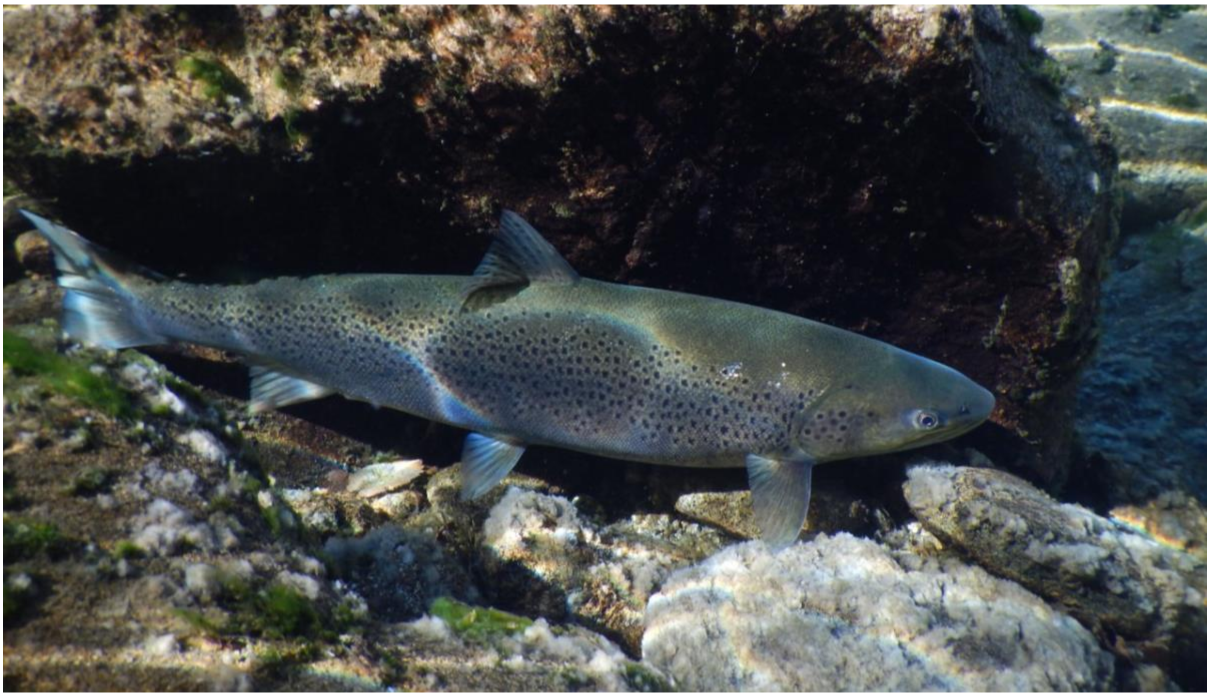
Behaviour of adult sea trout in a regulated lake



by

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Cover photo: adult sea trout in the Aurland watercourse, by Ulrich Pulg

Abstract

Norwegian rivers and lakes are highly regulated for hydropower, which affects freshwater ecosystems and anadromous fish species, such as sea trout (*Salmo trutta*). Lakes provide important habitats for sea trout before, during, and after spawning, however, there is limited knowledge on how hydropower affects the behaviour of sea trout in lakes. To investigate the impacts of hydropower on the behaviour of adult sea trout in lakes, I conducted an acoustic telemetry study using novel acceleration sensors. A total of 31 adult sea trout were captured by angling in river Aurlandselva, Norway, and tagged between July 20 and August 12, 2021. In addition to acceleration sensors, the tags were instrumented with sensors for temperature and depth, which provided information on the sea trout's presence and behaviour in lake Vassbygdevatnet. Results during the spawning migration showed that there was a large prevalence of sea trout in the lake, where sea trout were less active compared to the riverine habitats. The discharge from the high-head storage plant into the lake had a minimal effect on the depth use and activity of sea trout in the lake. However, the results indicated that hydropower regulations were linked to the spatial effect of the depth use and activity of sea trout in the lake. The seasonal increase in activity of sea trout in the lake might indicate that sea trout spawn in the lake, which occurs in several trout populations. Because sea trout exhibit a larger variation of life history strategies compared to Atlantic salmon (*Salmo salar*) and there is likely a niche differentiation between the two species, management efforts based on the ecology of Atlantic salmon can misrepresent the requirements of sea trout populations. Additionally, the large prevalence of spawners in the lake during autumn will likely cause an underestimation of the actual size of the sea trout population in rivers with lakes during annual stock assessment.

Table of contents

1 Introduction

Freshwater comprises only a small fraction of the Earth, yet freshwater habitats are disproportionately threatened by overexploitation, pollution, and regulation (Dudgeon *et al*. 2006; Grill *et al*. 2019; Reid *et al*. 2019; WWF 2020). Salmonids and other species that rely on freshwater are therefore vulnerable (Klemetsen *et al*. 2003), and changes to the rivers and lakes can have substantial impacts on resident and migratory trout populations (Peiman *et al*. 2017; Birnie-Gauvin *et al*. 2018). Hydropower regulations can cause changes to the natural water flow, such as the timing, magnitude, and variability of the water flow (Poff *et al*. 1997; Stanford *et al*. 1996). Hydrological changes affect both the biotic and abiotic environment upstream and downstream of modified areas by altering the movement of sediments and organic resources, availability of habitat types, shelters, and forage opportunities, and the distribution, abundance, and richness of species (Vannote *et al*. 1980; Poff *et al*. 1997; Poff & Hart, 2002). The effects of regulation and modifications of rivers on freshwater fish are frequently studied (e.g., Schwinn *et al*. 2017; Birnie-Gauvin et al. 2018) and restoration interventions (e.g., fishways, barrier removal, gravel augmentation) are increasingly implemented to improve habitat connectivity and quality, among others (e.g., Roni *et al*. 2008; Pulg *et al*. 2011; Koed *et al*. 2019; Pulg *et al*. 2022). In contrast, there is a lack of studies about how hydropower impacts lake habitat for anadromous species (Lennox *et al*. 2021).

Norwegian rivers and lakes are highly exploited to generate hydropower due to a topography with a high abundance of freshwater systems across different altitudes, steep mountains, and high annual precipitation (Alfredsen *et al*. 2022). In contrast to most hydropower regulations around the world that produce energy by implementing physical barriers such as dams and weirs in rivers (Anderson *et al*. 2015; Belletti *et al*. 2020), Norway also utilises high-head storage plants due to the natural topography of mountains (Alfredsen *et al*. 2022). Storage plants exploit the potential energy of water from reservoirs that often discharge into lakes, which are important habitats for anadromous brown trout (or sea trout, hereafter referred to as sea trout, *Salmo trutta*) and Atlantic salmon (*Salmo salar*; Klemetsen *et al*. 2003). The intake of high-head storage plants is often in the deeper part of reservoirs, which results in the transfer of hypolimnetic water (i.e., bottom-layered water) through turbines and into a fjord, river, or a reservoir such as a natural lake or artificial reservoir (Heggenes *et al*. 2021). The hypolimnetic water is approximately 4 ºC and the storage plant will therefore transfer cool water during summer and warm water during winter (Saltveit, 2006; Heggenes *et al*. 2021). More than 30 % of Norwegian rivers have lakes, in which many are highly exploited to generate hydroelectricity (Alfredsen *et al*. 2022).

The Aurland watercourse, Western Norway, consists of two main anadromous river stretches separated by a lake. The watercourse is heavily regulated by several hydropower plants, including Norway's third largest hydropower plant that has an artificial outlet running into the lake Vassbygdevatnet (Aurland 1, high-head storage plant; Ugedal *et al*. 2019). Assessments of the sea trout population in Aurland have concluded that hydropower regulation is the main driver of the continued poor condition of the sea trout population (VRL

2019; VRL 2022). The supply of mountain water from the high-head storage plant affects the natural hydromorphological condition of the lake Vassbygdevatnet as the storage plant transports water from the reservoir that ends up in the lake. Thus, the discharge alters the stratification and water chemistry of the lake, and supplies the lake with allochthonous resources (i.e., resources originating from another location; Ugedal *et al*. 2019; Heggenes *et al*. 2021). An important priority is therefore to investigate how hydropower discharge affects the behaviour of fish in lakes.

A previous tagging study of trout revealed an altered depth behaviour in lake Vassbygdevatnet that was seemingly modified by the discharge into the lake from the high-head storage plant (Lunde, 2014). Alteration of habitats can affect behaviour and accelerate energy depletion of animals (Jeffrey *et al*. 2015), for instance through increased activity. With the novel tool of acceleration sensors, this study aims to provide insight into the lake use and activity of sea trout by measuring their movement in the three spatial axes. By using acoustic transmitters (i.e., tags) with an acceleration sensor, I aimed to test whether adult sea trout in Aurland utilise lake Vassbygdevatnet before spawning and whether their behaviour is affected by discharge from the high-head storage plant. In addition to the acceleration sensor, the tags were instrumented with temperature and depth sensors to reveal patterns and differences in habitat use, depth use, and activity. I hypothesised that: 1) the lake is an important habitat for sea trout before spawning, and that 2) the activity of sea trout differs between the rivers and the lake. To test whether the high-head storage plant affected sea trout behaviour in the lake, I hypothesised that 3) the high-head storage plant discharge alters depth use of sea trout, and 4) the high-head storage plant discharge affects activity of sea trout during the spawning migration.

2 Methods

2.1 Study site

The study was conducted in the Aurland watercourse in Vestland county, Norway (Figure 1). The watercourse consists of the two main rivers, Vassbygdelva and Aurlandselva, that are separated by the lake Vassbygdevatnet. River Vassbygdelva has an anadromous stretch of approximately 4.7 km and runs upstreams into lake Vassbygdevatnet (Ugedal *et al*. 2019). The main sea trout river, Aurlandselva, runs downstream from the lake with a stretch of about 7.8 km before it ends in the fjord Aurlandsfjorden, an arm in the Sognefjord about 170 km from the open ocean. With a length of 3.3 km, the lake covers an area of 1.9 km^2 with an average depth of 42 m and maximum depth of 65 m. The Aurland watercourse has a total anadromous stretch of more than 15 km (Ugedal *et al*. 2019). The watercourse was previously known throughout Norway for its large populations of Atlantic salmon and especially sea trout. However, following the implementation of the hydropower plants, both species' populations exhibited a dramatic decline by the late 1980s (Ugedal *et al*. 2019). Today, the sea trout population dominates while the salmon population is still significantly reduced and has been protected since 1989 (Jensen *et al.* 1993; Pulg *et al.* 2022). Still, the sea trout in the river Aurlandselva attracts anglers and has large recreational value to the anglers and great socio-economic importance to the local community.

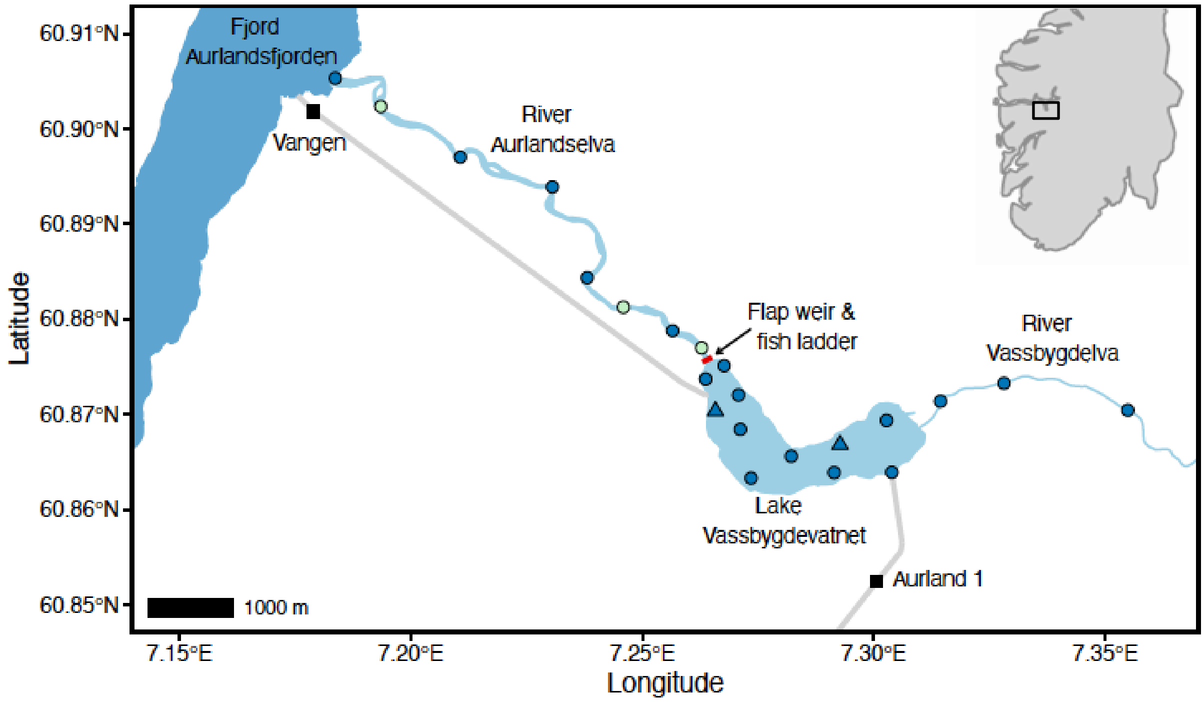

Figure 1. Map of Aurland water system with the location of receivers (circles, triangles) deployed prior (blue) and post (green) tagging, the 'Aurland 1' high-head storage plant, 'Vangen' storage plant, and the flap weir and fish ladder at the outlet of Lake Vassbygdevatnet (red line). Two synchronization transmitters were placed with two of the receivers in the lake (triangles).

2.1.1 Hydropower plant

The implementation of the hydropower system in Aurland began in 1969 and lasted until 1989 (Ugedal *et al.* 2019). Today, the hydropower system consists of five power plants, which together with 14 reservoirs and several tunnels, regulate the Aurland watercourse (Ugedal *et al.* 2019). Two of these power plants directly influence the lake Vassbygdevatnet in Aurland (Figure 1). The 'Aurland 1' plant is a high-head storage plant (850 m in head height, 840 MW) with its outlet running into the southeastern part of Vassbygdevatnet and is the largest station in the watercourse. Aurland 1 constitutes the primary supply of water into the lake by transporting water from the mountain reservoir. Therefore, the lake surface temperature is colder than normal during summer and warmer during the winter, which results in a low thermal stratification of the lake (Ugedal *et al.* 2019). The 'Aurland 4' storage plant (55 m in head height, 38 MW), also known as 'Vangen', has its intake in the western part of lake Vassbygdevatnet that leads to a tunnel running down to the power plant close to the fjord. The intake is at 7-19 m depth and has a diameter of approximately 40 m. The Vangen station is operating from September 15 until the end of April, and during this period a flap weir located in the beginning of the river Aurlandselva is elevated, thereby regulating the water flow downstream in the river (Figure 1). While Vangen is operating, Aurlandselva has a mandatory minimum discharge of 3 m^3/s that is upheld by release of water over the flap weir (Økland *et al*. 1995). The lake functions as a natural reservoir while Vangen is operating. A fish ladder along the flap weir allows for migration between lake and river.

2.1.2 Discharge data

The high-head storage plant, Aurland 1, released an average discharge of 20.97 m^3/s (± 16.95) into the lake during the study period (July 20 - November 14, 2021), with a minimum discharge of 0 m^3/s and a maximum discharge of 108.46 m^3/s (Figure 2). Before the flap weir was elevated, the downstream river, Aurlandselva, had an average discharge of 27 m^3/s (± 10.40) and a minimum and maximum discharge of 3.75 and 51.11 m^3/s, respectively (Figure 2). After the elevation of the flap weir, the average discharge was 4.25 m^3/s (± 0.54), the minimum discharge was 2.96 m^3/s, and the maximum discharge was 8.13 m^3/s in Aurlandselva (Figure 2). Discharge data for the study period were provided by the hydropower company Hafslund ECO (Appendix 11).

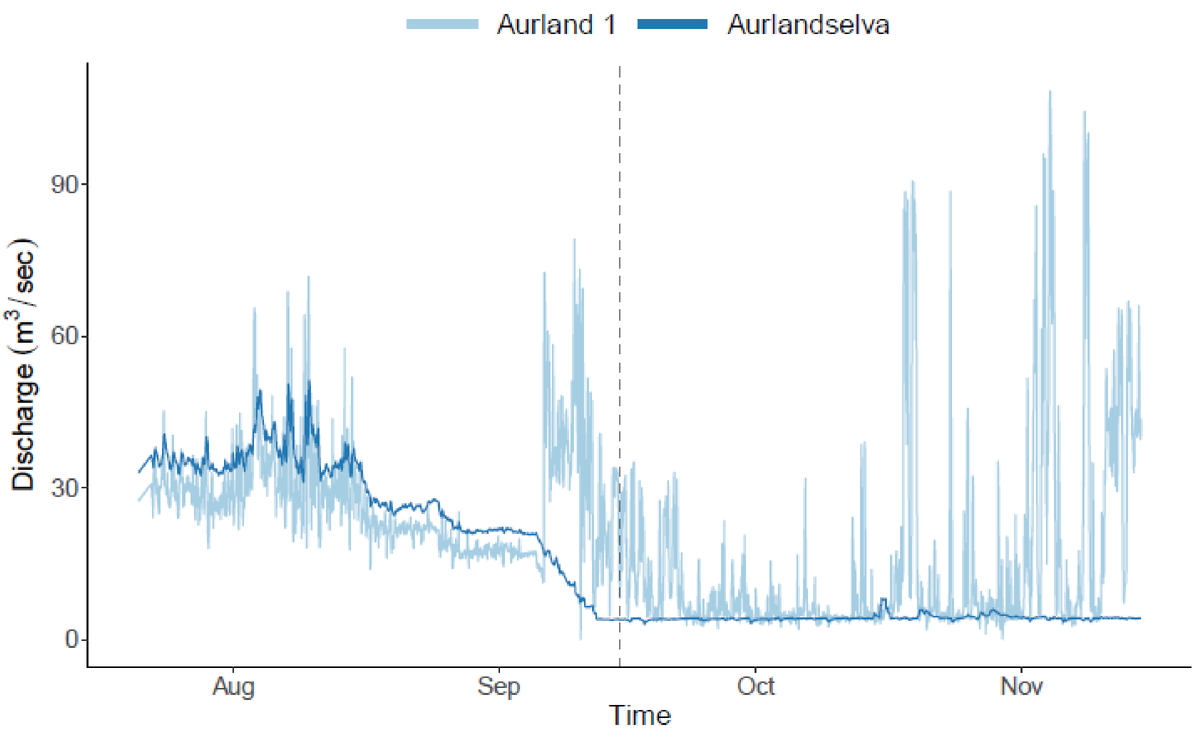

Figure 2. Water discharge (m^3/sec) from the high-head storage plant (Aurland 1) with outlet in lake Vassbygdevatnet, and water discharge in the downstream river (Aurlandselva) during the study period (July 20 - Nov. 14, 2021). Vertical dashed line indicates the elevation of the flap weir (Sep.15).

2.2 Study design

All sea trout were captured, tagged, and released between July 20 and August 12, 2021. Prior to capturing fish, a total of 19 TBR 700 and 700L acoustic receivers (Thelma Biotel AS, Trondheim, Norway) were deployed in the Aurland water system: three in river

Vassbygdelva; five in river Aurlandselva; and eleven in lake Vassbygdevatnet (Figure 1, Appendices 9 & 10). Two synchronizing transmitters ("sync tags") were deployed with two receivers to correct clock drift of the receivers in the lake. Three additional receivers were deployed September 2 in river Aurlandselva after all fish were captured, tagged, and released, to maximize the coverage in the river during the autumn migration and spawning (Figure 1). Data were retrieved from all 22 receivers on November 15 and 16, 2021.

2.3 Sampling

Sea trout were captured by angling along river Aurlandselva and tagged with acoustic transmitters ("tags"), with a total of 31 fish (540 ± 102 mm total length) tagged (Figure 3, Appendix 1). Sea trout were kept in keepnets or tubes for a minimum of 30 minutes to provide a recovery period. Maximum holding time prior to tagging was less than one day for all fish. After tagging, the recovery of all fish was observed for 10 to 15 minutes in keepnets or containers with fresh river water after which the fish were released. To ensure that the tag burden was less than 2 % of body weight (e.g., Jepsen *et al.* 2005; Smircich & Kelly, 2014), the lower weight limit was converted to a lower length limit of fish by using Fulton's condition formula (Robinson *et al.* 2008). The minimum total fish length requirement was set to 38 cm, however, the smallest fish tagged was 41.5 cm in total fish length. Thus, the maximum tag burden was approximately 1.59 % of the fish's body weight. Each sea trout was visually assessed prior to surgery. To avoid selection of sea trout, all captured sea trout in the present study were assessed suitable for tagging, and visible wounds or marks were noted. Every fish was tagged and released close to its capture site (hereafter referred to as tagging site, Figure 3). Approval of the project was given by the Norwegian Food Safety Authority (FOTS, application nr. 23016), and handling and tagging of sea trout was conducted according to the animal welfare regulations. Certification of tagging abilities is provided in Appendix 3.

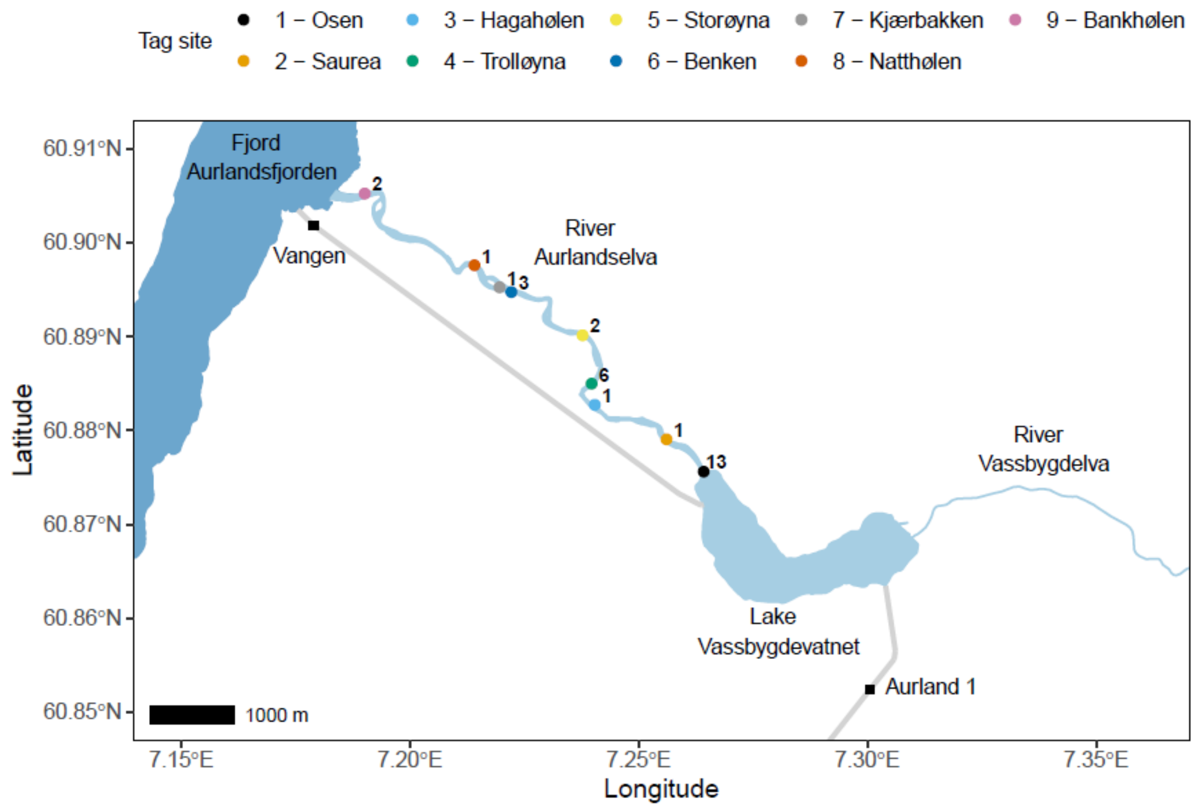

Figure 3. Map of Aurland watercourse and the sites where sea trout were tagged (circles, colour coded) in river Aurlandselva. The number by each site indicates the number of fish tagged at the given site. Tagging sites are numbered from 1 to 9, with tagging site 1 at the confluence and tagging site 9 by the river mouth.

2.4 Tagging procedure

Prior to surgery, each sea trout was anaesthetized with 1.5-2 mL Aqui-S in a container with 50 L water until equilibrium was lost (6-9 min). At the end of the anaesthetic period, a gill sample was taken with scissors sterilized 2 min in bleach, 2 min in distilled water, and 2 min in ethanol. The gill sample was taken for another study and the findings from the sample is therefore not used in the present study. The fish was placed supine in a tube where fork length (mm) and total length (mm) were measured prior to the surgical incision. A silicone tube with running water containing 50 % dose of the anaesthetics was placed in its mouth to maintain anaesthesia and oxygenation during surgery. A 15-18 mm incision was performed with a sterile scalpel approximately 3 cm posterior to the pectoral fins and 1-2 mm from the linea alba. The sterilized acoustic tag was placed into the abdomen, followed by three interrupted sutures to close the incision (Appendix 2). The surgery, including the anaesthetic period, lasted for approximately 16 minutes. The fish was placed into a keepnet or a container with fresh water after which a scale sample was taken (results from scale reading were not used in the present study) and its recovery was supervised for about ten to fifteen minutes before the fish was released.

2.5 Acoustic telemetry

2.5.1 Acoustic transmitters

A 13 mm acoustic tag (LP13-ADT, Thelma Biotel AS, Trondheim, Norway) was surgically implanted in the sea trout. The tag had a length of 33.3 mm, diameter of 13 mm, and weighed 11.5 grams. The acoustic tag generates sound at 150 dB with a frequency of 69 kHz, and at a random time interval between every 60 and 120 sec, which is decoded by passive acoustic receivers. Each sensor in each tag (i.e. each sea trout) has its own unique ID that is registered by the receiver when it detects the transmission. The unique IDs therefore makes it possible to separate the sensors in each tag and each sea trout. In this study, the acoustic tags had three different sensors that measured the acceleration ('activity' is hereafter used as a proxy for acceleration), temperature, and depth. Thus, there were three unique IDs assigned to each specimen. All sea trout are hereafter identified by their first unique sensor ID (e.g., for the first tagged sea trout with ID = 4667, 4668, and 4669, ID = 4667 was used). The sensors in the tags had a range of 0 to 25.5, hence any depth detections below 25.5 m were registered as 25.5 m, and any acceleration or temperature detections above 25.5 were registered as 25.5.

2.5.2 Passive acoustic receivers

TBR 700 and 700L passive acoustic receivers (Thelma Biotel AS, Trondheim, Norway) were deployed in parts of the watercourse in Aurland (Figure 1). These receivers are battery-driven loggers with a battery lifetime of eight months. The hydrophone on top of the receiver registers and logs the time and the ID of all signals emitted from each fish when tagged fish are within the range of the receiver. In addition, the hydrophone registers the water temperature and any possible background noise at intervals of ten minutes. Because centres of activity (position estimates) were used for data analyses, the sync tags were used for checking that the range of the receivers in the lake overlapped (Simpfendorfer *et al*. 2002). The range of the receivers in the rivers were not checked.

2.6 Data analysis

All preparation, visualization, and statistical analyses of data were conducted in R-Studio 4.1.2 (R Core Team, 2021). Acoustic telemetry and detection data are prone to false detections (Simpfendorfer *et al*. 2015), which is necessary to account for. False detections were identified and removed with cleaning tools in the *dplyr* package (Wickham *et al*. 2022). Data were visualized with the *ggplot2* package (Wickham, 2016) and model interpretations were visualized with the *gratia* package (Simpson, 2021). All codes for data preparation, visualization, statistical analyses are given in Appendix 5 and 6.

All generalized additive models (GAMs) used in the data analyses were implemented with the *bam()* function from the *mgcv* package (Wood, 2017), which is suitable for larger datasets. Additionally, a gamma distribution with a log link function was used in all the GAM models. The gamma distribution was used because the response variable of the different models was continuous and positive (Zuur *et al*. 2009). The collinearity between explanatory variables was checked with the *ggpairs()* function from the *GGally* package (Schloerke *et al*. 2021) to exclude variables that were correlated. To test whether the smoothers (term to account for non-linear variation over time) followed the same pattern, the *concurvity()* function from the *mgcv* package was used. The function calculates three measures of concurvity (worst, observed, and estimate), and by using the concurvity values from the most pessimistic measure (worst), values above 0.8 indicates strong presence of concurvity (Cuthbert *et al.* 2022) and therefore similar patterns between two smoothers.

The raw dataset of 4 012 680 detections was filtered so that only data from the study period (July 20 - November 14, 2021) and the unique IDs from the S64K-69kHz protocol were retained in the dataset, leaving 3 821 738 detections. One individual ID (ID 4697) died or lost its tag on August 26, 2021, a month after tagging. For this individual; only detections up until August 26, 2021, were included. One fish (ID 4685) was never detected, giving a final sample size of 30 sea trout and a dataset of 3 738 182 detections.

A total of nine detections from three sea trout (ID 4673, 4709, 4736) were manually removed, as these nine detections were unlikely to occur due to the setup of the lake receiver array. A detailed description of the manual removal is given in Appendix 4.

To account for any more potential false detections, three filtering codes with different criteria were constructed and any detections that met the criteria were removed (Appendix 5). The dataset was first filtered by grouping the dataset by fish ID, then calculating the speed (metre per second) and distance (metre) from the previous detection. Therefore, the first detection from each unique fish had a distance and speed equal to zero. The three filtering codes were: 1) detections from one of the river receivers where the previous detection was in the lake and the distance calculated was greater than 1000 metres; 2) detections from a lake receiver with a previous detection from one of the river receivers and a calculated distance greater than 1000 metres; and 3) any detections with a distance larger than 800 metres and with a speed greater than 5 m/s. The speed criteria was set to 5 m/s as it is unlikely that salmonids swim faster than 5 m/s over longer distances (Farrell *et al.* 2003; Palstra *et al.* 2020). The final filtered dataset consisted of 3 287 639 detections and 30 sea trout.

To calculate average position (i.e., longitude and latitude) and average sensor data (i.e. activity, temperature, and depth), a new time frame was calculated by grouping the dataset by fish ID followed by calculating a 15-minute time interval. The average position and sensor data were then calculated based on the new time interval. With the new 15-minute time interval, the final dataset with average position and sensor data consisted of 799 338 detections.

2.6.1 Hypothesis 1: Habitat use

In order to analyze the habitat use and movement of the tagged sea trout, the movement data were filtered with the *dplyr* package (Wickham *et al.* 2022) and visualized with the *ggplot2* package (Wickham, 2016).

To investigate if there was a seasonal effect on the number of sea trout in the lake, a generalized linear model was built with poisson distribution by using the *glm()* function. All individuals were assigned to either river or lake per minute throughout the study. Thus, undetected minutes per individual were interpolated by using the previous habitat a fish was detected in. Day of year (denoted as *day*) and the number of sea trout that could have been in the lake (calculated by offset; denoted as *total*) were used as explanatory variables, and number of sea trout in the lake (denoted as *lake*) was used as response variable. The model was given as:

Model 1.1
lake ~ day + offset(log(total)), family = "Poisson", data=mod1

2.6.2 Hypothesis 2: Effect of habitat on activity

To test whether habitat (lake or river) had an effect on the activity, a GAM model was built. There was high correlation between day of year and discharge in the downstream river (-0.835), and high correlation between day of year and temperature (-0.944, temperature measured from temperature sensor in the tags). Temperature and the discharge in the downstream river were therefore removed, to retain the temporal structure of the variance in the models.

Average activity based on accelerometer data (or acceleration, denoted as *accel* in the models) was included as the response variable, while *habitat* (lake or river, as factor), day of year (denoted as *day*), and time of day (denoted as *time*) were included as explanatory variables. The unique fish ID (denoted as a factor *individual*) variable was included as a random effect. A smoother (denoted *s()* in the model) was used for each of the temporal variables (day and time) to account for non-linear variation over time. When the wiggliness of values of a variable differ substantially, it can be useful to include an interaction in the smoother, which informs the model to apply a separate smoother for each level of a factor (Pedersen *et al*. 2019). The term '*by=habitat*' was included in each of the temporal smoothers so that a smoother was fitted to each level of habitat (i.e., lake and river). For the random effect of fish ID, a smoother was used to account for nestedness and repeated measurements of observations, with "re" specifying that the basis for smoothing (bs) is adjusted to the random effect of the variable and k equals to the sample size (k = N = 30). The amount of wiggliness (k) was adjusted to the other smoothers.

Because the dataset was built up by repeated measurements from the same sea trout individuals over time, an autocorrelation term was included to test if the autocorrelation structure improved the model. The autocorrelation term was calculated based on the first model and then included in the second model. Akaike Information Criterion (AIC; Johnson & Omland, 2004) was used to compare the fit of the two models. The final models were:

Model 2.1
accel ~ habitat + s(day, by=habitat, k=40) + s(time, by=habitat, k=10)+ s(individual, bs="re", k=30), data=mod2, method="fREML", family=Gamma(link="log")

Model 2.2
accel ~ habitat + s(day, by=habitat, k=40) + s(time, by=habitat, k=10) + s(individual, bs="re", k=30), AR.start=starting_timepoint, rho=rho_value, data=mod2.1, method="fREML", family=Gamma(link="log")

2.6.3 Hypothesis 3: Effect of high-head storage plant discharge on depth use in the lake

To test if there was an effect of the discharge from the high-head storage plant on the depth use of the sea trout in the lake, two GAM models were built with- and without the discharge as an explanatory variable. The models were built by the average depth (denoted as *depth*) as response variable, and the explanatory variables day of year (denoted as *day*), time of day (denoted as *time*), and a bivariate smoother to account for the spatial interaction between longitude (denoted as *longitude*) and latitude (denoted as *latitude*). The spatial smoother had a k-value of 125 to allow for large spatial variation. A smoother was also used for each of the two temporal variables to account for seasonal- and daily variation in depth use. To account for the random effect of individual sea trout, the fish IDs (denoted as a factor *individual*) was included in a smoother, with k equal to the number of sea trout detected in the lake (k = N = 26). A calculated autocorrelation structure was included in both models. In the second model, the discharge data from the high-head storage plant Aurland 1 (denoted as *AU1*) was included as an additional explanatory variable. To test whether the discharge data improved the model, AIC model comparison was implemented. The best fitted model was then visualized for inspection of the explanatory variables. The two models were:

Model 3.1
depth ~ s(longitude, latitude, k=125) + s(day, k=40) + s(time, k=10)+ s(individual, bs="re", k=26), AR.start=starting_timepoint, rho=rho_value, data=mod3.1, method="fREML", family=Gamma(link="log")

Model 3.2
depth ~ s(AU1, k=10) + s(longitude, latitude, k=125) + s(day, k=40) + s(time, k=10)+ s(individual, bs="re", k=26), AR.start=starting_timepoint, rho=rho_value, data=mod3.1, method="fREML", family=Gamma(link="log")

2.6.4 Hypothesis 4: Effect of high-head storage plant discharge on activity in the lake

To test if there was an effect of the discharge from the high-head storage plant on the activity of sea trout in the lake, two GAM models were built with- and without discharge as an explanatory variable. Day of year (denoted as *day*) and time of day (denoted as *time*) were included to test whether there was a temporal effect on the activity in the lake, with a smoother for each of the temporal variables to account for non-linear temporal variation. The spatial interaction between longitude (denoted as *longitude*) and latitude (denoted as *latitude*) was included as a bivariate smoother. A smoother was used for the random effect of fish IDs (denoted as a factor *individual*). The average depth (denoted as *depth*) and an autocorrelation term were included in both models. The final two models were built with the activity (denoted as *accel*) as response variable, depth, day of year, time of day, and the spatial interaction of longitude and latitude as explanatory variables, and the unique fish ID as random effect. The second model had the discharge data as an additional explanatory variable (denoted as *AU1*). The AIC was used to test whether the discharge from the high-head storage plant improved the model. The explanatory variables of the best fitted model were then inspected visually. The final two models were:

Model 4.1
accel ~ depth + s(longitude, latitude, k=125) + s(day, k=40) + s(time, k=10)+ s(individual, bs="re", k=26), AR.start=starting_point, rho=rho_value, data=mod4.1, method="fREML", family=Gamma(link="log")

Model 4.2
accel ~ depth + s(AU1, k=10) + s(lon, lat, k=125) + s(day, by=habitat, k=40) + s(time k=10)+ s(individual, bs="re", k=26), AR.start=starting_point, rho=rho_value, data=mod4.1, method="fREML", family=Gamma(link="log")

3 Results

<u>3.1 Hypothesis 1: Habitat use</u>

During the study period (July 20 - November 14, 2021), a high percentage of the tagged sea trout were detected in the lake (87 %, N=26), among which half were tagged at the confluence of the river and the lake (N=13) and half ascended from their tagging sites in the downstream river (N=13, Figure 4, 5, Appendix 1). The remaining 13 % of the sea trout stayed in the river throughout the study (N=4, Figure 4, 5). A few sea trout ascended to the upstream river (13 %, N=4, Figure 4, 5). Out of the sea trout tagged at the confluence, nearly 70 % remained in the lake (N=9, Figure 4, 5). None of the 30 sea trout were detected by the receiver at the river mouth of the downstream river. A more detailed description of the transitions of sea trout between the rivers and the lake is summarized in Figure 5.

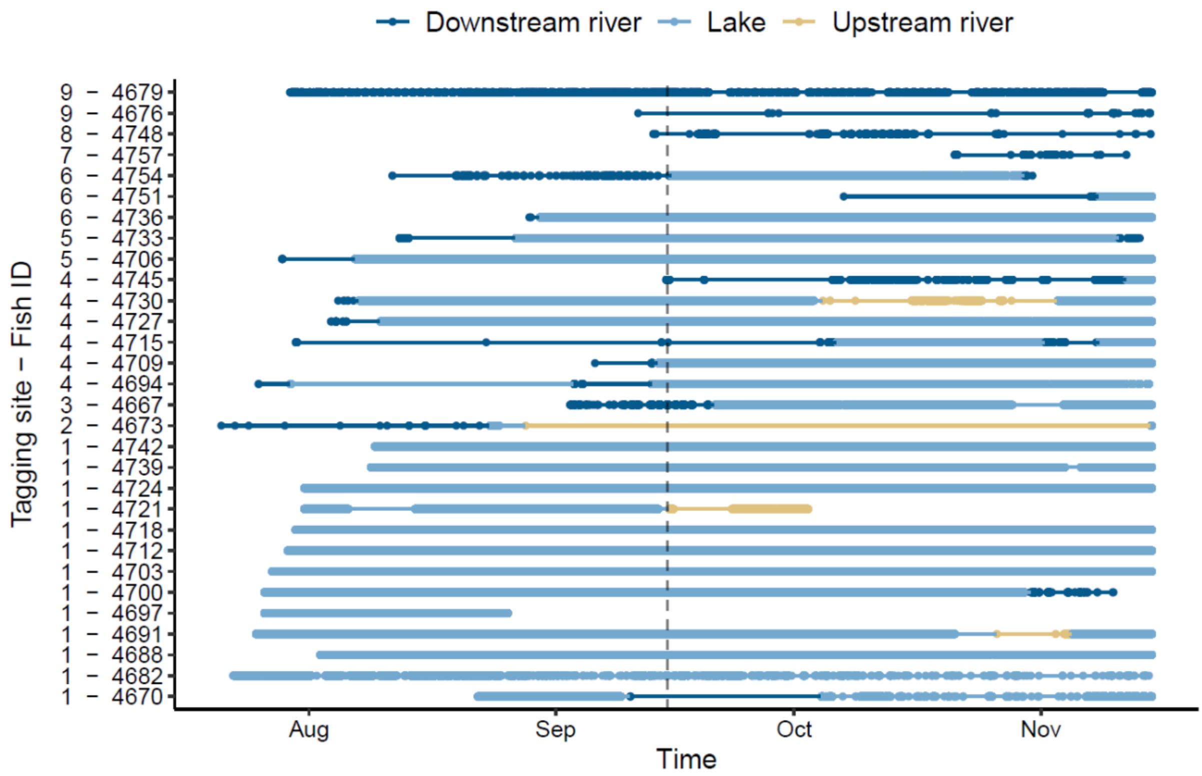

Figure 4. Habitat use of 30 tagged sea trout during the study period (July 20 - Nov. 14, 2021, x-axis). Y-axis represents tagging site (1-9; Figure 2) and unique fish ID. Vertical dashed line indicates when the flap weir was elevated (Sep. 15). Thin lines are drawn between detections (dots).

Out of the sea trout that ascended to the lake, 57 % ascended before (N=8) and 43 % ascended after (N=6) the elevation of the flap weir (Sep. 15, Figure 4, 5). A total of six sea trout descended from the lake to the downstream river, in which 33 % descended before (N=2) and 77 % descended after (N=4) the elevation of the flap weir (Figure 4, 5). Thus, the sea trout that ascended or descended after the flap weir was elevated used the fish ladder. All sea trout that remained in the river throughout the study ascended from their tagging site.

The generalized linear model showed that there was a significant effect of day of year on the number of sea trout in the lake ($z = 3.031$, $p = 0.00244$), such that there were more sea trout in the lake later in the study compared to earlier in the study.

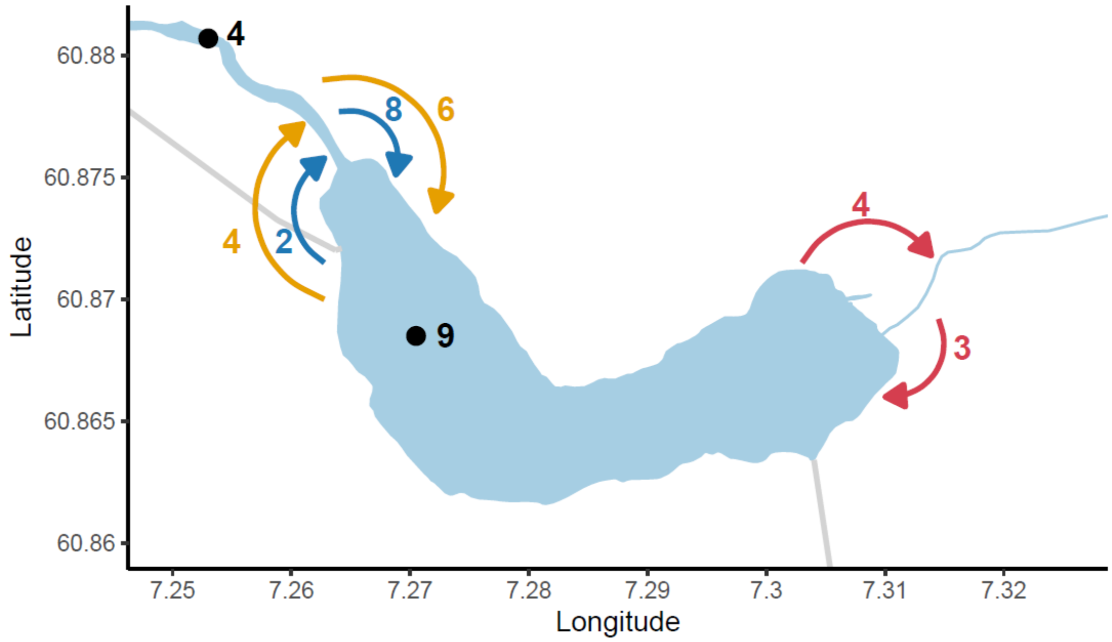

Figure 5. Number of sea trout moving between habitats or remained within one habitat throughout the study (July 20 to Nov. 14, 2021). Movement between downstream river and lake before (blue) and after (orange) elevation of the flap weir (Sep. 15), movement between the lake and the upstream river (red), and black points indicate how many sea trout that remained within the given habitat.

<u>3.2 Hypothesis 2: Effect of habitat on activity</u>

There was a difference in the sea trout activity between lake and river habitats, with sea trout being more active in the rivers than in the lake (Figure 6). The average log transformed activity of all detected sea trout combined was 2.26 (SD = 0.736, median = 2.20) in the lake and 2.96 (SD = 0.616, median = 2.94) in the rivers.

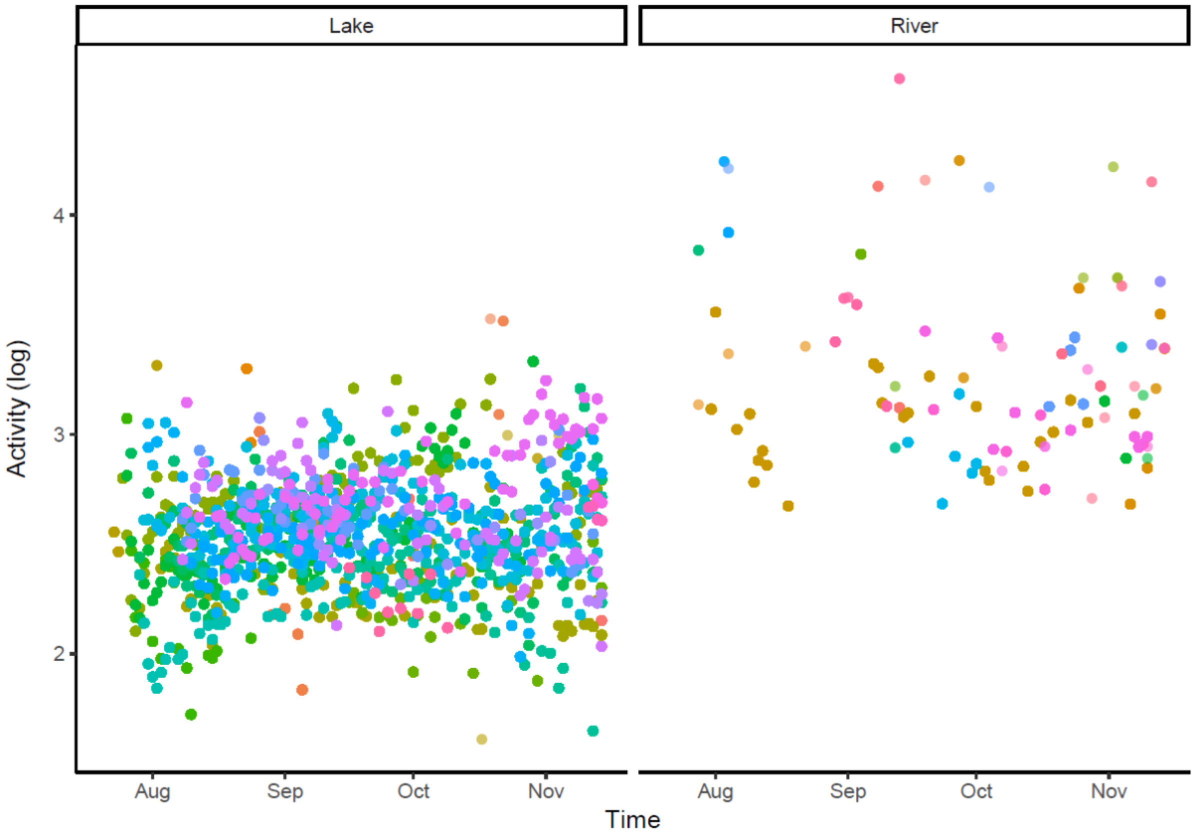

Figure 6. The average activity (log transformed) per day of sea trout in the two habitats: lake (Vassbygdevatnet) and river (Aurlandselva and Vassbygdelva). Colours represent different sea trout individuals.

The Akaike Information Criterion (AIC) test resulted in a lower AIC value for the model with the autocorrelation term (Model 2.2) compared to the model without (Model 2.1, Table 1). Sea trout were more active during the day than the night in both the lake and the rivers, however the effect size was small (ToD, Appendix 7). Throughout the study period, there was an overall decrease in the sea trout activity in the rivers, while the activity of sea trout in the lake slightly increased by mid-November when data were recovered (DoY, Appendix 7).

Table 1. Model selection based on Akaike Information Criterion (AIC) between models without autocorrelation term (Model 2.1) and with autocorrelation term (Model 2.2). Degrees of freedom denoted as df. The lowest value of AIC indicates the best fitted model. Difference in AIC denoted as ΔAIC.

Model	**df**	**AIC**	**ΔAIC**
Model 2.1	95.60446	5 446 527	+ 7014
Model 2.2	95.54288	5 439 513	0

3.3 Hypothesis 3: Effect of high-head storage plant discharge on depth use in the lake

All 26 sea trout mainly utilised the upper water column of the lake throughout the study period with an overall mean depth use of 3.7 m (SD = 3.7). However, 81 % of the sea trout were detected at the tag depth limit (25.5 m). Total sea trout length did not affect the depth used in the lake.

The second model that included the high-head storage plant discharge (Model 3.2) had a lower AIC (ΔAIC = 4099) than the model without the discharge (Model 3.1, Table 2). Thus, the second model with discharge as an explanatory variable was a better fit and therefore contributed to explaining more of the variance compared to the model without the discharge. The best fitted model showed that the effect of discharge on the depth used in the lake was minimal around the mean value of the discharge (20.97 ± 16.95 m^3/sek, Figure 2; Figure 7. A). When the discharge approached approximately 90 m^3/s, sea trout used deeper water layers more than at lower discharge, which followed with an immediate use of more shallow water layers as the discharge approached 100 m^3/s. There was a minimal effect of the discharge on the depth used in the lake compared to the effect of individual variation in depth use. Six sea trout exploited deeper parts of the lake to a larger extent than the rest of the sea trout (Figure 7. C). Sea trout were at deeper depths during the night (Figure 7. D) and used the deeper habitats more as the study period progressed (Figure 7. B). The spatial interaction between longitude and latitude revealed that the sea trout exploited deeper areas in the southwestern part of the lake and were closest to the surface in the northwestern part of the lake (Figure 8).

Table 2. Model selection based on Akaike Information Criterion (AIC) between models without (Model 3.1) and with (Model 3.2) high-head storage plant discharge as explanatory variable. Degrees of freedom are denoted as df. The lowest value of AIC indicates the best fitted model. Differences in AIC are denoted as ΔAIC.

Model	**df**	**AIC**	**ΔAIC**
Model 3.1	193.1262	6 491 302	+4099
Model 3.2	202.1155	6 487 203	0

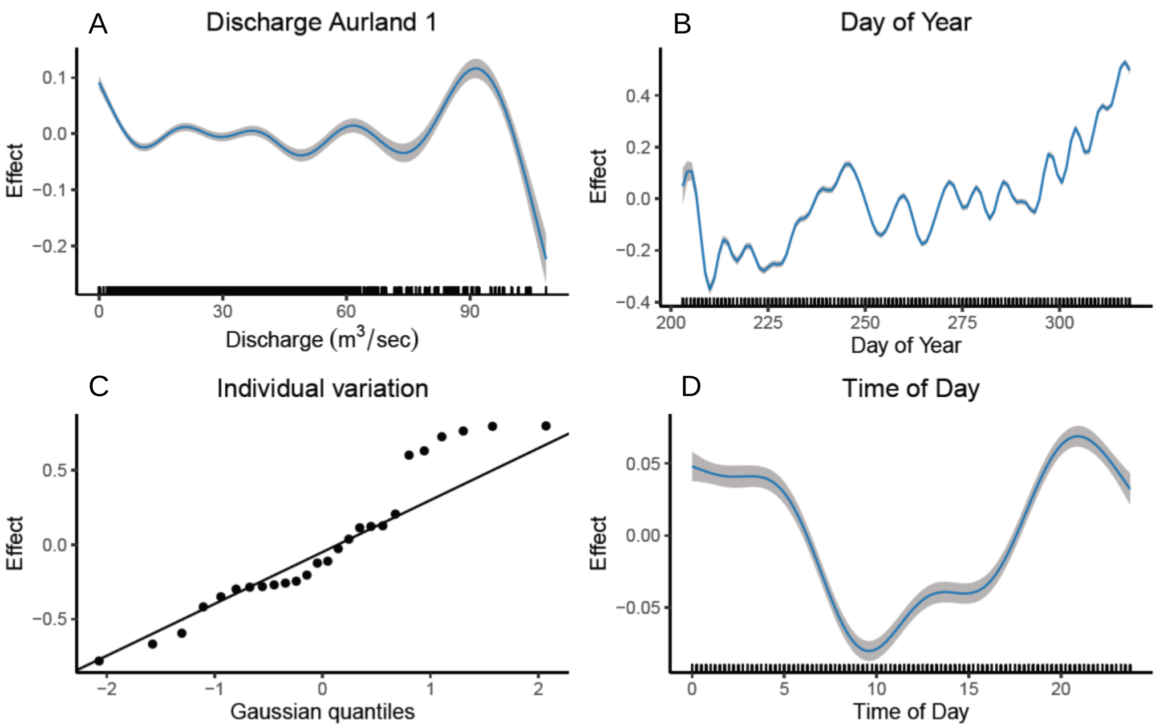

Figure 7. Visualization of the effect of the explanatory variables on depth use in the lake. **A**: effect of discharge from high-head storage plant (Aurland 1); **B**: effect of day of year; **C**: effect of individual variation; **D**: effect of time of day.

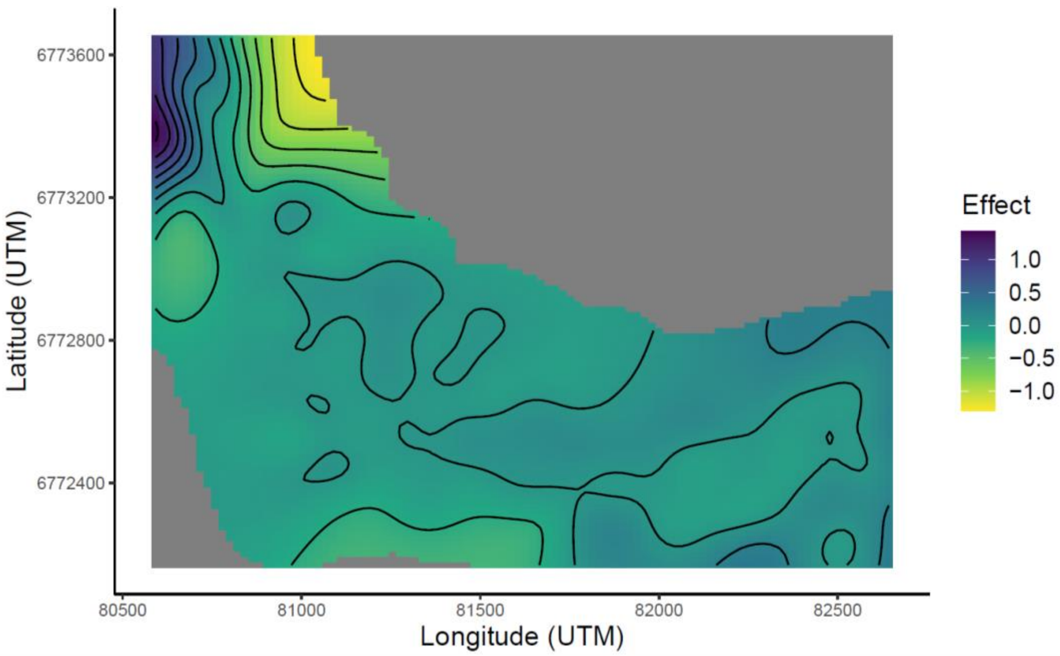

Figure 8. Contour plot of the posterior distributions of the spatial smoother from the generalized additive model on the effect of discharge on the depth use of sea trout in the lake (log transformed, colour coded). Longitude (UTM) and latitude (UTM) on x-axis and y-axis, respectively. Darker colour indicates deeper depth use (Effect).

3.4 Hypothesis 4: Effect of high-head storage plant discharge on activity in the lake

The model with the storage discharge (Model 4.2) had a better fit (ΔAIC = 2344) than the model without the discharge as an explanatory variable (Model 4.1, Table 3). The discharge had an minimal effect on the activity in the lake, until the discharge approached approximately 90 m^3/s and the discharge effect on the activity increased (Figure 9. A). There was a small increase in activity throughout the study (Figure 9. B). Time of day had a relatively small effect on the activity, however, sea trout were more active during the day than during the night (Figure 9. D). The sea trout activity was negatively correlated with depth use such that they were less active at deeper depths (mdepth, Appendix 8). The longitude and latitude spatial interaction on activity in the lake indicated that sea trout were more active in the northwestern area and in the eastern area of the lake (Figure 10).

Table 3. Akaike Information Criterion (AIC) model selection between the models without (Model 4.1) and with (Model 4.2) the high-head power plant discharge as an explanatory variable. Degrees of freedom are denoted as df. The lowest value of AIC indicates the best fitted model. Differences in AIC are denoted as ΔAIC.

Model	**df**	**AIC**	**ΔAIC**
Model 4.1	185.1357	5 310 819	+2344
Model 4.2	193.4499	5 308 475	0

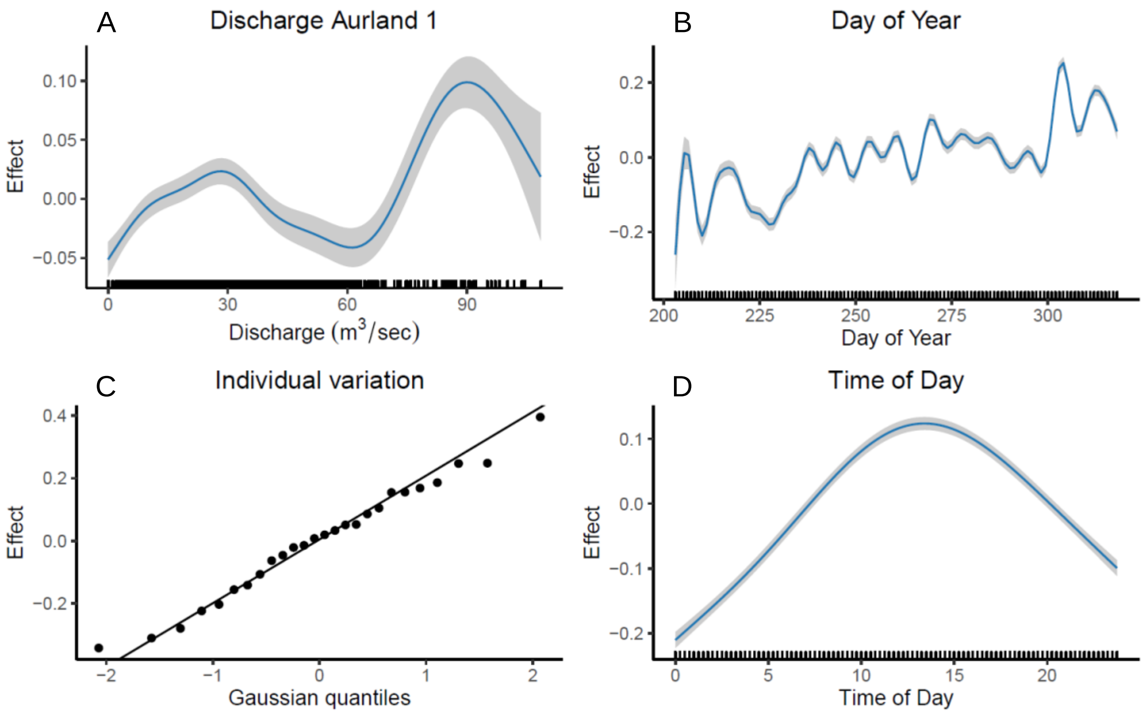

Figure 9. Visualization of the effect of the explanatory variables on activity in the lake. **A**: effect of discharge from high-head storage plant (Aurland 1); **B**: effect of day of year; **C**: effect of individual variation; **D**: effect of time of day.

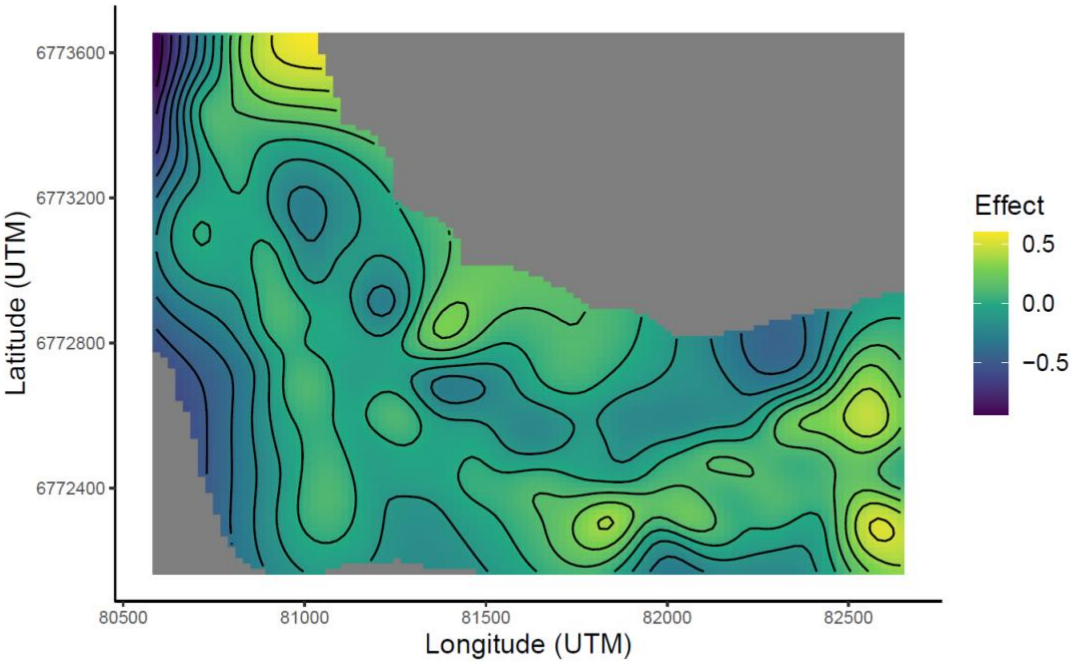

Figure 10. Contour plot of the posterior distributions of the spatial smoother from the generalized additive model on the activity of sea trout in the lake (log, colour coded). Longitude (UTM) and latitude (UTM) on x-axis and y-axis, respectively. Brighter colour indicates higher activity.

4 Discussion

This study investigated the habitat use of adult sea trout before spawning and whether the sea trout's activity differed between the riverine and lacustrine environments. Additionally, the study tested whether the depth use and activity of adult sea trout in lake Vassbygdevatnet were affected by the discharge from the high-head storage plant. The lake offered an important habitat for the sea trout before spawning, supporting previous findings from the same lake (Lunde, 2014). In the lake, the depth use and activity were affected by discharge from the high-head storage plant. Ultimately, the results suggest that the effect of the hydropower discharge was relatively small. However, hydropower regulation might have caused a spatial effect on the depth use and activity of sea trout in the lake. Given that most sea trout inhabited the lake during the spawning migration, the lake might conceal a significant part of the sea trout population during annual stock assessments.

4.1 Hypothesis 1: Habitat use

Most sea trout in this study were detected at some point in the lake Vassbygdevatnet, suggesting that the lake provided an important habitat for the adult sea trout during the spawning migration. The large number of sea trout inhabiting the lake indicates that there is an advantage to seeking refuge in the lake compared to remaining in the rivers before spawning. Although this may be the normal behaviour of sea trout in Aurland, changes in the river flow regime can have affected the behaviour and distribution of fish in the watercourse, and reduced the availability of prey and spawning habitats (Banks, 1969; Vannote *et al*. 1980;

Poff *et al*. 1997; Poff & Hart, 2002; Westrelin *et al*. 2018). The water level in the upstream river, Vassbygdelva, is unnaturally low due to the hydropower regulations (Ugedal *et al*. 2019), and sea trout may therefore be more vulnerable to predation above the lake (e.g., by otters; Van Dijk *et al*. 2020). During summer, the hydropower regulations have also caused a warming in the upstream river, Vassbygdelva, coincident with a cooling in the downstream river, Aurlandselva (Saltveit, 2006; Ugedal *et al*. 2019). Furthermore, both the downstream and upstream rivers are subject to angling during summer. Consequently, the lake may be used as a refuge by sea trout because of these anthropogenic stressors or to avoid predators. An alternative explanation is that lakes provide feeding grounds, which is observed by pre-spawning trout in Norwegian lakes (L'Abée-Lund *et al*. 1992; Amundsen & Knudsen 2009; Jensen *et al*. 2012; Hanssen *et al*. 2022). Hanssen et al. (2022) documented predation of Atlantic salmon smolts by adult sea trout in lake Evangervatnet after spawning (April-June). Additionally, the lake might offer refuge for energy conservation or thermoregulation (i.e., seek certain water temperatures) before spawning (Newell & Quinn, 2005; Mathes *et al*. 2010; Mulder *et al*. 2018).

Although brown trout exhibit a variety of life history strategies (e.g., sea-run trout, freshwater residents; Klemetsen *et al*. 2003), the high prevalence of sea-run trout (i.e., sea trout) in the lake in the present study is consistent with the use of lakes by trout in previous studies (e.g., Jonsson, 1989; L'Abée-Lund *et al.* 1992; Andersson *et al*. 2020). In contrast, Atlantic salmon spend less time in lakes than sea trout (Kennedy and Allen, 2016; Nilsen, 2021.), despite being closely related. For instance, Atlantic salmon in the Vosso river system mainly used the lakes as aid in migration (Nilsen, 2021), while trout forage in the lake Evangervatnet (Haugen *et al.* 2017; Hanssen *et al*. 2022). Because sea trout are morphologically less adapted to strong water currents in rivers compared to Atlantic salmon (Jonsson & Jonsson, 2011), these two closely related species might use freshwater habitats differently. When sea trout and Atlantic salmon sympatrically inhabit river systems with lakes, competition on resources and habitat might have caused a spatial segregation whereby Atlantic salmon dominate in rivers and sea trout dominate in lakes. Both sea trout and Atlantic salmon inhabit the Aurland watercourse, however, the abundance of spawners between the two species differs substantially. In 2018, approximately 60 Atlantic salmon spawners and 840 sea trout spawners were registered by drift diving in the two anadromous rivers in Aurland (Skoglund *et al*. 2019a; Skoglund *et al*. 2019b). Because Atlantic salmon are stocked by a hatchery into both the upstream and downstream rivers (Ugedal *et al*. 2019), the low abundance of Atlantic salmon spawners indicates that the mortality of Atlantic salmon is high. In contrast, the last stocking of sea trout by a hatchery was conducted in 1999 in the Aurland watercourse (Ugedal *et al*. 2019), thus, the sea trout population might be better adapted to the watercourse compared to the Atlantic salmon population.

4.2 Hypothesis 2: Effect of habitat on activity

Sea trout were more active in the rivers than in the lake. The lower degree of activity by sea trout in the lake indicates that the sea trout spent less energy in the lake than in the rivers (e.g., Briggs & Post, 1997; Lowe *et al*. 1998; Cooke *et al*. 2016). The high survival rate of sea trout following spawning (Bendall *et al*. 2005; Haraldstad *et al*. 2018) indicates that sea trout exhibit a sufficient strategy for conserving and allocating their energy storages. Strategic allocation and conservation of energy might be promoted by habitat preference whereby they can limit behaviours that are energy-depleting. Because the activity registered in the rivers in this study is likely caused by the active movement required to ascend rivers or maintain position against flowing water (Hynes, 1970), sea trout in this study likely exploited the lake Vassbygdevatnet as a habitat for energetic refuge (Newell & Quinn, 2005; Mathes *et al*. 2010).

There was temporal variation in the activity of sea trout in both lake- and river habitats. Sea trout exhibited an increase in activity throughout the study in the lake that could be explained by spawning activity near the end. Because the spawning period of sea trout in Aurland lasts from October to early January (Pulg, pers.comm), the higher activity of sea trout near the end of the observation period could indicate spawning or spawning-related behaviour. Sea trout have been observed spawning in lake Vassbygdevatnet in Aurland (Pulg, pers.comm.), and there are an increasing number of studies on the presence of spawning in lakes in sea trout populations (Birnie-Gauvin *et al*. 2019). In lake Røldalsvatnet, Norway, redds were observed and the presence of trout spawners were further verified by using gillnets (Brabrand *et al*. 2002). Thus, the seasonal increase in activity exhibited by sea trout in the present study might be a result of spawning or spawning-related activity in the lake.

In contrast to the observed increasing activity in the lake, there was a reduction in activity in the rivers throughout the study period. After the flap weir at the confluence of the lake and the river was elevated (Sep. 15), the water flow in the river was greatly reduced. Reduced water flow can result in a greater difficulty to ascend rivers (Thorstad *et al*. 2003b). Berg & Berg (1989) found that larger-sized sea trout resided longer at sea when the water level fell in August, which could indicate difficulties for upriver migration. Alternatively, adult sea trout commonly seek deep pools in rivers (Bunnell *et al*. 1998; Arnekleiv & Rønning, 2004), where there is a lower necessity to be active due to reduced water flow. Hence, the hydropower regulations may partially explain the reduced activity of sea trout in the river.

The diel activity of sea trout was similar in the lake and the rivers. Sea trout were consistently more active during the day than the night in both habitats. Other studies have mostly found nocturnal or crepuscular peaks in activity of trout (Bunnell *et al*. 1998; Young, 1999; Bremset, 2000; Björnsson, 2001; Ovidio *et al*. 2002; Barry *et al*. 2020), which is consistent with the diel activity of other salmonids (e.g., Jakober *et al*. 2000; Huusko *et al*. 2007; Harrison *et al*. 2013). Fish are thought to be least active during the day to minimise the risk of predation by otters, birds, or piscivorous fish species. Hence, the higher activity observed during midday in both the lake and river habitats in this study is relatively unique. A higher activity of sea trout during the day in lake Vassbygdevatnet may indicate that the relatively large sea trout are not prone to predation. Alternatively, the higher activity during the day than during the night might be due to spawning or spawning-related movement (e.g., searching for spawning grounds), as have been demonstrated with Chinook salmon (McMichael *et al*. 2005).

4.3 Hypothesis 3: Effect of high-head storage plant discharge on depth use in the lake

Trout were mostly found near the surface of the lake, but the high-head storage plant discharge had an effect on the depth use of sea trout in the lake. However, the effect of the discharge was small and based on few detections at extremely high discharge levels, which were rare. Additionally, the depth used in the area of the discharge was not distinctively different from most of the remaining lake, where the impact was predicted to be the most extreme. Collectively, the model outputs suggested that there was a minimal effect of discharge on depth use in the lake.

There were spatial and temporal effects on the depth use of sea trout in the lake. Sea trout were detected more frequently in shallow water layers during the day than during the night, which is aligned with the activity peak of the sea trout in the present study. Because sea trout are visual feeders (Klemetsen *et al.* 2003), sea trout might utilise daylight to feed at the surface. Interestingly, the use of the deeper water in the southwestern area, relative to the remaining lake, coincides with the intake location of the storage plant (Vangen, located at 7-19 m depth). A radio tracking study conducted by Økland *et al*. (1995) did not locate trout inside of the intake. However, sea trout have been observed to aggregate around the area of the intake, most likely because they are attracted by the inflow of water (Lunde, 2014). A potential attraction could be a result of sea trout mistaking the flow of water into the tunnel as the path to the downstream river when they search for suitable spawning grounds. To demonstrate the effect of the inflow of water into the tunnel on the behaviour of sea trout, a future study can periodically manipulate the storage plant operations during the spawning migration. In exorheic lakes, such as Vassbygdevatnet that have an outlet to a downstream river, it is of interest to whether more fish descend to the river during the spawning period when there is no other outflow of water than to the downstream river.

The varying depth used among sea trout (i.e., random effect intercept) was larger than the effect of the other parameters and contributed to explaining a large part of the variation in the data. Six sea trout used on average deeper habitats than the remaining sea trout throughout the study. The individual variation in depth use is potentially a result of differences in personalities among sea trout. For instance, the ‘shy-bold continuum’ proposed by Wilson et al. (1993) suggests that personality traits affect the observed behavioural variations among individuals. For the vertical behaviour of sea trout in lake Vassbygdevatnet, the ‘shy-bold continuum’ can potentially contribute to explaining the individual variation in depth preference. Shy individuals, compared to bold individuals, are more likely to remain at deeper depths to limit their exposure to threats (e.g., fishing, terrestrial or avian predators). Additionally, the individual vertical movement differences observed in the present study might be a result of individual fitness because vertical movement is costly (Strand *et al*. 2005). Thus, sea trout that exhibited a greater vertical movement in lake Vassbygdevatnet might have higher fitness or have a more bold personality than the remaining sea trout.

4.4 Hypothesis 4: Effect of high-head storage plant discharge on activity in the lake

The high-head storage plant discharge affected the activity of sea trout in the lake, although the effect was small. Because the inflow of water from the high-head storage plant affects the stratification of the lake (Ugedal *et al*. 2019), and temperature is closely related to energy consumption and activity (Brown *et al*. 2004), it is likely that there is an effect of discharge on the activity of sea trout that is not accounted for by the change in discharge. It is also important to point out that although the addition of discharge improved the model on the activity of sea trout in the lake, the effect was small and the shape of the fit was seemingly impacted by a few extreme values. Thus, the discharge from the high-head storage plant did not have a strong effect on the activity of sea trout in the lake.

The higher activity of sea trout observed in the eastern part of the lake may indicate that there was an effect from the high-head storage plant discharge, despite the model not accounting for the discharge location directly. The additional supply of water from the high-head storage plant into the surface layer of the lake caused a higher surface flow that could result in an increase in activity of sea trout, particularly around the discharge area. Swimming towards discharging water will require higher activity of sea trout. Thus, it is likely that the observed increase in activity around the Aurland 1 discharge is caused by the outflow of water. However, because acoustic telemetry relies on sound, this method of tracking aquatic animals is susceptible to environmental conditions (e.g., discharging water) influencing the detection range (Huveneers *et al*. 2016; Crossin *et al*. 2017). Thus, it is important for future studies, where lakes are subjected to discharging water from storage plants or river mouths, to deploy several receivers around the outlet of the discharging area. More receivers can result in an overall improved detection probability. For instance, positioning individuals by trilateralization of receiver detections (i.e., overlapping receiver ranges such that more accurate positions of fish can be calculated) around the outlet can also give more data on the effect of discharging water on the behaviour of fish in lakes.

4.5 Methodological limitations

River receivers were deployed in areas that likely affected the distribution of data. The receivers in the rivers were not deployed in areas subjected to the greatest water velocity, but in deep pools or other relatively calm areas with higher detection probability. Thus, the receivers could not detect data from when the sea trout potentially were the most active (i.e., areas with greatest flow) in the rivers. Therefore, the activity of sea trout in the rivers was potentially higher than what was decoded by the receivers, indicating that the difference between activity in the rivers and the lake was likely greater than the observed activity difference.

Tagging of fish can potentially cause unwanted stress and reduced fitness from capture, holding, anaesthetics, or the tagging process (Arlinghaus *et al*. 2007; Cooke & Sneddon, 2007; Cooke *et al*. 2010; Baktoft *et al*. 2013). Catch-and-release angling can for instance cause physical damage to fish (Arlinghaus *et al*. 2007; Cooke & Sneddon, 2007; Colotelo & Cooke, 2011) or affect migration patterns (Thorstad *et al*. 2003a). However, sea trout have shown low mortality from catch-and-release angling (Blyth & Bower, 2022). Prior to tagging, all fish had a minimum holding time of 30 minutes in keepnets or tubes after being caught. The minimum holding time enabled sea trout to regain homeostasis as internal tagging procedures require use of anaesthetics that can elicit unwanted behavioural effects (Cooke *et al*. 2011). Consequently, after the tagging procedure, all sea trout were observed to ensure recovery of regained equilibrium, responsiveness, and motor functionality before being released. Tagging of fish can alter the behaviour of fish (Cooke *et al*. 2011). However, there are several studies that do not indicate long-term effect on the behaviour of tagged fish (Hondorp *et al.* 2015; Hubbard *et al.* 2020). Thus, the behaviour of the tagged sea trout in the present study is likely representative of the behaviour of non-tagged sea trout.

4.6 Implications for management

The large prevalence of sea trout inhabiting the lake during the spawning migration demonstrates that the lake provided an important habitat for sea trout, where they likely conserved energy prior to spawning. Based on factors, such as hydropower regulations and overfishing, assessment of Norwegian sea trout populations has concluded that only 25 % of the populations are in a good condition (VRL, 2022). Additionally, the sea trout population assessment is based on drift dive spawning count conducted in rivers. Because a large portion of the sea trout in the present study inhabited the lake during the annual river drift dive spawning count (usually conducted in mid- to late October; Skoglund *et al*. 2019b; Skoglund *et al*. 2021), the lake Vassbygdevatnet in Aurland potentially concealed a significant number of spawning sea trout. Thus, the results from the spawning count are potentially underestimated. In general, stock assessment of several Norwegian river systems might be underestimated given that about 30 % of river systems in Norway contain lakes (Hanssen *et al*. 2021). Therefore, the possibility of lake-residing fish should be taken into consideration when management efforts are made based on spawning stocks.

With the increasing demand of renewable energy, lakes are likely to become increasingly exploited for development and hydropower (Hirsch *et al*. 2017). Given that lakes provide such important habitat for sea trout, effects of hydropower on this habitat may render sea trout particularly vulnerable. However, the effect of hydropower regulations on the lake ecology of salmonids is generally poorly documented (Lennox *et al*. 2021), despite being among the most frequently studied fish species globally (Birnie-Gauvin *et al*. 2019). Because sea trout and Atlantic salmon exhibit different life history strategies (Klemetsen *et al*. 2003), hydropower mitigation efforts based on the ecology of Atlantic salmon can misrepresent the requirements of sea trout. Consequently, current management mitigations and regulations might not be sufficient. Management and the hydropower industry should further invest in research on the lake ecology of sea trout to provide necessary knowledge on the requirements of sea trout populations.

Based on the observed higher activity of sea trout around the discharging water from the high-head storage plant, it is likely that the storage plant ultimately caused an increase in activity due to the altered water regime, especially in this area of the lake. Thus, storage plants, which are highly exploited in Norway, might contribute to increased energy depletion of sea trout and likely other fish species inhabiting regulated lakes. Because availability of energy is fundamental for the physiology, behaviour, and movement of fish (Shepard *et al.* 2013), storage plants might affect the fitness and success of fish on an individual and population scale in regulated watercourses. Thus, management should evaluate how the seasonal habitat use and behaviour of sea trout and other freshwater fish species might be affected by hydropower regulations, especially when sea trout rely on sufficient energy storage for spawning.

The use of deeper habitats by sea trout around the area of the intake of the storage plant, Vangen, can potentially be caused by an attraction to the inflow of water. Because the discharge in the downstream river is severely reduced while Vangen is operating (i.e., also during the spawning period), spawners might be attracted by the flow of water into the tunnel when searching for the lake outlet to spawn in the river. Thus, management should consider increasing the river flow in the downstream river during the spawning period to guide fish towards the river.

5 Conclusion

This study discovered that the lake offered an important habitat for sea trout during their spawning migration. The activity of sea trout was higher in the rivers than in the lake, indicating that the lake offered a refuge where sea trout could conserve energy by being less active. Additionally, there was a seasonal difference in activity of sea trout between the lake and river habitats; sea trout were more active in the lake later during the study while they were more active in the rivers earlier in the study. This could indicate that spawning or spawning-related movement might have occurred in the lake as the spawning period approached. Combining tracking with acceleration sensors can potentially help reveal if sea trout spawn in lakes. Although there was a minimal effect of discharge from the high-head storage plant on both depth use and activity of sea trout in the lake, the model outputs revealed a potential spatial effect of hydropower regulation on a critical habitat to migrating sea trout. Because lakes are likely to become increasingly exploited to generate hydroelectricity, sea trout and other freshwater species are particularly vulnerable where such modifications are made. Consequently, further research on the effect of storage plants on the lake behaviour of fish is needed, as sea trout exhibited a clear preference of the lake as habitat during the spawning migration.

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7 Appendices

Appendix 1.

Appendix 1. Tagging data for the 31 tagged sea trout individuals. Unique transmitter ID (ID); the date (Date) and site (Site) of capturing, tagging, and release; total fish length (TL (mm)); if detected (x) or not detected (-) in lake (Lake) and river (River) habitat; and maximum depth registered in lake (Depth (metre)).

ID	Date	Site	TL (mm)	Lake	River	Depth (metre)
4667	20.07.2021	3 - Hagahølen	472	x	x	25.5
4670	20.07.2021	1 - Osen	455	x	x	25.5
4673	20.07.2021	2 - Saurea	494	x	x	16.3
4676	21.07.2021	9 - Bankhølen	566	-	x	
4679	21.07.2021	9 - Bankhølen	463	-	x	
4682	21.07.2021	1 - Osen	428	x	-	11.6
4685	22.07.2021	9 - Bankhølen	787	-	-	
4688	24.07.2021	1 - Osen	555	x	-	25.5
4691	25.07.2021	1 - Osen	712	x	x	25.5
4694	25.07.2021	4 - Trolløyna	587	x	x	25.5
4697	26.07.2021	1 - Osen	469	x	-	25.5
4700	26.07.2021	1 - Osen	602	x	x	25.5
4703	27.07.2021	1 - Osen	450	x	-	25.5
4706	27.07.2021	5 - Storøyna	551	x	-	25.5
4709	28.07.2021	4 - Trolløyna	563	x	x	25.5
4712	29.07.2021	1 - Osen	587	x	-	25.5
4715	29.07.2021	4 - Trolløyna	538	x	x	25.5
4718	30.07.2021	1 - Osen	416	x	-	25.5
4721	31.07.2021	1 - Osen	540	x	x	22.9
4724	31.07.2021	1 - Osen	419	x	-	25.5
4727	02.08.2021	4 - Trolløyna	522	x	-	25.5
4730	03.08.2021	4 - Trolløyna	470	x	x	25.5

4733	03.08.2021	5 - Storøyna	525	x	-	25.5
4736	03.08.2021	6 - Benken	415	x	x	25.5
4739	08.08.2021	1 - Osen	425	x	-	25.5
4742	09.08.2021	1 - Osen	466	x	-	25.5
4745	09.08.2021	4 - Trolløyna	612	x	x	13.7
4748	10.08.2021	8 - Natthølen	535	-	x	
4751	10.08.2021	6 - Benken	676	x	x	16.4
4754	11.08.2021	6 - Benken	685	x	x	25.5
4757	12.08.2021	7 - Kjærbakken	765	-	x	

<u>Appendix 2.</u>

Appendix 2. Picture of a tagged sea trout (left) and the acoustic transmitter (right).

Appendix 3.

Versjon 26.11.2020

Praksisattest

Navn: Lotte Dahlmo

Attesten gjelder for arbeid med laks og/eller sjøaure.

Prosedyre (sett kryss)	Score	Dato	Signatur veileder
Håndtering	1		✓ 1
Bedøvelse	1		✓ 1
PIT-merking (skalpell)	1		
PIT-merking (merke pistol)	1		
Floy-merking			
CWT-merking			
Akustikk-merking	1 1		✓ 1
Avliving (slag mot hodet)	1		✓ 1
Avliving overdose			
Avliving elektrisk bedøving			
Gjelleprøver	1		✓ 1
Kliniske tegn på gassblæresyke			
Blodprøve			
Histologi gjeller			
Histologi hud			
Fettfinneklipping			
Annet:			

Score 1 betyr mestrer teknikken nok til å kunne arbeide alene

Score 2 betyr mestrer teknikken nok til å lære andre

Appendix 3. Certification of tagging abilities

Appendix 4.

Appendix 4. Detailed description of manually filtering of detections

One sea trout (ID 4673) was detected twice by the lower receiver in the upstream river, Vassbygdelva, on August 28 and November 14. However, the sea trout was detected six times on the receivers in the western part of the lake between these two detections, without being detected by any of the six receivers in the eastern part of the lake. The sea trout was frequently detected by these six receivers in the eastern part of the lake prior to the first river detection on August 28, and it is unlikely that the sea trout passed these receivers without being detected once by at least one of the receivers. Therefore the six lake detections between October 01 and November 13 were removed. The first two detections from the second fish (ID 4709) were registered by one of the lake receivers, yet the following detections were registered in the river, the first one by the receiver closest to where the sea trout was tagged 2 km downstream of the lake. These two first lake detections were therefore removed. Despite being tagged nearly 3.8 km from the confluence of the lake, the first detection of the third sea trout (ID 4736) was in the lake. The following three detections were registered by two different river receivers as the sea trout ascended the river and entered the lake. This first detection was therefore removed. The manually filtered dataset consisted of 3 738 173 detections.

Appendix 5.

Appendix 5. R-codes

```
#### load in data ####
aur0 <- read_csv("C:/Users/losv/OneDrive - University of Bergen/Aurland/AurUiB/Feb/
aurland-new.csv") %>%
  mutate(dtz=with_tz(dt_utc, "CET"))
aur1 <- aur0 %>%
  dplyr::select(Receiver, lat, lon, dt, dt_utc, dtz, ID, Data, oid, dmy, sensor, TL, Angler) %>%
  mutate(Receiver=as.numeric(Receiver)) %>%
  dplyr::filter(!is.na(sensor)) %>%
  replace_na(list(lon=7.238081)) %>%
  replace_na(list(lat=60.88436)) %>%
  dplyr::filter(ID>4660 & ID<4800) %>%
  dplyr::filter(!is.na(lon)) %>%
  dplyr::filter(dt <=as.POSIXct("2021-11-15", tz="Europe/Oslo")) %>% # ("2021-11-15
CEST")) funker også
  dplyr::filter(oid!=4685) %>%
  replace_na(list(Angler="Bjornar")) %>%
  mutate(Habitat=case_when(
    (lon> 7.263 & lon< 7.309)~"Lake",
    (lon< 7.2629 | lon> 7.31)~"River")) %>%
  mutate(lonC=lon, latC=lat) %>%
  mutate(yr="2021") %>%
  unite(tag, dmy, yr, sep= " ") %>%
  mutate(tag=lubridate::mdy(tag)) %>%
  mutate(tagdt=lubridate::hms("06:00:00")) %>%
  unite(tag, tag, tagdt, sep = " ") %>%
  mutate(tag=lubridate::ymd_hms(tag)) %>%
  rename(dt_cet=dt) %>%
```

```
  rename(dt=dtz)

#### change the projection system to UTM ####
require(rgdal)
coordinates(aur1) <- ~lon+lat
proj4string(aur1) <- CRS("+init=epsg:4326")
aur1<-spTransform(aur1, CRS("+proj=utm  +zone=33 +datum=WGS84"))
aur1<-aur1 %>% as_tibble()

#### filter out dead individual ####
aur1 <- aur1 %>%
  dplyr::filter(oid!=4697 | oid==4697 & dt<="2021-08-26 00:00:00") # correct time


#### filter for speed and distance ####
d_fun<-function(x1, x2, y1, y2) {
  sqrt(((x1-x2)^2)+(y1-y2)^2)
}

options(scipen=999)

# create six new columns: llon, llat, ldt, dist, time, speed
aur1 = aur1 %>%
  arrange(dt) %>%
  group_by(oid) %>%
  mutate(llon=lag(lon, default=first(lon)), # create llon column (previous lon detection)
         llat=lag(lat, default=first(lat)),  # create llat column
         ldt=(lag(dt, default=first(dt)))) %>% # create ldt (previous time detection)
  mutate(dist=d_fun(llon, lon, llat, lat), # create distance column
         time=as.numeric(dt-ldt)) %>% # create time passed since last detection
  mutate(speed=dist/time) # create speed column

# speed and distance filters
aur1 = aur1 %>%
  group_by(oid) %>%
  mutate(fil=case_when(lag(Habitat)=="Lake" & dist>1000~"FALSE",T~"TRUE")) %>%
  dplyr::filter(fil=="TRUE") # keep the true detections

aur1 = aur1 %>%
  group_by(oid) %>%
  mutate(sdfil=case_when(speed>5 & dist>800~"FALSE", T~"TRUE")) %>%
  dplyr::filter(sdfil=="TRUE")
```

```
aur1 <- aur1 %>%
  group_by(oid) %>%
  mutate(fil2=case_when(lag(Habitat)=="River" & dist>1000~"FALSE", T~"TRUE")) %>%
  dplyr::filter(fil2=="TRUE")

#### combine aur1 and eco1 and temp1 (eco)####
# make identical column with eco
aur1 = aur1 %>%
  arrange(dt) %>%
  mutate(dt60=dt)

minute(aur1$dt60) = 0
second(aur1$dt60) = 0

eco0 <- read_excel("C:/Users/losv/OneDrive - University of
Bergen/Aurland/AurUiB/Aur/Eco.xlsx")
eco1 = eco0 %>%
  as_tibble() %>%
  mutate(Dato=if_else(str_detect(DT, "^\\d"), DT, NA_character_)) %>%
  fill(Dato) %>%
  mutate(Tid=if_else(str_detect(DT, "^\\d"), "Time 01", DT),
         Tid=str_remove(Tid, "Time "),
         Tid=as.numeric(Tid),
         Tid=Tid-1,
         Tid=paste(Dato, Tid),
         dt_utc=dmy_h(Tid)) %>%
  mutate(dt=force_tz(dt_utc, "CET"))

eco1 = eco1 %>%
  dplyr::filter(dt <= as.POSIXct("2021-11-14 23:00:00")) %>%
  dplyr::filter(dt >= as.POSIXct("2021-07-20")) %>%
  dplyr::select(-DT, -Dato, -Tid, -dt_utc) %>%
  arrange(dt) %>%
  mutate(dt60=(dt)) %>%
  dplyr::select(-dt) %>%
  group_by(dt60) %>%
  summarise(AU1m=mean(AU1), AU4=AU4, Vassbygdelvi=mean(Vassbygdelvi),
dt60=dt60, Aurlandselva=Skjærshølen) %>%
  distinct()

### get the temperature
```

```
require(readxl)
temp0 <- read_excel("C:/Users/losv/OneDrive - University of
Bergen/Aurland/AurUiB/Aur/EcoVannTemp.xlsx")

temp1 = temp0 %>%
  as_tibble() %>%
  mutate(Dato=if_else(str_detect(DT, "^\\d"), DT, NA_character_)) %>%
  fill(Dato) %>%
  mutate(Tid=if_else(str_detect(DT, "^\\d"), "Time 01", DT),
         Tid=str_remove(Tid, "Time "),
         Tid=as.numeric(Tid),
         Tid=Tid-1,
         Tid=paste(Dato, Tid),
         dt_utc=dmy_h(Tid)) %>%
  mutate(dt=force_tz(dt_utc, "CET")) %>%
  mutate(Aurlandselva=SkjærshølenVann)

temp1 = temp1 %>%
dplyr::filter(dt <= as.POSIXct("2021-11-14 23:00:00")) %>%
#  dplyr::filter(dt >= as.POSIXct("2021-07-20")) %>%
  dplyr::select(-DT, -Dato, -Tid, -dt_utc) %>%
  arrange(dt) %>%
  mutate(dt60=dt) %>%
  dplyr::select(-dt) %>%
  group_by(dt60) %>%
  summarise(Aurlandselva=mean(Aurlandselva), Vassbygdelvi=mean(VassbygdelviVann),
            VassbydelviTemp=mean(VassbygdelviTemp),
VassbygdevatnetTemp=mean(VassbygdvatnTemp), dt60=dt60) %>%
  distinct()

temp1 %>%
  dplyr::filter(dt60 <= as.POSIXct("2021-10-31 04:00:00")) %>%
  dplyr::filter(dt60 >= as.POSIXct("2021-10-31 02:00:00")) %>% view

# combine aur1 and eco1 and temp1
aurmeta = left_join(aur1, eco1, by="dt60")
aurmeta = left_join(aurmeta, temp1, by=c("dt60", "Vassbygdelvi", "Aurlandselva"))%>%
  ungroup()

aurmeta %>% colnames
# plot over water flow - fix superscript
water = aurmeta %>%
```

```
  pivot_longer(AU1m:Aurlandselva, names_to = "waterflow")
water1 = aurmeta %>%
  pivot_longer(AU1m:AU4, names_to = "waterflow")

#### azimuth and lunar ####
aurmeta = aurmeta %>%
  rename(lonU=lon, latU=lat) %>%
  mutate(getSunlightPosition(dt, lat=60.87, lon=7.25, keep="azimuth")) %>%
  mutate(lunphase=lunar.phase(dt)) %>%
  mutate(luni=lunar.illumination(dt, shift=+2)) %>%
  dplyr::select(-fil, -sdfil, -fil2) %>%
  dplyr::select(-lon,-lat)

#### average sensor data ####
# create 15 min time intervals
aurmean = aurmeta %>%
  mutate(dt15=round_date(dt, "15 min")) %>%
  dplyr::select(-dt60)

# get the mean of sensor data
aurmean1 = aurmean %>%
  dplyr::select(dt, oid, Data, sensor) %>%
  arrange(oid, dt) %>%
  mutate(dt15=round_date(dt, "15 min")) %>%
  group_by(oid, dt15, sensor) %>%
  summarise(mean=mean(Data)) %>%
  mutate(maccel=case_when(sensor=="accel"~mean)) %>%
  mutate(mtemp=case_when(sensor=="temp"~mean)) %>%
  mutate(mdepth=case_when(sensor=="depth"~mean))

aurmean1.1 = aurmean1 %>%
  dplyr::select(-sensor, -mean)

aurmean1.1 = aurmean1.1 %>% # combine the rows
  group_by(oid, dt15) %>%
  summarise(maccel=max(maccel, na.rm=T),
            mtemp=max(mtemp, na.rm=T),
            mdepth=max(mdepth, na.rm=T))

aurmean1.1 = aurmean1.1 %>% # change -Inf to NA
  mutate(maccel=replace(maccel, maccel=="-Inf", NA)) %>%
  mutate(mtemp=replace(mtemp, mtemp=="-Inf", NA)) %>%
```

```
  mutate(mdepth=replace(mdepth, mdepth=="-Inf", NA))


#### average azimuth and luni data ####
aurmean2 = aurmean %>%
  dplyr::select(dt, oid, azimuth, luni) %>%
  arrange(oid, dt) %>%
  mutate(dt15=round_date(dt, "15 min")) %>%
  group_by(oid, dt15) %>%
  summarise(maz=mean(azimuth), mluni=mean(luni))

#### average long and lat position ####
# lonU and latU
aurmean3 = aurmean %>%
  dplyr::select(dt, oid, lonU, latU) %>%
  arrange(oid, dt) %>%
  mutate(dt15=round_date(dt, "15 min")) %>%
  group_by(oid, dt15) %>%
  summarise(mlon=mean(lonU), mlat=mean(latU))

# lonC and latC
aurmean4 = aurmean %>%
  dplyr::select(dt, oid, lonC, latC) %>%
  arrange(oid, dt) %>%
  mutate(dt15=round_date(dt, "15 min")) %>%
  group_by(oid, dt15) %>%
  summarise(mlonC=mean(lonC), mlatC=mean(latC))

# llon and llat
aurmean5 = aurmean %>%
  dplyr::select(dt, oid, llon, llat) %>%
  arrange(oid, dt) %>%
  mutate(dt15=round_date(dt, "15 min")) %>%
  group_by(oid, dt15) %>%
  summarise(mllon=mean(llon), mllat=mean(llat))

#### combine all data frames ####
aurmean5 %>% colnames()

mean0 = aurmean %>%
  dplyr::select(-dt, -ID, -Data, -sensor, -lonC, -latC, -lonU, -latU, -llon, -llat, -ldt, -dist, -time,
-speed, -date, -azimuth, -luni)
```

```
# combine mean sensor data
mean1 = left_join(mean0, aurmean1.1, by=c("oid", "dt15"))
mean1 = mean1 %>% dplyr::select(-dt_utc, -dt_cet)
mean1 = mean1 %>% distinct(., .keep_all = T)

# combine mean azi and luni
mean2 = left_join(mean1, aurmean2, by=c("oid", "dt15"))

# combine mean lon and lat
mean3 = left_join(mean2, aurmean3, by=c("oid", "dt15"))

# combine mean lonC and latC
mean4 = left_join(mean3, aurmean4, by=c("oid", "dt15")) # added on Feb 3 2022

# combine mean llon and llat
mean5 = left_join(mean4, aurmean5, by=c("oid", "dt15")) # added on Feb 19 2022

##### mean6 with DoY and ToD ####
mean6 = mean5 %>%
mutate(DoY=as.numeric(format(dt15, format='%j'))) %>%
  mutate(ToD=
         (as.numeric(format(dt15, format='%H')))+
         (as.numeric(format(dt15, format='%M'))/60)+
         (as.numeric(format(dt15, format='%S'))/3600))

#### get the capture sites ####
trout <-
gsheet2tbl('https://docs.google.com/spreadsheets/d/1G9Ll78xzcXAppZGvQ6sPjLQWgPAah
vCH3wCry9xtWMU/edit?usp=sharing') %>%
  as_tibble %>%
  dplyr::select(Transmitter, "Capture", slat, slon, site) %>%
  dplyr::filter(!is.na(Transmitter)) %>%
  rename(oid=Transmitter, capture="Capture")

dfs = trout %>%
  count(site)
trout = left_join(trout, dfs, by="site")

#### create DoY and ToD ####
habitat = aur1 %>%
  dplyr::select(dt, oid, Habitat, tag) %>%
```

```
  ungroup() %>%
  arrange(oid, dt) %>%
  mutate(DoY=as.numeric(format(dt, format='%j'))) %>%
  mutate(ToD=
         (as.numeric(format(dt, format='%H')))+
         (as.numeric(format(dt, format='%M'))/60)+
         (as.numeric(format(dt, format='%S'))/3600)) %>%
  mutate(id = data.table::rleid(Habitat)) %>%
  arrange(oid, dt)

#### time spent in habitat - aur1 dt ####
# habitat spent overview
hab2 = habitat %>%
  group_by(oid, id, Habitat) %>%
  dplyr::summarise(time_spent=difftime(max(dt), min(dt), units="days")) %>%
  group_by(oid, Habitat) %>%
  dplyr::summarise(time_spent_new=sum(time_spent))

options(digits=11)

hab2 = hab2 %>%
  group_by(oid) %>%
  mutate(TiH=as.numeric(time_spent_new)) %>%
  mutate(tot=sum(TiH)) %>%
  mutate(per=(TiH/tot)*100)

# all columns
habview = left_join(habitat, hab2, by=c("oid", "Habitat")) %>%
  arrange(oid, dt)

#### combine habitat overview and tagging site ####
det = left_join(habview, trout, by="oid")

#### plot undetected river lake distribution new 09 mars ####
unhabitat = aur1 %>%
  dplyr::select(dt, oid, Habitat, tag) %>%
  arrange(oid, dt)

sp = seq(from=as.POSIXct("2021-07-20 00:00:00", tz="Europe/Oslo"),
        by=60, to=
         as.POSIXct("2021-11-15 00:00:00 CEST")+
         as.difftime(10, units="hours")) %>%
```

```
  as_tibble %>%
  dplyr::rename(dti=value)

unhabitat = unhabitat %>%
  mutate(dti=round_date(dt, "min")) %>%
  select(oid, Habitat, dti, tag) %>%
  split(., .$oid) %>%
  purrr::map(~distinct(.x)) %>%
  purrr::map(~full_join(sp %>% mutate(i="i"), .x, by="dti")) %>%
  purrr::map(~fill(.x, tag, .direction = "downup")) %>% # checked all individuals that this is
correct
  map_dfr(~fill(.x, oid, .direction = "downup")) %>%
  mutate(Habitat=replace_na(Habitat, "Undetected")) %>%
  mutate(DoY=lubridate::yday(dti)) %>%
  mutate(ToD=lubridate::hour(dti)+
         (lubridate::minute(dti)/60)+
         (lubridate::second(dti)/3600))

# to check that tag filling is correct
# undet %>% dplyr::filter(oid==4757) %>% distinct(tag) %>% view
unhabitat = unhabitat %>%
  arrange(oid, dti) %>%
  dplyr::select(-i) %>%
  dplyr::filter(oid==4697 & dti<ymd_hms("2021-08-26 00:00:00") | oid!=4697) %>%
  mutate(id=data.table::rleid(Habitat))

unhab2 = unhabitat %>%
  group_by(oid, id, Habitat) %>%
  dplyr::summarise(time_spent=difftime(max(dti), min(dti), units="days")) %>%
  group_by(oid, Habitat) %>%
  dplyr::summarise(time_spent_new=sum(time_spent))

options(digits = 11)

unhab2 = unhab2 %>%
  group_by(oid) %>%
  mutate(TiH=as.numeric(time_spent_new)) %>%
  mutate(tot=sum(TiH)) %>%
  mutate(per=(TiH/tot)*100)

unhabview = left_join(unhabitat, unhab2, by=c("oid", "Habitat")) %>%
  arrange(oid, dti)
```

```
mod = left_join(mean6, trout %>% dplyr::select(-n), by="oid")

### hypothesis 1
a<-aurmeta %>%
  mutate(dti=dt)
second(a$dti)=0

#  mutate(dti=round_date(dt, "1 min")) %>%
a = a %>%
  mutate(dti=round_date(dti, "min")) %>%
  arrange(dt) %>%
  split(.$oid) %>%
  purrr::map(~left_join(., seq(as.POSIXct("2021/7/20 00:00"), as.POSIXct("2021/11/15
00:00"),
                              by = "min") %>%
                           as_tibble %>%
                           dplyr::rename(dti=value)))

time_seq<-seq(as.POSIXct("2021/7/20 00:00"),
              as.POSIXct("2021/11/15 00:00"),
              by = "min") %>%
  as_tibble %>%
  dplyr::rename(dti=value)

a<-aurmeta %>%
  mutate(dti=round_date(dt, "min")) %>%
  select(oid, tag, Habitat, dt, dti, lonC, Receiver) %>%
  arrange(dt) %>%
  split(., .$oid) %>%
  purrr::map(~distinct(.x)) %>%
#  purrr::map(~right_join(., time_seq)) %>%
  purrr::map(~full_join(time_seq %>% mutate(i="i"), .x, by="dti")) %>%
  purrr::map(~fill(.x, tag, .direction = "downup")) %>%
  purrr::map(~fill(.x, Habitat, .direction = "down")) %>%
  purrr::map(~filter(.x, dti>tag)) %>%
  purrr::map(~fill(., Habitat, .direction = "up")) %>%
  map_dfr(~fill(.x, oid, .direction = "downup"))

b<-a %>%
#  bind_rows() %>%
  group_by(oid, tag) %>%
```

```
  tidyr::fill(Receiver, lonC, Habitat, .direction="down") %>%
  arrange(dti) %>%
  ungroup() %>%
  dplyr::select(dti, oid, tag, Receiver, lonC, Habitat)

b<-b %>% mutate(habitat=case_when(
  (lonC> 7.263 & lonC< 7.309~"Lake"),
  (lonC> 7.31)~"River",
  (lonC< 7.2629)~"River"))

b %>%
  dplyr::filter(!is.na(oid)) %>%
  distinct(Habitat, oid, yd=date(dti)) %>%
  group_by(Habitat, yd) %>%
  count() %>%
  ggplot(aes(yd, n, fill=Habitat))+
  geom_col()+
  theme_classic()

c = b %>%
  dplyr::filter(!is.na(oid)) %>%
  distinct(Habitat, oid, yd=date(dti)) %>%
  group_by(Habitat, yd) %>%
  count() %>%
  right_join(b %>%
        dplyr::filter(!is.na(oid)) %>%
        distinct(Habitat, oid, yd=date(dti)) %>%
        group_by(yd) %>%
        summarise(nt=n())) %>%
  dplyr::filter(Habitat=="Lake")

glm(n ~ yd + offset(log(nt)), family="poisson", data=c) %>% summary

### hypothesis 2
mod1 = mod %>%
  mutate(site=as.factor(site)) %>%
  mutate(foid=as.factor(oid)) %>%
  mutate(Habitat=as.factor(Habitat)) %>%
  mutate(capture=as.factor(capture))

# checking correlation
require(GGally)
```

```
corrM1 = mod1 %>% ungroup() %>% dplyr::select(Habitat, mluni, site, DoY, ToD,
Aurlandselva, mtemp)
ggpairs(corrM1, aes(alpha=0.4), lower = list(combo=wrap("facethist", binwidth=0.5)))

# basic model
m1.10 = bam(maccel ~ Habitat +
              s(DoY, by=Habitat, k=40) +
              s(ToD, by=Habitat, k=5) +
              s(foid, bs="re", k=30),
            data=mod1, method="fREML",
            family=Gamma(link="log"),
            discrete = T)

k.check(m1.10, subsample = 5000, n.rep=400)
gam.check(m1.10)
plot(m1.10)
summary(m1.10)

## autocorrelation
valRhoM1 = acf(resid(m1.10), plot=FALSE)$acf[2]
mod1.1 = mod1

mod1.1 = mod1.1 %>%
  select(oid, dt15) %>%
  arrange(dt15) %>%
  group_by(oid) %>%
  summarise(dt15=min(dt15)) %>%
  mutate(start=TRUE) %>%
  right_join(mod1.1) %>%
  mutate(start=case_when(is.na(start)~FALSE, T~T))

# include autocorrelation
m1.20 = bam(maccel ~ Habitat +
              s(DoY, by=Habitat, k=40) +
              s(ToD, by=Habitat, k=5) +
              s(foid, bs="re", k=30),
            data=mod1.1, method="fREML",
            family=Gamma(link="log"),
            discrete = T,
            AR.start=mod1.1$start, rho=valRhoM1)
k.check(m1.20, subsample = 5000, n.rep=400)
gam.check(m1.20)
```

```
summary(m1.20)
draw(m1.20)

# model selection
AIC(m1.10, m1.20)

# check concurvity()
concurvity(m1.20, full=T)

### hypothesis 3
mod2 = mod %>%
  dplyr::filter(Habitat=="Lake") %>%
  mutate(Rec = as.numeric(Receiver==1739)) %>%
  mutate(site=as.factor(site)) %>%
  mutate(foid=as.factor(oid))

# correlation
corrM2 = mod2 %>% ungroup() %>% dplyr::select(Habitat, mluni, site, DoY, ToD, mtemp,
AU1m)
ggpairs(corrM2, aes(alpha=0.4), lower = list(combo=wrap("facethist", binwidth=0.5)))

# basic model
m2.10 = bam(mdepth ~
              s(mlon, mlat, k=125) +
              s(DoY, k=40) +
              s(ToD, k=10) +
              s(foid, bs="re", k=26),
            data=mod2,
            method="fREML",
            family=Gamma(link="log"),
            discrete = T)

k.check(m2.10, subsample = 5000, n.rep=400)
gam.check(m2.10)

## autocorrelation
valRhoM2 = acf(resid(m2.10), plot=FALSE)$acf[2]
mod2.1 = mod2

mod2.1 = mod2.1 %>%
  select(oid, dt15) %>%
  arrange(dt15) %>%
```

```
  group_by(oid) %>%
  summarise(dt15=min(dt15)) %>%
  mutate(start=TRUE) %>%
  right_join(mod2.1) %>%
  mutate(start=case_when(is.na(start)~FALSE, T~T))

# include autocorrelation
m2.20 = bam(mdepth ~
              s(mlon, mlat, k=125) +
              s(DoY, k=40) +
              s(ToD, k=10) +
              s(foid, bs="re", k=26),
            data=mod2.1,
            method="fREML",
            family=Gamma(link="log"),
            discrete = T,
            AR.start=mod2.1$start, rho=valRhoM2)

k.check(m2.20, subsample = 5000, n.rep=400)
gam.check(m2.20)
summary(m2.20)
AIC(m2.10, m2.20)

# include discharge
m2.30 = bam(mdepth ~
              s(AU1m, k=10) +
              s(mlon, mlat, k=125) +
              s(DoY, k=40) +
              s(ToD, k=10) +
              s(foid, bs="re", k=26),
            data=mod2.1,
            method="fREML",
            family=Gamma(link="log"),
            discrete = T,
            AR.start=mod2.1$start, rho=valRhoM2)

k.check(m2.30, subsample = 5000, n.rep=400)
gam.check(m2.30)
summary(m2.30)
plot(m2.30)
AIC(m2.20, m2.30)
```

```
concurvity(m2.30, full=F)

### hypothesis 4
mod3 = mod %>%
  dplyr::filter(Habitat=="Lake") %>%
  mutate(site=as.factor(site)) %>%
  mutate(foid=as.factor(oid)) %>%
  mutate(TL=as.numeric(TL))

# checking correlation
library(GGally)
corrM3 = mod3 %>% ungroup() %>% dplyr::select(Habitat, mluni, site, DoY, ToD, AU1m,
TL)
ggpairs(corrM3, aes(alpha=0.4), lower = list(combo=wrap("facethist", binwidth=0.5)))

# basic model
m3.10 = bam(maccel ~ mdepth +
              s(mlon, mlat, k=125) +
              s(DoY, k=40) +
              s(ToD, k=10) +
              s(foid, bs="re", k=26),
            data=mod3,
            method="fREML",
            family=Gamma(link="log"),
            discrete = T)

k.check(m3.10, subsample = 5000, n.rep=400)
gam.check(m3.10)

## autocorrelation
valRhoM3 = acf(resid(m3.10), plot=FALSE)$acf[2]
mod3.1 = mod3

mod3.1 = mod3.1 %>%
  select(oid, dt15) %>%
  arrange(dt15) %>%
  group_by(oid) %>%
  summarise(dt15=min(dt15)) %>%
  mutate(start=TRUE) %>%
  right_join(mod3.1) %>%
  mutate(start=case_when(is.na(start)~FALSE, T~T))
```

```
# include autocorrelation
m3.20 = bam(maccel ~ mdepth +
        s(mlon, mlat, k=125) +
        s(DoY, k=40) +
        s(ToD, k=5) +
        s(foid, bs="re", k=26),
      AR.start=mod3.1$start, rho=valRhoM3,
      data=mod3.1,
      method="fREML",
      family=Gamma(link="log"),
      discrete = T)

k.check(m3.20, subsample = 5000, n.rep=400)
gam.check(m3.20)
summary(m3.20)
AIC(m3.10, m3.20)

# include discharge
m3.30 = bam(maccel ~ mdepth +
        s(AU1m, k=10) +
        s(mlon, mlat, k=125) +
        s(DoY, k=40) +
        s(ToD, k=5) +
        s(foid, bs="re", k=26),
      AR.start=mod3.1$start, rho=valRhoM3,
      data=mod3.1,
      method="fREML",
      family=Gamma(link="log"),
      discrete = T)

k.check(m3.30, subsample = 5000, n.rep=400)
gam.check(m3.30)
summary(m3.30)
plot(m3.30, pages = 1, all.terms = TRUE)
AIC(m3.20, m3.30)
concurvity(m3.30, full=F)
```

Appendix 6.

Appendix 6. R-codes for figures

Figure 1. Map of Aurland watercourse and receiver locations

```
tr <- opq(bbox = 'Aurland Norway') %>% # opq defines a bounding box
  add_osm_feature(key = 'name') %>%
  osmdata_sf()

coord <-
gsheet2tbl('https://docs.google.com/spreadsheets/d/1h1KAS5IU08DqiRPs2_1cPoiUUzqAqQ
_AmFeiLXtVHb4/edit#gid=1259876854') %>%
  as_tibble %>%
  dplyr::filter(!is.na(lon)) %>%
  dplyr::select(Habitat, Receiver, lat, lon, type, acc, dep) %>%
  mutate(Receiver=as.factor(Receiver))

power =
gsheet2tbl('https://docs.google.com/spreadsheets/d/1h1KAS5IU08DqiRPs2_1cPoiUUzqAqQ
_AmFeiLXtVHb4/edit#gid=1259876854') %>%
  as_tibble() %>%
  dplyr::select(lat, lon, type) %>%
  dplyr::filter(type=="Vangen" | type=="Aurland 1")

#### aurland map base ####
aurlandmap = tr$osm_polygons %>%
  dplyr::filter(grepl("Vassbygdivatne", name)) %>%
  ggplot()+
  geom_sf(fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_multipolygons %>%
          dplyr::filter(grepl("Aurlandsfjor", name)),
        fill="skyblue3", colour="skyblue3")+
  geom_sf(data=tr$osm_multipolygons %>%
          dplyr::filter(grepl("Aurlandselvi", name)),
        colour="#a6cee3", fill="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302575", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302574", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
```

```
          dplyr::filter(grepl("298302571", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302572", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302573", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%
          dplyr::filter(grepl("298302569", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  theme_classic()+
  coord_sf(xlim=c(7.15, 7.36),
         ylim=c(60.850, 60.91))+
  geom_segment(aes(x=7.26424, y=60.87209, xend=7.26371, yend=60.87202),
             colour="lightgrey", size=1)+ # Vangen short
  geom_segment(aes(x=7.26371, y=60.87202, xend=7.25884, yend=60.87325),
             colour="lightgrey", size=1)+ # Vangen short
  geom_segment(aes(x=7.25884, y=60.87325, xend=7.17898, yend=60.90183),
             colour="lightgrey", size=1)+ # Vangen long
  geom_segment(aes(x=7.17898, y=60.90183, xend=7.1755, yend=60.9035),
             colour="lightgrey", size=1)+ # Vangen short fjord
  geom_segment(aes(x=7.30401, y=60.86341, xend=7.30613, yend=60.85653),
             colour="lightgrey", size=1)+ # Aurland 1 short
  geom_segment(aes(x=7.30613, y=60.85653, xend=7.30586, yend=60.85563),
             colour="lightgrey", size=1)+ # Aurland 1 short2
  geom_segment(aes(x=7.30586, y=60.85563, xend=7.30056 , yend=60.85240),
             colour="lightgrey", size=1)+ # Aurland 1 long
  geom_segment(aes(x=7.30056, y=60.85240, xend=7.29159 , yend=60.84685),
             colour="lightgrey", size=1)+ # Aurland 1 long
  geom_segment(aes(x=7.263, y=60.8755, xend=7.265, yend=60.876), # Dam across
Aurlandselva
             colour="red3", size=1)+
  labs(x="Longitude", y="Latitude")+
  geom_point(data=power,
           aes(lon, lat), pch=15, inherit.aes=F, size=2)+
  theme(text = element_text(colour = "black"), axis.text = element_text(colour="black"),
      axis.line = element_line(colour="black"), axis.ticks = element_line(colour = "black"))

library(ggspatial)
aurlandrec = aurlandmap +
  geom_point(data=coord %>%
```

```
          as_tibble() %>%
          dplyr::filter(Receiver!=437) %>%
          mutate(lon=as.numeric(lon), lat=as.numeric(lat)) %>%
          distinct(lon, lat, acc, dep),
         aes(lon, lat, shape=acc, fill=dep),
         inherit.aes = F, size=2)+
  scale_shape_manual(values=c(21, 24))+
  scale_fill_manual(values=c("#ccebc5", "#1f78b4"))+
  theme(legend.position = "none",
      panel.border = element_rect(colour = "black", fill=NA, size=.35),
      axis.line = element_line(size=.35))+
  annotate("text", x = 7.28, y=60.8589, label = "Lake \n Vassbygdevatnet",
        colour="black", size=3)+
  annotate("text", x = 7.23, y=60.90, label = "River \n Aurlandselva",
        colour="black", size=3)+
  annotate("text", x = 7.338, y=60.878, label = "River \n Vassbygdelva",
        colour="black", size=3)+
  annotate("text", x = 7.16699, y=60.90912, label = "Fjord \n Aurlandsfjorden",
        colour="black", size=3)+
  annotate("text", x = 7.314, y=60.85270, label = "Aurland 1",
        colour="black", size=3)+
  annotate("text", x = 7.17801, y=60.89864, label = "Vangen",
        colour="black", size=3)+
  annotate("text", x = 7.285, y=60.8792, label = "Flap weir & \n fish ladder",
        colour="black", size=3)+
  geom_segment(aes(x=7.2735, y=60.879, xend=7.266, yend=60.8764),
          arrow=arrow(length=unit(0.1, "cm")), colour="black")+ #gray26
  annotation_scale(width_hint=0.1, bar_cols = "black",
           line_col="black", style="bar", unit_category="metric", text_col = "black")+
  coord_sf(xlim=c(7.15, 7.36),
        ylim=c(60.852, 60.91))+
#  theme(panel.grid.major = element_line(colour="black"))+
  theme(panel.background = element_blank(),
      plot.background = element_blank(),
      text = element_text(colour = "black"), axis.text = element_text(colour="black"),
      axis.line = element_line(colour="black"), axis.ticks = element_line(colour = "black"))
```

Figure 2. Water flow in high-head storage plant and downstream river, Aurlandselva

```
waterflow = water %>%
  dplyr::filter(waterflow=="Aurlandselva" | waterflow=="AU1m") %>%
  ggplot(aes(dt60, value, colour=waterflow))+
```

```
  geom_line()+ # aes(linetype=waterflow)
  xlab(label = "Time")+
  ylab(bquote('Water flow'~(m^3/sec)))+
  scale_color_manual(values=c("#a6cee3", "#1f78b4"),
                    labels=c("Aurland 1", "Aurlandselva"))+
  theme(legend.key.width = unit(1.5, "cm"),
#        legend.key.height = unit(5, "cm"),
        legend.position = "top",
        legend.text = element_text(size=14),
        legend.title = element_blank(),
        axis.text = element_text(size=12),
        axis.title = element_text(size=14),
        legend.margin=margin(t = 0, unit='cm'))+
  geom_vline(xintercept = as.POSIXct(as.Date("2021-09-15")), linetype="dashed", alpha
=0.5)+
  guides(color = guide_legend(override.aes = list(size = 2)))
```

Figure 3. Map of Aurland watercourse and tagging sites in downstream river, Aurlandselva

```
trout <-
gsheet2tbl('https://docs.google.com/spreadsheets/d/1G9Ll78xzcXAppZGvQ6sPjLQWgPAah
vCH3wCry9xtWMU/edit?usp=sharing') %>%
  as_tibble %>%
  dplyr::select(Transmitter, "Capture", slat, slon, site) %>%
  dplyr::filter(!is.na(Transmitter)) %>%
  rename(oid=Transmitter, capture="Capture") %>%
  dplyr::filter(oid!=4685)
dfs = trout %>%
  count(site)
trout = left_join(trout, dfs, by="site")

trout = trout %>%
  mutate(n=as.character(n)) %>%
  mutate(pct = paste0("(", n,")")) %>%
  unite("tag", c("site", "capture"), remove=F, sep = " - ") %>%
  unite("tag", c("tag", "pct"), remove=F, sep = " ") %>%
  unite("sitetagged", c("site", "pct"), remove=F, sep= " - ") %>%
  unite("tagsite", c("site", "capture"), remove=F, sep = " - ")

tagsitecolours <- c("#000000", "#E69F00", "#56B4E9", "#009E73", "#F0E442",
"#0072B2","#999999", "#D55E00", "#CC79A7")

maptagging = tr$osm_polygons %>%
```

```
dplyr::filter(grepl("Vassbygdivatne", name)) %>%
ggplot()+
geom_sf(fill="#a6cee3", colour="#a6cee3")+
geom_sf(data=tr$osm_multipolygons %>%
          dplyr::filter(grepl("Aurlandsfjor", name)),
        fill="skyblue3", colour="skyblue3")+
geom_sf(data=tr$osm_multipolygons %>%
          dplyr::filter(grepl("Aurlandselvi", name)),
        colour="#a6cee3", fill="#a6cee3")+
geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302575", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302574", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302571", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302572", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302573", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
geom_sf(data=tr$osm_lines %>%
          dplyr::filter(grepl("298302569", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
theme_classic()+
coord_sf(xlim=c(7.15, 7.36),
         ylim=c(60.850, 60.91))+
geom_segment(aes(x=7.26424, y=60.87209, xend=7.26371, yend=60.87202),
             colour="lightgrey", size=1)+ # Vangen short
geom_segment(aes(x=7.26371, y=60.87202, xend=7.25884, yend=60.87325),
             colour="lightgrey", size=1)+ # Vangen short
geom_segment(aes(x=7.25884, y=60.87325, xend=7.17898, yend=60.90183),
             colour="lightgrey", size=1)+ # Vangen long
geom_segment(aes(x=7.17898, y=60.90183, xend=7.1755, yend=60.9035),
             colour="lightgrey", size=1)+ # Vangen short fjord
geom_segment(aes(x=7.30401, y=60.86341, xend=7.30613, yend=60.85653),
             colour="lightgrey", size=1)+ # Aurland 1 short
geom_segment(aes(x=7.30613, y=60.85653, xend=7.30586, yend=60.85563),
             colour="lightgrey", size=1)+ # Aurland 1 short2
```

```
  geom_segment(aes(x=7.30586, y=60.85563, xend=7.30056 , yend=60.85240),
              colour="lightgrey", size=1)+ # Aurland 1 long
  geom_segment(aes(x=7.30056, y=60.85240, xend=7.29159 , yend=60.84685),
              colour="lightgrey", size=1)+ # Aurland 1 long
  labs(x="Longitude", y="Latitude")+
  geom_point(data=power,
            aes(lon, lat), pch=15, inherit.aes=F, size=1.5)

trout = trout %>%
  dplyr::select(-oid) %>%
  distinct(tag, slon, slat, sitetagged, tagsite, n)

tagsitenumber = maptagging +
  geom_point(data=trout %>%
              as_tibble() %>%
              mutate(slon=as.numeric(slon), slat=as.numeric(slat)),
            aes(slon, slat, colour=tagsite), inherit.aes=F, size=1.7)+
  scale_colour_manual(values=tagsitecolours)+
  geom_text(data=trout %>%
             as_tibble() %>%
             mutate(slon=as.numeric(slon), slat=as.numeric(slat)),
           aes(slon, slat, label=n), fontface="bold", inherit.aes = F, size=2.7, nudge_x = 0.0027,
nudge_y=0.001)+
  theme(legend.position = "top",
        legend.text = element_text(size=9.2),
        legend.title = element_text(size=9.2),
        panel.border = element_rect(colour = "black", fill=NA, size=.35),
        axis.line = element_line(size=.35))+
  labs(colour="Tag site")+
  annotate("text", x = 7.28, y=60.8586, label = "Lake \n Vassbygdevatnet",
           colour="black", size=3)+
  annotate("text", x = 7.24, y=60.90, label = "River \n Aurlandselva",
           colour="black", size=3)+
  annotate("text", x = 7.338, y=60.878, label = "River \n Vassbygdelva",
           colour="black", size=3)+
  annotate("text", x = 7.16699, y=60.90912, label = "Fjord \n Aurlandsfjorden",
           colour="black", size=3)+
  annotate("text", x = 7.314, y=60.85270, label = "Aurland 1",
           colour="black", size=3)+
  annotate("text", x = 7.17801, y=60.89864, label = "Vangen",
           colour="black", size=3)+
  annotation_scale(width_hint=0.1, bar_cols = "black",
```

```
                    line_col="black", style="bar", unit_category="metric", text_col = "black")
```

Figure 4. Habitat use

```
hyp0 = mean6
hyp1 = left_join(hyp0, trout, by="oid")
hyp1 = hyp1 %>%
  mutate(Hab=case_when(
    (mlonC> 7.263 & mlonC< 7.309~"Lake"),
    (mlonC> 7.31)~"Upstream river",
    (mlonC< 7.2629)~"Downstream river"))

habitatuse = hyp1 %>%
  arrange(oid, dt15) %>%
  ggplot(aes(dt15, paste(site, " - ", oid), colour=Hab %>% factor, group=oid %>% factor))+
  geom_point(size=1)+
  geom_line(size=.6)+
  scale_colour_manual(values = c("#045a8d","#74a9cf", "#dfc27d"))+
  labs(x="Time", y="Tagging site - Fish ID")+
  theme(legend.text = element_text(colour="black", size=12),
        axis.text = element_text(colour="black", size=10),
        axis.title = element_text(colour="black", size=12),
        legend.position = "top", legend.title = element_blank(),
        axis.title.y = element_text(margin = margin(r=10)))+
  geom_vline(xintercept = as.POSIXct(as.Date("2021-09-15")), linetype="dashed", alpha
=0.5)
```

Figure 5. Habitat use and transitions

```
mapcurve <- tr$osm_polygons %>%
  dplyr::filter(grepl("Vassbygdivatne", name)) %>%
  ggplot()+
  geom_sf(fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_multipolygons %>%
           dplyr::filter(grepl("Aurlandsfjor", name)),
          fill="skyblue3", colour="skyblue3")+
  geom_sf(data=tr$osm_multipolygons %>%
           dplyr::filter(grepl("Aurlandselvi", name)),
          colour="#a6cee3", fill="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
           dplyr::filter(grepl("298302575", osm_id)),
          fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
           dplyr::filter(grepl("298302574", osm_id)),
```

```
        fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302571", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302572", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  geom_sf(data=tr$osm_lines %>%  # stretch of vassbygdelva
          dplyr::filter(grepl("298302573", osm_id)),
        fill="#a6cee3", colour="lightblue")+
  geom_sf(data=tr$osm_lines %>%
          dplyr::filter(grepl("298302569", osm_id)),
        fill="#a6cee3", colour="#a6cee3")+
  theme_classic()+
  coord_sf(xlim = c(7.25, 7.325), ylim = c(60.86, 60.881))+
  geom_segment(aes(x=7.26424, y=60.87209, xend=7.26371, yend=60.87202),
             colour="lightgrey", size=1)+ # Vangen short
  geom_segment(aes(x=7.26371, y=60.87202, xend=7.25884, yend=60.87325),
             colour="lightgrey", size=1)+ # Vangen short
  geom_segment(aes(x=7.25884, y=60.87325, xend=7.17898, yend=60.90183),
             colour="lightgrey", size=1)+ # Vangen long
  geom_segment(aes(x=7.17898, y=60.90183, xend=7.1755, yend=60.9035),
             colour="lightgrey", size=1)+ # Vangen short fjord
  geom_segment(aes(x=7.30401, y=60.86341, xend=7.30613, yend=60.85653),
             colour="lightgrey", size=1)+ # Aurland 1 short
  geom_segment(aes(x=7.30613, y=60.85653, xend=7.30586, yend=60.85563),
             colour="lightgrey", size=1)+ # Aurland 1 short2
  geom_segment(aes(x=7.30586, y=60.85563, xend=7.30056 , yend=60.85240),
             colour="lightgrey", size=1)+ # Aurland 1 long
  geom_segment(aes(x=7.30056, y=60.85240, xend=7.29159 , yend=60.84685),
             colour="lightgrey", size=1)+ # Aurland 1 long
  labs(x="Longitude", y="Latitude")+
  #  geom_point(data=power,
  #             aes(lon, lat), pch=15, inherit.aes=F, size=1.5)
  scale_y_continuous(labels=c(60.86, 60.865, 60.870, 60.875, 60.880), breaks = c(60.860,
60.865, 60.870, 60.875, 60.880))+
  scale_x_continuous(labels=c(7.25, 7.26, 7.27, 7.28, 7.29, 7.30, 7.31, 7.32), breaks = c(7.25,
7.26, 7.27, 7.28, 7.29, 7.30, 7.31, 7.32))

arrowmap = mapcurve +
  geom_curve(aes(x=7.264, xend=7.2688, y=60.8777, yend=60.8751),
           arrow = arrow(type = "closed", length = unit(0.04, "npc")),
```

```
            colour= "#1f78b4", size=1, angle=90, curvature=-0.5, linetype="solid")+
  geom_curve(aes(x=7.2626, xend=7.2722, y=60.879, yend=60.8736),
            arrow = arrow(type = "closed", length = unit(0.04, "npc")),
            colour= "#E69F00", size=1, angle=90, curvature=-0.95, linetype="solid")+
  geom_curve(aes(x=7.2621, xend=7.2607, y=60.8735, yend=60.8771),
            arrow = arrow(type="closed", length = unit(0.04, "npc")),
            colour="#1f78b4", size=1, angle=90, curvature = -0.45, linetype="solid")+
  geom_curve(aes(x=7.2627, xend=7.258, y=60.8719, yend=60.8778),
            arrow = arrow(type="closed", length = unit(0.04, "npc")),
            colour="#E69F00", size=1, angle=90, curvature=-1, linetype="solid")+
  geom_curve(aes(x=7.303, xend=7.3139, y=60.8715, yend=60.87179),
            arrow = arrow(type="closed", length = unit(0.04, "npc")),
            colour="#d53e4f", size=1, angle=90, curvature = -0.6, linetype="solid")+
  geom_curve(aes(x=7.316, xend=7.3120, y=60.8712, yend=60.8671),
            arrow = arrow(type="closed", length = unit(0.04, "npc")),
            colour="#d53e4f", size=1, angle=90, curvature = -0.6, linetype="solid")+
  annotate("text", x = 7.2695, y=60.8778, label = 'bold("8 (0)")', parse=T,
          colour="#1f78b4", size=4.5)+
  annotate("text", x = 7.277, y=60.8778, label = 'bold("5 (1)")', parse=T,
          colour="#E69F00", size=4.5)+
  annotate("text", x = 7.2576, y=60.8739, label = 'bold("2 (1)")', parse=T,
          colour="#1f78b4", size=4.5)+
  annotate("text", x = 7.251, y=60.874, label = 'bold("4 (1)")', parse=T,
          colour="#E69F00", size=4.5)+
  annotate("text", x = 7.308, y=60.8739, label = 'bold("4 (2)")', parse=T,
          colour="#d53e4f", size=4.5)+
  annotate("text", x = 7.32, y=60.8686, label = 'bold("3 (1)")', parse=T,
          colour="#d53e4f", size=4.5)
```

Figure 6. Activity in lake vs rivers

```
hyp2 = hyp1

habitataccel = hyp2 %>%
  mutate(tid=as.Date(dt15)) %>%
  group_by(oid, tid) %>%
  summarise(m=mean(maccel), tid=tid, oid=as.factor(oid), Habitat=Habitat) %>%
  ggplot(aes(tid, log(m), colour=oid))+
  geom_point(alpha = 0.6)+
#  stat_summary(geom = "line", fun = "mean", colour="black")+
  scale_shape_manual(values = 19)+
  labs(x="Time", y="Activity (log)")+
  theme(legend.position="none",
```

```
      axis.title.y = element_text(margin = margin(r=10)))+
  facet_wrap(~Habitat)
```

Figure 7. Visualisation of model

```
mod2au1 = draw(m2.30,
              select = smooths(m2.30)[1],
              smooth_col = "#1f78b4")+
  xlab(bquote('Discharge'~(m^3/sec)))+
  ylab("Effect")+
  ggtitle("Discharge Aurland 1")+
  theme(plot.title = element_text(hjust = .5))

mod2doy = draw(m2.30,
              select = smooths(m2.30)[3],
              smooth_col = "#1f78b4")+
  labs(x="Day of Year", y="Effect")+
  ggtitle("Day of Year")+
  theme(plot.title = element_text(hjust = .5))

mod2tod = draw(m2.30,
              select = smooths(m2.30)[4],
              smooth_col = "#1f78b4")+
  labs(x="Time of Day", y="Effect")+
  ggtitle("Time of Day")+
  theme(plot.title = element_text(hjust = .5))

mod2oid = draw(m2.30,
              select = smooths(m2.30)[5],
              smooth_col = "#1f78b4")+
  labs(x="Gaussian quantiles", y="Effect")+
  ggtitle("Individual variation")+
  theme(plot.title = element_text(hjust = .5))

library(gridExtra)
figuremod2 = arrangeGrob(mod2au1, mod2doy, mod2oid, mod2tod, nrow=2)
```

Figure 8. Visualisation of spatial interaction from model

```
mod2spatial = draw(m2.30, n_contour = 14,
    continuous_fill = ggplot2::scale_fill_viridis_c(direction = -1),
    select = smooths(m2.30)[2],
    rug = NULL)+
  labs(x="Longitude (UTM)", y="Latitude (UTM)")+
```

```
  ggtitle(" ")+
  theme(axis.title = element_text(size=14),
        legend.title = element_text(size=14),
        legend.text = element_text(size=12))
```

Figure 9. Visualisation of model

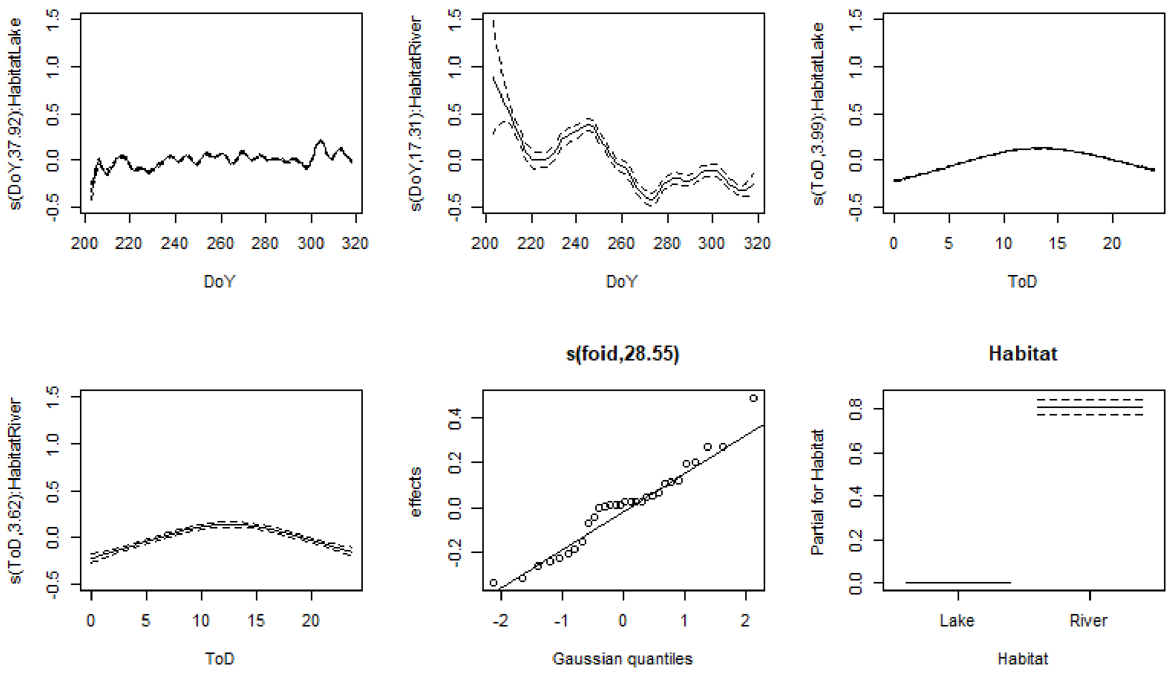
```
mod3au1 = draw(m3.30,
               select = smooths(m3.30)[1],
               smooth_col = "#1f78b4", scale = "fixed")+
  xlab(bquote('Discharge'~(m^3/sec)))+
  ylab("Effect")+
  ggtitle("Discharge Aurland 1")+
  theme(plot.title = element_text(hjust = .5))

mod3doy = draw(m3.30,
               select = smooths(m3.30)[3],
               smooth_col = "#1f78b4")+
  labs(x="Day of Year", y="Effect")+
  ggtitle("Day of Year")+
  theme(plot.title = element_text(hjust = .5))

mod3tod = draw(m3.30,
               select = smooths(m3.30)[4],
               smooth_col = "#1f78b4")+
  labs(x="Time of Day", y="Effect")+
  ggtitle("Time of Day")+
  theme(plot.title = element_text(hjust = .5))

mod3oid = draw(m3.30,
               select = smooths(m3.30)[5],
               smooth_col = "#1f78b4")+
  labs(x="Gaussian quantiles", y="Effect")+
  ggtitle("Individual variation")+
  theme(plot.title = element_text(hjust = .5))

library(gridExtra)
figuremod3 = arrangeGrob(mod3au1, mod3doy, mod3oid, mod3tod, nrow=2)
```

Figure 10. Visualisation of spatial interaction in model

```
mod3spatial = draw(m3.30, n_contour = 14,
                   continuous_fill = ggplot2::scale_fill_viridis_c(direction = 1),
```

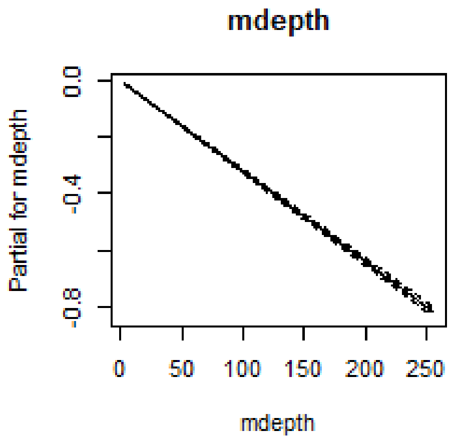
```
              select = smooths(m3.30)[2],
              rug = NULL)+
labs(x="Longitude (UTM)", y="Latitude (UTM)")+
ggtitle(" ")+
theme(axis.title = element_text(size=14),
     legend.title = element_text(size=14),
     legend.text = element_text(size=12))
```

<u>Appendix 7.</u>



Appendix 7. Visualization of model output from hypothesis 2.

Appendix 8.



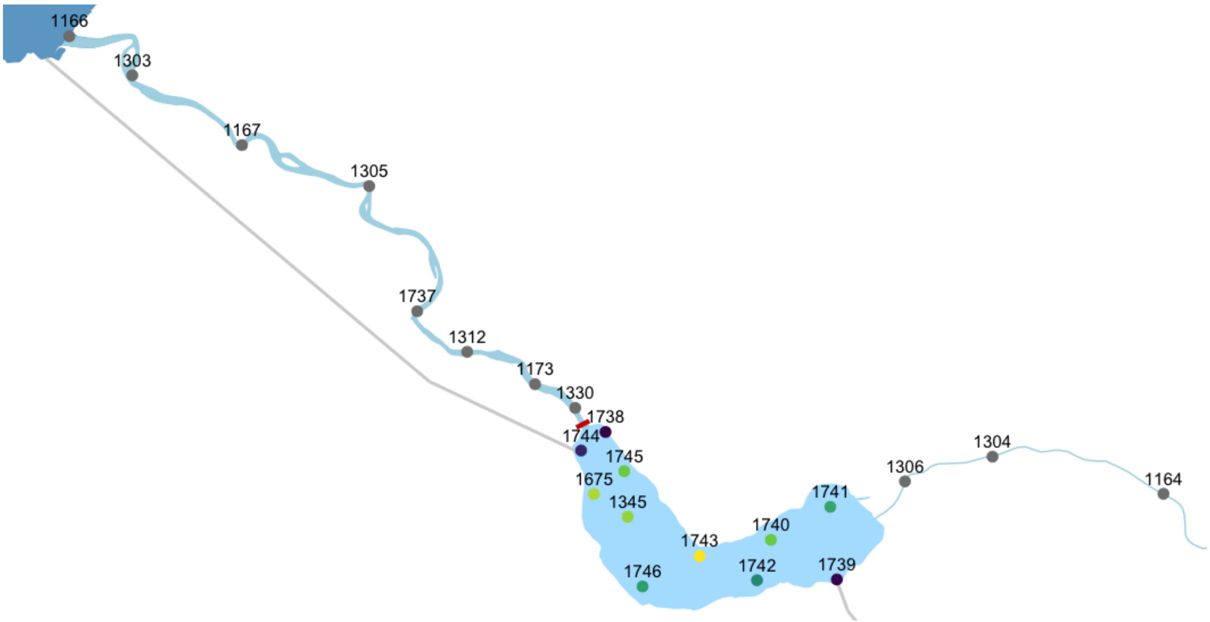
Appendix 8. Visualization of the effect of depth on activity from hypothesis 4.

Appendix 9.

	Receiver	Detections	Habitat	lon
1	1303	1	River	7.193488
2	1167	43607	River	7.210661
3	1305	623	River	7.230566
4	1737	7334	River	7.238081
5	1312	9455	River	7.245900
6	1173	5243	River	7.256526
7	1330	1637	River	7.262809
8	1744	408423	Lake	7.263729
9	1675	468887	Lake	7.265745
10	1738	462696	Lake	7.267554
11	1745	481819	Lake	7.270487
12	1345	443390	Lake	7.271018
13	1746	278524	Lake	7.273356
14	1743	305035	Lake	7.282288
15	1742	231813	Lake	7.291260
16	1740	245232	Lake	7.293433
17	1741	272709	Lake	7.302728
18	1739	140241	Lake	7.303759
19	1306	3	River	7.314415
20	1304	15063	River	7.328116
21	1164	2	River	7.354871

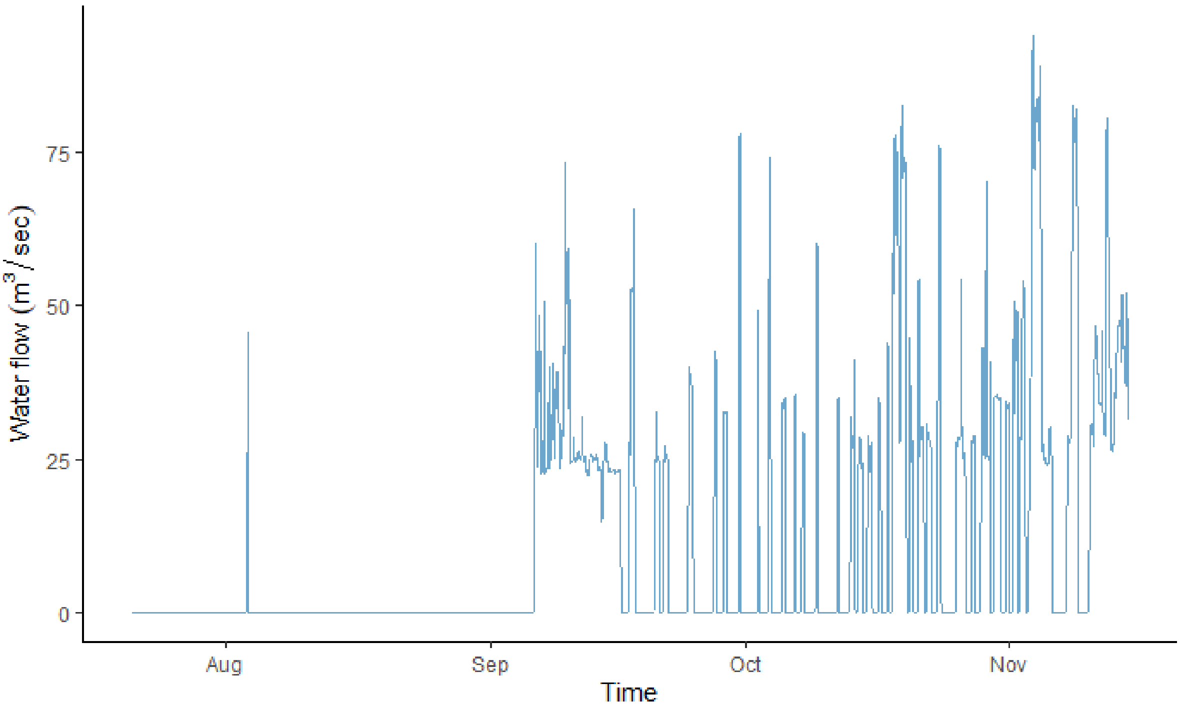
Appendix 9. Number of detections per receiver throughout det study, arranged after increasing longitude (lon) such that receiver nr. 1303 is closest to the fjord and receiver nr. 1164 is furthest up in the upstream river, Vassbygdelva.

Appendix 10.



Appendix 10. Overview of all the receivers and the receiver identification.

Appendix 11.



Appendix 11. Discharge data from Vangen.