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# Swimming behaviour of Atlantic salmon kelts migrating past a hydropower plant dam: Effects of hydraulics and dam operations

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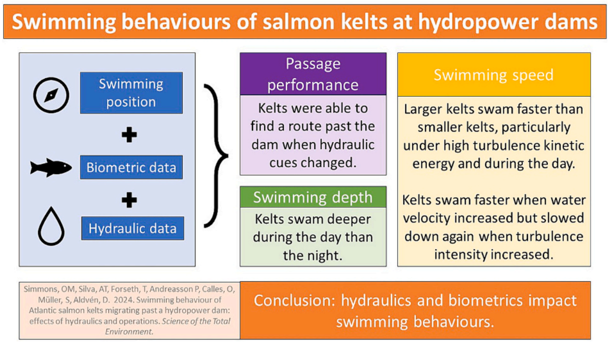
## HIGHLIGHTS

- Assessed kelt behaviour near a hydropower dam with telemetric and hydraulic data
- Kelts used hydraulic cues to navigate past dam.
- Kelt swimming depth varied with time of day and hydraulic conditions.
- Kelt swimming speed directly affected by water velocity and turbulence.

## GRAPHICAL ABSTRACT


Swimming behaviours of salmon kelts at hydropower dams

Kelts were able to find a route past the dam when hydraulic cues changed.

Kelts swam deeper during the day than the night.

Larger kelts swam faster than smaller kelts, particularly under high turbulence kinetic energy and during the day.

Kelts swam faster when water velocity increased but slowed down again when turbulence intensity increased.

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Conclusion: hydraulics and biometrics impact swimming behaviours.

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## ABSTRACT

Hydropower plants commonly impede the downstream migration of Atlantic salmon (*Salmo salar*) kelts. Thus, understanding the effects of hydraulic conditions on kelt behaviour and passage performance at dams is crucial for developing effective mitigation measures. In this study, we investigated the influence of hydraulic conditions on kelt passage performance and swimming behaviour at a Norwegian hydropower plant. We combined biological data from 48 kelts collected via acoustic telemetry with hydraulic data modelled using computational fluid dynamics. We assessed kelt passage performance using metrics such as time-to-pass, total number of detections, and total number of detections per day. Additionally, we analysed swimming depths and speeds in relation to the hydraulic conditions created by different dam operating conditions. We found that the dam operation schedule impacted the kelts' ability to find a route past the dam. Though kelts could have passed the dam throughout the study period via a submerged pipe at the dam (which had seemingly sufficient discharge for the kelts to find), 98 % of the kelts instead waited for a spill gate to open partway through the study period. The swimming depth analysis indicated diel variation, with kelts swimming nearer to the water surface during the night. We found that swimming speed increased with increasing kelt body length, particularly under high turbulence kinetic energy and during the day. Furthermore, kelts swam faster as water velocity increased, but

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slowed down again as turbulence intensity increased. Our findings reveal the effects of hydraulic conditions and dam operations on the migration behaviour of Atlantic salmon kelts. This provides valuable insights for developing strategies to optimise dam operations and improve fish passage performance, including the need to spill enough water to increase passage success and will contribute to sustainable management of Atlantic salmon populations in regulated rivers.

## 1. Introduction

Hydropower plants (HPPs) play a significant role in generating renewable energy, which is increasingly important as the world transitions from a fossil fuel-based economy to a green economy (Zarfl et al., 2015). However, their presence can negatively affect aquatic ecosystems, such as degrading river connectivity, which adversely impacts migratory species (Liermann et al., 2012). This is particularly true for fish that must undertake several long-distance migrations during their life cycle (Forseth et al., 2017). One example is the Atlantic salmon (*Salmo salar*), a highly valued anadromous fish with several migratory life stages. As juveniles (termed 'smolts'), Atlantic salmon migrate from their natal river to the sea, where they spend a year or more growing and maturing, before returning as adults to freshwater to reproduce. After spawning, they may migrate back to the sea to recondition. During this post-spawning downstream migration, they are called 'kelts'. (Klemetsen et al., 2003). Thus, in hydropower-regulated rivers, Atlantic salmon may pass HPPs multiple times during their life cycle.

Migration in HPP-regulated rivers can pose significant challenges to the survival and reproductive success of adult Atlantic salmon (Babin et al., 2021b; Thorstad et al., 2008). Passage through HPP dams can lead to increased energy costs, delayed migration, and even mortality from impingement on racks, blade strikes, shear stress, and exposure to gas supersaturation, all of which can affect the overall resilience of salmon populations (Babin et al., 2021b; Calles et al., 2012; Rubenstein et al., 2023; Sigourney et al., 2015). Such challenges for migrating Atlantic salmon have long been recognised, particularly during their upstream migration to the spawning grounds. As a result, solutions like fish ladders were developed to facilitate their upstream journey (Williams et al., 2012). Later, the importance of the smolt downstream migration was also recognised and downstream fish passage solutions were implemented for this life stage (Nyqvist et al., 2018; Silva et al., 2018). However, downstream passage solutions for kelts, which are substantially larger than smolts but can have low individual condition factors, have been relatively overlooked (but see Nyqvist et al. (2017b) as an exception). This relative neglect of kelts may be attributed, in part, to a limited understanding of their fundamental ecology, as scientists have historically focused more on other Atlantic salmon life stages or on semelparous salmonid species (Birnie-Gauvin et al., 2019).

Kelts can play an important role in population resilience among Atlantic salmon. Not all populations have salmon that survive reproduction to become kelts, but for those that do, kelts can make an outsize contribution to producing new Atlantic salmon cohorts (Reid and Chaput, 2012). This is because kelts can return to freshwater after marine reconditioning for a subsequent round of spawning. In doing so, kelts become repeat spawners, which typically have a larger body size than first-time spawners (Chaput, 2012). Repeat spawners are, therefore, typically more fecund, producing more eggs than their smaller conspecifics (Fleming, 1996; Heinimaa and Heinimaa, 2004; Moffett et al., 2006; Thorpe et al., 1984). Additionally, repeat spawners are thought to make important genetic contributions to Atlantic salmon populations by passing on the genes that have granted them the fitness to survive multiple risky marine migrations (Birnie-Gauvin et al., 2019). With many Atlantic salmon populations declining in abundance throughout their native range (Chaput, 2012; Mills et al., 2013), kelts need appropriate and efficient downstream passage solutions to mitigate the negative impacts of HPPs during migration.

The swimming behaviour of kelts near HPPs must be better understood to devise effective downstream passage solutions. Many different factors affect swimming behaviours of migratory fish species (Cooke et al., 2022). Among these are biotic factors, including inter- and intraspecific interactions like resource competition and predator-prey dynamics (Shaw, 2020). Additionally, abiotic factors exert an impact on fish swimming behaviour, including water temperature, discharge rates, water chemistry, and hydraulic conditions (Hubley et al., 2008; Thorstad et al., 2012). Of the abiotic factors, much focus has been given to the effect of water temperature, as fish display behavioural thermoregulation when moving to areas with optimal temperatures for their metabolic processes (Cooke et al., 2022). Yet, hydraulic characteristics, such as water velocity and turbulence, also influence swimming behaviour (Liao, 2007; Silva et al., 2020; Silva et al., 2012). These variables are particularly relevant when studying movement past HPP dams, which alter the river's natural hydraulic conditions (Renöfält et al., 2010). The ways water velocity and turbulence affect swimming behaviour vary by species and life stage (e.g. Ben Jebria et al. (2021); Goettel et al. (2015); Silva et al. (2012); Tritico and Cotel (2010)). In general, fish avoid accelerating and decelerating water velocities, which could be a strategy to prevent injury or migration delays, respectively (Coutant and Whitney, 2000; Enders et al., 2012). Water velocity may also influence rheotaxis, where fish are more likely to display positive rheotaxis (i.e. orient head-first into the flow) as the flow velocity increases (Coombs et al., 2020). Turbulence is known to increase the energetic costs of locomotion, so fish may avoid areas with high turbulence (Enders et al., 2003; Wilkes et al., 2017). The effect of these hydraulic variables is life stage and body size dependent, with, for example, large individuals better equipped to cope with, or simply less affected by, higher levels of turbulence (Hockley et al., 2014).

To date, only a handful of studies have attempted to evaluate how Atlantic salmon kelts behave during downstream passage at HPPs. Broadly, HPPs cause delays for kelts during migration (Babin et al., 2021a; Baktoft et al., 2020). This might be due to relatively slow migration rates through HPP reservoirs (Babin et al., 2021a) or to kelts making multiple attempts to find a safe way to pass the HPPs (Nyqvist et al., 2016). Migratory delays can result in increased energy expenditure, with kelts that experienced a 30-day delay losing 4–5 % of their energy reserves (Baktoft et al., 2020). This could have negative survival consequences as kelts already have low energy reserves after spawning (Jonsson et al., 1991). Route choice past HPPs varies based on the available routes, such as spillways, bypasses, or turbines (Babin et al., 2021a; Nyqvist et al., 2017a; Nyqvist et al., 2016). Passage survival also varies based on the available routes, with some studies reporting a 100 % survival rate past an HPP (i.e. Baktoft et al. (2020)) and others reporting rates as low as 51 % (Babin et al., 2021a). Survival rates depend on the passage routes available to the kelts, with higher mortality when kelts must pass via turbines. Mortality may be cumulative, with low overall survival rates for kelts that must migrate past numerous HPPs (i.e. Nyqvist et al. (2016); Nyqvist et al. (2017a)). While metrics such as migration rates, passage performance, and survival rates are most commonly reported in the literature, fewer studies have undertaken a detailed analysis of kelt behaviour during such migrations (Simmons et al., *in review*). For example, Babin et al. (2021a) examined the swimming behaviours of kelts at the Mactaquac Generating Station, NB, Canada, and found that kelts tend to be surface-oriented and that migration rates (measured in km day $^{-1}$) increased with higher water temperatures and lower water velocities. They included water velocity in their analysis of passage success and found that higher velocities led to lower passage rates. However, this analysis lacked the fine-scale resolution required to assess how water velocity impacts swimming behaviour at a smaller scale (for example, movements measured in $\mathrm{m\ s^{-1}}$ instead of $\mathrm{km\ day^{-1}}$). Given the importance of hydraulic conditions for swimming behaviours across fish species and life stages (Ben Jebria et al., 2021; Goettel et al., 2015; Silva et al., 2012; Tritico and Cotel, 2010), the influence of such conditions on kelts represents a critical knowledge gap.

Herein, we aimed to better understand the swimming behaviours of Atlantic salmon kelts as they approached and passed the dam by (1) assessing their passage performance, (2) analysing their swimming depth patterns before dam passage, and (3) evaluating the effects of various hydraulic, temporal, and biological factors on the kelts' swimming speeds. Our study was conducted at the Bjørset intake to the Svorkmo HPP on the River Orkla, central Norway. The findings of this study are expected to contribute to a broader understanding of the ecological implications of HPP dams on migratory Atlantic salmon kelts. Ultimately, this should contribute information to inform the development of effective management strategies to enhance fish migration and ensure the sustainability of Atlantic salmon populations in hydropower-regulated rivers.

## 2. Methods

### 2.1. Study site

The River Orkla, central Norway, has five hydropower plants (HPP), including the Svorkmo HPP, which is the HPP the furthest downstream. Our work occurred at the intake of the Svorkmo HPP in the forebay of the Bjørset Dam (see Szabo-Meszaros et al. (2021) or Baktoft et al. (2020) for detailed descriptions and figures of the study site). The study site was approximately 500 m long, with an average depth of 2.3 m and a maximum depth of 3.7 m. The Bjørset dam has four spillways. The top-opening spillway crest gates were closed over winter, gradually opening from the 30th of April. During the study period, only the gate on the northern side of the dam, closest to the intake to the turbines and hereafter referred to as the 'first gate', was opened. First, it was opened to approximately 40 % on the 30th of April, allowing kelts to pass the dam via this route, then to approximately 60 % on the 2nd of May and to approximately 70 % on the 5th of May (Table 1). There are pool-weir-type fish passes at both ends of the dam. Neither fish pass was in operation during the study period. Immediately adjacent to the fish pass near the first gate, a pipe connects the upstream part of the river with the river downstream of the dam. The pipe, which was originally designed to spill water but could be used by fish passing the dam, was open throughout the study period and had a mandatory minimum flow of approximately 4 $\mathrm{m^3 s^{-1}}$.

### 2.2. Sampling and tagging

Between the 9th and 20th of April 2016, forty-eight Atlantic salmon kelts (46 female and 2 male) were captured via rod and reel at the study site (n = 16) or on river reaches 0.8–10.5 km upstream (n = 34). The timing of the fieldwork was selected based on many years of observations of Atlantic salmon kelts in the River Orkla in general, and on the intake racks at this HPP in particular. Each kelt was anaesthetised using 0.7 ml of 2-phenoxyethanol per litre of water (Baktoft et al., 2020). Their body lengths (± 0.01 m) and mass (± 0.1 kg) were measured and ranged from 0.73–1.040 m and 1.4–7.1 kg, respectively. Subsequently, each kelt was internally tagged with an acoustic transmitter containing a pressure sensor (Lotek MM-M-11-28-PM [76 kHz], 12 × 65 mm length; Lotek Wireless Inc., Newmarket, ON, Canada). The incision from the tagging was closed with two sutures (Ethicon Perma-hand, 5–0/FS-2). Throughout the surgery, the kelts were exposed to a diluted concentration of the anaesthetic solution to maintain their sedated state. After recovering from the anaesthetic, the kelts were released at the same location in the river where they were initially caught.

A network of twenty-four autonomous acoustic receivers (WHS3250, 76 kHz, Lotek Wireless Inc.) was deployed upstream of the Bjørset dam to monitor the kelts' 3D movements (see Baktoft et al. (2020) for a description of the network). The receiver network operated from the 16th of April 2016, to the 1st of June 2016. The acoustic receivers were precisely positioned by a GNSS receiver (Trimble Geo7x) with a VRS service that ensured accuracy up to 2 cm. The network was tested by dragging tags through the study area and simultaneously recording the tags' positions with a high-resolution GPS. Each receiver was securely attached to the riverbed using weighted structures or was mounted to dam concrete. Each kelt's position was estimated every 2.5 s.

Each kelt's trajectory was estimated following the procedure from Baktoft et al. (2019) using the YAPS package in R (Baktoft et al., 2017). An example of the trajectories was previously published in Baktoft et al., 2020. During the study, there were instances when the kelts migrated upstream beyond the range of the receivers. Consequently, their trajectories were fragmented. Kelts were considered to have passed the dam on the date that they were last detected by the receivers. In this study, all kelts passed the dam during the study period.

For more information about the study site and sampling procedures, refer to Baktoft et al. (2020).

### 2.3. Hydraulic characterisation of the river

#### 2.3.1. Operational and hydraulic scenarios

During the study, the kelts experienced varying hydraulic conditions resulting from the different operational activities of the HPP. To understand kelt swimming behaviour as a response to varying hydraulic conditions near the HPP, we used computational fluid dynamics (CFD) modelling to characterise the hydraulic conditions of the study area. Based on the HPP operation activities and concomitant variations in flow discharge, four different scenarios were modelled (Table 1). Scenario 1 represented the longest period, lasting for nearly two weeks, while the remaining scenarios lasted fewer than four days each (Table 1).

**Table 1**

Discharge regimes at the Bjørset Dam for the first spillway, the intake tunnel, and the pipe under the different hydraulic scenarios. All discharge values are mean values for a given period and are provided in $\mathrm{m^3 s^{-1}}$.

| Scenario | Start date | End date | Length of scenario (days) | % opening of first gate | Spillway discharge | Intake tunnel discharge | Pipe discharge | Total discharge | Discharge ratio between dam and tunnel |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 2016-04-17 01:00:00 | 2016-04-30 21:00:00 | 13.8 | 2.26 | 0.0 | 22.4 | 4.0 | 26.3 | 0.00 |
| 2 | 2016-04-30 21:00:01 | 2016-05-02 00:00:00 | 1.1 | 41.91 | 8.0 | 28.8 | 4.0 | 40.9 | 0.28 |
| 3 | 2016-05-02 00:00:01 | 2016-05-03 19:00:00 | 1.8 | 60.41 | 22.3 | 38.6 | 4.0 | 64.8 | 0.58 |
| 4 | 2016-05-03 19:00:01 | 2016-05-07 16:00:00 | 3.9 | 70.51 | 38.4 | 45.4 | 0.5 | 84.3 | 0.85 |

### 2.3.2. CFD modelling

The hydraulic characteristics of the 200-metre river reach upstream of the Bjørset Dam were modelled through CFD. The flow velocity components, turbulence kinetic energy (TKE), and its dissipation rate ($\epsilon$) for the four hydraulic and operational scenarios were simulated using the pimpleFoam utility from the OpenFOAM platform (Greenshields, 2015). Bathymetry data were collected in the same area for which the hydraulic data was modelled using a SonTek M9 Acoustic Doppler Current Profiler (ADCP) deployed from a boat. The bathymetry data were used as input for the CFD model and the velocity measurements to validate the results from the CFD output. The CFD model was calibrated and validated by adjusting the surface roughness parameters to optimise the correlation between the modelled and measured cross-sectional velocities. The calibration was conducted along a transect under a flow condition of 129 $m^3s^{-1}$. The values from the ADCP and CFD had a Pearson's correlation of $R^2 = 0.74$. Further information can be found in Szabo-Meszaros et al., 2019. From the CFD modelling output, time-average water velocities ($V_{av}$) and turbulence intensities (TI; Basse (2019)) were calculated as:

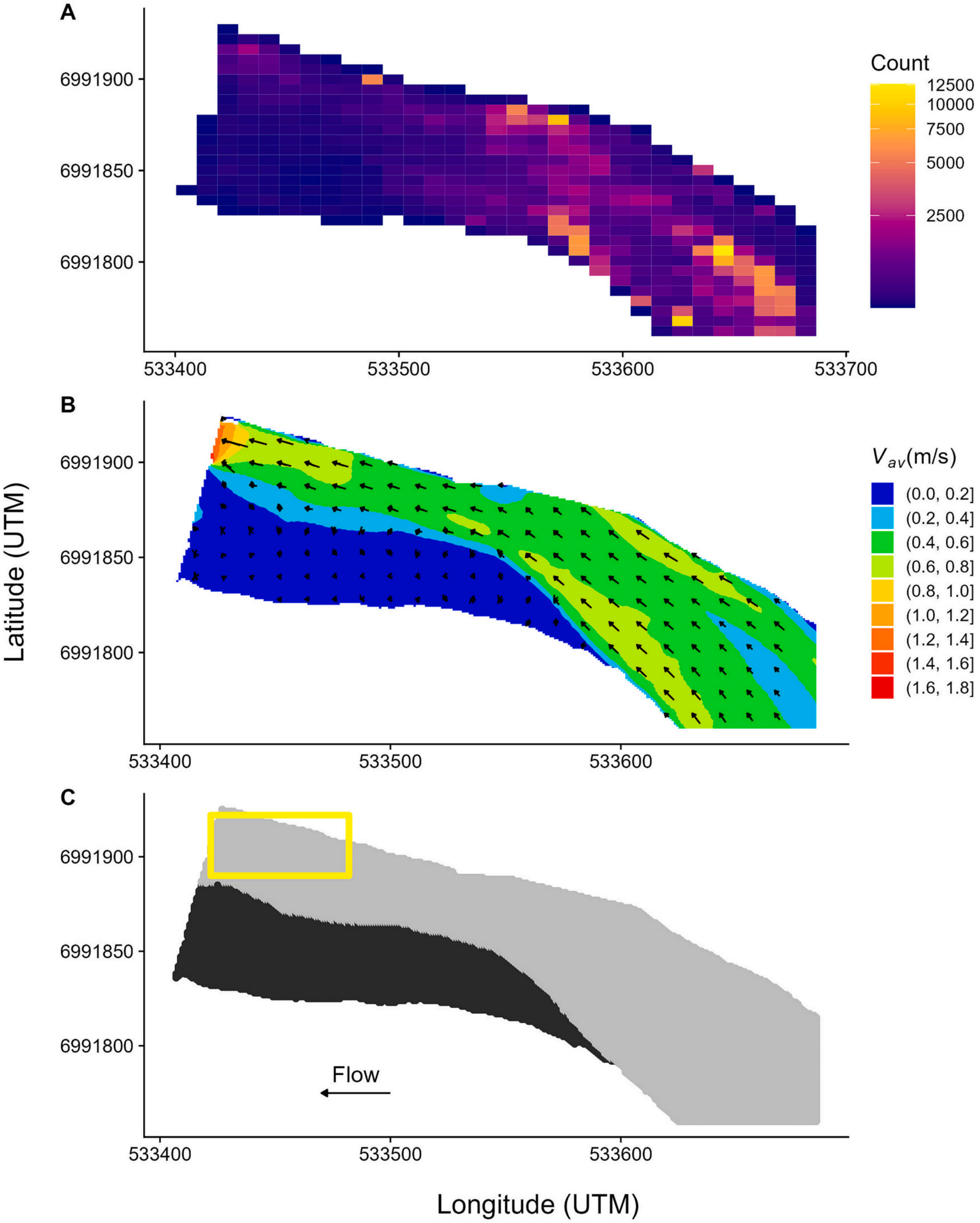

**Fig. 1.** Maps of the area with kelt tracks and hydraulic data, at a depth of 1.1 m below the surface. The top map shows how the number of detections varies across the area and uses a logarithmic scale (A), the middle map shows the resultant velocities, where the colour indicates magnitude and the arrow indicates direction (B), and the bottom map shows the recirculation area in black and the exploration area within the yellow box (C). A depth of 1.1 m below the surface was selected, as this is the depth with the most detections.

$$V_{av} = \sqrt{V_x^2 + V_y^2 + V_z^2}$$

where $V_x$, $V_y$, and $V_z$ are the water velocities in the longitudinal, latitudinal, and vertical directions, and

$$TI = \frac{\sqrt{\frac{2}{3}TKE}}{V_{av}}$$

### 2.3.3. Areas of interest

Upon plotting the hydraulic data, two distinct areas with different hydraulic conditions were identified. There was a recirculation area, located in front of the southern end of the dam, which differs from the remaining study area that had a more unidirectional flow pattern (Fig. 1). It is well-established that high levels of turbulence, such as those found in areas of recirculation, can greatly impact fish swimming performance (Lacey et al., 2012; Liao, 2007; Silva et al., 2020). Consequently, this "recirculation area" was considered the first area of interest. This selection was also supported by the fewer kelt detections in this zone when the kelt tracks were plotted with the hydraulic data, suggesting the hydraulic condition played a role in influencing the route choice of the kelts. A second area of interest was in front of the first gate, where there was a pronounced acceleration of flow. Given that it is well-known that water speed and acceleration influences Atlantic salmon behaviour (Enders et al., 2012; Silva et al., 2020), this second area, referred to as the "exploration area", was anticipated to trigger potential "searching and avoidance" behaviours in the kelts as they attempted to pass the dam.

## 2.4. Statistical analysis

From the fish tracking data, it was observed that approximately 75 % of the detections were recorded during scenario 1, which occurred before the first gate was opened. In this scenario, water velocities throughout the study area were generally low, and the kelt tracks appeared to indicate arbitrary fish movements. As the gate was opened further, the water velocities also increased and the kelts began to migrate past the dam, leading to fewer detections throughout the study area. This resulted in an unbalanced data set, where three-quarters of the data came from scenario 1 and only one-quarter came from the remaining scenarios. This imbalance in the data set was considered to be unimportant for evaluating the passage performance for the kelts. However, it could impact the statistical analysis of swimming depths and speeds, as there were very few detections made in the areas and scenarios with the highest water velocities. To address this issue, we focused on the last two days of scenario 1 for the swimming depth and swimming speed analysis. This subset consisted of slightly over 500,000 detections from scenario 1, representing approximately 41 % of the total detections in the data set (compared to 75 % when considering all dates). Furthermore, for the swimming depth and speed analysis, we excluded data from two kelts that had considerably fewer detections compared to the others ($N_{detections} = 28$ and $N_{detections} = 154$), accounting for only 0.001 % and 0.006 % of all detections, respectively.

### 2.4.1. Kelt passage performance

To assess the passage performance of the kelts, we first recorded the amount of time it took for each kelt to pass the dam after it was tagged. Three metrics were estimated in accordance with Trancart et al. (2019), and evaluated for the different areas of interest:

1. Time-to-pass ("TTP"), defined as the time difference between the first and last position recorded within the area of interest for each kelt. This metric was calculated for detections within the exploration area and measured in hours.
2. Total-number-of-detections ("TND"), defined as the total number of detections recorded within the area of interest for each kelt. This metric was calculated for detections within the exploration area and recirculation zone.
3. Total-number-of-detections-per-day ("TND per day"), defined as the total number of detections recorded within the area of interest on each day of the study period. This metric was calculated for detections within the exploration area and recirculation zone.

Additionally, a fourth metric was calculated as the percent-detections ("% TND"), defined as the percentage of positions recorded in both the exploration area and recirculation zone compared to the total number of positions recorded across the whole study area for each kelt.

### 2.4.2. Kelt swimming depths

Swimming depth data were recorded at each position via the pressure sensor in each tag. To account for differences in river depth throughout the site, we calculated the 'relative swimming depth' as the ratio of the swimming depth from the tag to the river depth at each position and converted this to a percentage. Thus, a relative swimming depth of 0 % indicated the kelt was swimming at the river surface, a relative swimming depth of 50 % indicated the kelt was swimming in the middle of the water column, and a relative swimming depth of 100 % indicated the kelt was swimming at the riverbed. Because bathymetry data were only available for the portion of the study site with hydraulic data (see Section 2.3.2), we only analysed swimming depths within this region.

Previous studies have shown that migrating fish swim closer to the water surface during the night than the day (Mehner, 2012). However, this behaviour has not been studied extensively in Atlantic salmon kelts. To assess whether there was a difference in swimming depth based on diel period, we used the R package lubridate to obtain sunrise and sunset data for each day of the study period at our study site and assigned each detection to be a day or night detection based on that daily diel data (Grolemund and Wickham, 2011). We then used a Wilcoxon test to assess whether there was a difference in swimming depth between the two diel periods. To explore the relationship between HPP operating schedule and kelt swimming depth preferences, we used a Kruskal-Wallis test how mean swimming depth varied between hydraulic scenarios. The swimming depths were analysed in R (R core team, 2021).

### 2.4.3. Swimming speed analysis

The kelt swimming speeds (m/s) were calculated as follows (Silva et al., 2020):

$$V_S = \sqrt{V_{S,x}^2 + V_{S,y}^2 + V_{S,z}^2}$$

where $V_{S,x}$, $V_{S,y}$, and $V_{S,z}$ are the swimming speeds in the directions of $x$, $y$, and $z$, respectively. These were calculated as follows:

$$V_{S,x} = V_{G,x} - V_{F,x};$$
$$V_{S,y} = V_{G,y} - V_{F,y};$$
$$V_{S,z} = V_{G,z} - V_{F,z}$$

where $V_{G,x}$, $V_{G,y}$, and $V_{G,z}$ are the ground speed components in the directions of $x$, $y$, and $z$, and $V_{F,x}$, $V_{F,y}$, and $V_{F,z}$ are the flow velocity vectors in the directions of $x$, $y$, and $z$.

To evaluate the effect of hydraulic conditions, diel period, and body length on kelt swimming speed, we used a linear mixed effects model with individual ID numbers as a random effect. A first-order autoregressive process was also included to account for the dependency of the current swimming speed on the previous speed for each fish. The hydraulic variables included in the model were based on the results from Silva et al. (2020), which produced a similar analysis for juvenile Atlantic salmon smolts and identified key variables that impacted both the swimming speed and swimming direction of those fish.

Before model construction, numeric variables were standardised by subtracting the mean value and dividing by the standard deviation using the R function scale. Next, pairs of explanatory variables were assessed with Pearson's correlation using the package corrplot (Wei and Viliam, 2021). If Pearson's $R^2$ exceeded 0.7 for a pair of explanatory variables, only the variable considered to be most biologically relevant was retained for the analysis. Thus, because of the high correlation between TKE and $\epsilon$, only TKE was included in the analysis as it has been shown to strongly affect other life stages of Atlantic salmon (Silva et al., 2020). Furthermore, we examined whether to include the three components of water velocity as covariates or the resultant water velocity as a covariate in the model. Previous research found that both the direction and magnitude of the components of water velocity impact swimming speed in Atlantic salmon smolts (Silva et al., 2020). However, there was a high correlation between the velocity components in the longitudinal and latitudinal directions at each position. Thus, to determine whether we

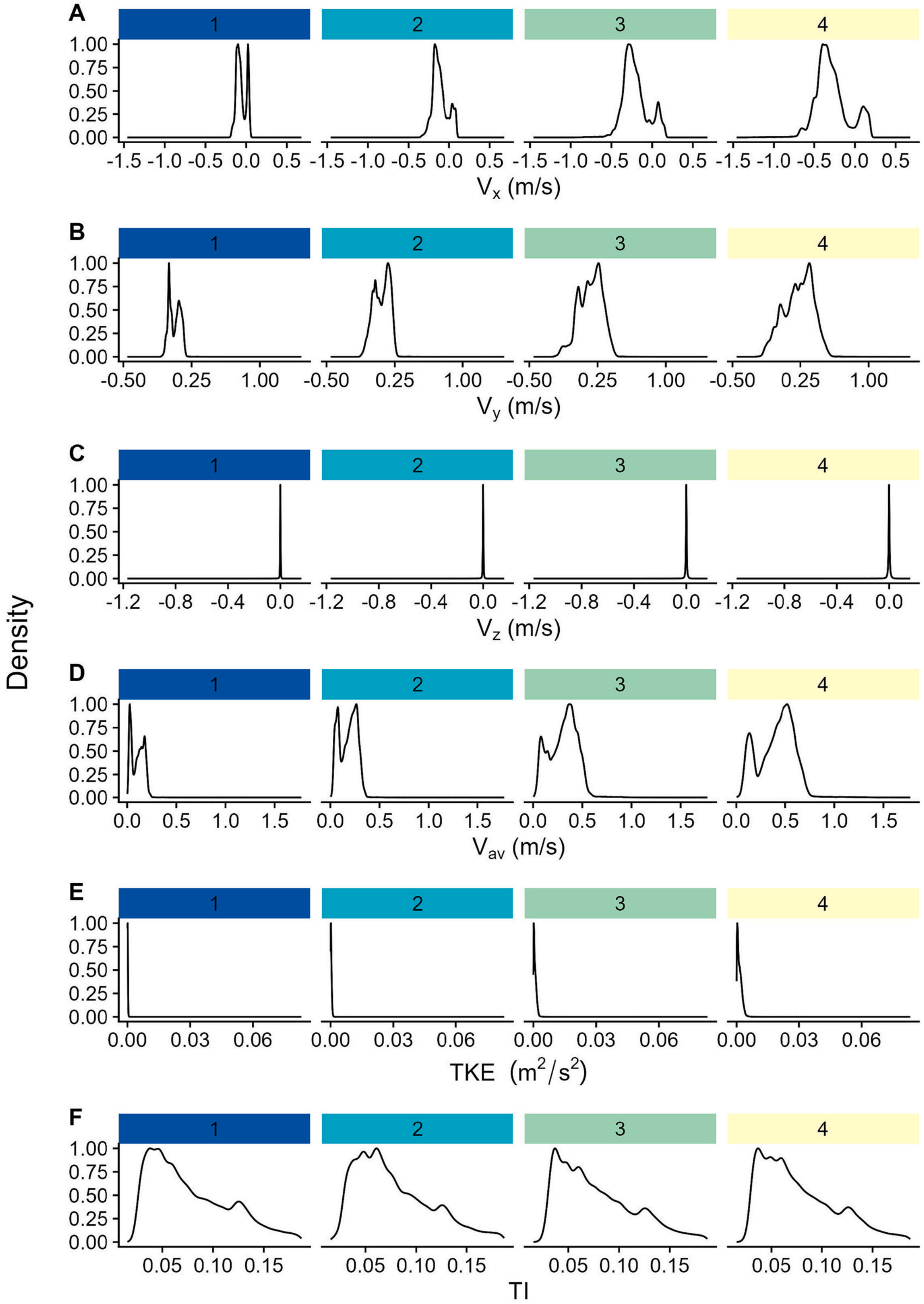

**Fig. 2.** Density distributions for each hydraulic variable under each of the four scenarios (where the first scenario is represented by the darkest coloured label and the subsequent scenarios represented by lighter labels).

would include the components, known to be biologically significant for smolts, or the resultant velocity, thus avoiding high levels of correlation in our covariates, we first tested two simple models: one with all three components and one with only the resultant velocity. These models also incorporated the AR1 random effect structure. Model comparison using the Wanatabe-Akaike information criterion (WAIC) revealed that the model with only the resultant water velocity had a lower WAIC, thus it was selected as the water velocity variable. After determining which velocity variable to use, the global model including the explanatory variables was built. We assessed model results to identify whether any covariates had 95 % credible intervals that included 0, which we interpreted to mean the covariate had a negligible effect on swimming speed. Any such covariates would then be iteratively removed, to build a candidate model set. The model with the lowest WAIC was considered to be the best model.

The modelling was conducted using INLA (Rue et al. (2009); software can be downloaded at www.r-inla.org) with the default priors. To assess model fit, cross-validatory predictive checks, including the conditional predictive ordinates and the probability integral transform values, were calculated and plotted as were additional diagnostic plots such as fitted versus observed values (Adrion and Mansmann, 2012; Ferkingstad et al., 2017).

For all analyses, figures were created using the R packages ggplot2, cowplot, and patchwork (Pedersen, 2022; Wickham, 2016; Wilke, 2020).

## 3. Results

### 3.1. Data summary

Most of the hydraulic variables had quite unsymmetrical distributions. There was some variation in the data between hydraulic scenarios, with the resultant velocity particularly displaying higher values in the later scenarios (Fig. 2.D.). The flow velocities ranged from −1.5 to 0.7, −0.5 to 1.5, and −1.2 to 0.2 m/s for the longitudinal ($V_x$), latitudinal ($V_y$), and vertical components ($V_z$), respectively (Fig. 2.A-c). The time-averaged flow velocity ($V_{av}$) ranged from 0.0 to 1.7 m/s (Fig. 2.D). The turbulence kinetic energy (TKE) ranged from $3 \times 10^{-7}$ to $8 \times 10^{-2}$ $m^2/s^2$ and turbulence intensity (TI) ranged from 0.01 to 0.18 (Fig. 2.*E*-F). More details about the hydraulic data can be found in Baktoft et al. (2020).

### 3.2. Kelt passage performance

All kelts passed the dam during the study period with no observed mortality. The time between when each kelt was tagged and when it was last detected ranged from 11 to 27 days, while the time between when each kelt was first detected on a receiver in the study area to when it was last detected ranged from 50 min to 17.5 days. Kelts that passed the dam during the second scenario took the least amount of time to pass the dam from the time they were tagged (mean = 16.3 days), while kelts that passed in the final scenario took the longest time between tagging and dam passage (mean = 22.9 days). Only one of the 48 kelts passed the dam before the first gate opened on the 30th of April during the first scenario, 12 kelts passed during the second scenario, 28 during the third scenario, and the final 7 during the final scenario. The discharge through the pipe during the first scenario ranged from 3.995 to 8.634 $m^3s^{-1}$, with a mean discharge of 4.198 $m^3s^{-1}$. This means that between 11.5 % and 28.5 % of the total discharge in the river passed through the pipe during the period before the gate opened. Nonetheless, the kelts chose to wait for the gate to open rather than migrate via the pipe. Overall, passage through the dam was slightly higher during the day (n = 26) than during the night (n = 22), which might be partly due to the days being longer than the nights.

The time-to-pass (TTP) from the time a kelt was first detected within the exploration area to when it was last detected at the dam ranged from 1.01 to 55.25 h, with a mean of 10.85 h. The mean total-number-of-detections (TND) in the exploration area was 4256, with a range of 16–81,019 detections. Differences in TND among scenarios were also observed, with most of the detections in the exploration and recirculation areas occurring during the third scenario, when the gate was opened at approximately 60 %. This is particularly striking given the length of the third scenario (approximately 2 days) relative to, for example, the first scenario (approximately 14 days). The percentage of detections in both areas was highest for fish that passed the dam during the fourth scenario but lowest for those that passed during the first scenario (Fig. 3A-C). In both areas of interest, the TND per day was highest on the 30th of April when the first gate was opened in the dam. The second highest TND per day in both areas was on the 2nd of May (Fig. 4).

### 3.3. Kelt swimming depth

The kelts had a mean swimming depth of 45 % below the water surface. Proximity to the surface was higher at night, when the mean swimming depth was 44.29 %, than during the day, when the mean swimming depth was 45.74 % ($W = 6 \times 10^{10}$, $p < 0.05$; Fig. 5A.). The relative swimming depth also varied by scenario ($H = 118{,}376$, $p < 0.05$), with the kelts swimming closer to the surface during the earlier scenarios (scenarios 1, 2, and 3; mean swimming depths of 48.32 %, 41.27 %, and 50.17 %, respectively), and closer to the bottom during scenario 4 (mean swimming depth of 73.34 %; Fig. 5B.).

### 3.4. Kelt swimming speed

The most parsimonious model, with the lowest WAIC, included all the explanatory fixed effects and two-way interactions (Table 2). Kelt body length positively influenced swimming speed, indicating that larger kelts swam faster than smaller kelts. However, when modified by water velocity and TKE, the interaction between body length and these hydraulic variables was negative, implying that as the water velocity and TKE increase, the effect of body length on swimming speed decreases (Fig. 6A and Fig. 6B.). In contrast, when the body length was modified by TI (which has a negative effect), the positive effect on swimming speed persists (Fig. 6C.). This suggests that, though larger fish tend to swim faster than smaller fish, as TI increases, the swimming speed for all fish decreases.

The kelts swam faster at night than during the day. However, the interaction between body length and diel period (with 'night' as the contrast level) is negative, suggesting that though larger kelts swim faster than smaller kelts, the difference is more pronounced during the day than at night. In other words, the disparity in the swimming speeds between large and small kelts was greater during the day than at night (Fig. 6D.).

There were also two interactions between hydraulic variables retained in the final model. The interaction between water velocity and TKE was positive, indicating that higher levels of both led to increased swimming speeds for the kelts (Fig. 6E.). In contrast, the interaction between water velocity and TI was negative, implying that while faster water velocities meant increased swimming speeds, the magnitude of this effect was diminished as the level of TI also increased (Fig. 6F.).

## 4. Discussion

This study is one of the first to attempt to couple hydraulic conditions to the various swimming behaviours of Atlantic salmon kelts. We found that most kelts passed the dam quickly after the first spillway opened. It was unexpected that only one kelt passed via the pipe before the gate opened, as the flow through the pipe was thought to be strong enough to attract the kelts. We also found that though the kelts exhibited some surface-oriented swimming behaviour, they also displayed diel

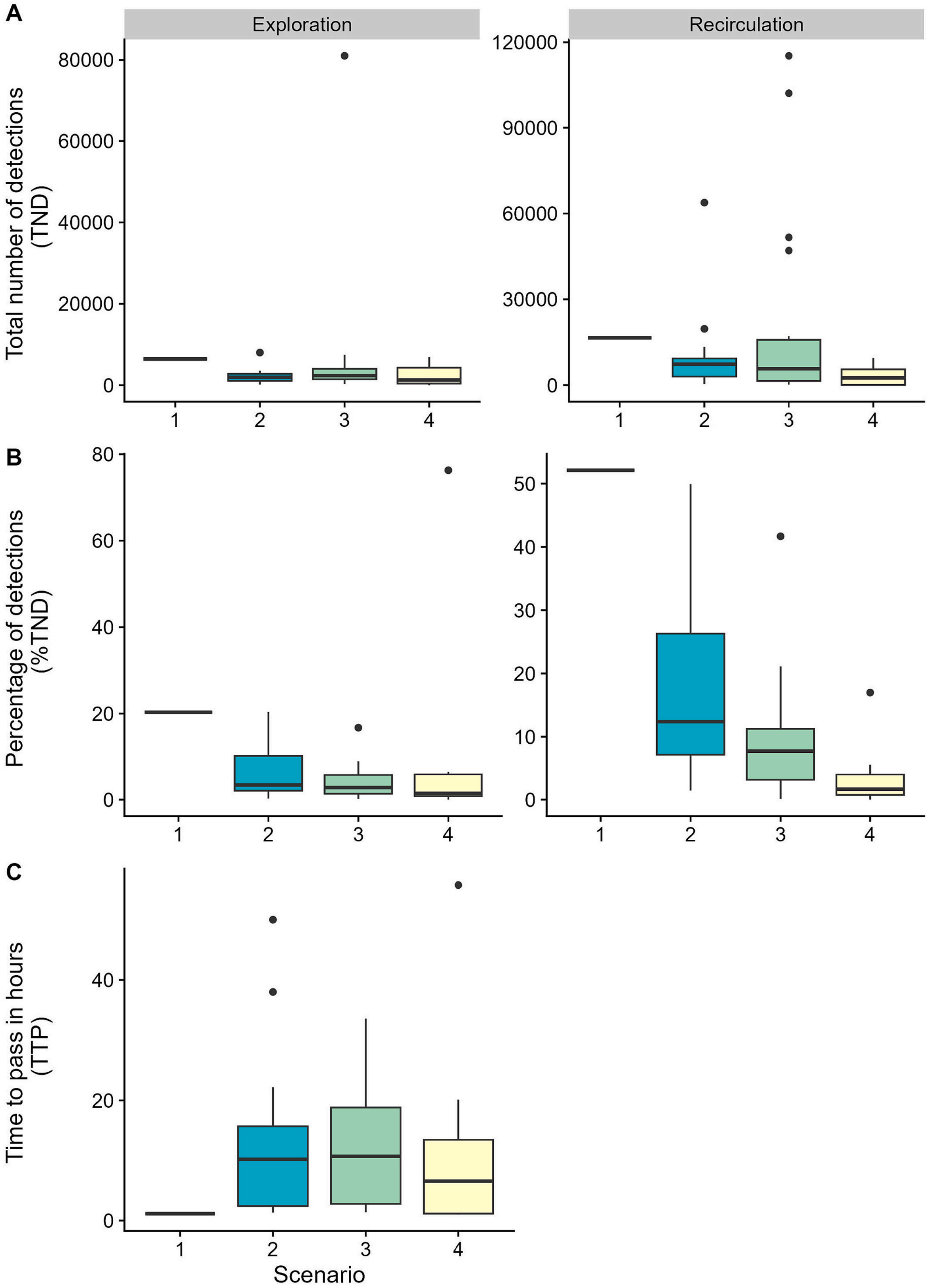

**Fig. 3.** Passage performance metrics for kelts last observed in each hydraulic scenario in the exploration and recirculation areas. Only one kelt passed the dam during the first hydraulic scenario, therefore the metrics for this kelt are represented by a single horizontal bar. Eighteen kelts passed the dam during the second scenario, twenty-two during the third scenario, and seven during the final scenario.

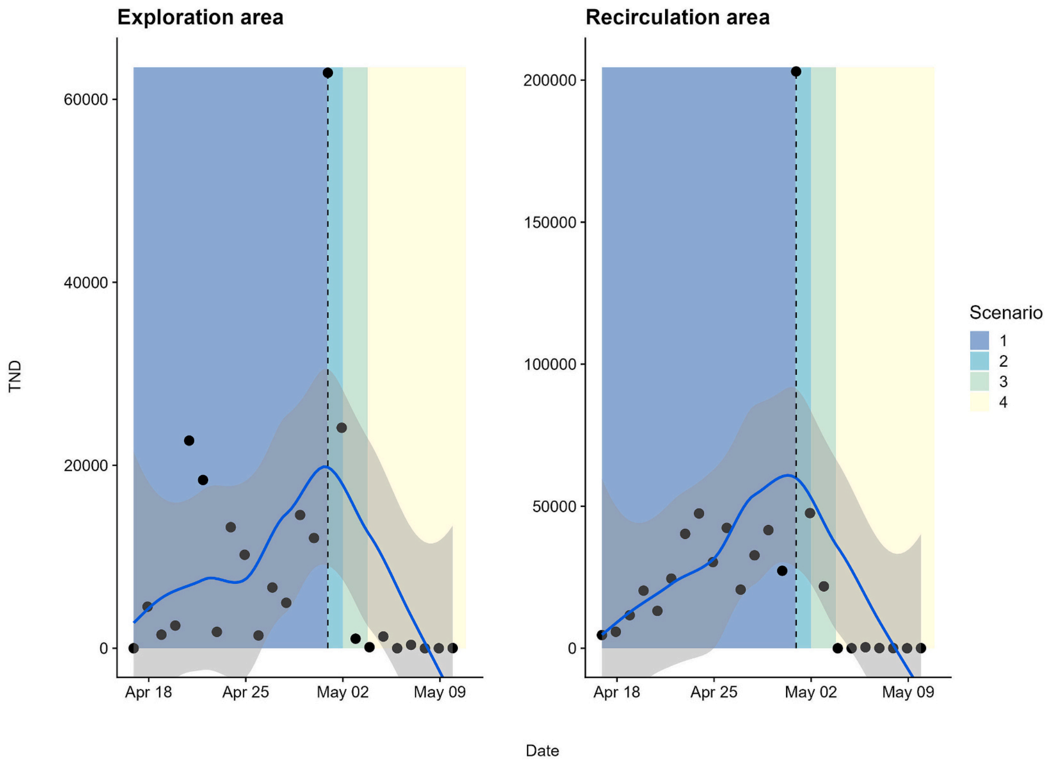

**Fig. 4.** The mean TND per day in the exploration and recirculation areas. The blue line represents a smoothing line for visual aid. The dashed vertical line indicates 30 April at 21:00, the date that the first gate opened. The background shading shows the hydraulic scenario, with the darkest shade representing the first scenario and the lighter shades representing each subsequent scenario. One kelt passed the dan during the first scenario, eighteen kelts passed during the second scenario, twenty-two during the third scenario, and seven during the final scenario.

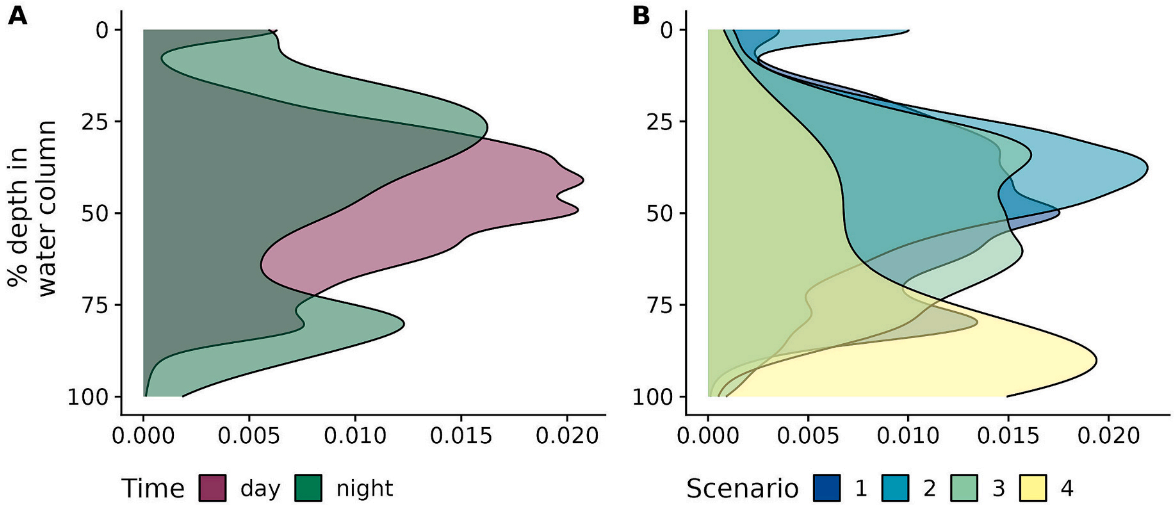

**Fig. 5.** Density distributions of relative kelt swimming depths by time and scenario, where a depth of 0 % indicates the surface and a depth of 100 % indicates the riverbed.

swimming depth patterns common among other fish species. Furthermore, we found that hydraulic conditions, including water velocity, turbulence kinetic energy (TKE) and turbulence intensity (TI), impacted swimming speed.

Before the first gate opened, the kelts were mostly unable to find a route past the dam, even though the pipe near one of the fishways could have been a passage route. Fish are known to follow flows when migrating downstream (Williams et al., 2012), but if that cue is not strong enough, they will not find the passage route. However, it seems that here, the flow should have been high enough for the kelts to find the pipe. More likely, the kelts could have struggled to find the pipe due to the site layout. The lateral entrance of the pipe is likely challenging for the kelts to locate as it is angled 90° to the direction of the main flow. 75 % of the Atlantic salmon kelts passed the dam within the first two days that the first gate opened, when the gate discharge was between 8 and 22.3 $m^3s^{-1}$. Not only did the discharge increase, but the water velocity in the area near the gate also increased. Additionally, there was a large increase in kelt detections in the exploration and recirculation areas, which were the closest areas to the dam, on both days. Combined, these results suggest that the kelts detected that a new route past the dam was

**Table 2**
Results from the most parsimonious model for swimming speed, indicating the mean, standard deviation, and 95 % credible interval of the posterior distributions for each variable.

| Type | Variable | Mean estimate | SD | 95 % credible interval |
|---|---|---|---|---|
| Intercept | Intercept | 0.2676 | 0.0212 | (0.2258, 0.3097) |
| Biological | Length | 0.0156 | 0.0073 | (0.0012, 0.0301) |
| Hydraulic | Vav | 0.0158 | 0.0007 | (0.0145, 0.0172) |
| | TI | −0.0207 | 0.0007 | (−0.022, −0.0194) |
| | TKE | 0.0283 | 0.0006 | (0.0271, 0.0295) |
| Temporal | $\text{Diel}_{\text{night}}$ | 0.0218 | 0.0003 | (0.0212, 0.0224) |
| Interaction | Length x Vav | −0.0019 | 0.0002 | (−0.0022, −0.0016) |
| | Length x TKE | −0.0018 | 0.0002 | (−0.0021, −0.0015) |
| | Length x TI | 0.0015 | 0.0002 | (0.0011, 0.0018) |
| | Length x $\text{Diel}_{\text{night}}$ | −0.0018 | 0.0003 | (−0.0023, −0.0013) |
| | Vav x TKE | 0.0009 | 0.0001 | (7e-04, 0.0011) |
| | Vav x TI | −0.0184 | 0.0004 | (−0.0192, −0.0176) |

available once the spillway gate had opened, either by detecting the increased discharge rates or the change in the water velocity. They likely used the change in hydraulic conditions as the cue to locate the spillway (Williams et al., 2012). While this is the most likely cue that allowed the kelts to navigate past the dam, it is also possible that there may have been auditory cues at play too, with the sound of the water passing the spillway potentially helping to guide the fish (Popper and Hawkins, 2019). Though it was demonstrated elsewhere that salmonid kelts have high survival rates when passing dams via spillways (Colotelo et al., 2014; Nyqvist et al., 2016; Wertheimer and Evans, 2005), it has also been established that migratory delays, such as when waiting for a spillway to open, can cause energy reserve depletion (Baktoft et al., 2020). The fact that so many kelts passed the dam so quickly after the spillway opened is a strong indication that they had been delayed waiting for the spillway to open. Opening the gate at the beginning of the migration period could mitigate the risk of delays for kelts in this river.

The kelts displayed a distinct diel swimming depth pattern at the Bjørset Dam, where they swam at deeper depths during the day than at night, which has been previously observed for other species and life stages (Mehner, 2012). In smaller fishes, this is often assumed to be an anti-predator response, where fish avoid visual predators by spending day hours in the darker deeper depths of the water column (Andersen et al., 2017; Hrabik et al., 2006). At night, these fish swim towards the surface as they search for their own prey or other food resources. It seems improbable that the kelts are avoiding predators by adopting this behaviour, as such large fish are unlikely to have many predators in the River Orkla. Perhaps this pattern reflects their predatory instincts if they are modifying swimming depth to search out smaller prey fishes. There is some evidence that steelhead kelts (*Oncorhynchus mykiss*) predate smaller fish and invertebrates as they migrate downstream (Penney and Moffitt, 2014), though there seems to be less evidence of Atlantic salmon kelts feeding during the riverine portion of their migration. Alternatively, the diel vertical migrations exhibited by the kelts may be a vestigial behaviour from when they were smolts that allowed them to avoid predation. Predation can be intense for smolts and post-smolts, so diel vertical migrations are adaptive for those life stages (Dieperink et al., 2002; Hvidsten and Lund, 1988; Jepsen et al., 2019; Thorstad et al., 2012). Alternatively, it may be a way to preserve energy, by staying near the riverbed where flow velocity is lower during the night, as salmonids have been shown to prefer negotiating passage routes during the day when they can see the routes better (Colotelo et al., 2014; Nyqvist et al., 2017b). Regardless of the underlying cause, Atlantic salmon kelts also exhibit the same diel vertical migration pattern at sea (Reddin et al., 2011), so this appears to be a common pattern in marine and freshwater habitats.

We also observed that the Atlantic salmon kelts swam at greatest depth during the fourth scenario when the gate opened the furthest. During this scenario, the surface flows near the spillway had the highest velocity. Perhaps the kelts were avoiding some of the higher water velocity areas. Alternatively, the remaining kelts might have spent more time near the riverbed searching for routes past the dam. It should be noted, however, that by the fourth scenario, most of the kelts had already passed the dam, with just seven kelts yet to make passage.

Body size is known to be an indicator of swimming capacity among fishes, with large individuals typically stronger and faster swimmers than small conspecifics (e.g. Rubio-Gracia et al. (2020)). In this study, not only did we show that larger kelts swim faster than smaller kelts, but that diel period and various hydraulic variables interact with body size to influence swimming speed. Firstly, the effect of body size was weaker at night and under increasing levels of TKE. This could occur if smaller kelts are not as active during the day as at night, and be an anti-predator response where smaller fish are less active in the daytime to avoid the attention of visual predators. There are likely few predators in the study area that would prey on the larger kelts. Interestingly, although Babin et al. (2021a) found that kelts migrated the same distance during night and day, they found there were slightly more night-time movements in an HPP reservoir at night. Perhaps in our study and in Babin et al. (2021a), the kelts took advantage of the darkness to explore more extensively for a route past the dam, with this behaviour even more pronounced for small kelts. The effect of body length on swimming speed is lessened at higher levels of TKE, suggesting that larger kelts swim even faster at higher levels of TKE, while smaller kelts are slowed more when TKE increases. This makes sense if larger fish are better able to harness the energy from the turbulence to propel themselves forward, as has been suggested in studies of upstream-migrating adult sockeye salmon (*Oncorhynchus nerka*) (Hinch and Rand, 2000). Smaller fish may be less able to do the same and, therefore, struggle more in areas with high levels of TKE. In contrast, it has been established among fish of various species and body sizes that as TI increases, swimming performance decreases (e.g. Silva et al. (2012); Lupandin (2005)). We found that swimming speed increased with body length in areas with low TI. The slowest swimming speeds occurred for kelts with small body sizes in areas with high TI. This suggests that body size confers an advantage when swimming in areas with high TI (Lupandin, 2005), where small fish swim even slower in high TI conditions than they would otherwise.

We also found that Atlantic salmon kelts swam faster in areas with higher water velocities, though the effect of water velocity on swimming speed was modified by the amount of turbulence. For example, the interaction between water velocity and TKE was positive, indicating that kelts swam fastest under conditions with high water velocities and high TKE. Again, if kelts can use the energy from TKE to propel themselves (Hinch and Rand, 2000), it makes sense that this would work in concert with water velocity to further increase their speeds. Conversely, we found the opposite result with TI, where the interaction between water velocity and TI was negative. This indicates that although increasing water velocities lead to increased swimming speeds, higher levels of TI mean the swimming speeds are not increased as much as they would otherwise be. In the swimming speed model, the interaction between water velocity and TI was the interaction with the largest effect size, further indicating that not only do higher levels of TI reduce swimming performance for migrating kelts, but that this interaction is particularly important for explaining variation in swimming speed.

It should be noted, however, that we focused primarily on hydraulic effects when evaluating factors that can affect kelt swimming speeds. We did this because these important variables have hitherto been overlooked when studying kelt migration in rivers. Nonetheless, several additional factors could influence kelt swimming behaviour. Firstly, water temperature is known to affect swimming depths and speeds. Babin et al. (2021a) found that the water temperature could affect the number of kilometres a kelt swam per day, and temperature affects kelt swimming speed in laboratory experiments (Booth et al., 1997). It would be interesting to add water temperature data to an analysis of kelt

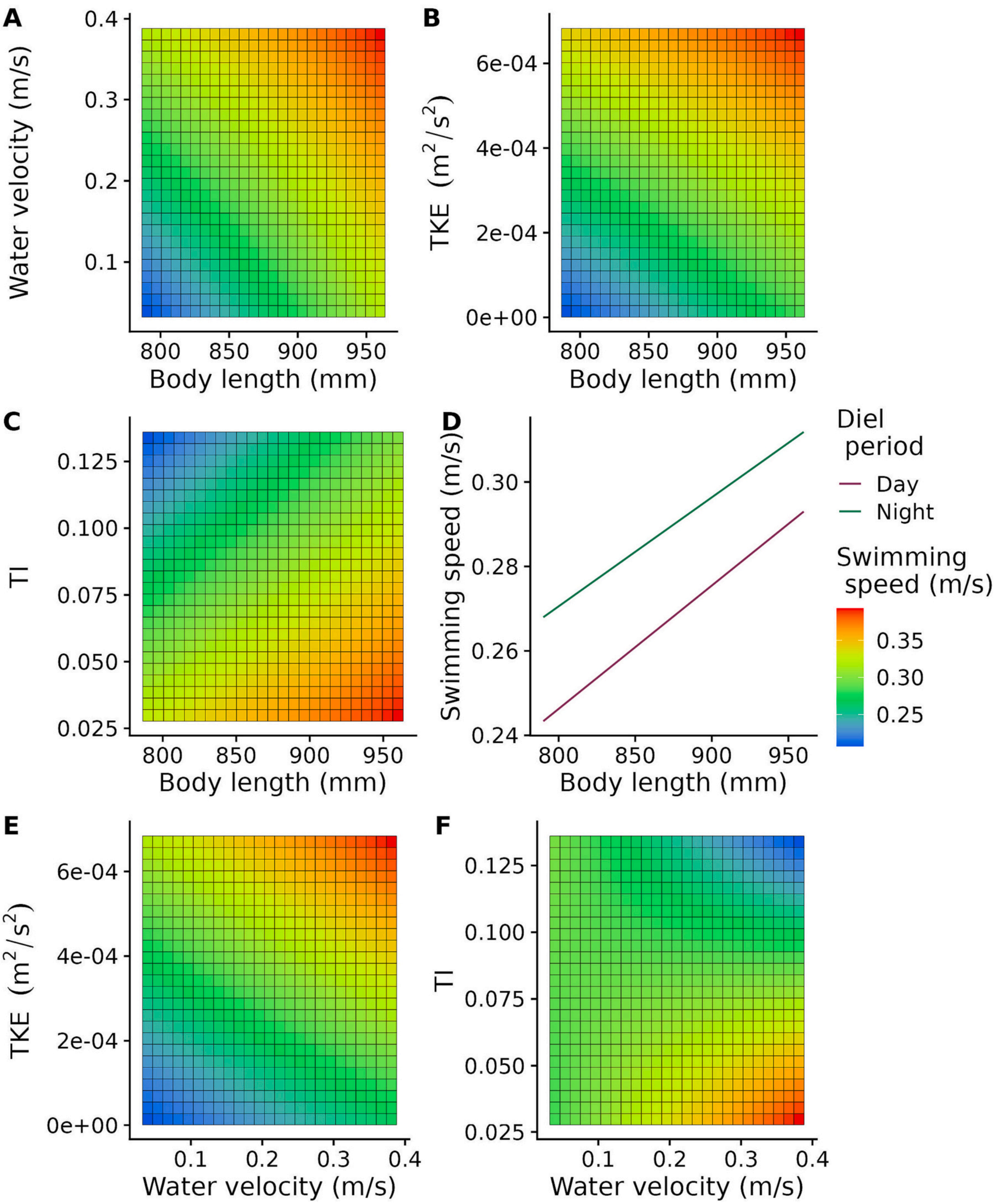

**Fig. 6.** Marginal effects of the interactions between the explanatory variables on kelt swimming speed in the most parsimonious model.

swimming behaviour in regulated rivers, which unfortunately we did not have. Furthermore, we could not assess the effect of different biological variables on kelt swimming behaviour. Perhaps kelt age, as well as the number of previous spawning migrations, may affect swimming behaviour. An older or more experienced kelt may be able to find the open spillway on the 30th of April more quickly. The extent to which kelts feed while waiting for a passage past the dam is poorly known, yet the presence of prey could impact swimming depth and speed (Penney and Moffitt, 2014). The swimming behaviour of the kelts may also vary based on their readiness to migrate. Kelts with lower energy reserves may be more likely to swim swiftly while looking for passage and also pass the dam earlier than kelts with better energy reserves. It would also be interesting to assess the effect of sex on swimming behaviour. Female salmonid kelts are known to have better condition after spawning than males, meaning they tend to have higher energy reserves (Nyqvist et al., 2016). Therefore, often male kelts migrate in the autumn shortly after spawning, while females may overwinter in the river and migrate in the spring (Nyqvist et al., 2017b; Nyqvist et al., 2016). In our study, only two of the kelts were males. Presumably, the other males had migrated in the autumn, or had had low overwinter survival.

To safeguard the downstream passage of Atlantic salmon kelts in the River Orkla, it is critical to incorporate knowledge of their swimming behaviour with the development of downstream passage solutions that allow the volitional movement of fish with minimal delay (Castro-Santos and Haro, 2010). To prevent delays, opening the spillway gate earlier in the spring could be a valuable strategy, though we acknowledge that additional spilling may be economically impractical. Thus, constructing a new downstream passage route with appropriate attraction flows that accounts for how the hydraulic conditions affect kelt swimming behaviour, and is operational for the entire migration period, is desirable.

## 5. Conclusion

This study is one of the first to investigate how hydraulic conditions influence Atlantic salmon kelt swimming behaviour in hydropower-regulated rivers. In particular, water velocity and turbulence have been shown to be key factors affecting swimming speed, while the diel period has been shown to affect swimming depth patterns. Further studies in controlled laboratory settings, where factors such as water temperature and biotic interactions are controlled or removed, would be useful for further elucidating the ways hydraulics affect swimming behaviours in kelts. This knowledge could also lead to the development of improved downstream passage solutions. Our study emphasizes the critical importance of early gate openings and customized downstream passage solutions that account for varying hydraulic conditions. These measures will contribute to Atlantic salmon kelt conservation and promote sustainable management practices.

## CRediT authorship contribution statement

**O.M. Simmons:** Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **A.T. Silva:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing – review & editing. **T. Forseth:** Writing – review & editing. **P. Andreasson:** Writing – review & editing. **S. Müller:** Writing – review & editing. **O. Calles:** Writing – review & editing. **D. Aldvén:** Funding acquisition, Project administration, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.171304.

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