Received: 6 October 2023 | Revised: 8 April 2024 | Accepted: 14 June 2024

DOI: 10.1002/aff2.192

AQUACULTURE, FISH and FISHERIES Open Access WILEY

ORIGINAL ARTICLE

Sea trout (*Salmo trutta*) activity and movement patterns in response to environmental cues in a fjord system

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Funding information
Sveriges Lantbruksuniversitet; Göteborgs jaktsällskap; Stockholms Universitet; Royal Swedish Academy of Sciences

Abstract

As a predatory fish that migrates between freshwater and marine environments, the sea trout (*Salmo trutta*) is important in linking these systems. This study investigated movement patterns of sea trout in a coastal fjord at the Swedish Skagerrak region from August 2018 to January 2019, using acoustic telemetry, while assessing these against environmental variables across different spatial and temporal scales. Six acoustic receivers were deployed in the fjord and a river, which flows into the upper reaches of the fjord, with the aim of detecting 20 sea trout that had been tagged with acoustic transmitters. Sea surface temperature and winds (east–west) affected movement patterns of the sea trout the most, while changes in atmospheric pressure were also important, but to a lesser extent. Sea surface temperature and atmospheric pressure both had a positive relationship with the number of detections, whereas stronger winds from the east (i.e. from land) resulted in more detections than stronger winds from the west (i.e. from the ocean). In addition, interesting diel (day–night) movement patterns were observed for some fish. A significant positive correlation was also discovered between the weight of the fish and the number of detections. This study offers insight in movements of sea trout that use coastal habitats and how environmental conditions can affect movement patterns in a fjord system. To further our understanding of sea trout movement patterns and connectivity, tracking from river, through fjord, out to sea and at a longer time scale with more variation in fish size would be valuable to understand more about the complex movement dynamics of this important species.

KEYWORDS
acoustic telemetry, connectivity, fish, river, *Salmonid*, sea surface temperature, seascape

1 | INTRODUCTION

Monitoring movements of fish is a key approach to understanding their behaviour, and how they are utilising their environment throughout a defined period in space and time (Hussey et al., 2015; Kristensen et al., 2021; Pittman et al., 2014). Fishes' movements are driven by the response to a multitude of environmental factors, such as temperature and salinity, and ecological processes, such as resource availability and predation (Freitas et al., 2021; Kristensen et al., 2018; Rooker et al., 2018). Therefore, it is imperative to understand how changes in the environment could affect movement patterns and connectivity strength of marine organisms.

FIGURE 1 A tagged sea trout in the recovery tank after surgery.

In temperate Northern Europe, the anadromous sea trout (*Salmo trutta*; Figure 1) is an important predatory fish using both fresh- and saltwater environments. Sea trout spawn in freshwater rivers and streams and the young hatch and migrate to the sea where they spend from less than a year up to several years before heading back to freshwater to reproduce; often but not always, they choose to spawn in their natal river (International Council for the Exploration of the Sea (ICES), 2020). On the west coast of Sweden, bordering the Skagerrak Sea, lies the Gullmar Fjord, which is characterised by deep trenches and shallow coastal shelves, comprising many different habitats and a rich biodiversity. Both juvenile and adult sea trout are known to utilise the coastal shallow-water habitats in this region, which likely have a strong functional significance for shelter and prey availability for the sea trout (Perry et al., 2018; Staveley et al., 2017).

In the nearby Baltic Sea, sea trout populations have substantially declined in recent years, most likely due to high exploitation rates and loss of habitat connectivity due to hydropower establishment (Degerman et al., 2012; ICES, 2020; Whitlock et al., 2017). However, more information regarding movement patterns and migration routes is required for better management of this important species (Degerman et al., 2012). In Kattegat, western Sweden, studies on sea trout migrating from river to sea have highlighted important time of day movement patterns as well as distinct mortality rates between years and age groups, potentially linked to river discharge (Aldvén et al., 2015). In the Skagerrak region around Denmark and Norway, much research has been conducted on sea trout movement patterns in relation to their migration routes between freshwater and the marine environment (Jensen et al., 2014; Kristensen et al., 2019). For instance, larger sea trout individuals were found to embark on longer sea migrations when compared to younger cohorts, probably linked to prey availability (Jensen et al., 2014; Knutsen et al., 2001). In Norway, some sea trout return to freshwater where they spend the colder winter months and subsequently return to the sea in summer (Thorstad et al., 2016), whereas other individuals stay in marine waters during winter and only migrate upstream to reproduce in freshwater during late summer and autumn; thus, this species shows individualistic behavioural patterns. To date, little research has been conducted on sea trout in the Swedish Skagerrak, especially in regard to movement patterns and connectivity.

This study aimed to reveal insight into the movements of younger sea trout that spend time within coastal environments. Specifically, using acoustic telemetry methods, multiple spatiotemporal scales (1–10 s/km; hours to months) were observed in order to further understand the connectivity of the sea trout and how the environment is influencing movements in a coastal fjord in western Sweden.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in the Gullmar Fjord on the Swedish Skagerrak coast (Figure 2). The main study area was at the mouth of the fjord (south-western part), whereas the outflow section of the major river Örekilsälven (in the interior, north-eastern part of the fjord) was part of the study design. The main inflow of freshwater into the fjord comes from this river, which is among the largest rivers on the Skagerrak coast. The surface water salinity varies between 15 and 25 PSU (practical salinity unit), whereas the sea temperature reaches about 20°C in summer and can be as low as 0°C during winter (Kristiansen & Aas, 2015; Pihl & Rosenberg, 1982). This part of Sweden is subjected to tides two times per day, where the amplitude is on average approximately 20 cm, and up to 35 cm during spring tides (Source: SMHI). Winds and atmospheric pressure also influence the water level in the area; the mean maximum water level is +95 cm, and the mean minimum is −70 cm (Sjöfartsverket, 2018).

2.2 | Acoustic telemetry setup

Five acoustic receivers (VR2; A–E) were placed just inside the southern side of the fjord (Figure 2). As sea trout are anadromous, an additional receiver (VR2W; F) was placed in a connected river, namely Örekilsälven, to observe possible spawning migrations or overwintering in freshwater (Figure 2). Range testing using the same receivers and types of transmitters had previously been conducted within the study area (Staveley et al., 2019). The mean detection range for receivers in unvegetated areas was 216 m, and in vegetated areas (i.e. eelgrass), it ranged between 94 and 114 m, depending on depth. This highlights the effect that underwater vegetation can have on signal range (Melnychuk, 2012; Swadling et al., 2020). The receiver array was deployed in the fjord (4.5–20 m depth) and river (2.5 m), where the receivers floated 1.5 m above the bottom using sub-surface and surface buoys (Table 1). The study ran from the 20 August 2018 to the 25 January 2019. Noteworthy is that an additional set of acoustic receivers was originally placed across the mouth of the fjord to detect seaward movement, but unfortunately due to severe winter storms, these receivers moved, and some not retrieved; therefore, subsequent data could not be used in this study.

Twenty sea trout were caught using a beach seine net (30 m in length, a maximum height of 3.5 m and a mesh size of 1 cm) that was deployed by boat and hauled onto land close to Kristineberg Centre

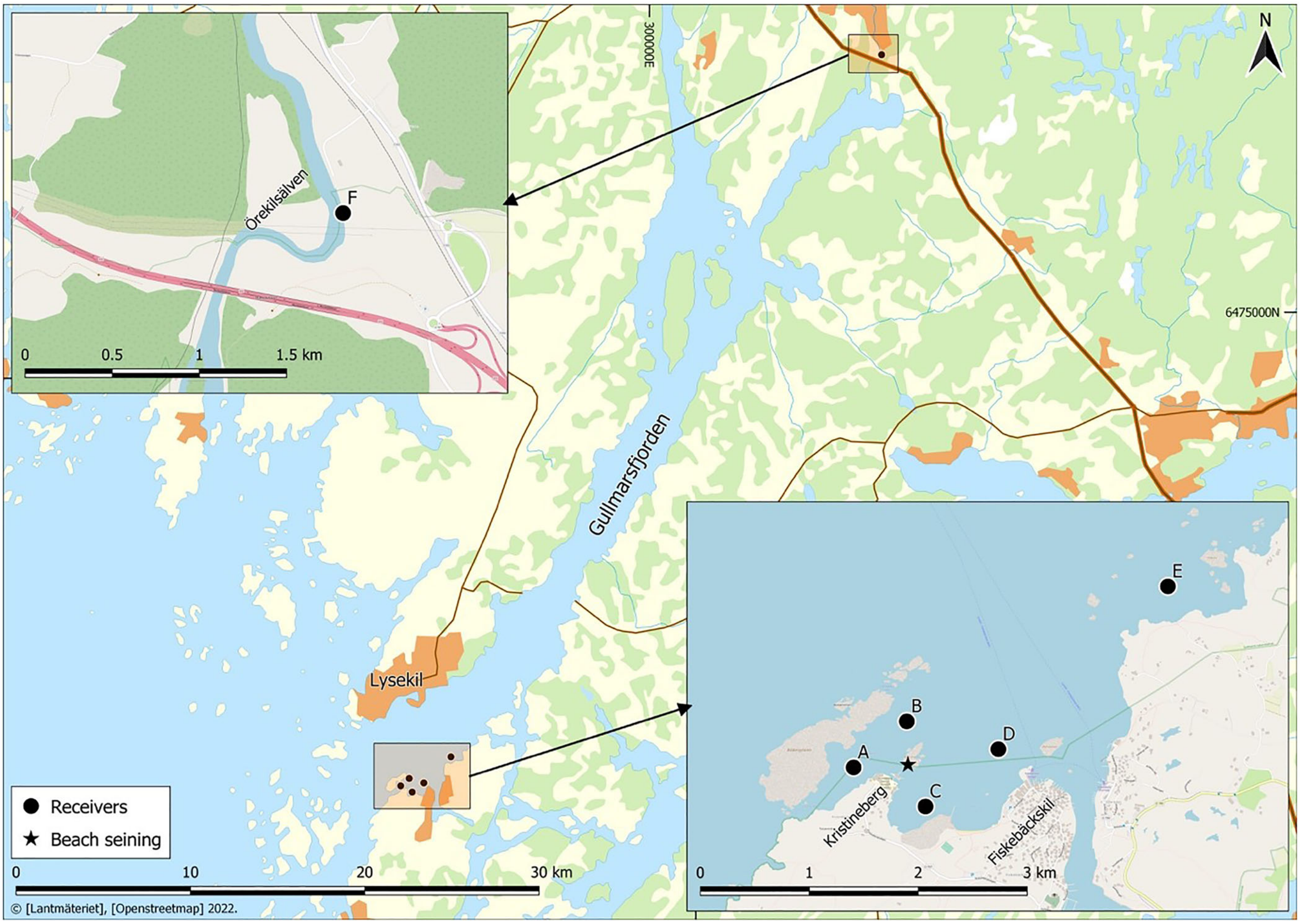

FIGURE 2 Acoustic telemetry receiver placements (A–F) in the area of the Gullmar Fjord, Sweden. The capture of the sea trout was located at the star (inset, bottom right). Kristineberg refers to Kristineberg Centre for Marine Research and Innovation.

TABLE 1 Receiver and detection information of the six receivers.

Receiver name	Model	Longitude	Latitude	Depth (m)	No. of detections	Placement
A	VR2	11.44321	58.24974	4.5	132,988	Fjord
B	VR2	11.44720	58.25217	13	25,159	Fjord
C	VR2	11.44891	58.24842	5	169,740	Fjord
D	VR2	11.45501	58.25138	20	8085	Fjord
E	VR2	11.46899	58.25802	11	221	Fjord
F	VR2W	11.69190	58.44650	2.5	0	River

for Marine Research and Innovation (Figure 2). Fishing was performed during 06:00–08:00 and 20:00–22:00, between the 17 and 20 August 2018. Caught sea trout were stored in covered containers with seawater until transported to the research station and transferred into larger tanks where they were held for a maximum time of 2.5 days before tagging.

All 20 sea trout were surgically implanted with ID-LP7 transmitters (Thelma Biotel; 17 mm long and weighed 1.1 g in water; frequency of 69 kHz; ping interval of 30–90 s). The battery was estimated to last 150 days with an automatic off-switch set to 180 days after start. Before surgery, fish were sedated with the anaesthetic MS-222 (0.1 g/L of seawater). A small incision of approximately 1 cm was made off-centre on the ventral side of the fish, between the pectoral and pelvic fins. The transmitter was sterilised and then inserted into the gut-cavity. The incision was closed with one suture and a surgeon's knot. The fish were placed into a recovery tank with running seawater until being released back into the sea (approximately 150 m from the area where caught) (Figure 1). All fish showed good signs of recovery and swam away effortlessly in a natural manner. During the study period, one transmitter failed to be detected by any receivers and not used further in the study; consequently, 19 fish were used in the analyses.

2.3 | Data analysis

Receivers were retrieved from the study area on the 25 January 2018. Detection data were downloaded and organised; non-study transmitter IDs were removed as well as likely false detections (i.e. single detections occurring within a 24-h period; Reubens et al., 2013) and adjusted for time drift. The first day of recorded detections was removed to account for handling stress and possible release trauma (Knickle & Rose, 2014).

The residency index (RI) is a measurement of the number of days the fish had been observed in the study area divided by the total number of days it had a possibility of being detected, that is the number of days in the study. RI is therefore a ratio between the number of days detected and the number of days the monitoring occurred (Espinoza et al., 2015). Average detections per day were also included in the correlation tests and used to quantify a degree of activity, for example how much a fish had been moving inside the study area if it was detected by receivers. This was calculated as the number of total detections throughout the study period divided by the number of days the fish had been observed in the study area. Spearman's rank correlation tests were used to determine relationships between the length or weight of fish and the average number of detections and the RI value.

In order to compare acoustic detections with environmental variables, weather data were retrieved from the long-term monitoring at Kristineberg located inside the study site. Data of atmospheric pressure (hPa), photosynthetically active radiation (PAR; μmol/m^2/s), sea level (mm), wind direction (°), wind speed (m/s) and sea surface temperature (SST; °C) were downloaded and averaged into daily (24 h) values. Wind speed and wind direction were modified into variables that measure a combination of speed and direction of the east-westerly (on- and offshore) and north-southerly (along shore) winds. Moon-illumination data (linked to potential movement patterns) were downloaded from timeanddate.com (2019). Additional information regarding the calculated moon illumination and wind speed and direction can be found in Supporting Information 1.

The number of daily detections was analysed using general linear mixed models (GLMMs), where environmental variables were classed as fixed and individual fish were classed as random factors. Prior to analyses, environmental predictor variables were transformed as necessary. Wind speed and PAR were log-transformed to assume normality. Predictor variables were tested for collinearity using the variance inflation factor (VIF), where only those with a score <3 were included in the models (i.e. SST, atmospheric pressure, wind speed and direction from east-west, wind speed and direction from north–south, and moon illumination). The variables PAR and sea level failed to reach the VIF cut-off score and therefore were omitted from further analyses. Daily detections were modelled with a zero-inflated negative binomial distribution and a log link in relation to the predictor variables above. If an individual left the study area at an early stage, not enough movement data could be gathered and used; therefore, an RI-limit was set at ≤0.02 (i.e. 3 or less days) and fish with lesser values were removed from the GLMM analysis (see Table 2). In this part of the analysis, each individual fish's detections were grouped into daily bins, covering the total number of detections from 00:00 to 23:59 UTM.

All analyses were performed in R version 3.6.1 (R core team, 2019) with packages 'Devtools' (Wickham & Chang, 2019), 'moments' (Komsta & Novomestky, 2015) 'car' (Fox & Weisberg, 2018), 'glmmTMB' (Brooks et al., 2017), 'bbmle' (Bolker & Team, 2017) and 'ggplot2' (Wickham, 2016). Statistical significance for all tests was based on a *p*-value of <0.05.

3 | RESULTS

3.1 | General patterns

From the 20 August 2018 to the 25 January 2019, 336,193 detections were recorded from the 19 successfully tagged sea trout. The fish with the lowest RI (017, RI = 0.01) failed to be detected after release, whereas the fish with the highest RI (004, RI = 0.89) was detected until the middle of January 2019 (Table 2; Figure 3). The average RI for all fish was 0.21, equivalent to being monitored for 31.5 days.

3.2 | Size-detection relationships

The majority of individuals had a total length of 21.5–28.5 cm (mean total length ± SD = 26.1 ± 1.9 cm) with a weight range of 108–236 g (mean weight ± SD = 177 ± 40 g). One sea trout (020) was much larger than the other specimens, with a total length of 52.5 cm and a weight of 1283 g (Table 2).

A significant positive correlation was found between the weight of the fish and the average number of detections (Table 3). This indicates that fish that weighed more were detected more often. No relationships were found between the weight or length of the fish and the RI (Table 3).

3.3 | Day–night patterns

Day–night movement patterns between specific areas were also discovered (Figure 4). For example, crepuscular movements (during sunset and sunrise) could clearly be observed from fish 005, which resided at receivers A and B during the day and moved to receiver C at night (Figure 4a). In contrast, some individuals exhibited much more stationary behaviour (Figure 4b). Statistical analyses were not performed on these diel patterns due to relatively low amounts of data. Nonetheless, important patterns were observed, highlighting individual connectivity traits of sea trout at specific spatiotemporal scales (e.g. 100 s/m; hourly daily).

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TABLE 2 Summary of information of the 20 tagged sea trout and associated detection details.

Fish ID	Weight (g)	Total length (cm)	Date last of detection	Days detected	Days monitored	RI
001	207	26.6	2018-08-21	2	2	0.01
002*	234	27	2018-09-09	21	21	0.14
003	108	21.5	2018-08-21	2	2	0.01
004*	217	27	2019-01-14	148	133	0.89
005*	236	28.5	2018-11-29	102	102	0.68
006	168	25.5	–	–	–	–
007*	167	25.5	2018-09-28	40	40	0.27
008	183	27	2018-08-21	2	2	0.01
009*	176	25.5	2019-01-02	136	45	0.30
010	144	24.5	2018-08-21	2	2	0.01
011*	108	23	2018-11-10	83	83	0.55
012	169	27	2018-08-24	5	3	0.02
013	199	28	2018-08-21	2	2	0.01
014*	225	28.5	2018-09-17	29	29	0.19
015*	136	24	2018-12-01	104	39	0.26
016*	127	24.5	2018-10-25	67	51	0.34
017	152	26	2018-08-20	1	1	0.01
018*	208	28	2018-09-12	24	24	0.16
019	199	27.5	2018-08-22	3	3	0.02
020*	1283	52.5	2018-09-22	34	34	0.23

Note: Fish ID 006 failed to be detected. The residency index (RI) is a measurement of the number of days the fish had been observed in the study area divided by the total number of days it had a possibility of being detected.
*Individuals that were included in the general linear mixed models (GLMM) analysis.

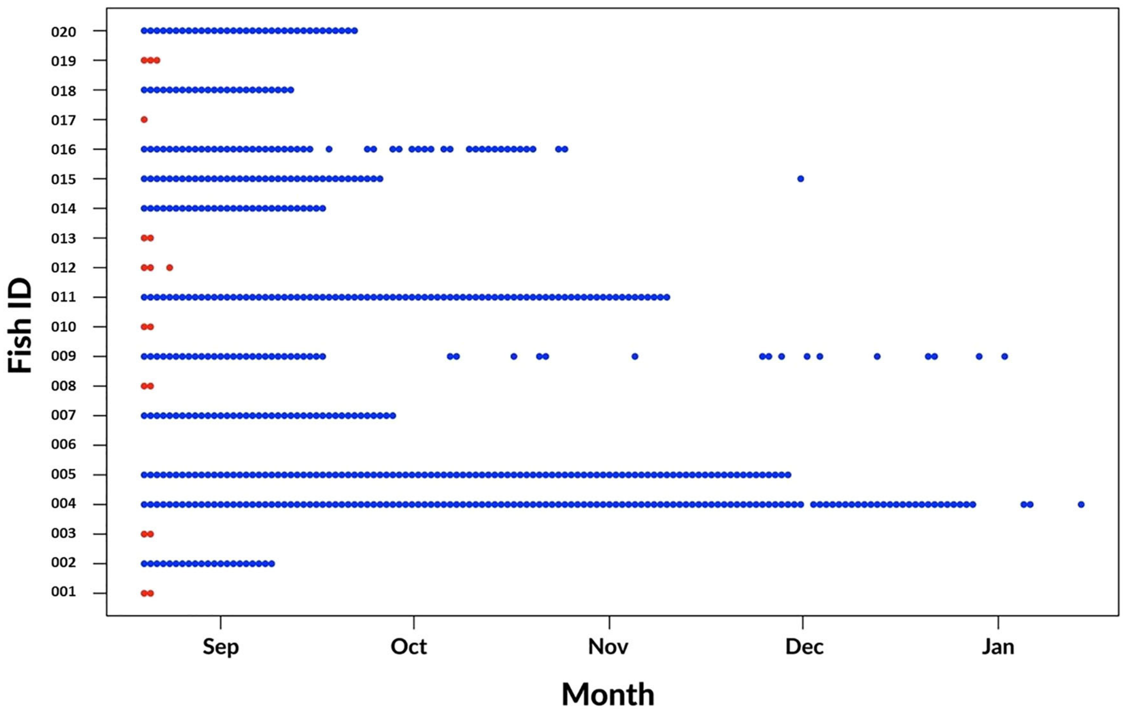

FIGURE 3 A presence plot showing how long each sea trout (Fish ID) was detected in the study area. Each circle represents one day. Blue circles indicate sea trout that were detected for more than 3 days and thus included in the general linear mixed models (GLMM) analysis.

TABLE 3 Correlation results for weight and length of fish against the average detections and residency index.

Response	Predictor	S	p-Value	rho
Weight	*Average detections*	589.52	**0.036**	0.482
	Residency index	976.85	0.558	0.143
Length	*Average detections*	714.38	0.115	0.373
	Residency index	1117.1	0.935	0.020

Note: Significant values ($p < 0.05$) are shown in bold. S = sum of all squared rank differences. Rho = strength of association between the two variables.

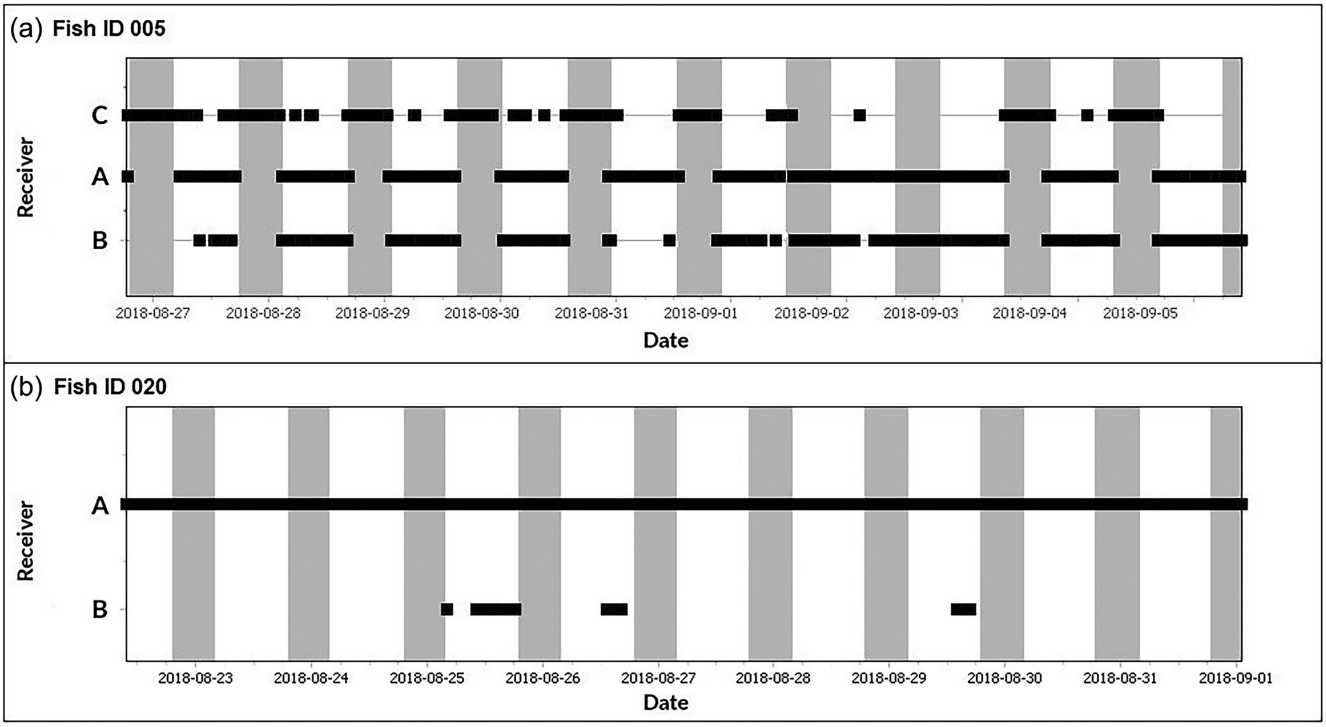

FIGURE 4 Receiver detections of two sea trout specimens, over time, exhibiting (a) diel and (b) stationary behaviour. The vertical white and grey stripes indicate the periods of day and night, respectively.

3.4 | Environmental variables influencing detections

Daily detections plotted against the modelled environmental variables (i.e. SST, atmospheric pressure, wind speed and direction from east–west, wind speed and direction from north–south, and moon illumination) are shown in Figure 5. From the GLMM output, SST and atmospheric pressure were found to positively affect the number of daily detections by sea trout in the Gullmar Fjord (Table 4). Wind speed and direction from the east to west were also significant according to the model, which meant that stronger winds from the east (positive values) resulted in more detections than stronger winds from the west (negative values) (Table 4).

4 | DISCUSSION

This study documented the movements of sea trout in a fjord environment from summer to winter. Various spatiotemporal scales were assessed (1–10 s/km; hours to months), and important information regarding juvenile activity and movement was established.

The most striking results of this study were the strong significance of SST and the east–west winds on the number of detections from the tagged sea trout. This emphasises the importance of such environmental factors and how they can affect the potential movement and connectivity of sea trout in a fjord environment. From an early age, fishes' physiology, morphology and movement are affected by environmental cues. Sea temperature is well documented to influence fish movement (Freitas et al., 2021; Kristensen et al., 2018; Staveley et al., 2019). In salmonids, temperature and light are the main factors that affect development, migration and survival (Björnsson et al., 2011; Drenner et al., 2012); therefore, it was not unsurprising that temperature was a significant factor in regard to sea trout activity in this study. As the water temperature decreases, perhaps thermoregulatory migrations towards shallower and warmer waters further inside the fjord occurred. However, individuals may have also moved slightly outside the detection range or suffered mortality; thus, no longer being detected for the remainder of the study period.

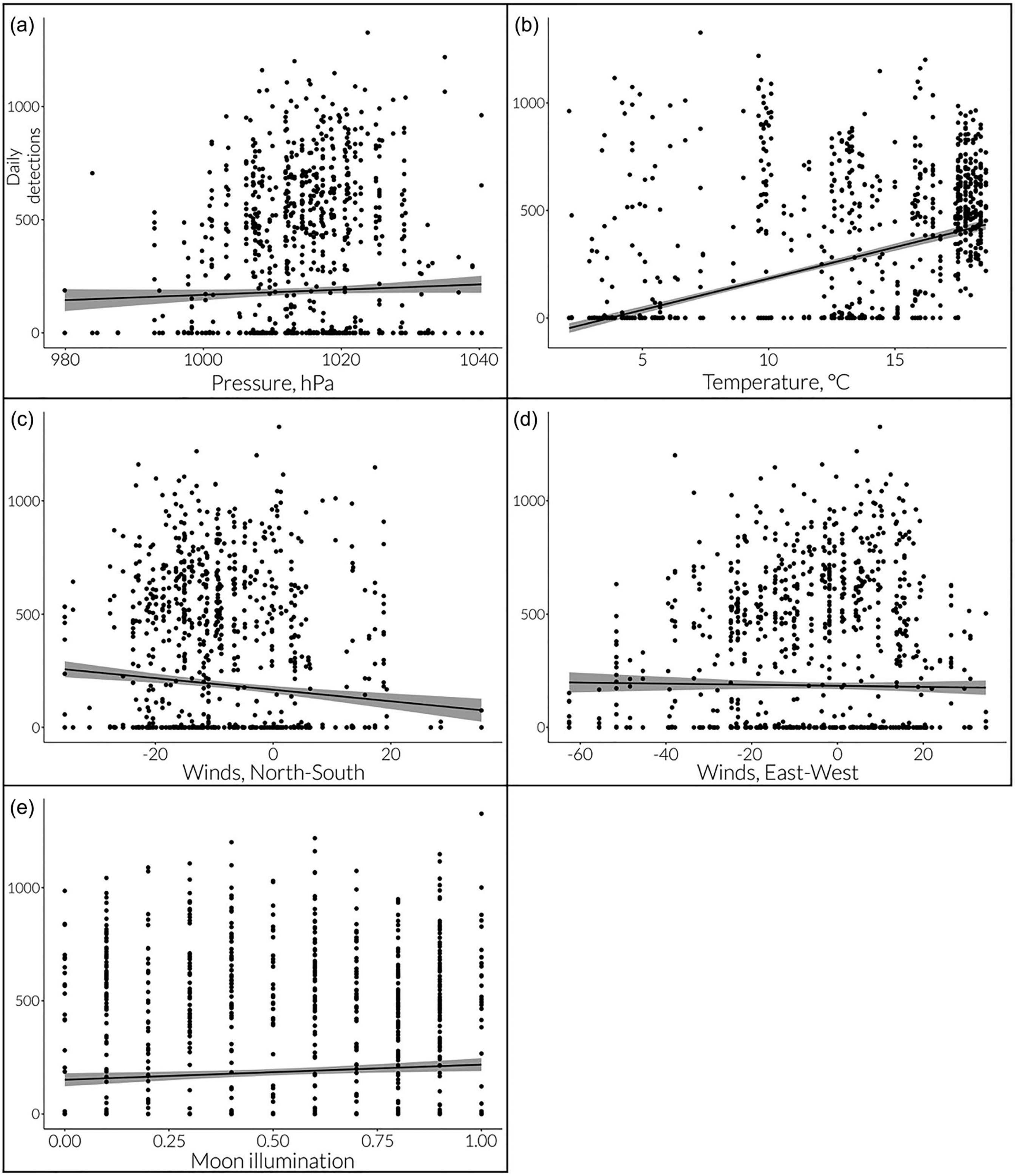

FIGURE 5 Scatterplots with regression lines and confidence intervals for the five weather variables (a–e) and the number of daily detections. The *y*-axis in each plot includes 'daily detections', whereas the *x*-axis contains the five different weather variables. Each plot has 1628 observations, which is a result of one data point being given each of the 148 study days for the 11 fish used in this analysis.

TABLE 4 Model results from the general linear mixed model (GLMM).

Predictor	Estimate	SE	*z*	*p*
SST	0.063	0.010	5.830	**<0.001**
Atmospheric pressure	0.010	0.004	2.122	**0.033**
Wind E–W	0.009	0.002	4.818	**<0.001**
Wind N–S	−0.004	0.003	−1.419	0.155
Moon illumination	0.050	0.108	0.466	0.641

Note: Significant values ($p < 0.05$) are shown in bold.
Abbreviation: SST, sea surface temperature.

Aside from influences of temperature upon sea trout activity and movement patterns, strong winds from the west (i.e. from the ocean) resulted in less detections than strong winds from the east. Even though wind strength is not typically associated with sea trout movements, it was of considerable interest that these significant patterns were found. From other predatory fish in Australia, wind strength has been shown to be a driver for the residing depth, as well as movements within and outside of acoustic arrays (Lédée et al., 2015, 2016). Previous studies have also reported that stronger winds can create better opportunities for predatory fish to catch prey throughout shallower areas and in the littoral zone (Gabel et al., 2011; Lédée et al., 2015). In a study investigating upstream migration of sea trout in Scotland, Ho et al. (2021) reported wind speed to negatively affect catches from fly fishing, which, as they discuss, could have been due to subsequent environmental factors such as higher turbidity, caused by increased wind strength. In addition, wind strength can have a considerable effect on receiver detection ranges (Kessel et al., 2014), which, in this case, may have caused a reduction in detections during stronger winds (i.e. above ca. 20 m/s). However, there were relatively fewer detections outside of this range which is likely due to fewer days with stronger winds as well as that these are predominantly during winter when sea trout might have also left the study area. Nevertheless, further investigations would need to be conducted to determine specific ecological connections in relation to the east–west wind patterns in this region.

Atmospheric pressure was also revealed to be a significant environmental factor that affected the number of detections of sea trout in this study. Here, a greater atmospheric pressure resulted in a significant increase in the number of detections. In contrast, other studies on trout found no significant correlations between atmospheric pressure and detections or movement (Rustadbakken et al., 2004; Schulz & Berg, 1992; Solomon, 1978). However, it was noted that increased swimming activity of trout sometimes occurred just before or during stormy weather, which is often correlated with the change of atmospheric pressure (Schulz & Berg, 1992). Moreover, on the Swedish east coast (on the island of Gotland in the Baltic Sea), sea trout freshwater migrations were shown to be influenced by atmospheric pressure, though it was reported that these findings also could be due to other environmental factors, such as temperature and wind direction (Bystedt, 2012).

The weight of the individual sea trout and the number of detections showed a significant positive correlation, which indicates that heavier fish may be more active or may also be a consequence of being in closer range of receivers. This may be a response that larger (heavier in this case) fish may spend more time in shallower areas, for example, in search of prey and causing intraspecific competition, forcing younger cohorts into more deep, offshore areas (Eldøy et al., 2015). In contrast, weight was not significantly correlated to sea trout residency, which shows that the number of time detected within the study period was irrelevant of fish size.

Diel movement patterns can often be observed in sea trout behaviour, with varying degrees of strength and consistency, depending on season (Eldøy et al., 2017; Haraldstad et al., 2017). Although insufficient data were available to show any significant conclusions regarding diel movement of sea trout in this study, it was apparent that in some cases, strong diel patterns occurred in the shallow-water areas of the fjord. This may offer some insight into local movement patterns within bays, perhaps in relation to seeking shelter or prey resources.

In the studied river, Örekilsälven, no detections were recorded from any of the tagged sea trout. This could be because fish specimens were not in the life stage to begin their migration back to freshwater, or that the tagged sea trout had their natal river elsewhere (as the sea trout in this study were caught near the fjord mouth). Indeed, immature sea trout are often known to return to their freshwater rivers to overwinter (Thorstad et al., 2016). However, as Olsen et al. (2006) reported from the Norwegian Skagerrak, juvenile sea trout were found to spend the winter period in coastal environments, particularly where large river systems are lacking. As sea trout can tolerate marine salinities and near-freezing waters (Thorstad et al., 2016), the benefits of overwintering in marine waters (i.e. increased prey abundance and less risk compared to freshwater migration) may be a likely factor for not choosing to return to the river environments (Olsen et al., 2006; Staveley et al., 2017). Results from this study indicate a few behavioural similarities to the trout of southern Norway, based on some individuals showing winter residency in the fjord; nonetheless, further investigation and longer time series would be necessary to understand movement patterns throughout the river-fjord-sea continuum.

5 | CONCLUSIONS

This study offers insight in the movement patterns of sea trout in a temperate fjord system on the Swedish Skagerrak coast and how contemporary environmental conditions can affect the movement and connectivity. Most strikingly, we found that sea trout movement patterns throughout the coastal seascape were related to SST and wind patterns (in turn linked to weather and climate change). To further our understanding of sea trout movement patterns and connectivity, future studies should track fish (of different size classes) and associated habitat utilisation across wide coastal seascapes – from river, through fjord and complex archipelagos, out to sea – over longer and critical time scales.

AUTHOR CONTRIBUTIONS

Thomas A. B. Staveley: Conceptualisation; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; writing—original draft. **Felix van der Meijs**: Data curation; formal analysis; investigation; methodology; visualization; writing—review and editing.**Martin Gullström**: Conceptualisation; funding acquisition; investigation; project administration; supervision; writing—review and editing.

ACKNOWLEDGEMENTS

This research was funded by Stockholm University and the Swedish University of Agricultural Sciences with additional grants from the Royal Swedish Academy of Sciences and Göteborgs Jagtsällskap. Thanks to the County Administration Board of Västra Götaland for the use of acoustic receivers. Appreciation goes to the staff at Kristineberg Centre for Marine Research and Innovation, University of Gothenburg, for assistance with logistics, boats and technical support throughout the study, as well as access to weather data.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Ethical and catch permits were acquired from the Swedish Board of Agriculture (reference numbers: 131-2014 and 109-2015) and the Swedish Agency for Marine and Water Management (reference number: 2620-18). All authors were certified to handle fish and perform surgery according to national guidelines.

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SUPPORTING INFORMATION

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

How to cite this article: Staveley, T.A.B., van der Meijs, F. & Gullström, M. (2024) Sea trout (*Salmo trutta*) activity and movement patterns in response to environmental cues in a fjord system. *Aquaculture, Fish and Fisheries*, 4, e192. https://doi.org/10.1002/aff2.192