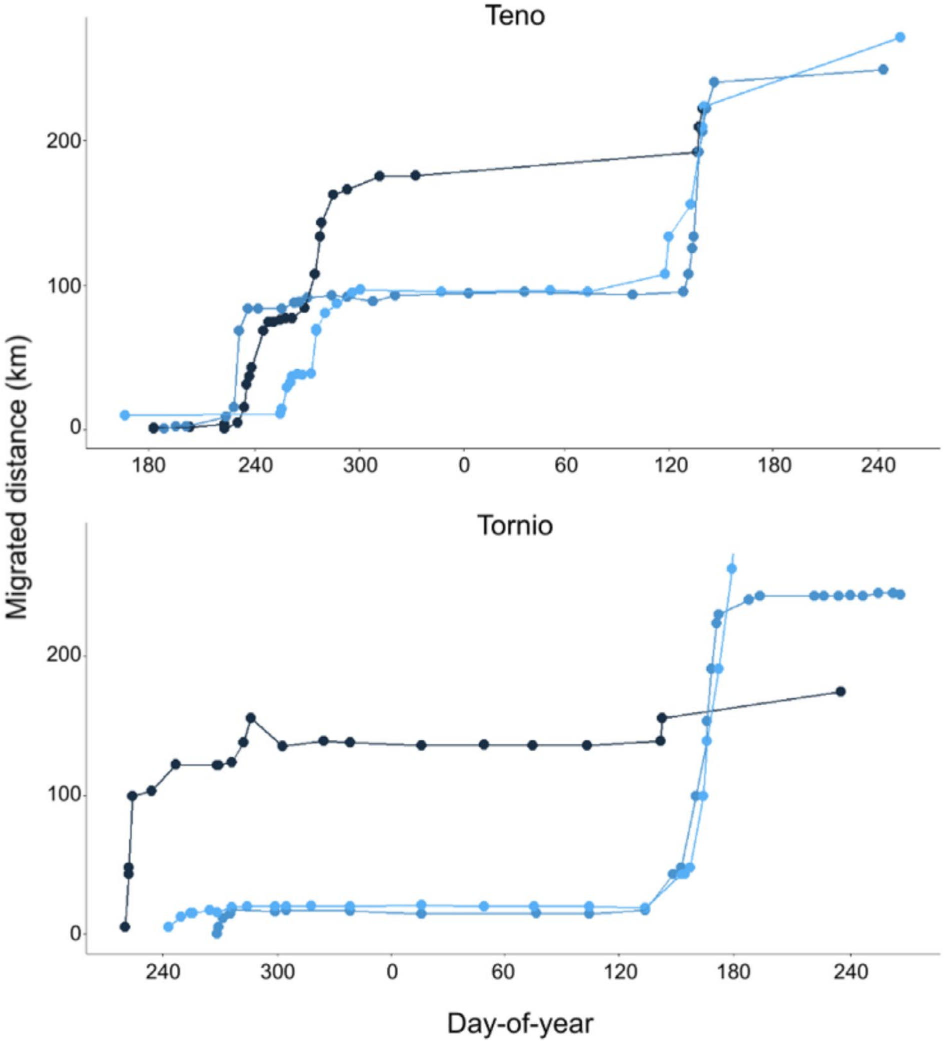

**FIGURE 4** | Example of the most common upstream spawning migration patterns of three sea trout tagged in Teno River (upper) and Tornio River (lower). All fish were caught in the lower reaches of the studied river systems. Dots represent observations, while migrated distance at observation (km from the sea, *y*-axis), and day-of-year of the observation. (*y*-axis) are shown on the axis. Colours are used to separate individual trout movements. Last observations (end destination of migration) are of trout entering estimated spawning habitat or spawning tributaries.

generally initiated migration upstream from overwintering habitats in mid- to late May, and the movements upstream were rapid once migration was initiated from overwintering habitats (Figure 4). Estimated median day of initiated migration was May 17th (±10 days) in the Teno- and May 23rd (±17 days) in the Tornio River, based on observations of the first movements upstream from overwintering habitats (Figure S1). Estimated median water temperature at initiation of upstream migration was 5°C (±3.7°C) in Teno and 8°C (±3.6°C) in the Tornio River, respectively (Figure S1). Individuals in both river systems were observed to spend more than 300 days in-river prior to entering spawning habitats (Figure 4; S2 and S3), which were located exclusively in tributaries (Huusko et al. 2023; Orell et al. 2017; Figure S4). Median distance from sea to spawning habitats of trout was 192 km (±77.8) and 241 km (±56.5), while median distance from pre-spawning overwintering habitats to spawning habitats was 111 km (±73.1) and 175 (±88.3) for trout tagged in Teno and Tornio rivers, respectively (Figure S1). Overall, migration speed (km day$^{-1}$) of sea trout during the open water season was significantly higher in the larger Tornio River (1.3 ± 12.0 km day$^{-1}$) than in the smaller Teno River (0.6 ± 7.8 km day$^{-1}$; Wilcoxon test, $W = 81{,}431$, $Z = -3.7$, $p < 0.0005$).

**TABLE 3** | Summary of best fitting General additive Mixes models (GAMM) for explaining migration speed of sea trout (*Salmo trutta* L.). Summary includes best fitting model (GAMM), coefficient of determination for goodness of fit (R squared ($R^2$)), and estimated deviance in migration speed explained by model (Deviance exp.), as well as minimised generalised cross-validation values (GCV) and number of observations included in generation of each model (*n*).

| River | Model | $R^2$ | Deviance exp. | GCV | *n* |
|---|---|---|---|---|---|
| Teno River | GAMM | 0.38 | 42.4% | 0.53 | 512 |
| Tornio River | GAMM | 0.56 | 60.9% | 0.57 | 373 |

### 3.2 | Modelling of Sea Trout Migration Speed

The best fitting GAMM models for sea trout migration speed of the Teno- and Tornio River populations explained roughly 42% and 61% of the deviance, respectively (Table 3). The best fitting model for the Teno River system was a model which included discharge ($m^3\ s^{-1}$), temperature (°C), change in discharge (log %), proportion of the migrated distance (%), and trout length-at-tagging (cm) as predictive variables (Table 4). The same environmental variables were also included in the best fitting model for the Tornio River system, but individual characteristics were not significantly influencing the results in the Tornio and were therefore excluded (Table 4). Tagging location and year-of-migration did not significantly influence modelling results in either system; neither did changing temperature (°C), sea age (years), or previous spawning experience (maiden vs. repeat spawner). Interactions between environmental variables failed to improve either model's results; therefore, the final models did not include interactions.

Increased discharge had a positive, non-linear impact on migration speed in both the Teno (Figure 5A) and Tornio River systems (Figure 6A; Table 4). Migration speed increased sharply with discharge in the Teno River until reaching a peak at ~1000 $m^3\ s^{-1}$, after which speed plateaued (Figure 5A). Model predictions suggests that migration speed would be 0.7 km $day^{-1}$ (95% CI = 0.4–1.4) at 100 $m^3\ s^{-1}$, increasing to 1.1 km $day^{-1}$ (0.6–2.0) at 250 $m^3\ s^{-1}$, and to 2.82 km $day^{-1}$ (1.5–5.3) at 500 $m^3\ s^{-1}$. Peak migration speed of ~7.9 km $day^{-1}$ (3.6–17.4) would be reached at discharges of 1000 $m^3\ s^{-1}$. Similarly, discharge had generally a positive effect on predicted speed in the Tornio River (Figure 6A). During low discharge conditions (~200 $m^3\ s^{-1}$) trout migration speed was predicted to be 0.6 km $day^{-1}$ (0.2–1.5), with speed increasing rapidly at discharges > 250 $m^3\ s^{-1}$. Peak speed of 10 km $day^{-1}$ (5.4–18.6) would be predicted at discharges of 1000 $m^3\ s^{-1}$, after which it tapered and decreased to 3.8 km $day^{-1}$ (1.3–11.0) at 2500 $m^3\ s^{-1}$. The relationship between migration speed and change in discharge was significant, non-linear (Table 4) and hump-shaped in both rivers (Figures 5B and 6B), with highest speed in both river at 0%–25% change in discharge. Migration speed peaked in the Teno around 0.8 km $day^{-1}$ (0.8–1.5) when change in discharge was ~0, while a 25% increase in discharge lead to a similar speed value of 0.8 km $day^{-1}$ (CI 0.5–1.5), and a 25% decrease to a value of 0.7 km $day^{-1}$ (0.4–1.3). Both increases and decreases in discharge of 50% had a negative impact on migration speed, causing a decrease to 0.7- (0.4–1.1) and 0.5 km $day^{-1}$ (0.25–1.0), respectively. Major increases in discharge over 100% would decrease speed further to < 0.6 km $day^{-1}$ (0.3–1.1) in the Teno. Migration speed peaked around 0% change in Tornio as well, and the peak was higher than for the Teno (3.4 km $day^{-1}$, 1.7–6.92). A discharge decrease of 25% lowered the predicted migration speed to 3.2 km $day^{-1}$ (1.5–6.6), while an 25% increase led to a decrease in speed to 1.86 km $day^{-1}$ (0.9–4.0). Increases or decreases of 50% led to speed decreasing to 1.3- (0.5–3.0) and 1.4 km $day^{-1}$ (0.6–3.5), respectively. Major increases (> 50%) in discharge had a linear decreasing influence on migration speed.

Temperature exhibited a significant, non-linear effect on migration speed in both the Teno- and Tornio River (Table 4). Migration speed generally increased with temperature (Figures 5C and 6C) as trout were most active in water temperatures above 15°C, while speed decreased as temperatures dropped below 10°C in both systems, reflecting seasonal variation in migration speed. Model predictions indicate that migration speed in the Teno would increase from 0.2 km $day^{-1}$ (CI 0.1–0.5) at 0°C, to 0.5 km $day^{-1}$ at 5°C (0.3–1.0), and to 0.8 km $day^{-1}$ (0.5–1.5) at 10°C. Migration speed would reach 1.5 km $day^{-1}$ (0.5–4.2) at peak temperatures of 20°C, which is a 78% increase in speed when compared to temperatures of 10°C. Increasing water temperature had a positive impact on trout migration speed in Tornio, as predicted speed was lowest during temperatures of ~5°C (3.09 km $day^{-1}$, CI 1.1–8.5) and increased to between 3.9 and 5.5 km day–1 during temperatures of 10°C–15°C. Peak migration speed was predicted at temperatures of > 20°C, with speed reaching 11.8 km $day^{-1}$ (5.3–26.9) at 20°C and 17.4 km $day^{-1}$ (4.3–70.8) at 25°C.

The relationship between migration speed and migrated distance (%) was highly flexible and nonlinear in both systems (Figures 5D and 6D, Table 4), as trout generally increased their migration speed from the lower river. Speed decreased markedly at the end of migration as spawning periods drew near, and as trout moved closer to spawning habitats (Figures 5D and 6D). The Teno model results indicated that migration speed would increase with migrated distance until the last quarter of the migration (Figure 5D), increasing from < 0.6 km $day^{-1}$ (0.3–1.1) at the lowest 10%- to 1.2 km $day^{-1}$ (0.7–2.0) at 70% of the total migrated distance. Speed was predicted to decrease considerably to 1.0 km $day^{-1}$ (0.6–1.7) at 80% of the total migration, and further to 0.5 km $day^{-1}$ (0.2–0.9) at the endpoint of the migration and arrival at spawning habitats. Similarly, migration speed in the Tornio (Figure 5D) was predicted to increase from ~0.6 km $day^{-1}$ (0.1–3.6) at the lowest 10%-, to a peak of 3.8 km $day^{-1}$ (1.9–7.8) at 70% of the total migrated distance. Speed was predicted to decrease considerably to 2.8 km $day^{-1}$ (1.5–5.1) at

**TABLE 4** | Fitted GAMM model results for migration speed of the sea trout (*Salmo trutta* L.) populations.

| Model | Variable | edf | *F* | *p* |
|---|---|---|---|---|
| *Teno River* | | | | |
| GAMM | Discharge ($m^3\ s^{-1}$, log) | 3.7 | 12.1 | *** |
| | Temperature (°C) | 2.8 | 9.1 | *** |
| | Proportion of migrated distance (log) | 8.7 | 4.0 | *** |
| | Percentage change in discharge (log) | 4.7 | 5.1 | *** |
| | Lenght-at-tagging | 3.6 | 3.3 | * |
| *Tornio River* | | | | |
| GAMM | Discharge ($m^3\ s^{-1}$, log) | 4.8 | 18.0 | *** |
| | Temperature (°C) | 5.6 | 3.3 | ** |
| | Proportion of migrated distance (log) | 6.5 | 3.6 | ** |
| | Percentage change in discharge (log) | 6.2 | 5.3 | *** |

*Note:* Variables included in model generation with effective degrees of freedom (edf), *F*-values and *p*-values for each variable. Variables include discharge conditions at observation (log $m^3\ s^{-1}$), temperature (°C), proportion of total migrated distance at observation (log), percentage change in discharge (log $m^3\ s^{-1}$) between observations, and length-at-tagging (cm). Statistical significance levels: *$p < 0.05$, **$p < 0.005$, ***$p < 0.0005$.

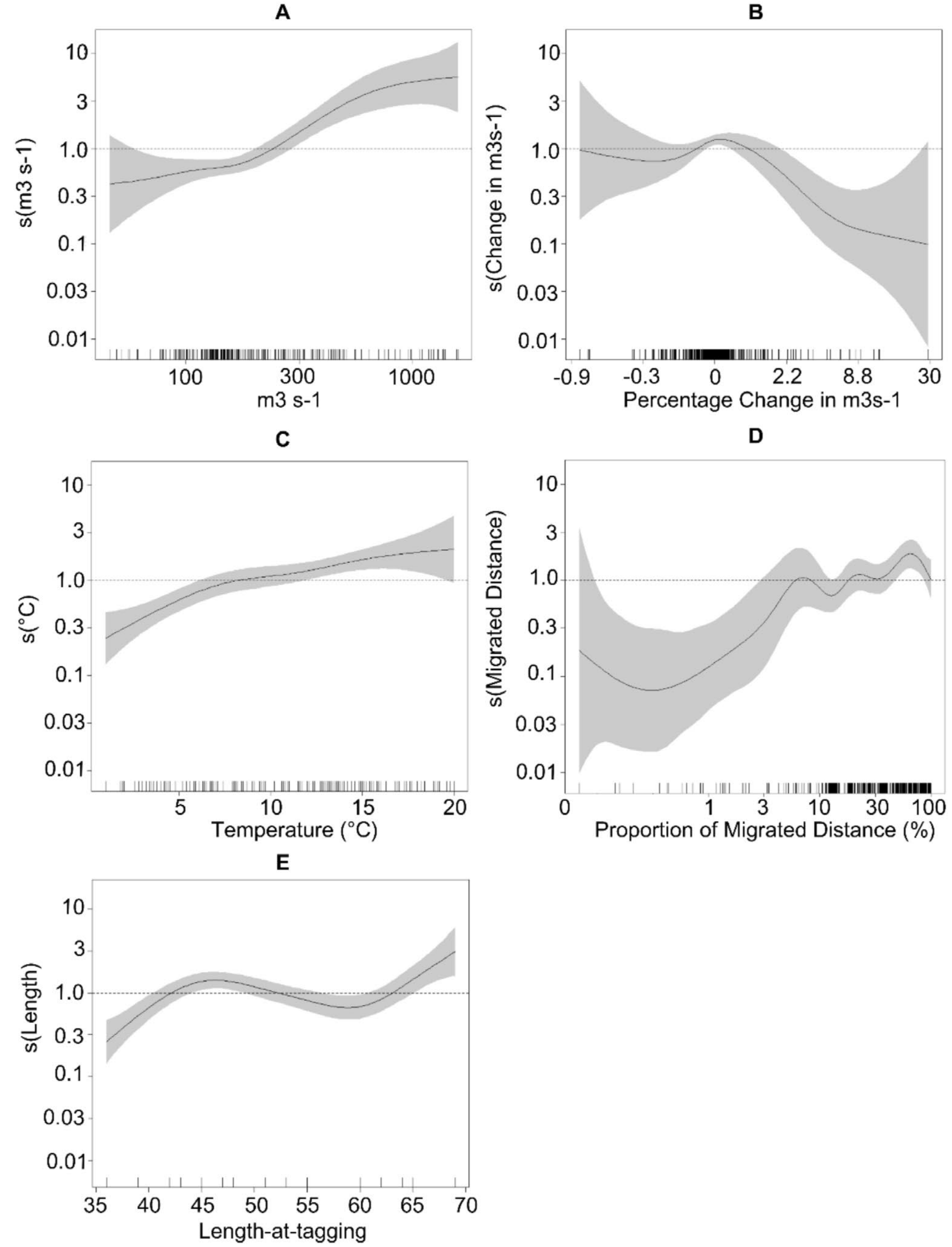

**FIGURE 5** | GAMM model smoothers illustrating the partial effect of covariates on sea trout (*Salmo trutta* L.) migration speed (km day$^{-1}$) in Teno River. Covariates illustrated from top left: (A) Discharge at observation (m$^3$ s$^{-1}$), (B) percentage change in discharge condition between observations (% given as decimals), (C) Temperature at observation (°C), (D) proportion of total migrated distance at observation (%), and (E) length-at-tagging (cm). Individual trout identity code was used as the random effect in the GAMM fitting. Solid lines represent the fitted GAMM function, which describe a variables effect on the response variable (sea trout speed), while the shadings are 95% approximate confidence limits for each smoother. Covariate values shown on *x*-axis, with partial effect shown on *y*-axis. Datapoints illustrated as a rug plot on the *x*-axis. Zero function, which indicates no effect of the covariate, illustrated by dashed line. Axis values normalised.

80% of the total migration, and further to 0.7 km day$^{-1}$ (0.4–1.2) at the end point of the migration.

Sea trout length had a significant effect on trout migration speed in the Teno River (Figure 5E, Table 4), as speed increased with trout size at tagging. Smaller individuals (< 40 cm at tagging) had a lower predicted speed of 0.5 km day$^{-1}$ than individuals between 40 and 60 cm which had predicted speed between 0.6 and 1.0 km day$^{-1}$. The model predicted highest migration speed for individuals > 65 cm, with speed of 65 cm individuals predicted to be 1.1 km day$^{-1}$ (0.6–2.0) while 70 cm trout would have a predicted speed of 2.8 km day$^{-1}$ (1.1–7.1).

## 4 | Discussion

The migration behaviour of the sea trout populations in this study demonstrates that the populations have developed similar

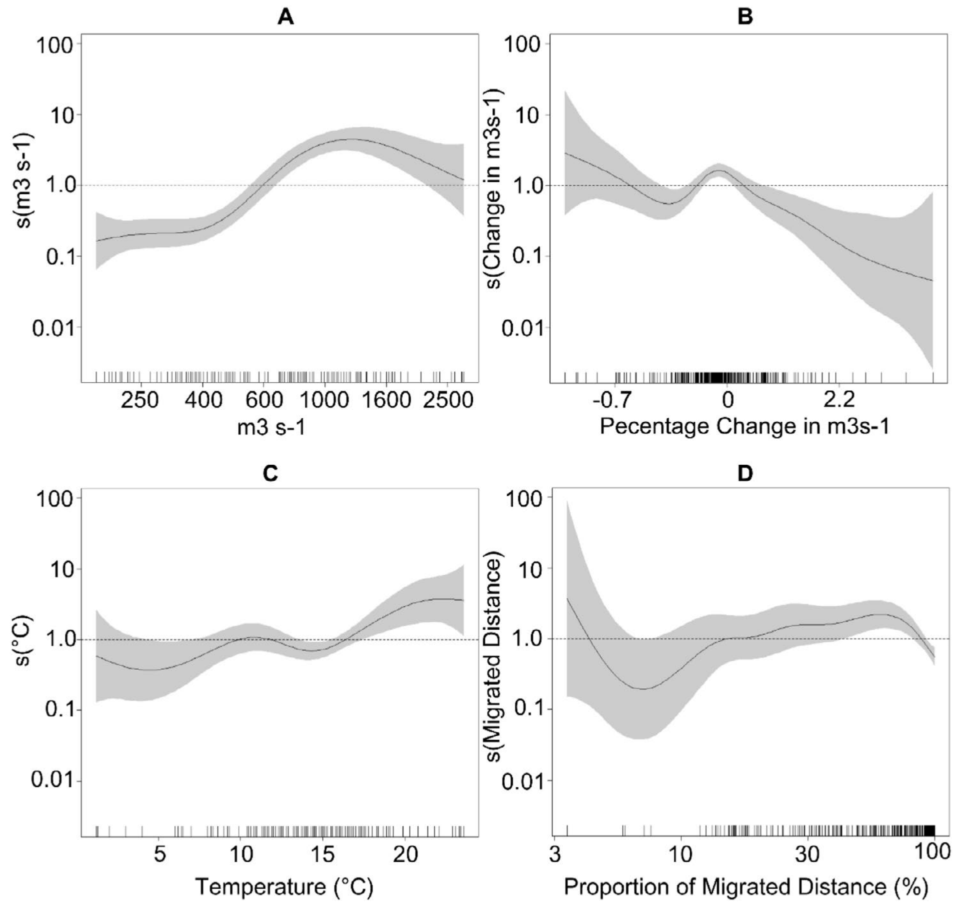

**FIGURE 6** | GAMM model smoothers illustrating the partial effect of covariates on sea trout (*Salmo trutta* L.) migration speed (km day$^{-1}$) in Tornio River. Covariates illustrated from top left: (A) Discharge at observation (m$^3$ s$^{-1}$), (B) percentage change in discharge condition between observations (% given as decimals), (C) Temperature at observation (°C), and (D) proportion of total migrated distance at observation (%). Individual trout identity code was used as the random effect in the GAMM fitting. Solid lines represent the fitted GAMM function, which describe a variables effect on the response variable (sea trout speed), while the shadings are 95% approximate confidence limits for each smoother. Covariate values shown on *x*-axis, with partial effect shown on *y*-axis. Datapoints illustrated as a rug plot on the *x*-axis. Zero function, which indicates no effect of the covariate, illustrated by dashed line. Axis values normalised.

responses to changes in the studied factors, as the populations displayed similar behavioural responses to variation in discharge and temperature and migrated distance. Furthermore, the populations had similar overwintering tactics, utilising the freshwater habitats for overwintering pre-spawning, extending the freshwater stay to one calendar year prior to the spawning event, which has not been reported for sea trout populations outside of these river systems. Collectively, the observed similarities in freshwater habitat utilisation, migration patterns and responses to changes in environmental conditions suggest that these populations have adapted similar behavioural responses to environmental change.

The two-year spawning migration strategy observed for sea trout in the studied rivers has to our knowledge only been reported for sea trout populations inhabiting these two large, high-latitude rivers (Huusko et al. 2023; Lähteenmäki et al. 2025; Orell et al. 2017). It is likely that the ambient river conditions can at least partly explain the adaptation of premature freshwater entry as part of the spawning migration strategy, considering the similarities in environmental conditions between the rivers and the observed migration behaviour reported in this study. Populations of both rivers were observed to have similar timing of freshwater entry, overwintering tactics, timing of upstream movements post-wintering, and similar responses to changes in conditions during the migration. The main observed difference between migrating trout in these rivers was the location of wintering habitats, which differed considerably between the two rivers. Wintering patterns of both immature and mature sea trout have been described in more detail in previous studies conducted in the Teno (Orell et al. 2017) and Tornio River (Huusko et al. 2023; Lähteenmäki et al. 2025), but the factors influencing the selection of wintering habitats are still largely unknown. River morphology is likely to influence the availability of suitable habitat and could therefore partly explain differences in wintering patterns in the studied rivers. These observations are further likely driven by the ambient conditions of the rivers since these large river systems have similar environmental characteristics in terms of temperature regimes and period of ice cover; however, the rivers differ in terms of river morphology, location of river outlet, the adjacent marine environment, and discharge conditions. Despite these differences, the observed responses to environmental change differed little across populations, suggesting that these geographically isolated populations have developed similar responses separately in both systems.

Freshwater entry a year prior to spawning has been reported for Atlantic salmon in rivers of NW Russia and the Kola peninsula (Studenov et al. 2008), in northern Norway and northeastern Canada (Power 1981). The fitness benefits of undertaking this type of migration strategy are still unclear, as there is considerable uncertainty about what factors are driving the strategy adaptation. Factors related to survival rates between freshwater and marine habitats are likely to influence habitat shifts (Werner and Gilliam 1984), and length of freshwater stay (Foldvik et al. 2024), as predation and fishing related mortality at sea has been reported to be considerable (e.g., Jensen et al. 2019; Jonsson and Jonsson 2009b; Whitlock et al. 2017). A recent study by Foldvik et al. (2024) indicated that optimal freshwater return date of Atlantic salmon varies depending on salmon size and mortality rates at sea, suggesting that timing of freshwater entry should coincide with conditions that improve survival, reduce energetic risks and with conditions that are suitable for upstream migrations. Consequently, freshwater entry into large river systems could improve survival and thereby fitness of maturing sea trout, influencing adoption of premature freshwater entry and prespawning overwintering in rivers that provide suitable overwintering conditions and habitats.

The observed responses to changes in environmental conditions are likely linked to individuals reacting to physiological constraints during upstream migration, since seasonal conditions are essential for upstream migration of anadromous salmonids, as river discharge and temperature facilitate or restrict migrations by altering energy expenditure and swimming performance (Lee et al. 2003; Videler and Weihs 1982). Collectively, changes in photoperiod, water temperature and discharge (Birnie-Gauvin et al. 2021; Dahl et al. 2004; Erkinaro et al. 1999; Jones and Petreman 2015; Quinn and Adams 1996; Robards and Quinn 2002), have been reported to work as environmental cues for salmonid migrations. The results of this study demonstrated that variation in discharge had an impact on migration speed. Trout migration speed increased with increasing discharge, and migration speed peaked when discharges reached ~1000 $m^3$ $s^{-1}$ in both rivers. Moderate increases or decreases in discharges also had a positive impact on the speed, while large increases or decreases generally had a negative effect on trout migration speed in these large, free-flowing rivers. It should be noted that trout were active throughout the open-water season in both river systems, highlighting that discharge conditions are not restricting migrations at any point during this period. Increased discharge has been reported to be important in facilitating movements of salmonids during the migration and in passage of barriers; however, major increases in discharge have also been reported to temporarily halt or slow salmonid movements (e.g., Jensen et al. 1989; Stuart 1958), due to the increased energy expenditure needed to maintain upstream movement against strong currents (Enders et al. 2005; Fenkes et al. 2016). This could be reflected in the observed changes in migration speed patterns during major discharge increases, and the decrease in speed at peak discharges in the Tornio River. These results provide further evidence that discharge can be important in influencing movements of anadromous salmonids, even in large river systems with discharge conditions which enable migration throughout the open-water season.

Water temperature was an important variable impacting migration in both studied river systems, as increasing temperature had a positive effect on migration speed, while speed decreased later in the migration as temperature declined prior to spawning. These observations reflect seasonal changes in river conditions, which inevitably influence movements of poikilothermic fish as movement and metabolic costs are temperature dependent (Jobling 1995; Lee et al. 2003). Migration speed was generally lower during water temperatures below 10°C, and the lowest speed was measured when temperatures dropped below 5°C. Sea trout were most active once temperature increased above 10°C, and migration speed seemed to peak at temperatures close to 20°C in both rivers, presumably reflecting the influence of thermal conditions on the swimming ability of salmonids (Salinger and Anderson 2006; Svendsen et al. 2004). Little is known about water temperatures' influence on migration speed of adult brown trout, but juveniles have been reported to reach maximum swimming performance at 16°C and to sustain 90% of maximum swimming performance in temperatures between 12°C and 19°C (Ojanguren and Brañta 2000). Optimal temperatures for swimming performance of mature pacific salmonids have been estimated to be ~16°C for sockeye (*Oncorhynchus nerka*) and chinook salmon (*Oncorhynchus tshawytscha*) (MacNutt et al. 2006; Salinger and Anderson 2006), and 15°C–18°C for rainbow trout (*Oncorhynchus mykiss*) as reported by Farrell et al. (1996). These observations of salmonid swimming performance in relation to experienced temperatures support the findings of this study, highlighting that sea trout migrating in these cold-climate rivers are responding to elevated temperatures by increasing migration speed. This is likely partly due to migration conditions improving as temperature increased in early summer, triggering migration upstream and due to increased temperatures facilitating movement. In addition to temperature, migrated distance impacted migration speed in both systems, as speed generally peaked prior to the last quarter of the migration and decreased as trout moved closer to spawning habitats. Migration upstream from overwintering habitats was initially rapid, as trout moved tens to hundreds of kilometres upstream without noticeable pause once the migration was initiated. The apparent lowered migration speed during the later stages of the migration could be due to trout searching for suitable habitat in their natal stream (Finstad et al. 2005), staying at close distance from the spawning areas and performing occasional short search movements, as described for Atlantic salmon (Karppinen et al. 2004; Økland et al. 2001). Moreover, decreasing temperature late in the migration could have an effect on migration speed since colder temperatures have been reported to influence swimming speed, oxygen consumption, and scope of activity of salmonids (Jonsson and Jonsson 2009a; Lee et al. 2003), which combined with increasing fatigue and lowered energy reserves could explain the decrease in speed late in the migration. Based on these observations it is likely that water temperature is influential for the adoption of the observed migration strategies, as ice cover and water temperatures are restricting movements during winter months, consequently influencing the observed pre-spawning overwintering tactics.

Length-at-tagging was observed to have a significant impact on migration speed in the Teno, but not in the Tornio River system. Body size has been reported to influence critical swimming speed in salmonids, with swimming speed increasing with body size (Cano-Barbacil et al. 2020). Differences in factors such as river morphology, experienced discharge and temperature conditions, migration distances, and post-wintering energy reserves could likely partly explain why size was significant in the Teno and not the Tornio River. The results also indicate that the differences in expected speed based on length are driven by trout at either end of the size range, since most individuals within the range had similar speed. These results regarding the difference in migration speed based on trout size should be interpreted with caution due to the relatively small sample size, yet it should be considered and further evaluated in future studies.

The models were able to explain some of the sea trout migration speed; however, there was considerable inter- and intrapopulation variation in individual migration behaviour that could not be explained. Due to tracking limitations (large river sizes, difficult terrain etc.), the number of observations in the upper reaches and the spawning tributaries of the Teno River was low, likely impacting the model fit. Furthermore, individual characteristics of fish (maturation stage, energy reserves, hormones, and stress levels), social interactions, genetics, or changes in water chemistry and olfactory cues (Banks 1969; Berdahl et al. 2017; Bett and Hinch 2016; Hansen and Jonsson 1991; Jonsson et al. 2007; Thorstad et al. 2008), which have shown to affect migration behaviour, could not be included in the model generation.

The observed migration strategy and behaviours of the studied sea trout populations highlight the plasticity of sea trout spawning migrations and life histories. The results of the study provide important information on how prevailing environmental conditions and migration distances influence movements of migrating sea trout in large, unregulated river systems, and in high-latitude rivers. The observed behavioural adaptations have developed independently in these high-latitude river systems, suggesting that similar adaptations could be observed in other northern river systems as well. Further investigation into the mechanisms influencing these adaptations is needed to improve our knowledge of how these adaptations influence life history, fitness, and survival of sea trout populations.

## 5 | Management Implications and Further Research

The results of this study provide important information on habitat utilisation, migration timing and the influence of river conditions for upstream movements of sea trout. These findings will not only inform management of the studied populations but also offer relevant implications for management of trout populations in watercourses with similar environmental conditions. Temperature and discharge conditions were highly influential for trout migration speed; therefore, environmental monitoring data could be utilised for dynamic fisheries management to allow trout to take advantage of optimal migration conditions by restricting fishing during these periods. Targeted fishing restrictions should also be implemented at (and in adjacency to) important wintering habitats and spawning tributaries, where trout migration speed was lowest and where trout presumably are more likely to be caught. Protecting wintering areas in early summer and the start of the fishing season would be especially important to limit fishing related mortality since these areas are repeatedly used across life stages as eventual spawners, immature trout, and spawned kelts are all inhabiting these freshwater habitats during this period. Protecting trout later in the migration as trout enter spawning tributaries is also of importance, since trout migration speed decreased further upstream which could lead to trout being more prone to be caught. These measures are especially relevant for populations that have suffered from declines, such as several populations in Finland which have been classified as endangered (Hyvärinen et al. 2019).

Future research should target expanding the approach of this study to include populations, from different regions, and in rivers of different sizes, allowing comprehensive analysis of how behaviour vary over larger spatiotemporal scales. Information on individual characteristics (maturation stage, energy reserves, genetics etc.) could be included in the analysis to provide valuable information on the migration behaviour. Biotelemetry tracking of migrant sea trout could further improve our understanding of the impact of environmental changes during migrations, by combining telemetry derived information of spatiotemporal movements with tracking of physiological parameters during the migration (Watanabe and Papastamatiou 2023). Additionally, information regarding thermal regulation behaviour (Linnansaari et al. 2023) during the migration will be of major importance to further evaluate the impacts of ambient environmental conditions on migration behaviour. Climactic changes in both riverine and marine habitats are expected to impact the migration of salmonids globally (Arevalo et al. 2021; Crozier et al. 2021; Thorstad et al. 2021). This highlights the need for further behavioural studies to understand population responses to changing conditions, allowing allocation of resources for targeted management efforts.

### Acknowledgements

The authors would like to thank all field personnel at the Natural Resources Institute Finland (Luke), the Swedish University of Agricultural Science (SLU), and employees of consultant Olli van der Meer for their contributions to planning and conducting the field work in the Tornio River. Thank you also to Narve Johansen from Tanavassdragets fiskeforvalting (TF) and Mika Linna for their contributions to the field work in the Teno River. Special thanks to the volunteered fishers that assisted in fishing trout.

### Funding

This study was funded by Lapland's Centre for Economic Development, Transport and the Environment, the Finnish–Swedish Transboundary River Commission, the Ministry of Agriculture and Forestry of Finland, the Swedish Agency for Marine and Water Management, the Natural Resources Institute Finland, Kempestiftelserna, the Swedish University of Agricultural Science, Åbo Akademi University, and Svenska Kulturfonden.

### Ethics Statement

Data was collected from previously conducted tagging studies (Huusko et al. 2023; Orell et al. 2017). Catching of a threatened species and fishing outside the regular fishing season was performed under a permit issued by Lapland's Centre for Economic Development, Transport and the Environment Lapland (permits: LAPELY 1579/5713-2007; 1471/5713-2017). All tagging, and handling procedures presented in this study complied with animal welfare laws, guidelines and policies as approved by the Regional State Administrative Agency for Southern Finland (permits: ESAVI/1170/04.10.03/2011; ESAVI/3109/04.10.07/2015 & ESAVI/9500/2020).

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

All data that support the findings of this study will be published in Mendeley Data, V1, DOI: https://doi.org/10.17632/6w9c6c7sst.1.

## References

Arevalo, E., A. Maire, S. Tétard, et al. 2021. "Does Global Change Increase the Risk of Maladaptation of Atlantic Salmon Migration Through Joint Modifications of River Temperature and Discharge?" *Proceedings of the Royal Society B* 288: 20211882. https://doi.org/10.1098/rspb.2021.1882.

Banks, J. W. 1969. "A Review of the Literature on the Upstream Migration of Adult Salmonids." *Journal of Fish Biology* 1: 85–136. https://doi.org/10.1111/j.1095-8649.1969.tb03847.x.

Berdahl, A., P. A. Westley, and T. P. Quinn. 2017. "Social Interactions Shape the Timing of Spawning Migrations in an Anadromous Fish." *Animal Behaviour* 126: 221–229. https://doi.org/10.1016/j.anbehav.2017.01.020.

Bett, N. N., and S. G. Hinch. 2016. "Olfactory Navigation During Spawning Migrations: A Review and Introduction of the Hierarchical Navigation Hypothesis." *Biological Reviews* 91: 728–759. https://doi.org/10.1111/brv.12191.

Birnie-Gauvin, K., X. Bordeleau, S. J. Cooke, et al. 2021. "Life-History Strategies in Salmonids: The Role of Physiology and Its Consequences." *Biological Reviews* 96: 2304–2320. https://doi.org/10.1111/brv.12753.

Birnie-Gauvin, K., X. Bordeleau, S. H. Eldøy, et al. 2023. "A Review of Iteroparity in Anadromous Salmonids: Biology, Threats and Implications." *Reviews in Fish Biology and Fisheries* 33: 1005–1025. https://doi.org/10.1007/s11160-023-09773-8.

Booth, R. K. 1998. "Swimming Performance of Anadromous Atlantic Salmon, *Salmo salar* L., During their Spawning Migration in the Exploits River, Newfoundland, Canada." Doctor of Philosophy Thesis, University of Waterloo, Ontario. 148.

Brönmark, C., K. Hulthén, P. A. Nilsson, et al. 2014. "There and Back Again: Migration in Freshwater Fishes." *Canadian Journal of Zoology* 92: 467–479. https://doi.org/10.1139/cjz-2012-0277.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer New York. https://doi.org/10.1007/b97636.

Campbell, J. S. 1977. "Spawning Characteristics of Brown Trout and Sea Trout *Salmo trutta* L. in Kirk Burn, River Tweed, Scotland." *Journal of Fish Biology* 11: 217–229. https://doi.org/10.1111/j.1095-8649.1977.tb04115.x.

Cano-Barbacil, C., J. Radinger, M. Argudo, F. Rubio-Gracia, A. Vila-Gispert, and E. Garcia-Berthou. 2020. "Key Factors Explaining Critical Swimming Speed in Freshwater Fish: A Review and Statistical Analysis for Iberian Species." *Scientific Reports* 10: 18947. https://doi.org/10.1038/s41598-020-75974-x.

Crisp, D. T. 1981. "A Desk Study of the Relationship Between Temperature and Hatching Time for the Eggs of Five Species of Salmonid Fishes." *Freshwater Biology* 11: 361–368. https://doi.org/10.1111/j.1365-2427.1981.tb01267.x.

Crozier, L. G., B. J. Burke, B. E. Chasco, D. L. Widener, and R. W. Zabel. 2021. "Climate Change Threatens Chinook Salmon Throughout Their Life Cycle." *Communications Biology* 4: 222. https://doi.org/10.1038/s42003-021-01734-w.

Dadswell, M., A. Spares, J. Reader, et al. 2022. "The Decline and Impending Collapse of the Atlantic Salmon (*Salmo salar*) Population in the North Atlantic Ocean: A Review of Possible Causes." *Reviews in Fisheries Science & Aquaculture* 30: 215–258. https://doi.org/10.1080/23308249.2021.1937044.

Dahl, J., J. Dannewitz, L. Karlsson, E. Petersson, A. Löf, and B. Ragnarsson. 2004. "The Timing of Spawning Migration: Implications of Environmental Variation, Life History, and Sex." *Canadian Journal of Zoology* 82: 1864–1870. https://doi.org/10.1139/z04-184.

Elliott, J. M. 1994. *Quantitative Ecology and the Brown Trout*, 240. Oxford University Press. https://doi.org/10.1093/oso/9780198546788.001.0001.

Elliott, J. M., and M. A. Hurley. 1998. "An Individual-Based Model for Predicting the Emergence Period of Sea Trout Fry in a Lake District Stream." *Journal of Fish Biology* 53: 414–433. https://doi.org/10.1111/j.1095-8649.1998.tb00990.x.

Enders, E. C., D. Boisclair, and A. G. Roy. 2005. "A Model of Total Swimming Costs in Turbulent Discharge for Juvenile Atlantic Salmon (*Salmo salar*)." *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1079–1089. https://doi.org/10.1139/f05-007.

Erkinaro, J., Y. Czorlich, P. Orell, et al. 2019. "Life History Variation Across Four Decades in a Diverse Population Complex of Atlantic Salmon in a Large Subarctic River." *Canadian Journal of Fisheries and Aquatic Sciences* 76: 42–55. https://doi.org/10.1139/cjfas-2017-0343.

Erkinaro, J., F. Økland, K. Moen, E. Niemelä, and M. Rahiala. 1999. "Return Migration of Atlantic Salmon in the River Tana: The Role of Environmental Factors." *Journal of Fish Biology* 55: 506–516. https://doi.org/10.1111/j.1095-8649.1999.tb00695.x.

Farrell, A. P., A. K. Gamperl, J. M. T. Hicks, H. A. Shiels, and K. E. Jain. 1996. "Maximum Cardiac Performance of Rainbow Trout (*Oncorhynchus mykiss*) at Temperatures Approaching Their Upper Lethal Limit." *Journal of Experimental Biology* 199: 663–672. https://doi.org/10.1242/jeb.199.3.663.

Fenkes, M., H. A. Shiels, J. L. Fitzpatrick, and R. L. Nudds. 2016. "The Potential Impacts of Migratory Difficulty, Including Warmer Waters and Altered Discharge Conditions, on the Reproductive Success of Salmonid Fishes." *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology* 193: 11–21. https://doi.org/10.1016/j.cbpa.2015.11.012.

Ferguson, A., T. E. Reed, T. F. Cross, P. McGinnity, and P. A. Prodöhl. 2019. "Anadromy, Potamodromy and Residency in Brown Trout *Salmo trutta*: The Role of Genes and the Environment." *Journal of Fish Biology* 95: 692–718. https://doi.org/10.1111/jfb.14005.

Finstad, A. G., F. Økland, E. B. Thorstad, and T. G. Heggberget. 2005. "Comparing Upriver Spawning Migration of Atlantic Salmon *Salmo salar* and Sea Trout *Salmo trutta*." *Journal of Fish Biology* 67: 919–930. https://doi.org/10.1111/j.0022-1112.2005.00792.x.

Foldvik, A., E. M. Ulvan, and T. Næsje. 2024. "Optimal Timing of Return Migration in Atlantic Salmon." *Fish and Fisheries* 25: 429–440. https://doi.org/10.1111/faf.12816.

Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. Third ed. Sage. https://www.john-fox.ca/Companion/.

García-Vega, A., J. F. Fuentes-Pérez, P. M. Leunda Urretabizkaia, J. Ardaiz Ganuza, and F. J. Sanz-Ronda. 2022. "Upstream Migration of Anadromous and Potamodromous Brown Trout: Patterns and Triggers in a 25-Year Overview." *Hydrobiologia* 849: 197–213. https://doi.org/10.1007/s10750-021-04720-9.

Gargan, P. G., W. R. Poole, and G. Forde. 2006. "A Review of the Status of Irish Sea Trout Stocks." In *Sea Trout: Biology, Conservation and Management*, 25–44. Blackwell Publishing Ltd. https://doi.org/10.1002/9780470996027.ch3.

Hansen, L. P., and B. Jonsson. 1991. "Evidence of a Genetic Component in the Seasonal Return Pattern of Atlantic Salmon, *Salmo salar* L." *Journal of Fish Biology* 38: 251–258. https://doi.org/10.1111/j.1095-8649.1991.tb03111.x.

Hartig, F. 2022. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models." R package version 0.4.6. http://florianhartig.github.io/DHARMa/.

Hastie, T., and R. Tibshirani. 1990. *Generalized Additive Models*, 352. John Wiley & Sons, Inc.

Hastie, T. J. 2017. *Statistical Models in S*. 1st ed, 624. Routledge. https://doi.org/10.1201/9780203738535.

Houston, A. I., and J. M. McNamara. 1999. *Models of Adaptive Behaviour: An Approach Based on State*, 378. Cambridge University Press.

Huusko, R., G. Hellström, M. Jaukkuri, S. Palm, and A. Romakkaniemi. 2023. "Spawning Migration of Salmon and Sea Trout in the Tornio River." In *Natural Resources and Bioeconomy Studies*, vol. 29, 53. Natural Resources Institute Finland, Swedish University of Agricultural Sciences.

Hyvärinen, E., A. K. Juslén, E. Kemppainen, A. Uddström, and U. M. Liukko. 2019. *Suomen lajien uhanalaisuus 2019-Punainen kirja: The 2019 Red List of Finnish Species*, 704. Ympäristöministeriö & Suomen ympäristökeskus.

Jensen, A. J., O. H. Diserud, B. Finstad, P. Fiske, and A. H. Rikardsen. 2015. "Between-Watershed Movements of Two Anadromous Salmonids in the Arctic." *Canadian Journal of Fisheries and Aquatic Sciences* 72: 855–863. https://doi.org/10.1139/cjfas-2015-0015.

Jensen, A. J., B. Finstad, and P. Fiske. 2019. "The Cost of Anadromy: Marine and Freshwater Mortality Rates in Anadromous Arctic Char and Brown Trout in the Arctic Region of Norway." *Canadian Journal of Fisheries and Aquatic Sciences* 76: 2408–2417. https://doi.org/10.1139/cjfas-2018-0428.

Jensen, A. J., B. Finstad, P. Fiske, N. A. Hvidsten, A. H. Rikardsen, and L. Saksgård. 2012. "Timing of Smolt Migration in Sympatric Populations of Atlantic Salmon (*Salmo salar*), Brown Trout (*Salmo trutta*), and Arctic Char (*Salvelinus alpinus*)." *Canadian Journal of Fisheries and Aquatic Sciences* 69: 711–723. https://doi.org/10.1139/f2012-005.

Jensen, A. J., B. O. Johnsen, and L. P. Hansen. 1989. *Effect of River Discharge and Water Temperature on the Upstream Migration of Adult Atlantic Salmon Salmo salar L. in the River Vefsna, northern Norway. In Salmonid Migration and Distribution Symposium*, 140–146. University of Washington.

Jensen, J. L. A., and A. H. Rikardsen. 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: 735–749. https://doi.org/10.1111/j.1095-8649.2012.03343.x.

Jobling, M. 1995. "Fish Bioenergetics." *Oceanographic Literature Review* 9: 785.

Jones, N. E., and I. C. Petreman. 2015. "Environmental Influences on Fish Migration in a Hydropeaking River." *River Research and Applications* 31: 1109–1118. https://doi.org/10.1002/rra.2810.

Jonsson, B. 1985. "Life History Patterns of Freshwater Resident and Sea-Run Migrant Brown Trout in Norway." *Transactions of the American Fisheries Society* 114: 182–194.

Jonsson, B., and N. Jonsson. 1993. "Partial Migration: Niche Shift Versus Sexual Maturation in Fishes." *Reviews in Fish Biology and Fisheries* 3: 348–365. https://doi.org/10.1007/BF00043384.

Jonsson, B., and N. Jonsson. 2009a. "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 Discharge." *Journal of Fish Biology* 75: 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x.

Jonsson, B., and N. Jonsson. 2009b. "Migratory Timing, Marine Survival and Growth of Anadromous Brown Trout *Salmo trutta* in the River Imsa, Norway." *Journal of Fish Biology* 74: 621–638. https://doi.org/10.1111/j.1095-8649.2008.02152.x.

Jonsson, B., and N. Jonsson. 2011. *Ecology of Atlantic Salmon and Brown Trout: Habitat as a Template for Life Histories. Fish & Fisheries Series*. Vol. 33, 708. Springer. https://doi.org/10.1007/978-94-007-1189-1_1.

Jonsson, B., N. Jonsson, and L. P. Hansen. 2007. "Factors Affecting River Entry of Adult Atlantic Salmon in a Small River." *Journal of Fish Biology* 71: 943–956. https://doi.org/10.1111/j.1095-8649.2007.01555.x.

Jonsson, B., and J. H. L'Abée-Lund. 1993. "Latitudinal Clines in Life-History Variables of Anadromous Brown Trout in Europe." *Journal of Fish Biology* 43: 1–16. https://doi.org/10.1111/j.1095-8649.1993.tb01175.x.

Jonsson, N., and B. Jonsson. 2002. "Migration of Anadromous Brown Trout *Salmo trutta* in a Norwegian River." *Freshwater Biology* 47: 1391–1401. https://doi.org/10.1046/j.1365-2427.2002.00873.x.

Karppinen, P., J. Erkinaro, E. Niemelä, K. Moen, and F. Økland. 2004. "Return Migration of One-Sea-Winter Atlantic Salmon in the River Tana." *Journal of Fish Biology* 64: 1179–1192. https://doi.org/10.1111/j.0022-1112.2004.00380.x.

Kennedy, R. J., J. Barry, W. Roche, R. Rosell, and M. Allen. 2022. "In-River Behaviour and Freshwater Return Rates of Sea Trout, *Salmo trutta* L., From Two Coastal River Populations." *Journal of Fish Biology* 101: 1008–1020. https://doi.org/10.1111/jfb.15162.

Klemetsen, A. 2013. "The Most Variable Vertebrate on Earth." *Journal of Ichthyology* 53: 781–791. https://doi.org/10.1134/S0032945213100044.

Klemetsen, A., P. A. Amundsen, J. B. Dempson, et al. 2003. "Atlantic Salmon *Salmo salar* L., Brown Trout *Salmo trutta* L. and Arctic Charr *Salvelinus alpinus* (L.): A Review of Aspects of Their Life Histories." *Ecology of Freshwater Fish* 12: 1–59. https://doi.org/10.1034/j.1600-0633.2003.00010.x.

L'Abée-Lund, J. H., B. Jonsson, A. J. Jensen, et al. 1989. "Latitudinal Variation in Life-History Characteristics of Sea-Run Migrant Brown Trout *Salmo trutta*." *Journal of Animal Ecology* 58: 525–542. https://doi.org/10.2307/4846.

Lähteenmäki, L., R. Huusko, G. Hellström, M. Snickars, and A. Romakkaniemi. 2025. "Two-Year Spawning Migration as a Life-History Strategy of Sea Trout (*Salmo trutta* L.) in Large, High-Latitude River Systems." *Ecology of Freshwater Fish* 34: e70002. https://doi.org/10.1111/eff.70002.

Lähteenmäki, L., P. Orell, A. Romakkaniemi, and M. Snickars. 2023. "Spawning Migration Behaviour of Sea Trout (*Salmo trutta* L.) in a Boreal River System: Effects of Discharge Conditions and Obstacles on Migratory Activity." *Journal of Fish Biology* 102: 479–491. https://doi.org/10.1111/jfb.15286.

Lee, C. G., A. P. Farrell, A. Lotto, S. G. Hinch, and M. C. Healey. 2003. "Excess Post-Exercise Oxygen Consumption in Adult Sockeye (*Oncorhynchus nerka*) and Coho (*O. kisutch*) Salmon Following Critical Speed Swimming." *Journal of Experimental Biology* 206: 3253–3260. https://doi.org/10.1242/jeb.00548.

Linnansaari, T., A. M. O'Sullivan, C. Breau, et al. 2023. "The Role of Cold-Water Thermal Refuges for Stream Salmonids in a Changing Climate—Experiences From Atlantic Canada." *Fishes* 8: 471. https://doi.org/10.3390/fishes8090471.

MacNutt, M. J., S. G. Hinch, C. G. Lee, et al. 2006. "Temperature Effects on Swimming Performance, Energetics, and Aerobic Capacities of Mature Adult Pink Salmon (*Oncorhynchus gorbuscha*) Compared With Those of Sockeye Salmon (*Oncorhynchus nerka*)." *Canadian Journal of Zoology* 84: 88–97. https://doi.org/10.1139/z05-181.

Miettinen, A., S. Palm, J. Dannewitz, et al. 2021. "A Large Wild Salmon Stock Shows Genetic and Life History Differentiation Within, but Not

Between, Rivers.” *Conservation Genetics* 22: 35–51. https://doi.org/10.1007/s10592-020-01317-y.

Nall, G. H. 1930. *The Life of the Sea Trout*. Seeley, Service & Company Limited.

Ojanguren, A. F., and F. Brañta. 2000. “Thermal Dependence of Swimming Endurance in Juvenile Brown Trout.” *Journal of Fish Biology* 56: 1342–1347. https://doi.org/10.1111/j.1095-8649.2000.tb02147.x.

Økland, F., J. Erkinaro, K. Moen, et al. 2001. “Return Migration of Atlantic Salmon in the River Tana: Phases of Migratory Behaviour.” *Journal of Fish Biology* 59: 862–874. https://doi.org/10.1111/j.1095-8649.2001.tb00157.x.

Orell, P., J. Erkinaro, T. Kanniainen, and J. Kuusela. 2017. “Migration Behavior of Sea Trout (*Salmo trutta*, L.) in a Large Sub-Arctic River System: Evidence of a Two-Year Spawning Migration.” In *Sea Trout: Science and Management: Proceedings of the 2nd International Sea Trout Symposium*, 396–410. Matador.

Östergren, J., and P. Rivinoja. 2008. “Overwintering and Downstream Migration of Sea Trout (*Salmo trutta L.*) Kelts Under Regulated Flows—Northern Sweden.” *River Research and Applications* 24: 551–563. https://doi.org/10.1002/rra.1141.

Palm, S., A. Romakkaniemi, J. Dannewitz, et al. 2019. *Tornionjoen lohi-, meritaimen- ja vaellussiikakannat – yhteinen ruotsalais-suomalainen biologinen selvitys sopivien kalastussääntöjen arvioimiseksi vuodelle 2019*, 55. Sveriges lantbruksuniversitet.

Power, G. 1981. “Stock Characteristics and Catches of Atlantic Salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in Relation to Environmental Variables.” *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1601–1611. https://doi.org/10.1139/f81-210.

Quinn, T. P., and D. J. Adams. 1996. “Environmental Changes Affecting the Migratory Timing of American Shad and Sockeye Salmon.” *Ecology* 77: 1151–1162. https://doi.org/10.2307/2265584.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Rikardsen, A. H., D. Righton, J. F. Strøm, et al. 2021. “Redefining the Oceanic Distribution of Atlantic Salmon.” *Scientific Reports* 11: 12266. https://doi.org/10.1038/s41598-021-91137-y.

Rikardsen, A. H., J. E. Thorpe, and J. B. Dempson. 2004. “Modelling the Life-History Variation of Arctic Charr.” *Ecology of Freshwater Fish* 13: 305–311. https://doi.org/10.1111/j.1600-0633.2004.00070.x.

Robards, M. D., and T. P. Quinn. 2002. “The Migratory Timing of Adult Summer-Run Steelhead in the Columbia River Over Six Decades of Environmental Change.” *Transactions of the American Fisheries Society* 131: 523–536. https://doi.org/10.1577/1548-8659(2002)131%3C0523:TMTOAS%3E2.0.CO;2.

Rochet, M. J. 2000. “A Comparative Approach to Life-History Strategies and Tactics Among Four Orders of Teleost Fish.” *ICES Journal of Marine Science* 57: 228–239. https://doi.org/10.1006/jmsc.2000.0641.

Salinger, D. H., and J. J. Anderson. 2006. “Effects of Water Temperature and Flow on Adult Salmon Migration Swim Speed and Delay.” *Transactions of the American Fisheries Society* 135: 188–199. https://doi.org/10.1577/T04-181.1.

Stuart, T. A. 1958. *The Migrations and Homing Behaviour of Brown Trout (Salmo trutta L.). Freshwater and Salmon Fisheries Research*, 27. H.M. Stationery Office.

Studenov, I., V. Antonova, N. Chuksina, and S. Titov. 2008. “Atlantic salmon of the Pechora River.” Project Report, SevPINRO, Arkhangelsk, 52.

Svendsen, J. C., A. Koed, and K. Aarestrup. 2004. “Factors Influencing the Spawning Migration of Female Anadromous Brown Trout.” *Journal of Fish Biology* 64: 528–540. https://doi.org/10.1111/j.0022-1112.2004.00319.x.

Thellman, A., K. J. Jankowski, B. Hayden, et al. 2021. “The Ecology of River Ice.” *Journal of Geophysical Research: Biogeosciences* 126: e2021JG006275. https://doi.org/10.1029/2021JG006275.

Thorstad, E. B., D. Bliss, C. Breau, et al. 2021. “Atlantic Salmon in a Rapidly Changing Environment—Facing the Challenges of Reduced Marine Survival and Climate Change.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 2654–2665. https://doi.org/10.1002/aqc.3624.

Thorstad, E. B., F. Økland, K. Aarestrup, and T. G. Heggberget. 2008. “Factors Affecting the Within-River Spawning Migration of Atlantic Salmon, With Emphasis on Human Impacts.” *Reviews in Fish Biology and Fisheries* 18: 345–371. https://doi.org/10.1007/s11160-007-9076-4.

Videler, J. J., and D. Weihs. 1982. “Energetic Advantages of Burst-And-Coast Swimming of Fish at High Speeds.” *Journal of Experimental Biology* 97: 169–178. https://doi.org/10.1242/jeb.97.1.169.

Waldman, J. R., and T. P. Quinn. 2022. “North American Diadromous Fishes: Drivers of Decline and Potential for Recovery in the Anthropocene.” *Science Advances* 8: eabl5486. https://doi.org/10.1126/sciadv.abl5486.

Watanabe, Y. Y., and Y. P. Papastamatiou. 2023. “Biologging and Biotelemetry: Tools for Understanding the Lives and Environments of Marine Animals.” *Annual Review of Animal Biosciences* 11: 247–267. https://doi.org/10.1146/annurev-animal-050322-073657.

Werner, E. E., and J. F. Gilliam. 1984. “The Ontogenetic Niche and Species Interactions in Size-Structured Populations.” *Annual Review of Ecology and Systematics* 15: 393–425. https://www.jstor.org/stable/2096954.

Whitlock, R. E., J. Kopra, T. Pakarinen, et al. 2017. “Mark-Recapture Estimation of Mortality and Migration Rates for Sea Trout (*Salmo trutta*) in the Northern Baltic Sea.” *ICES Journal of Marine Science* 74: 286–300. https://doi.org/10.1093/icesjms/fsw152.

Winkler, D. W., C. Jørgensen, C. Both, et al. 2014. “Cues, Strategies, and Outcomes: How Migrating Vertebrates Track Environmental Change.” *Movement Ecology* 2: 1–15. https://doi.org/10.1186/2051-3933-2-10.

Wood, S. N. 2011. “Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models.” *Journal of the Royal Statistical Society (B)* 73: 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Wootton, R. J. 1984. “Introduction: Strategies and Tactics in Fish Reproduction.” In *Fish Reproduction: Strategies and Tactics*, 410. Academic Press.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Sea trout migration characteristics and habitat selection. **Figure S2:** Migration patterns of each radio-telemetry tagged sea trout in the Teno River. **Figure S3:** Migration patterns of each radio-telemetry tagged sea trout in the Tornio River. **Figure S4:** Map of the studied river systems (Tornio River on the left; Teno on right) with pre-spawning wintering locations shown in blue, and spawning habitats in red.