Ecological Informatics 85 (2025) 102967

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

Combining habitat selection, behavioural states, and individual variation to predict fish spatial usage near a barrier

Rachel Mawer [a,1,*], Jelger Elings [a,2], Stijn P. Bruneel [a,b], Ine S. Pauwels [b], Eliezer Pickholtz [c], Renanel Pickholtz [d], Johan Coeck [b], Peter L.M. Goethals [a]

[a] *Department of Animal Sciences and Aquatic Ecology, Ghent University, Ghent, Belgium*
[b] *Research Institute for Nature and Forest (INBO), Brussels, Belgium*
[c] *Independent Researcher, East Brunswick, NJ, USA*
[d] *School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel*

ARTICLE INFO

Keywords:
Step selection functions
Acoustic telemetry
Hydropower
Individual based model
Fine-scale telemetry
Fish migration

ABSTRACT

Riverine barriers are threatening freshwater fish migration, with major impacts on fish populations. Effective management requires understanding of fish movement and behaviour as they approach a barrier and fish pass, which can inform optimal mitigation options and barrier management. Here, the movements of upstream migrating barbel *Barbus barbus* and grayling *Thymallus thymallus* near a barrier were analysed and results used to develop predictive models. Fish were tracked via 2D acoustic telemetry. Hidden Markov models were used to distinguish behavioural states and step selection functions were applied to determine habitat selection by the fish in each state. Model results were explored to assess the benefits of including behavioural state and understand state-specific habitat preferences, then cross-validated and used to develop an individual based model to predict fish spatial usage. Little difference existed in habitat selection between states and individual variation was high, limiting general trends that could be described. Overall, barbel preferred deeper or faster water while for grayling, few trends could be described. Under the tested flow conditions, high spatial usage was predicted in the area directly downstream of the barrier. In addition, barbel usage was high in the area by and downstream of the fish pass entrance but not for grayling, which may indicate a need to improve pass attractiveness for grayling. The predictive model produced directed upstream movements of fish similar to those expected for upstream migrating freshwater fish, highlighting model potential for fish passage applications in future iterations. The high individual variability in fish behaviour drives the need for individual-based approaches for predicting fish movement.

1. Introduction

Understanding animal movement is an important step towards conservation and management, informing management approaches such as protected areas, fishing quotas or mitigation methods for barriers (Calles et al., 2021; Dwyer et al., 2020). Many animals undertake migrations as essential steps of their life cycles, enabling animals to use and exploit different habitats at different stages of their lives (Dingle, 2014). Interrupting animal migrations can lead to catastrophic impacts upon populations (Bolger et al., 2008), as highlighted in freshwater fish which have experienced major declines in recent decades (WWF, 2022). The decline of freshwater fish is in part attributed to the increase in riverine barriers (Silva et al., 2018). In Europe, over a million barriers fragment rivers, negatively impacting fish populations in numerous ways, such as blocking or delaying migrations (Belletti et al., 2020; Pelicice et al., 2015; Silva et al., 2018).

Fish passes are a common tool for barrier mitigation. Fish passes provide an alternative route past a barrier for fish, yet success is highly context dependent and passage efficiencies are often insufficient (Bunt et al., 2012; Hershey, 2021). With more barriers set to be constructed (Zarfl et al., 2015), there is pressing need to develop effective fish passage solutions, which in turn drives a need to study fish movement as

---

* Corresponding author at: School of Biological and Marine Sciences, University of Plymouth, Plymouth, UK
E-mail address: rachel.mawer@ugent.be (R. Mawer).

[1] Current affiliation: School of Biological and Marine Sciences, University of Plymouth, UK

[2] Current affliation: Department of Fish Ecology and Evolution, EAWAG, Swiss Federal Institute for Aquatic Science and Technology, Switzerland

https://doi.org/10.1016/j.ecoinf.2024.102967
Received 14 June 2024; Received in revised form 17 December 2024; Accepted 17 December 2024

they approach barriers and fish passes. Understanding fish movement, habitat usage and behaviours can assist barrier management to provide favourable conditions for migrating fish (Silva et al., 2018; Williams et al., 2012). In addition, such knowledge can be used to parameterise tools, such as individual based models (IBMs) to simulate fish movement near a barrier. IBMs are powerful and transferable predictive tools, capable of predicting fish movement in novel scenarios – for example, at barriers where data are lacking (Mawer et al., 2023b) – and can account for individual variation in behaviour. Accounting for individual variation is an important consideration in fish pass design. Typically, fish pass design does not consider for the wide natural variation across a population, rather focusing on the average fish (Birnie-Gauvin et al., 2019), and a growing body of literature highlights how a "one size fits all" approach is not sustainable (Birnie-Gauvin et al., 2019; Crawford et al., 2024; Jones et al., 2020). Fish may vary in different attributes – for example habitat preferences (Capra et al., 2017; Mawer et al., 2023a), burst swimming speeds (Birnie-Gauvin et al., 2019), sustained swimming speeds (Jones et al., 2020) and activity levels (Nyqvist et al., 2024) – which can then influence their success at finding and passing a fish pass. Ignoring such variations could lead poor predictive outcomes, for example over-estimating predicted fish passage efficiencies. One major benefit of IBMs is their ability to simulate many different individuals representing the range of variation observed in wild populations – for example swimming ability and total length (Zielinski et al., 2018). Already, IBMs have been applied to fish passage problems with great success. For example, IBMs have been applied to predict passage efficiency for downstream migrating salmon smolts, with high transferability to other sites, (Goodwin et al., 2014) and upstream migrating carp (Gilmanov et al., 2019). IBM development requires knowledge on (often species-specific) fish behaviour to guide simulations, such as habitat preferences and individual variation, which in turn requires data on fish movement near a barrier.

With fine-scale acoustic telemetry, fish positional data can be recorded every few seconds as fish move in the vicinity of a barrier, enabling further understanding on the behaviour of migrating fish (Mawer et al., 2023a; Orrell and Hussey, 2022). Hydraulic modelling can provide data on different hydraulic parameters, such as water depth and water velocity, across the study site and describe potential hydraulic habitats fish may encounter. Analysing telemetry and hydraulic data in conjunction can then shed light upon habitat selection and preference. A suitable method for analysing fine-scale habitat selection is applying step selection function (SSFs) models. With SSFs, habitat parameters at steps taken by tagged fish are compared to habitat at randomly generated steps to compare habitat usage to availability (Thurfjell et al., 2014). By fitting SSFs to individual animals, individual variability in habitat selection can be quantified (Mawer et al., 2023a; Sells et al., 2022). Habitat selection may also differ with behavioural state, e.g. if undergoing directed movements vs searching behaviours (Picardi et al., 2022; Whittington et al., 2022). Hidden Markov models (HMMs) can delineate behavioural states from animal telemetry, often using movement parameters such as step length or turning angle (Langrock et al., 2012). Incorporating behavioural state into SSFs can result in different interpretations of habitat selection (Picardi et al., 2022). Combining HMMs and SSFs to analyse migrating fish movement could be used to understand the parameters influencing observed movement patterns and usage, leading to predictive models for barrier management.

Here, habitat selection of migrating fish is analysed for different behavioural states and used to predict spatial usage of the two study species near a barrier with fish pass outflow, expanding on previous work by Mawer et al. (2023a). The paper proceeds in three steps: 1) analysing habitat selection in different behavioural states, building upon earlier work where the behavioural state was not defined (Mawer et al., 2023a), to determine whether habitat selection differs between states and if accounting for state improves the model; 2) cross-validating resulting models to optimise predictive capability; and 3) using the resulting predictive models to create an IBM to predict spatial usage by the fish as they approached the fish pass under different river discharges.

2. Methods

2.1. Study site

Movement of migrating fish was studied in the downstream section of the Altusried hydropower plant (HPP) on the river Iller in southern Germany (Fig. 1), to evaluate fish behaviour downstream of the barrier. The HPP has a capacity of 7.8 MW and a 525 m fish pass provides an alternative route for migrating fish to pass the HPP. A 2D acoustic receiver array consisting of 16 180 kHz HR2 VEMCO receivers was installed in the downstream area of the HPP, with two further receivers in the fish pass itself (Fig. 1A).

2.2. Data collection

Common barbel (*Barbus barbus*) and grayling (*Thymallus thymallus*) were caught and tagged during their spawning migration in 2018. Twenty-two barbel (total length (mean ± standard deviation): 469 ± 73 mm; weight: 1356 ± 592 g) were caught and tagged between May 17th and May 29th. Twenty five grayling (total length: 367 ± 56 mm; weight: 630 ± 270 g) were caught and tagged between March 28th and April 11th. Tagged fish data are available in the supplementary files. Captured fish were anaesthetised with phenoxy-ethanol (10 ml per 50 l water) and a VEMCO 180 kHz V9 acoustic tag was surgically implanted into the abdomen. After recovering, fish were released near the most downstream receiver in the array (Fig. 1A). For more details on data collection, see Mawer et al. (2023a).

Hydraulic data were collected and used to model the hydraulic environment for eight flow discharge scenarios (discharge from 10 to 80 m^3s^{-1}, in jumps of 10 m^3s^{-1}). Bathymetry was derived from a combination of drone images (using Structure from Motion methodology in shallow and dry areas) and from measurements taken at cross sections approximately 10–15 m apart. Measurements were taken via an echosounder in deeper waters with shallower areas surveyed by wading. Hydraulic models were made using Hydro_AS-2D (Nujic, 2016) and provided data on water velocity, water depth, spatial velocity gradient (SVG) and flow and SVG direction at a resolution of 0.5 × 0.5 m (supplementary files). The hydraulic models were calibrated using water elevation measurements every 10 m along the shoreline during a flow rate of 10 m^3s^{-1}. Hydraulic models covered the area of the array, up to around 500 m downstream of the HPP (Fig. 1A). Temperature data were collected by the acoustic receivers in 15 min intervals. The median value across receivers was taken to describe the temperature of the study site at a point in time.

2.3. Data analysis

The methodological framework is summarised in Fig. 2.

2.3.1. Track preparation

Tracks analysed in this study were identical to those previously analysed by Mawer et al. (2023a). Fish positions were calculated with a novel algorithm (see supplementary files) and analysed to detect when fish entered within 10 m of the fish pass entrance, at least 2 h after prior detections in that area. From each of these resulting detections near the fish pass, the preceding one hour of data (where available) were taken and were assumed to represent a distinct attempt by the fish to locate the fish pass, hereafter referred to as approach tracks. The approach tracks were further filtered as described in Mawer et al. (2023a) to retain tracks demonstrating directed movements towards the fish pass entrance. Data were limited to within the known spawning migration period for both species, based on previous analysis in the river stretch (Epple, 2020), to between date of tagging and June 16th for barbel, and to April 16th for grayling.

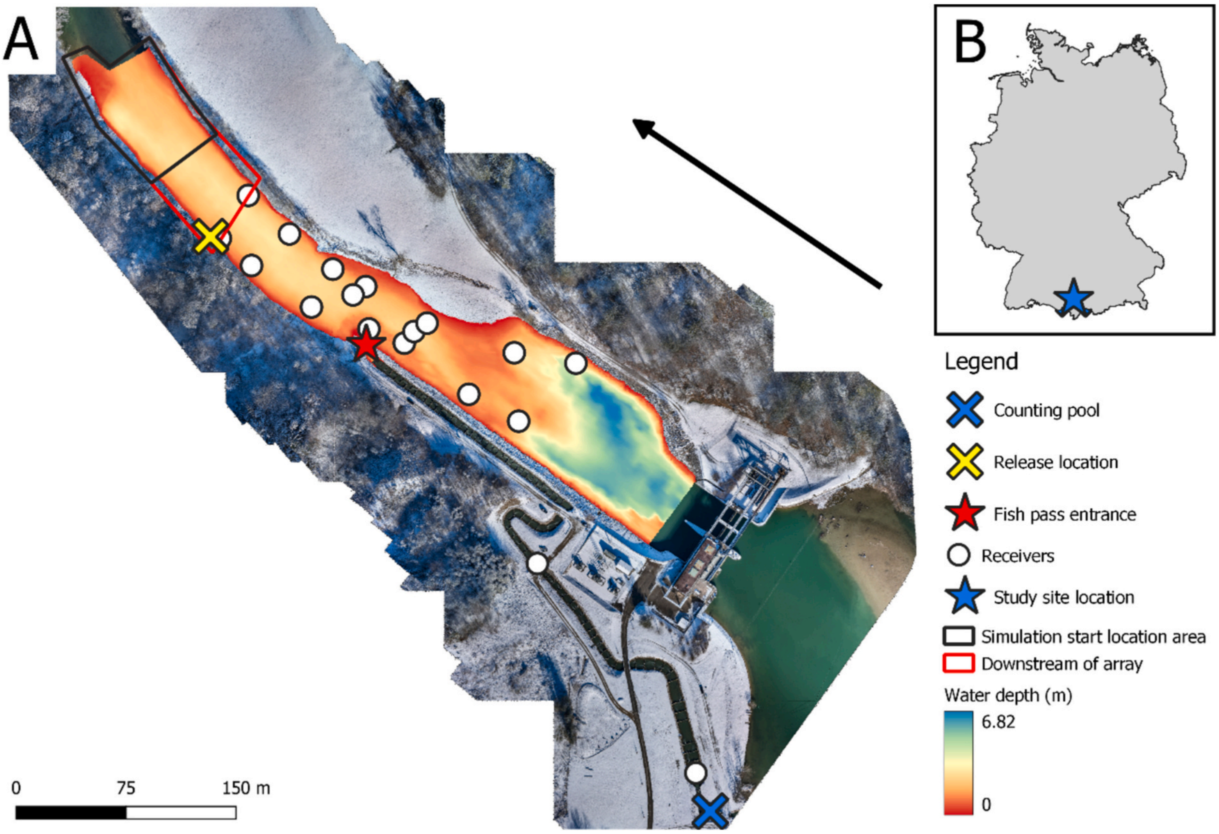

Fig. 1. A) Map of the study site, with the direction of river flow shown by the black arrow. Environmental data for water depth at discharge 40 m^3s^{-1} is shown to demonstrate the extent of available data. The black box represents the area in which simulations could begin while the red box marks the area downstream of the acoustic array: simulated positions in this area were removed from further analysis. B) Blue star: the location of the study site within Germany. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

As both HMMs and SSFs require positions at regular intervals, positions were interpolated to 20 s intervals using a continuous-time correlated random walk state-space model via the R package “crawl” (Johnson et al., 2008). Eighty-seven tracks for 31 fish (20 barbel and 11 grayling) were analysed. Some individuals approached the fish pass multiple times, with a mean number of tracks per fish of 2.8, ranging from 1 to 9. All barbel were caught in the fish ladder or counting pool while 8 of the 11 grayling were caught downstream. A two-stage approach was used to combine HMMs and SSFs: fit HMMs to the entire population, use the HMMs to split the data into behavioural states, then fit SSFs to each state separately (Fig. 2), to progress from the SSF analysis of Mawer et al. (2023a), where behavioural states were not distinguished.

2.3.2. *Hidden Markov modelling*

HMMs were fitted to all tracks for a species using the R package “momentuHMM” (McClintock and Michelot, 2018). A two-state HMM was fitted to the data of all fish per species to identify a transit state, representing longer directed movements (state 1), and a searching/resting state, showing movement in a restricted area (state 2), previously reported for migrating freshwater fish near a barrier (Elings et al., 2023b). States were defined by straightness index (SI), the ratio of total travelled distance to displacement where values approaching 1 indicate straightness and values approaching 0 indicate tortuosity (Elings et al., 2023b). SI was calculated over windows of 1, 5 and 10 min and separate HMMs were fitted using each SI window, to determine which served as a better data stream for the HMMs. No environmental covariates were included in the HMMs.

Resulting HMMs were compared via Akaike’s Information Criterion (AIC) to identify the optimal HMM. The optimal HMM was then used to split data for each fish into two behavioural states, using the Viterbi algorithm to classify each step as state 1 or 2 (Viterbi, 1967). The difference between step length and turning angle distributions in each state were tested with Kolmogorov-Smirnov tests.

2.3.3. *Explore: Drivers behind movement in each behavioural state*

The first stage in the analysis was to explore whether the parameters explaining observed fish movement differed between behavioural states and compare results to models fitted without behavioural state distinction by Mawer et al. (2023a), hereafter referred to as the both-states data/models.

Data for each behavioural state were prepared separately for SSF analysis per fish. For consistency, data were prepared with the same methods as Mawer et al. (2023a). A gamma and a von Mises distribution were fitted to step lengths and turning angles respectively for each fish and the distributions were used to generate random steps as a measure of habitat availability. Ten random steps were generated within the river. Environmental data (supplementary file) were added to the start and end points of steps. Time of day for each step was categorised as day, dusk, night, or dawn.

For modelling, step length was log transformed and directional covariates were transformed to their cosines, which converted angles from being on a circular scale to a linear scale between −1 and 1. All explanatory covariates (environmental data and movement data) were then standardised prior to statistical analysis, by subtracting the mean value and dividing by the standard deviation. For consistency with the previous analysis on the both-states data, the same mean and standard deviations were used to standardise values as used by Mawer et al. (2023a).

Conditional logistic regression models were fitted to each data set

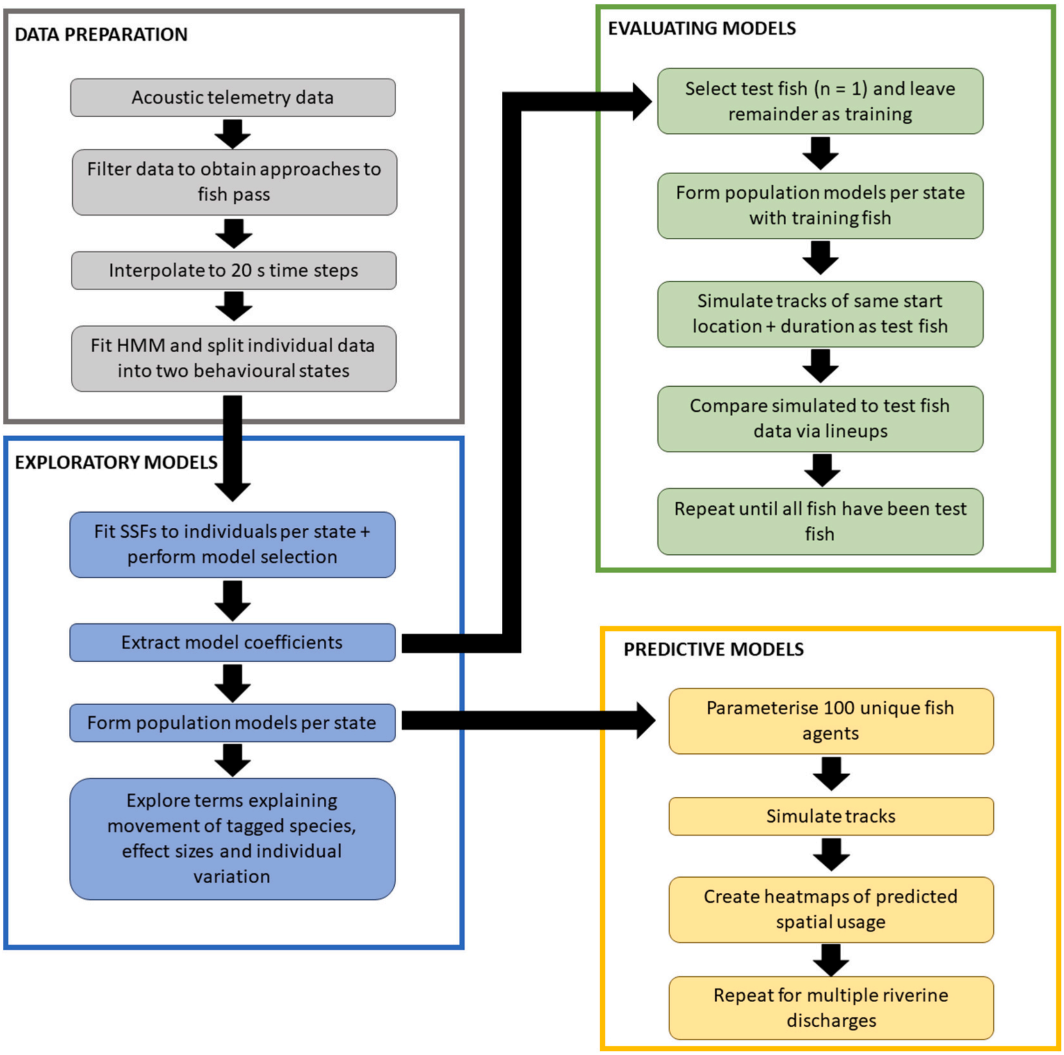

Fig. 2. The modelling process of this paper, going from fish positional data to a predictive individual based model, using hidden Markov models (HMMs) and step selection functions (SSFs). For details on the analysed tracks, see Mawer et al. (2023a).

(per state and per individual fish) to identify parameters influencing the selection of a step by fish, stratifying the analysis by step ID. The response variable of the model was whether a step was true (e.g. taken by the fish) or false (random steps generated as a use of habitat availability). A saturated model was fitted and backwards model selection was applied to determine the parameters best explaining the observed data. Main effect terms were: water velocity, depth, SVG, difference between fish and water velocity angles, and difference between fish and SVG angles at the end of steps; the logarithm of the step length; and the cosine of the turning angle. Two-way interactions were included, shown in Table 1. Terms were removed one-by-one and models were compared using AIC. A more complex model was retained if its AIC was at least two units lower than a simpler model. Final individual models were saved and model performance assessed via the concordance statistic, a

Table 1
Two-way interactions included in the saturated models for every fish. Interactions between the same parameter signifies interactions between the value of that parameter at the start and at the end of steps. Interactions involving time of day were only included if multiple time periods were present in the data. Interactions between log(SL) and other parameters used the parameter value at the start of the step. Terms abbreviated in the table are: spatial velocity gradient (SVG) and step length (SL).

	Water velocity	Depth	SVG	Difference between fish and velocity angle	Difference between fish and SVG angle	Time of day	Temperature	log (SL)
Water velocity	X	X	X	X	X	X		X
Depth	X	X	X	X	X	X		X
SVG	X	X	X	X	X	X		X
Difference between fish and velocity angle	X	X	X	X	X	X		X
Difference between fish and SVG angle	X	X	X	X	X	X		X
Time of day	X	X	X	X	X			X
Temperature								X
log(SL)	X	X	X	X	X	X	X	

measure of the model's discriminative ability (Therneau, 2024). The concordance values for each species in state 1 and 2 were compared to values for the both-states data via *t*-tests, to assess whether accounting for behavioural state improved overall model fit.

Population models were formed for each behavioural state per species. If a model term was not retained in an individual's model, the coefficient's value was set to zero for that individual, i.e. no effect (Morrison et al., 2015). Per species, state and model term, any coefficients that fell outside the inner fences of a boxplot (less than Q1–1.5*IQR, more than Q3 + 1.5*IQR, where Q1 and Q3 are the first and third quartiles, and IQR is the interquartile range) were identified as outliers and removed. Outliers were also removed in this manner from the both-states data, to enable comparisons between models. Mean coefficient size and standard error were calculated per term. A t-test was applied to determine whether the resulting mean was significantly different from zero. If the mean was not significantly different from zero, the term was assumed to have no cohesive effect on the studied population. Habitat selection between each behavioural state and with and without separation of behavioural states was compared with paired t-tests. Differences in habitat selection with capture location was not tested. All barbel analysed were caught in the fish pass or counting pool (i.e. had already located and entered the pass) thus there was no difference, while out of the analysed grayling, few were caught in the counting pool ($n = 3$) compared to downstream ($n = 8$).

2.3.4. *Evaluate: Cross-validating models for prediction*

Using the optimal model structures obtained in *Explore*, model predictive capability was evaluated via cross-validating using simulated tracks (Fig. 2). Initially, the model structures were used to refit models to each fish with unstandardised environmental data, to enable simulation using the available environmental rasters. The models of Mawer et al. (2023a) were also cross-validated. Further mentions of states in this section refer only to evaluating the behavioural SSFs.

One fish was set aside as a test fish with the remaining fish of that species forming the training fish. The process was repeated until every fish had been the test fish once. Within each species and state, a population model was created via averaging coefficients for the training fish as previously described. A covariance matrix of coefficients for the population model was also created, again with coefficient outliers removed. A (state-specific) selection function was parameterised for the test fish by selecting coefficient values from a multivariate normal distribution described by the mean and covariance matrix of the population model.

Training fish movement kernels were extracted, described by the step length distribution (a gamma distribution) and the turning angle distribution (a von Mises distribution) and adjusted based on coefficients in the individual models (Avgar et al., 2016). As movement kernel parameters cannot be negative, any values that became negative after adjustment were discarded. The test fish movement kernel was parameterised from a normal distribution described by the mean and standard deviation of the movement kernel parameters for the training fish. Separate movement kernels were created per state.

Data from the test fish track were used to inform simulations for 19 simulated agents, in terms of duration, state sequence and start location. If the test fish had multiple tracks, the following process was repeated for every track of the test fish. A simulation would start at the same location (and state) as the real track. At each time step, 20 potential steps were generated from the (state-specific) movement kernel and the selection probability of each step assessed via the (state-specific) selection function. A step would be chosen from a multinomial distribution and the process repeated until the simulated track covered the same duration as the real track. Fish could only move where environmental data were available (see Fig. 1A). If the state switched, the selection function and movement kernel would change. For addressing missingness in the real track, simulated data were only retained if the corresponding step was available in the real data.

Model predictive ability was assessed using a lineup protocol (Fieberg et al., 2023). Track appearance, spatial distribution of used locations as heatmaps, histograms of used habitat parameters, and histograms of movement parameters were compared between simulated and real tracks. Plots were created of data from the 19 simulated agents and from the test fish, with the plot of the test fish data located at a random position among all the plots for a given data type. Five observers were provided with unique lineups and visually examined every plot, selecting one they believed was the real track. Using the observations, a *p*-value for every plot was determined via a goodness-of-fit test as described by Fieberg et al. (2023), where the null hypothesis is that data and models are consistent and the alternative is that the data are distinct from the models as observers could identify the real data from the simulated. The smaller the resulting p-value, the stronger the evidence that the model did not capture the data. A p-value threshold of 0.05 was used, where the null hypothesis would be rejected if $p \leq 0.05$. The test was sensitive: if one of the five observers correctly identified the real fish, the null hypothesis would be rejected.

Performance of the both-states SSFs and the behavioural state SSFs were compared. In addition, note was also made whether the models could not capture the patterns of a fish who was an outlier in some/many terms in *Explore*.

2.3.5. *Predict: Predicting spatial usage of fish in the vicinity of a barrier*

The population model formed in subsection *2.3.2 Explore* was used to predict spatial movement of barbel and grayling when approaching the fish pass via an IBM (Fig. 2). Simulations were conducted separately per species and discharge.

A total of 100 individual fish agents were parameterised as described in subsection *2.3.4 Evaluate*, using data from all fish of a species. For similarity to real data, fish agents could have multiple tracks and the number of tracks was determined via a Poisson distribution parameterised by the mean number of tracks per fish in the data (barbel, mean = 5.714; grayling, mea*n* = 3.769).

The behavioural state sequence was determined by using the transition matrix of the fitted HMMs, which describes the probability of moving from one state to the other or remaining in a given state. The initial state was selected at random and the states for subsequent steps selected using the probabilities of the transition matrix (Klappstein et al., 2023).

Tracks started at a random location in the lower 100 m of the study site (Fig. 1A). Twenty potential steps were generated with the agent's state-specific movement kernel and steps were assessed via the state-specific selection function. A step was chosen from a multinomial distribution and the process was repeated for a total of 179 steps of 20 s, equal to one hour duration. Simulations were conducted for three discharge levels (20, 50 and 80 m^3s^{-1}), representing low, medium and high discharge scenarios, with one hundred unique agents per scenario. Resulting tracks were used to create heatmaps of predicted usage in the study site. All positions downstream of the acoustic array (Fig. 1A) were removed to reduce bias in predicted distributions due to start locations.

3. Results

3.1. *Hidden Markov modelling*

Using SI over a 10 min window produced the optimal HMM and was used to split the data (Fig. 3, Table 2). State 1 was directed movement, which we interpreted to represent a fish in transit while state 2 showed restricted movement, characteristic of searching and/or resting behaviours (Fig. 3B). Step length and turning angle distributions differed significantly between states ($p < 0.001$). Across all fish, steps were distributed roughly evenly between states, though not on an individual level and some individuals only had tracks in one state. For state 2, three fish had fewer than 25 steps (having 7, 14 and 19 steps) and these fish were removed from further analysis of state 2 habitat selection due to

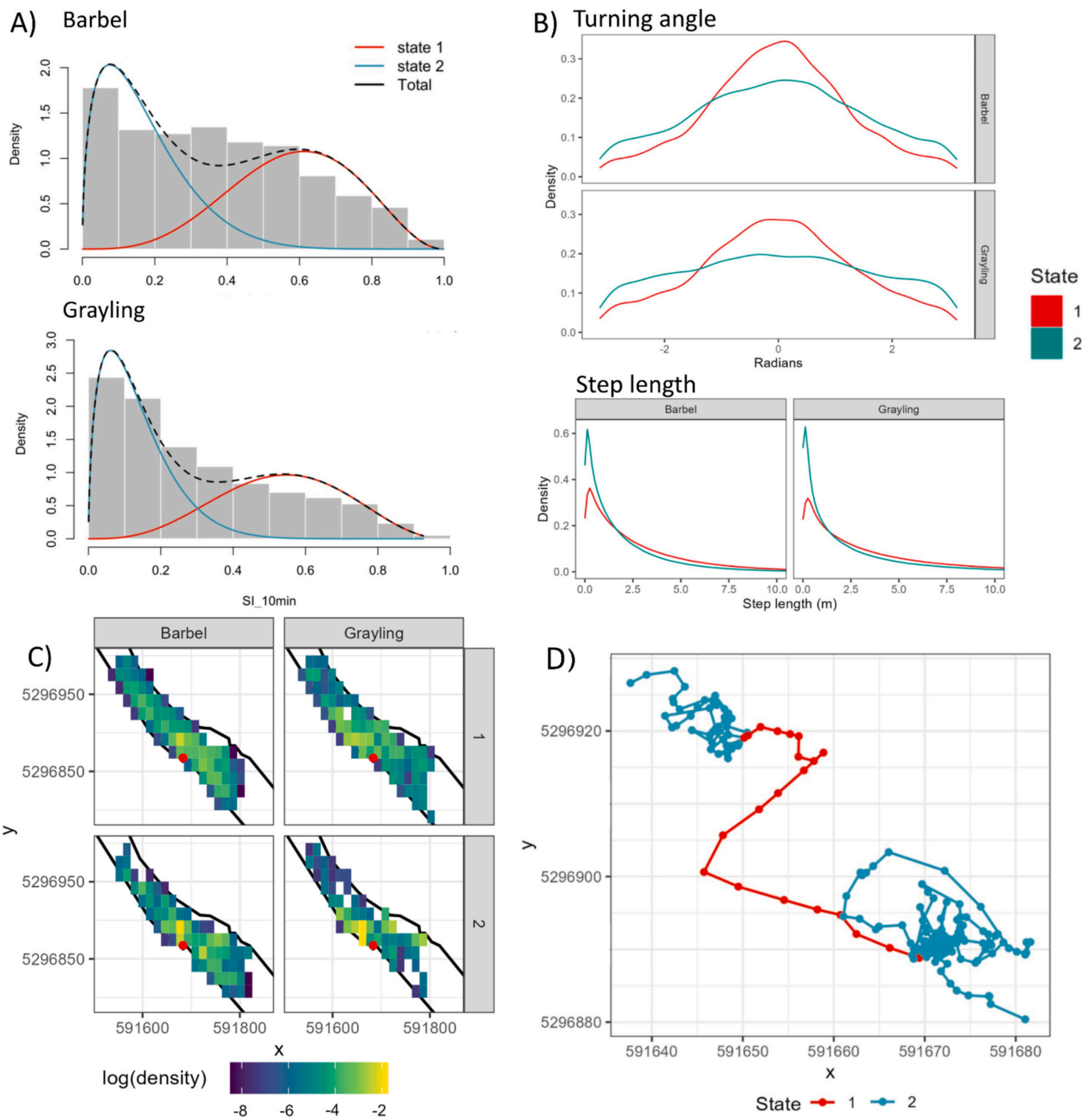

Fig. 3. Hidden Markov model outputs fitted to tracks of fish approaching the fish pass. A) Straightness index over 10 min (SI_10min) distributions for state 1 (transit) and state 2 (resting/searching) for barbel and grayling. B) Step length and turning angle distributions per species and state. C) Heatmaps of used locations per state per species, with the fish pass location shown in red. D) Example track coloured by state. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Akaike's information criterion (AIC) table for the candidate hidden Markov models (HMMs) for barbel and grayling.

HMM straightness index window	AIC, barbel	AIC, grayling
1 min	−4411.500	−1059.698
5 min	−7819.125	−2679.722
10 min	−8470.161	−3638.908

low data quantity.

3.2. *Exploratory analysis*

3.2.1. *Model performance*

Splitting data into behavioural states improved model concordance for three out of four species-state combinations (Table 3) compared to the models of Mawer et al. (2023a). However, the difference was not significant (paired *t*-test, $p > 0.05$). One fish had a concordance of 1 in state 2: the model for this fish returned NA for all coefficients, indicating issues with model fitting, and did not influence the population model.

Table 3
Mean and standard deviations (SD) for step selection function model concordances for each behavioural state, and for the previous models where behavioural state was not distinguished.

Species	State 1			State 2			Both-states (Mawer et al., 2023a)		
	Mean ± SD	Maximum	Minimum	Mean ± SD	Maximum	Minimum	Mean ± SD	Maximum	Minimum
Barbel	0.68 ± 0.05	0.81	0.63	0.66 ± 0.08	0.93	0.58	0.67 ± 0.06	0.81	0.60
Grayling	0.72 ± 0.09	0.91	0.61	0.70 ± 0.11	1	0.62	0.67 ± 0.06	0.81	0.57

3.2.2. *Habitat selection in behavioural states*

Common terms influencing step selection were apparent for each species and state. For barbel, over 80 % of fish had water velocity, depth, the difference between fish and velocity angle, and log(step length) in their state 1 (transit) models while over 80 % had log(step length), depth and SVG in their state 2 (resting/searching) models. While SVG was more prevalent in barbel state 2 models, that was not true for grayling. In state 1, 80 % of grayling models had SVG but only 37.5 % of state 2 models had SVG. Other terms in >80 % of grayling state 1 and state 2 models were log(step length), depth and water velocity. The inclusion of log(step length) and cos(turning angle) in many individual models indicate the movement kernels used to generate the random steps in the SSF were inaccurate.

Population trends for each behavioural state are shown in Fig. 4. Individual variation in coefficient size was large and in some cases contrasting effects existed where fish had the opposite response to the mean. For example, in both states barbel on average preferred faster water velocity, but some individuals had no preference and others avoided faster flows. The high individual variation prevented generalisations on the population level for many terms, as resulting means were not significantly different to zero (Fig. 4). Further discussion concerns only terms where the population model coefficient was significantly different to zero unless stated otherwise.

Overall, great overlap existed between state models. In general, barbel preferred faster water velocities in both states. In addition, both barbel states had a positive interaction between depth and SVG, meaning preference for one was stronger when the other was high. In addition, barbel moved less in faster water velocities in both states. Both barbel and grayling moved faster in deeper waters in both states. Grayling also had a negative interaction between water velocity and depth in state 1: in state 1, grayling preferred fast shallow water and deep slow water over fast deep and slow shallow areas. The state 1 coefficients overlapped with state 2, though the latter was not significantly different from zero.

Few terms were significantly different between states and differences between state only existed for barbel for: depth and the interaction between log(step length) with the angle between fish and SVG. Specifically, barbel selected for deeper waters in state 1 and had no depth preference in state 2 (Fig. 4). In addition, the interaction between log (step length) and the difference between fish and SVG angle was only present in the barbel state 1 population model, though its effect was not significant. In barbel state 1, coefficients for the interaction between log (step length) and depth, and the interaction between log(step length) and the difference between fish and SVG angle differed from the both-states model. The latter interaction was only present in state 1 and was not significantly different to zero on average. Comparing state 1 and the both-states model, barbel tended to move further when present in deeper water in state 1 compared to the both-states model, though the difference was small. No barbel state 2 model coefficients differed from both-states model coefficients.

3.3. *Model evaluation*

Both groups of models (both-states models and behavioural state models) could capture fish movement and habitat usage patterns. Considering all lineup plots made (nine per fish) and resulting goodness-of-fit test results, simulated data were consistent with the real data for 61 % of lineups for the behavioural state SSFs and 63 % for the both-states models ($p < 0.05$). Full summaries for every plot are provided in the supplements. Model performance differed with species: for barbel, 63 % were consistent for the behavioural state SSFs and 67 % for the both-states models. For grayling, both model types had 57 % of lineups showing simulated data being consistent with the real data. Model performance also differed with plotted data (Fig. 5). The presence of outliers in coefficients did not affect the ability of the models to capture movement and habitat usage of individual fish.

3.4. *Prediction*

The models including HMMs captured spatial usage better and were used to create predictive models. Model coefficients are shown in the supplements. Predictive maps of spatial usage are shown for barbel and grayling (Fig. 6). Example tracks for the first 6 grayling to enter the array at 20 $m^3 s^{-1}$ are shown in Fig. 7.

4. Discussion

Here, two aspects of animal behaviour – behavioural state and habitat selection – were combined to understand parameters driving fine-scale fish movement and to predict fish movement in an anthropogenically altered river system. In the context of the study, little difference existed in habitat selection between behavioural states and individual variation in habitat selection was high. Models including behavioural state though were better at capturing spatial usage patterns by fish. Together, combining HMMs and SSFs provided a route from real fish data to developing an IBM for predicting fish spatial usage that could have applications beyond the immediate context of this study.

From an exploratory point of view, accounting for behavioural state for habitat selection analysis had little benefit in this context. Model concordance did not significantly differ with and without behavioural state. Moreover, most coefficient values did not differ significantly between either state with the both-states models. The lack of difference between behavioural states may be related to the specific context of our work. Other studies combining HMM and SSFs found habitat selection differences between states but such studies operated on much coarser scales than the work presented here, e.g. 6 h time steps (Picardi et al., 2022). By comparison, this paper represents work on a very fine temporal scale (20 s time steps) and data were filtered for tracks where fish approach the fish pass. Given the defined tracks and very fine temporal scale, it may be possible that fish motivation in this context is largely consistent between behavioural states and fish select similar hydraulic cues when transiting and when searching/resting when approaching the fish pass. At coarser scales, habitat preference differences may emerge between states. Despite the lack of difference in habitat preference, including behavioural state did improve model ability to capture fish spatial usage patterns. Further research into fish habitat selection and behavioural state at this scale is needed.

Some constraints of the study data should be acknowledged with regards to the habitat selection analysis. One aspect is that both the hydraulic model and fish movement are in 2D. Hydraulic parameters will vary in the water column while the fish likely use varying depths. As a result, the hydraulic conditions a fish actually experienced may be poorly captured. The use of 3D models for the hydraulic environment (Ben Jebria et al., 2023; Goodwin et al., 2006) as well as using acoustic

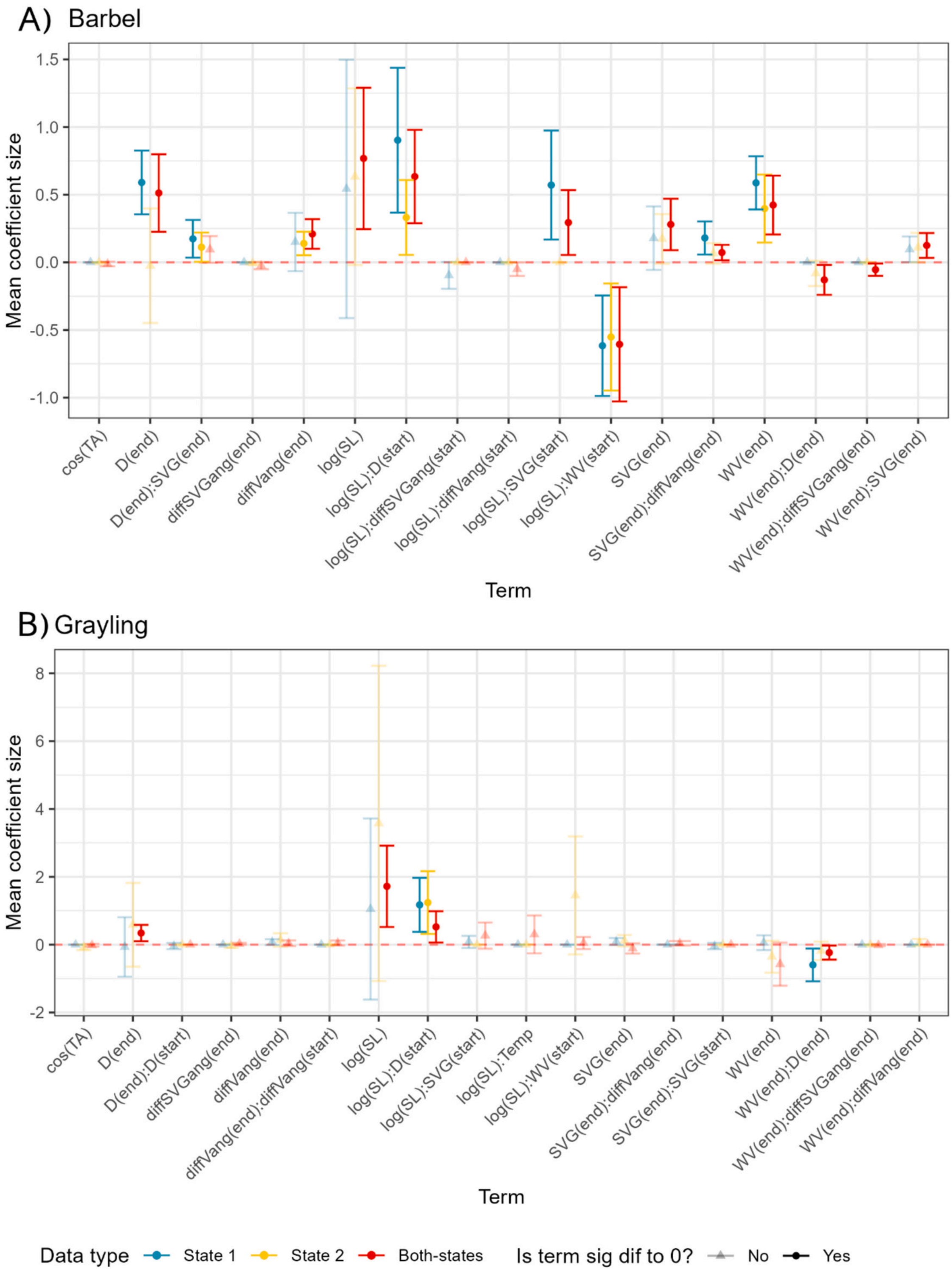

Fig. 4. General trends for barbel (A) and grayling (B) in the both-states (Mawer et al., 2023a), state 1 (directed movement) and state 2 (resting/searching) models. Mean coefficient sizes are plotted and error bars show the 95 % confidence interval (± 2 standard errors). Only terms where the mean coefficient is significantly different to zero for one of the data types are shown. Low-opacity triangular points show where a term was not significantly different to zero in the t-test. Terms are abbreviated for brevity as follows: water velocity (WV), depth (D), spatial velocity gradient (SVG), difference between fish and SVG angle (diffSVGang), difference between fish and water velocity angle (diffVang), temperature (Temp), time of day (TOD), step length (SL), turning angle (TA).

tags with pressure sensors to obtain fish vertical position (Runde et al., 2020) could address this in future telemetry studies. Another consideration is that several of the fish tracked in this study were caught in the fish pass itself. Given fish can have spatial learning behaviours (Burt De Perera and Holbrook, 2012; Fabre et al., 2014), it is possible they remembered the location and route. Regarding possible habituation, the analysis included multiple approaches to the fish pass by individual fish. Fish did not take identical routes on subsequent approaches, though the impact upon habitat selection analyses is unknown. Ideally, all fish should have been caught and tagged downstream of the study site and in

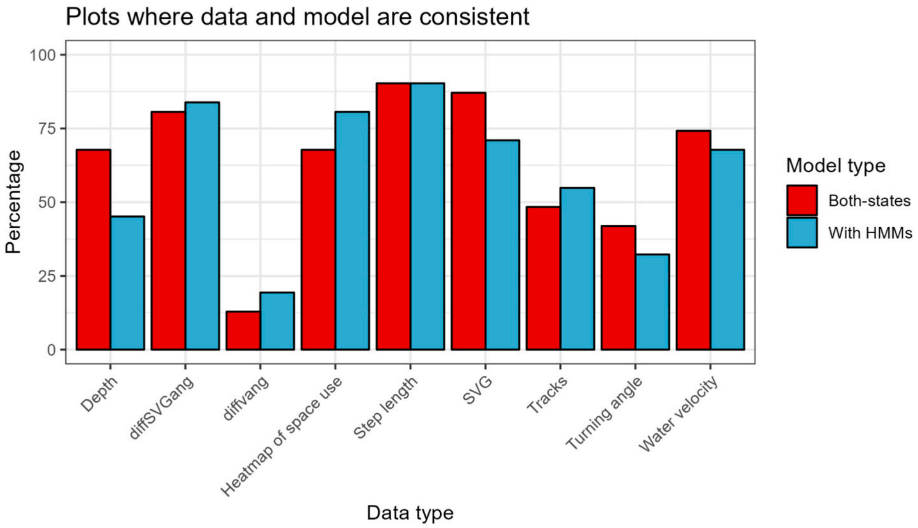

Fig. 5. Percentage of lineup plots for each data type where models and fish data were consistent in the goodness-of-fit tests. Abbreviated terms in the figure are: spatial velocity gradient (SVG), difference between fish and SVG angle (diffSVGang), difference between fish and water velocity angle (diffVang), and hidden Markov models (HMMs).

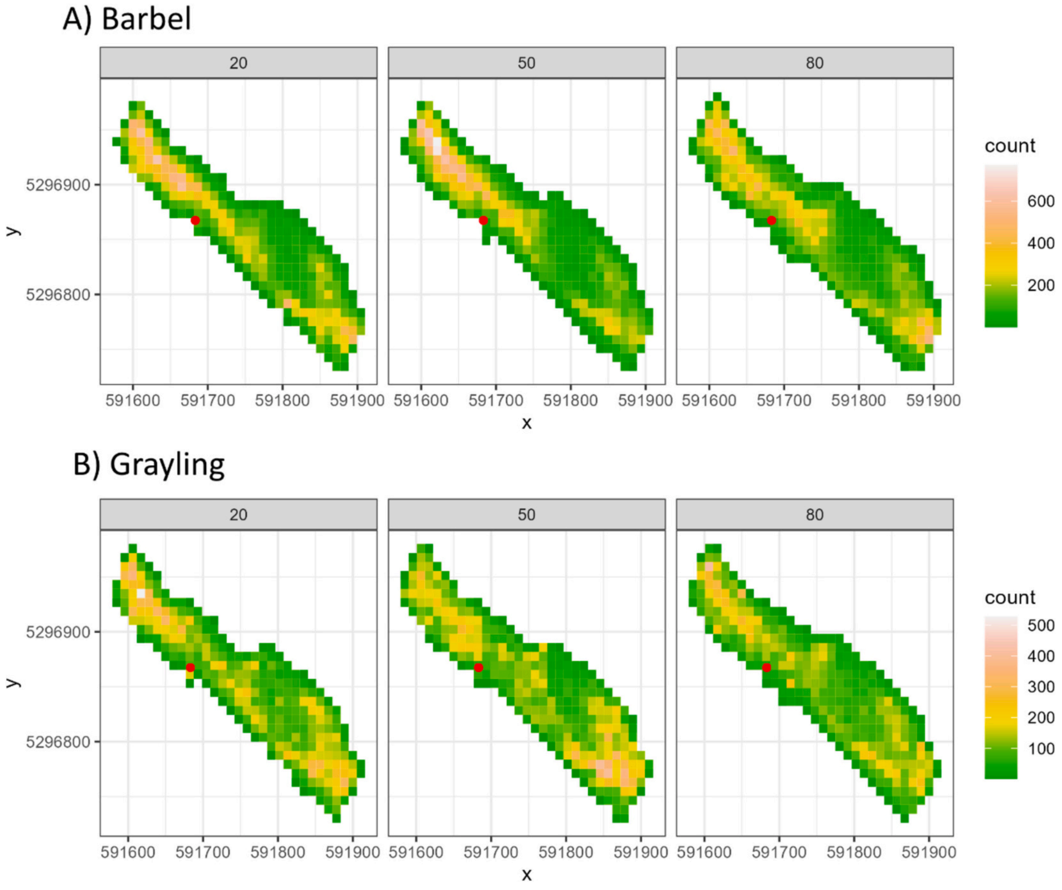

Fig. 6. Predicted spatial distribution of barbel (A) and grayling (B). Each plot is for a separate discharge (20 m^3s^{-1}, 50 m^3s^{-1} and 80 m^3s^{-1}). The red dot represents the fish pass location. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

advance of the spawning migration, limiting familiarity with the study site. However, this was not possible – in winter, catch efficiencies were too low for a successful tagging campaign while if fish were caught and tagged the previous year, there would be no guarantee of sufficient return rates for this study and it is possible a large proportion would not return. Another constraint is the assumption that fish were attempting to migrate. There is no certainty of the actual motivation of the tagged fish – were they attempting to migrate or were they simply using the study site for another purpose? This issue was addressed in two ways. Firstly, data were limited to the known migratory periods of barbel and grayling in this river system (Epple, 2020). Then, the selection of tracks as detailed in *Methods* occurred to identify periods where fish approached

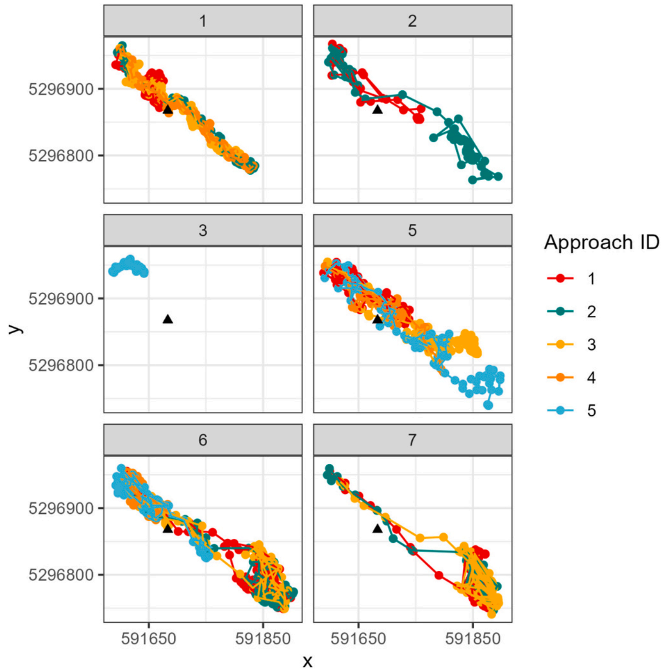

Fig. 7. Tracks for the first six grayling agents to enter the acoustic array for discharge 20 m^3s^{-1}. Tracks are coloured by ID, where agents had multiple tracks. The fish pass location is represented by the black triangle.

the fish pass, under the assumption that these represented attempts to migrate. Ultimately, the motivation of fish in this study cannot be known definitively and it is possible some of the tracks analysed during this study showed non-migratory behaviour. Regardless, models still provided insight into habitat selection and spatial usage by fish, and the predictive model could produce upstream movements.

Considerations must be paid to the behavioural states themselves when interpreting results. Two behavioural states were described: a combined resting/searching state where movement involves shorter step lengths and larger turns; and a transiting state featuring more directed movement of longer step lengths. Previous effort to create a three state model in this context, by splitting resting and searching, did not produce a statistically acceptable model (Elings et al., 2023b). In part, this is due to difficulty with scale and positioning error. At increasingly fine scales, the impact of positioning error upon step length and turning angle parameters becomes relatively greater (Jerde and Visscher, 2005), which is why using the traditionally-used step length and turning angle was not appropriate for this study (Elings et al., 2023b). In the context of this paper, if a fish spends an extended period in one place, apparent movement might be due to positioning error rather than actual fish movement (i.e. when a searching fish covers 2 m in a 20 s time step and positioning error also equals 2 m, both states cannot confidently be separated). Such errors make the designation of separate resting and searching states challenging (Elings et al., 2023b). It is possible that when resting (i.e. not travelling far) habitat selection will differ from searching (i.e. moving) and that having both behaviour in one state in this paper obscures patterns. However, the distinction of those behaviours cannot yet be made and further developments in both acoustic telemetry positioning and HMMs may be needed.

The distinction of resting and searching behaviours may hold additional benefit when comparing habitat selection of the two species in this study, barbel and grayling. Results considering state 2, the resting/searching state, can be interpreted differently depending on the behaviour, and it is possible between and within species that the state is more resting or more searching for some individuals than others. Specifically, in the resting/searching state (state 2), few grayling had spatial velocity gradient (SVG) in their models. Previous work with HMMs in this system showed a tendency to switch from transit to resting/searching behaviour in areas of higher SVG (Elings et al., 2023b) and adding attraction flows is noted as a key attribute for fish searching for a fish pass (Castro-Santos et al., 2017; Piper et al., 2012). If state 2 is predominantly resting behaviour for grayling, rather than searching, the lack of SVG may not be of concern – if searching, one could presume grayling may be influenced by SVG whereas if resting that may not be the case. By comparison, a higher proportion of barbel had SVG in their state 2 models compared to state 1. For barbel, this could be interpreted as SVG being more important for guiding fish movement when searching, provided that state 2 mainly shows searching behaviours. However, considering general trends, mean SVG selection did not differ between states for barbel nor did it differ significantly from zero. Moreover, ultimately these results are highly open to interpretation and dependent on what behaviours are actually captured by the HMM-defined behavioural states. Further development of fine-scale HMMs could assist in delineating these behaviours, and better informing future models.

Individual variation was high in both species and states. Across taxa, individual animals in a population can vary across a range of metrics, from habitat selection (Capra et al., 2017; Gillingham and Parker, 2008; Lesmerises and St-Laurent, 2017) and other aspects of spatial usage e.g. residency (Williamson et al., 2021) to physiological variation which may drive behavioural differences (Norin et al., 2024). Historically, fish passage science has taken a reductionist approach ignoring individual variation and considering only the average fish, at the risk of fish passage (Birnie-Gauvin et al., 2019; Jones et al., 2020). The results of this paper reiterate the results of Mawer et al. (2023a) and adds to a growing body of fish passage literature highlighting a need to account for individual variation in both analysis and predictions (Birnie-Gauvin et al., 2019; Crawford et al., 2024; Jones et al., 2020; Nyqvist et al., 2024). While mean values are important, researchers should also strive to report the variability in studied fish. Such variation is then informative for predictive modelling approaches, like IBMs, where it can be used to parameterise varying individual fish for simulation. Through better accounting for and reporting individual variation in freshwater fish, fish passage science can move towards fish passage solutions that cover the wide range of variation present in fish populations.

Though individual variation in habitat selection was high, some commonalities emerged, providing insight into parameters governing the movement of the studied fish. For example, barbel on average preferred faster water velocities. Such preferences for faster flow agrees with wider literature describing barbel as rheophilic (Britton and Pegg, 2011). Yet, this trend was not universal across barbel, with some individuals avoiding faster flows. The high individual variation prevented generalisations of the relationships between fish and many model terms. In some cases, terms were present in many models but due to contrasting effects across the studied fish, means were not significantly different to zero – for example, SVG. SVG is an important cue for navigating fish (Elings et al., 2023a, 2023b) and can attract or repel fish, depending on context (Enders et al., 2012; Piper et al., 2012). Mean SVG values were positive across models suggesting that, while not a universal trend, many fish preferred higher SVG values. For grayling, the individual variation prevented generalisations of many terms, which had wide confidence intervals. Such individuality means that management tools for prediction must consider individual behaviours (Sells et al., 2022), and even contrasting behaviours. It is important for future studies on fish behaviour in the context of passage to account and describe individual variation in behaviours to facilitate future IBMs. The predictive IBM developed here is one such tool, enabling agents with varying movement and habitat preferences to be parameterised.

Predicted spatial usage of barbel and grayling differed with discharge and species, though commonalities emerged. Specifically, all predictions showed high usage in the most upstream area of the study site. This usage was noticeable greater for grayling compared to barbel. In addition, predicted usage was high in the lower central extent of the acoustic array which may in part be related to the fact that all tracks started downstream thus passed through this area upstream. Moreover, while some tracks moved upstream, some remained in the downstream section of the acoustic array, reflecting favourable habitat in the area. In this area, SVG was typically higher due to flow from the fish pass while water velocity was faster compared to the upstream area. For barbel, high usage in this area was particularly pronounced while for grayling it was less distinct. Patterns of predicted usage for barbel and grayling below the barrier and in the downstream section of the array suggest barbel may have greater success at locating the fish pass. Barbel were predicted to use the area around the fish pass entrance more than the upstream region, with stronger usage at the lower discharges compared to the high discharge scenario. Facilitating such conditions experienced in lower discharges in this area, e.g. by altering riverbed design, could assist barbel during the migratory period. By comparison, highest grayling usage occurred in the upstream area, suggesting they may be more attracted to that area than the fish pass. As a result, there may be a need to improve pass attractiveness for grayling. For both species, future research could involve developing hydraulic models for new configurations, e.g. flow attractions or alternate fish pass locations, and applying the IBMs to the new hydraulic rasters to predict how potential mitigation measures may affect fish spatial usage.

Direct recommendations from the IBM in this paper should be taken cautiously. Though the IBM can capture fish movement and spatial usage in this context, there are some caveats and limitations in the data that hamper recommendations. For both species and all discharges, high usage was predicted directly downstream of the barrier and predicted usage patterns resemble the distribution of water depth in this area. Few data were available on fish movement in this area, yet it is not known whether this is due to a decision by the fish or constraints of the data. This region was beyond the extent of the 2D acoustic telemetry array, meaning fish positions in this area would have a high associated positioning error (Roy et al., 2014). As a result, while few calibrating data were available in this region, we cannot know whether fish use it or not. Secondly, and related, the water in this region was deeper than elsewhere in the study site, generally exceeding 4 m depth and reaching up to 7 m. As linear modelling is used, usage in areas with habitat values beyond that of the calibrating data may be exaggerated. However, positive selection for deeper water was only present on average for barbel in state 1: in other models, the mean was near zero. As a result, preference for and avoidance of deeper waters was likely represented in the range of simulated agents and other habitat preferences may influence usage in this area. This issue could have possibly been abated by using generalised additive models (GAMs) for fitting the SSFs, enabling flexible relationships rather than linear. However, GAMs are computationally more demanding and take longer to fit, drastically increasing the time for model selection. Moreover, previous early non-linear modelling on this data indicated that relationships were near-linear thus using GAMs may have had little benefit alongside the many disadvantages for this study (Mawer et al., 2023a).

The IBM of this manuscript is one within a growing body of IBMs for fish passage. Compared to many existing IBMs, reviewed by Mawer et al. (2023b), the IBM featured in this manuscript exploited existing tools in movement ecology (Sells et al., 2023; Signer et al., 2024) as opposed to developing an IBM completely from scratch. Such an approach – analysing with a SSF then using model outputs to predict – could provide a more accessible route to simulating fish movement in the fish passage context. The IBM in this paper relies upon selection for and against hydraulic parameters. Hydraulic parameters are commonly used in fish passage IBMs (Mawer et al., 2023b), with other IBMs modelling movement towards preferences (Gao et al., 2016; Tan et al., 2018). While the IBM of this paper can predict spatial usage and produce upstream movements, further adjustments may be needed before it could be used for predicting fish passage. Within the range of existing fish passage IBMs and wider literature, there are several other elements that can influence fish movement. For example, potential behavioural mechanisms (e.g. attraction to or rejection of a route when water acceleration is above a threshold) are not included, where encountering certain flow characteristics cause simulated fish to reject a route (Goodwin et al., 2014). Such behaviour has been reported in literature for salmonids and eels (Enders et al., 2012; Piper et al., 2015), though their inclusion in a SSF-based IBM may be dependent on time step of the study. For example, this paper concerns movement on a 20 s time step while fish may be responding to flow acceleration on even finer scales (e.g. < 5 s). Future developments in acoustic telemetry and SSF application may assist inclusion of such behaviours. Moreover, fatigue metrics can be of particular importance during upstream migration, where fish may need to overcome challenging flows (Katopodis et al., 2019) and can be incorporated into IBMs. For example, Gilmanov et al. (2019) enabled fatigue to influence fish movement in their IBM, where fish moved to minimise accumulated fatigue, using water velocity and fish swimming velocity to determine fatigue. Such an approach could work with future SSF-based IBM like that of this paper, using water velocity and water velocity angles to derive potential energetic costs of true and random steps to a fish, thereby providing an input for simulations.

With increasing interest towards fine-scale tracking of freshwater fish near barriers, SSFs present an opportunity to gain in-depth insight into the parameters shaping observed movement patterns. Including HMMs had little overall benefit in the presented study site, perhaps due to the fine-scale nature of the study, but yielded some benefits to predicting fish spatial usage. Ongoing developments in the applications of both SSFs and HMMs open the door for further applications to freshwater fish telemetry, and can be used to develop and IBM as seen in this paper. The framework demonstrated in this paper, moving from fish positional data to an IBM capable of predicting spatial usage patterns, highlights the future potential for other telemetry studies seeking to understand and predict fine-scale fish movement in the barrier environment.

Funding statement

The analysis presented here was carried out within the RIBES project (RIver flow regulation, fish BEhaviour and Status). The project has received funding from the European Union Horizon 2020 Research and Innovation Programme under the Marie Sklodowska-Curie Actions, Grant Agreement No. 860800. The study setup and data collection were funded by the European Union's Horizon 2020 (H2020) research and innovation program FITHydro (https://www.fithydro.wiki/index.php), under Grant Agreement No. 727830.

CRediT authorship contribution statement

Rachel Mawer: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jelger Elings:** Writing – review & editing, Formal analysis, Data curation, Conceptualization. **Stijn P. Bruneel:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Ine S. Pauwels:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization. **Eliezer Pickholtz:** Writing – review & editing, Formal analysis. **Renanel Pickholtz:** Writing – review & editing, Formal analysis. **Johan Coeck:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Peter L.M. Goethals:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Rachel Mawer reports financial support was provided by Horizon Europe. Jelger Elings reports financial support was provided by Horizon

Europe. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful for the efforts of colleagues and partners, who conducted the fieldwork in harsh weather conditions to test and install the receiver array, and to catch and tag the studied fish. Special thanks goes to the field experts of INBO: Raf Baeyens, Nico De Maerteleire and Sebastien Pieters, and to PhD student Jenna Vergeynst. We are grateful to Matthias Schneider and Ianina Kopecki at sje Ecohydraulic Engineering GmbH for their expertise and for the hydraulic data. We are grateful to the German catching and tagging experts: Thomas Lechner (IBF Umwelt), Tobias Epple (Augsburg University) and Johannes Naumann (IBF Umwelt). We thank Dale Webber and Stephanie Smedboll (VEMCO/Innovasea) for their guidance in testing and setting up the receiver array. We are grateful for the support of the hydropower plant operator BEW (Bayerische Elektrizitätswerke). We also thank James Campbell for his assistance with coding the function for simulating movement. Lastly, we would like to thank John Fieberg for discussions about validating step selection functions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2024.102967.

Data availability

Data are available at doi:https://doi.org/10.5281/zenodo.14313343 (fish positions) and doi:https://doi.org/10.5281/zenodo.14318807 (hydraulic rasters). Code is available at doi:https://doi.org/10.5281/zenodo.14318846.

References

Avgar, T., Potts, J.R., Lewis, M.A., Boyce, M.S., 2016. Integrated step selection analysis : bridging the gap between resource selection and animal movement. Methods Ecol. Evol. 619–630. https://doi.org/10.1111/2041-210X.12528.

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., Fernandez Garrido, P., Garcia-Vazquez, E., Garrido, S., Giannico, G., Gough, P., Jepsen, N., Jones, P.E., Kemp, P., Kerr, J., King, J., Łapińska, M., Lázaro, G., Lucas, M.C., Marcello, L., Martin, P., McGinnity, P., O'Hanley, J., Olivo del Amo, R., Parasiewicz, P., Pusch, M., Rincon, G., Rodriguez, C., Royte, J., Schneider, C.T., Tummers, J.S., Vallesi, S., Vowles, A., Verspoor, E., Wanningen, H., Wantzen, K.M., Wildman, L., Zalewski, M., 2020. More than one million barriers fragment Europe's rivers. Nature 588, 436–441. https://doi.org/10.1038/s41586-020-3005-2.

Ben Jebria, N., Carmigniani, R., Drouineau, H., De Oliveira, E., Tétard, S., Capra, H., 2023. Coupling 3D hydraulic simulation and fish telemetry data to characterize the behaviour of migrating smolts approaching a bypass. J. Ecohydraul. 8, 144–157. https://doi.org/10.1080/24705357.2021.1978345.

Birnie-Gauvin, K., Franklin, P., Wilkes, M., Aarestrup, K., 2019. Moving beyond fitting fish into equations: progressing the fish passage debate in the Anthropocene. Aquat. Conserv. Mar. Freshwat. Ecosyst. 29, 1095–1105. https://doi.org/10.1002/aqc.2946.

Bolger, D.T., Newmark, W.D., Morrison, T.A., Doak, D.F., 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecol. Lett. https://doi.org/10.1111/j.1461-0248.2007.01109.x.

Britton, J.R., Pegg, J., 2011. Ecology of European barbel Barbus barbus: implications for river, fishery, and conservation management. Rev. Fish. Sci. 19, 321–330. https://doi.org/10.1080/10641262.2011.599886.

Bunt, C.M., Castro-Santos, T., Haro, A., 2012. Performance of fish passage structures at upstream barriers to migration. River Res. Appl. 28, 457–478. https://doi.org/10.1002/rra.1565.

Burt De Perera, T., Holbrook, R.I., 2012. Three-dimensional spatial representation in freely swimming fish. Cogn. Process. 13, 107–111. https://doi.org/10.1007/s10339-012-0473-9.

Calles, O., Elghagen, J., Nyqvist, D., Harbicht, A., Nilsson, P.A., 2021. Efficient and timely downstream passage solutions for European silver eels at hydropower dams. Ecol. Eng. 170, 106350. https://doi.org/10.1016/j.ecoleng.2021.106350.

Capra, H., Plichard, L., Bergé, J., Pella, H., Ovidio, M., McNeil, E., Lamouroux, N., 2017. Fish habitat selection in a large hydropeaking river: strong individual and temporal variations revealed by telemetry. Sci. Total Environ. 578, 109–120. https://doi.org/10.1016/j.scitotenv.2016.10.155.

Castro-Santos, T., Shi, X., Haro, A., 2017. Migratory behavior of adult sea lamprey and cumulative passage performance through four fishways. Can. J. Fish. Aquat. Sci. 74, 790–800.

Crawford, R.M.B., Gee, E.M., Hicks, B.J., Nolte, D., Dupont, D.W.E., Franklin, P.A., 2024. Accounting for Interspecies and Intraspecies Variation in Swimming Performance for Fish Passage Solutions, pp. 1–11. https://doi.org/10.1111/1365-2664.14828.

Dingle, H., 2014. Migration : The Biology of Life on the Move, 2nd ed. Oxford University Press.

Dwyer, R.G., Krueck, N.C., Udyawer, V., Heupel, M.R., Chapman, D., Pratt, H.L., Garla, R., Simpfendorfer, C.A., 2020. Individual and population benefits of marine reserves for reef sharks. Curr. Biol. 30, 480–489.e5. https://doi.org/10.1016/j.cub.2019.12.005.

Elings, J., Bruneel, S., Pauwels, I.S., Schneider, M., Kopecki, I., Coeck, J., Mawer, R., Goethals, P.L.M., 2023a. Finding navigation cues near fishways. Biol. Rev. https://doi.org/10.1111/brv.13023.

Elings, J., Mawer, R., Bruneel, S., Pauwels, I.S., Pickholtz, E., Pickholtz, R., Coeck, J., Schneider, M., 2023b. Linking fine - scale behaviour to the hydraulic environment shows behavioural responses in riverine fish. Mov. Ecol. 1–23. https://doi.org/10.1186/s40462-023-00413-1.

Enders, E.C., Gessel, M.H., Anderson, J.J., Williams, J.G., 2012. Effects of decelerating and accelerating flows on juvenile salmonid behavior. Trans. Am. Fish. Soc. 141, 357–364. https://doi.org/10.1080/00028487.2012.664604.

Epple, T., 2020. Eine ganzheitliche Betrachtung von Maßnahmen zur Förderung potamodromer Fischarten in subalpinen Flüssen am Beispiel der mittleren Iller Fischaufstiegsbewegungen durch Fischwanderhilfen, deren Eignung als Lebensräume und Auswirkungen von Restaurierungsma. Universität Augsburg.

Fabre, N., García-Galea, E., Vinyoles, D., 2014. Spatial learning based on visual landmarks in the freshwater blenny Salaria fluviatilis (Asso, 1801). Learn. Motiv. 48, 47–54. https://doi.org/10.1016/j.lmot.2014.10.002.

Fieberg, J., Freeman, S., Signer, J., 2023. Evaluating goodness-of-fit of animal movement models using lineups. bioRxiv. https://doi.org/10.1101/2023.09.26.559591.

Gao, Z., Andersson, H.I., Dai, H., Jiang, F., Zhao, L., 2016. A new Eulerian-Lagrangian agent method to model fish paths in a vertical slot fishway. Ecol. Eng. 88, 217–225. https://doi.org/10.1016/j.ecoleng.2015.12.038.

Gillingham, M., Parker, K., 2008. The importance of individual variation in defining habitat selection by moose in northern British Columbia. Alces 44, 7–20.

Gilmanov, A., Zielinski, D., Voller, V., Sorensen, P., 2019. The effect of modifying a CFD-AB approach on fish passage through a model hydraulic dam. Water (Switzerland) 11, 1–16. https://doi.org/10.3390/w11091776.

Goodwin, R.A., Nestler, J.M., Anderson, J.J., Weber, L.J., Loucks, D.P., 2006. Forecasting 3-D fish movement behavior using a Eulerian-Lagrangian-agent method (ELAM). Ecol. Model. 192, 197–223. https://doi.org/10.1016/j.ecolmodel.2005.08.004.

Goodwin, R.A., Politano, M., Garvin, J.W., Nestler, J.M., Hay, D., Anderson, J.J., Weber, L.J., Dimperio, E., Smith, D.L., Timko, M., 2014. Fish navigation of large dams emerges from their modulation of flow field experience. Proc. Natl. Acad. Sci. USA 111, 5277–5282. https://doi.org/10.1073/pnas.1311874111.

Hershey, H., 2021. Updating the consensus on fishway efficiency: a meta-analysis. Fish Fish. 22, 735–748. https://doi.org/10.1111/faf.12547.

Jerde, C.L., Visscher, D.R., 2005. GPS measurement error influences on movement model parameterization. Ecol. Appl. 15, 806–810. https://doi.org/10.1890/04-0895.

Johnson, D.S., London, J.M., Lea, M.A., Durban, J.W., 2008. Continuous-time correlated random walk model for animal telemetry data. Ecology 89, 1208–1215. https://doi.org/10.1890/07-1032.1.

Jones, P.E., Svendsen, J.C., Börger, L., Champneys, T., Consuegra, S., Jones, J.A.H., De Leaniz, C.G., 2020. One size does not fit all: inter- and intraspecific variation in the swimming performance of contrasting freshwater fish. Conserv. Physiol. 8. https://doi.org/10.1093/conphys/coaa126.

Katopodis, C., Cai, L., Johnson, D., 2019. Sturgeon survival: the role of swimming performance and fish passage research. Fish. Res. 212, 162–171. https://doi.org/10.1016/J.FISHRES.2018.12.027.

Klappstein, N.J., Thomas, L., Michelot, T., Michelot, T., 2023. Flexible hidden Markov models for behaviour-dependent habitat selection. Mov. Ecol. 11, 1–13. https://doi.org/10.1186/s40462-023-00392-3.

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., Morales, J.M., 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology 93, 2336–2342. https://doi.org/10.1890/11-2241.1.

Lesmerises, R., St-Laurent, M.H., 2017. Not accounting for interindividual variability can mask habitat selection patterns: a case study on black bears. Oecologia 185, 415–425. https://doi.org/10.1007/s00442-017-3939-8.

Mawer, R., Bruneel, S.P., Pauwels, I.S., Elings, J., Pickholtz, E., Pickholtz, R., Schneider, M., Coeck, J., Goethals, P.L.M., 2023a. Individual variation in the habitat selection of upstream migrating fish near a barrier. Mov. Ecol. 11, 1–18. https://doi.org/10.1186/s40462-023-00414-0.

Mawer, R., Pauwels, I.S., Bruneel, S.P., Goethals, P.L.M., Kopecki, I., Elings, J., Coeck, J., Schneider, M., 2023b. Individual based models for the simulation of fish movement near barriers: current work and future directions. J. Environ. Manag. 335, 117538. https://doi.org/10.1016/J.JENVMAN.2023.117538.

McClintock, B.T., Michelot, T., 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. Methods Ecol. Evol. 9, 1518–1530. https://doi.org/10.1111/2041-210X.12995.

Morrison, C.D., Boyce, M.S., Nielsen, S.E., 2015. Space-use, movement and dispersal of sub-adult cougars in a geographically isolated population. PeerJ 2015. https://doi.org/10.7717/peerj.1118.

Norin, T., Rowsey, L.E., Houslay, T.M., Reeve, C., Speers-Roesch, B., 2024. Among-individual variation in thermal plasticity of fish metabolic rates causes profound variation in temperature-specific trait repeatability, but does not co-vary with behavioural plasticity. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 379, 20220488. https://doi.org/10.1098/rstb.2022.0488.

Nujic, M., 2016. Hydro_AS-2D Ein zweidimensionales Strömungsmodell für die wassrwirtschaftliche Praxis.

Nyqvist, D., Tarena, F., Candiotto, A., Comoglio, C., 2024. Individual activity levels and presence of conspecifics affect fish passage rates over an in-flume barrier. Ecol. Freshw. Fish 1–11. https://doi.org/10.1111/eff.12787.

Orrell, D., Hussey, N., 2022. Using the VEMCO positioning system (VPS) to explore fine-scale movements of aquatic species: applications, analytical approaches and future directions. Mar. Ecol. Prog. Ser. 687, 195–216. https://doi.org/10.3354/meps14003.

Pelicice, F.M., Pompeu, P.S., Agostinho, A.A., 2015. Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. Fish Fish. 16, 697–715. https://doi.org/10.1111/faf.12089.

Picardi, S., Mathews, S., Coates, P., Kolar, J., Dahlgren, D., Neil, S.O., 2022. Behavioural state- - dependent habitat selection and implications for animal translocations. J. Anim. Ecol. 624–635. https://doi.org/10.1111/1365-2664.14080.

Piper, A.T., Wright, R.M., Kemp, P.S., 2012. The influence of attraction flow on upstream passage of European eel (Anguilla anguilla) at intertidal barriers. Ecol. Eng. 44, 329–336. https://doi.org/10.1016/j.ecoleng.2012.04.019.

Piper, A.T., Manes, C., Siniscalchi, F., Marion, A., Wright, R.M., Kemp, P.S., 2015. Response of seaward-migrating european eel (Anguilla anguilla) to manipulated flow fields. Proc. R. Soc. B Biol. Sci. 282, 1–9. https://doi.org/10.1098/rspb.2015.1098.

Roy, R., Beguin, J., Argillier, C., Tissot, L., Smith, F., Smedbol, S., De-Oliveira, E., 2014. Testing the VEMCO positioning system: spatial distribution of the probability of location and the positioning error in a reservoir. Anim. Biotelemet. 2. https://doi.org/10.1186/2050-3385-2-1.

Runde, B.J., Michelot, T., Bacheler, N.M., Shertzer, K.W., Buckel, J.A., 2020. Assigning fates in telemetry studies using hidden Markov models: an application to deepwater groupers released with descender devices. N. Am. J. Fish Manag. 40, 1417–1434. https://doi.org/10.1002/nafm.10504.

Sells, S.N., Costello, C.M., Lukacs, P.M., Roberts, L.L., Vinks, M.A., 2022. Grizzly bear habitat selection across the northern continental divide ecosystem. Biol. Conserv. 276, 109813. https://doi.org/10.1016/j.biocon.2022.109813.

Sells, S.N., Costello, C.M., Lukacs, P.M., Roberts, L.L., Vinks, M.A., 2023. Predicted connectivity pathways between grizzly bear ecosystems in Western Montana. Biol. Conserv. 284, 110199. https://doi.org/10.1016/j.biocon.2023.110199.

Signer, J., Fieberg, J., Reineking, B., Schlägel, U., Smith, B., Balkenhol, N., Avgar, T., 2024. Simulating animal space use from fitted integrated <scp>step-selection functions</scp> (<scp>iSSF</scp>). Methods Ecol. Evol. 15, 43–50. https://doi.org/10.1111/2041-210X.14263.

Silva, A.T., Lucas, M.C., Castro-Santos, T., Katopodis, C., Baumgartner, L.J., Thiem, J.D., Aarestrup, K., Pompeu, P.S., O'Brien, G.C., Braun, D.C., Burnett, N.J., Zhu, D.Z., Fjeldstad, H.P., Forseth, T., Rajaratnam, N., Williams, J.G., Cooke, S.J., 2018. The future of fish passage science, engineering, and practice. Fish Fish. 19, 340–362. https://doi.org/10.1111/faf.12258.

Tan, J., Tao, L., Gao, Z., Dai, H., Yang, Z., Shi, X., 2018. Modeling fish movement trajectories in relation to hydraulic response relationships in an experimental fishway. Water (Switzerland) 10. https://doi.org/10.3390/w10111511.

Therneau, T., 2024. A Package for Survival Analysis in R. R package version 3.8-3. https://doi.org/10.32614/CRAN.package.survival.

Thurfjell, H., Ciuti, S., Boyce, M.S., 2014. Applications of step-selection functions in ecology and conservation. Mov. Ecol. 2, 1–12. https://doi.org/10.1186/2051-3933-2-4.

Viterbi, A.J., 1967. Error bounds for convolutional codes and an asymptotically optimum decoding algorithm. IEEE Trans. Inf. Theory 13, 260–269. https://doi.org/10.1109/TIT.1967.1054010.

Whittington, J., Hebblewhite, M., Baron, R.W., Ford, A.T., Paczkowski, J., 2022. Towns and trails drive carnivore movement behaviour, resource selection, and connectivity. Mov. Ecol. 10, 17. https://doi.org/10.1186/s40462-022-00318-5.

Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M., Travade, F., 2012. Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. River Res. Appl. 28, 407–417. https://doi.org/10.1002/rra.1551.

Williamson, M.J., Tebbs, E.J., Dawson, T.P., Curnick, D.J., Ferretti, F., Carlisle, A.B., Chapple, T.K., Schallert, R.J., Tickler, D.M., Harrison, X.A., Block, B.A., Jacoby, D.M.P., 2021. Analysing detection gaps in acoustic telemetry data to infer differential movement patterns in fish. Ecol. Evol. 11, 2717–2730. https://doi.org/10.1002/ece3.7226.

WWF, 2022. Living Planet Report 2022: Building a Nature-Positive Society. Gland, Switzerland.

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., Tockner, K., 2015. A global boom in hydropower dam construction. Aquat. Sci. 77, 161–170. https://doi.org/10.1007/S00027-014-0377-0.

Zielinski, D.P., Voller, V.R., Sorensen, P.W., 2018. A physiologically inspired agent-based approach to model upstream passage of invasive fish at a lock-and-dam. Ecol. Model. 382, 18–32. https://doi.org/10.1016/j.ecolmodel.2018.05.004.