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Migration Delays at Head-of-Tide Weirs are a Function of Tidal Cycles and River Flows in Anadromous Twaite Shad *Alosa fallax*

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Abstract

Riverine barriers can have significant negative impacts on the spawning migrations of anadromous fishes, with barriers of low passage efficiency limiting access to upstream spawning areas. Even fish that pass a barrier can be negatively affected via migration delays and energetic costs. The spawning migrations of 74 twaite shad *Alosa fallax* were tracked at two head-of-tide weirs on a bifurcated channel in the River Severn's upper estuary, western England, to test how barriers in tidal areas can affect river entry and incur migration delays. Although the weirs had a combined passage efficiency of 98.9%, median passage time was 19.8 h, with the longest passage time being 16.8 days, and those passing fastest being relatively large fish that approached during spring tides and higher river flows. A higher proportion of fish approached and passed the weir on the larger channel that generally had the dominant flow, yet the weir on the other channel had the higher probability of passage, with the effect of elevated river levels being less important, and individuals approaching this weir were less delayed. With river level being a function of the cyclical nature of the lunar and daily tidal cycles, temporal variation in passage efficiencies was predictable. As the environmental conditions that stimulated the entry of fish into the upper estuary were largely unrelated to the conditions facilitating weir passage, there was a high potential for migration delays at these barriers that potentially incurred considerable energetic costs.

Keywords Estuary movements · Acoustic telemetry · Fish tracking · Tidal barriers · Estuarine dynamics · Route choice

Introduction

European rivers are highly fragmented (Belletti et al., 2020) and while most artificial barriers are of low head height (Grill et al., 2019; Jones et al., 2019), even these barriers can impede the movements of fish (Carpenter-Bundhoo et al., 2020). As anadromous fishes return to freshwater to reproduce, they might have to navigate multiple low-head barriers to reach their spawning grounds (van Puijenbroek et al., 2019). Failure to reach these upstream areas can result in individuals either failing to reproduce or spawning in sub-optimal habitat (Twardek et al., 2022) and can also result in hybridisation between taxonomically similar species through sharing spawning grounds (Antognazza et al., 2021a, 2021b; Hasselman et al., 2014; Taillebois et al., 2020).

The initiation of the spawning migrations of anadromous species is primarily driven by abiotic conditions, with the timing of river entry often being a function of factors such as river temperature and flow (Keefer et al., 2009), or photoperiod (Yeldham et al., 2023). Where the fish are entering

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an anthropogenically modified river, then the most downstream weir encountered upon river entry is likely to be the first major barrier encountered in the spawning migration (Lothian et al., 2024; Thorstad et al., 2008). Where such barriers impede upstream passage, they can elevate mortality rates due to increased energy expenditure and/or increased vulnerability to predation (Alcott et al., 2020; Castro-Santos & Letcher, 2010). For surviving fish, the spawning migration can be delayed (Alcott et al., 2021; Davies et al., 2021; Silva et al., 2019) and, for iteroparous species, this can have carry-over effects via reduced return rates and so affect lifetime fecundity (Castro-Santos & Letcher, 2010). Where these barriers to migration are located at—or are downstream of—the normal tidal limit (NTL), they potentially block access to suitable freshwater spawning habitats. However, investigating how barriers in these locations influence the upstream migrations of fish using telemetry methods can be challenging due to the need to capture individuals in the areas downstream, where sampling can be difficult due to factors including high tidal flows (Grote et al., 2014; Silva et al., 2017). Although this can be at least partially overcome through deployment of specialised equipment from boats (e.g., Breine et al., 2017; Grote et al., 2014; Kelly et al., 2007), these can sometimes result in damage to the fish, making them unsuitable for tagging, and/or incur high capture mortality rates (Mack et al., 2021).

Barriers with high passage efficiencies are rarely considered as major impediments to fish migrations. Yet, these barriers can still cause migration delays, especially if only passable under certain environmental conditions, such as episodes of elevated river level (Davies et al., 2023; Mameri et al., 2021; Reinfelds et al., 2020) and higher water temperature (Davies et al., 2023; Starrs et al., 2011). Elevated river levels reduce the head difference across a barrier (the difference in river level upstream and downstream of the barrier) (El-Belasy, 2013), which usually facilitates passage, especially where this results in the barrier being drowned out above a threshold level (Keller et al., 2012). Higher water temperatures increase passage efficiencies by elevating the passage motivation of individual migrants and/or increasing their swimming capacity (Garcia-Vega et al., 2023). Barrier passage can also be influenced by individual traits, such as body size; while some barriers are passed more easily by smaller individuals (Newton et al., 2018), the selection at most barriers is for the passage of larger individuals (Starrs et al., 2011).

Twaite shad *Alosa fallax* Lacépède 1803 are distributed through eastern coastal waters of the Atlantic Ocean from north Africa to northern Europe, with their spawning migrations in their southern distribution commencing in February, but as late as May in the most northern populations (Aprahamian et al., 2003). Imperilled across its range (Aprahamian et al., 2003; Wilson & Veneranta, 2019), twaite shad are listed on Annex II and V of the European Union Habitats Directive (Council of the European Communities, 1992) and on Appendix III of the Bern Convention (Convention on the conservation of European wildlife and natural habitats, 1979). In Britain, its known spawning distribution is limited to rivers draining into the Bristol Channel, including the River Severn (Aprahamian et al., 2003; Wilson & Veneranta, 2019), with the species vulnerable in Britain and endangered in England according to IUCN red list criteria (Nunn et al., 2023).

In the lower non-tidal reaches of the River Severn, twaite shad spawning migrations are impeded by a series of navigation weirs (Antognazza et al., 2021a, 2021b; Bolland et al., 2019). Passage rates at these weirs can be low, but with twaite shad also identified as spawning downstream of these weirs (Davies et al., 2023). Accessing these spawning areas still requires individual twaite shad to pass one of two head-of-tide weirs located at the NTL on separate arms of a bifurcated channel. Although these weirs are not considered as major migration barriers (in terms of passage efficiency), the extent to which they delay spawning migrations, and the factors that could cause these delays, remain untested. Although both weirs can be drowned out by high river levels and during periods of high tidal influence (i.e. spring tides), they do not feature any alterations that would facilitate fish passage during low flow/neap tide periods when the tide does not reach the structures.

The arrival of migrating twaite shad into the upper Severn estuary is driven mainly by photoperiod rather than the tidal cycle or river flow (Yeldham et al., 2023). Consequently, individuals potentially arrive at head-of-tide weirs when conditions are unsuitable for passage (neap tides, low river flows), which could result in delays to arrival at upstream spawning areas, as well as incurring energetic costs. Twaite shad can be tracked over multiple spawning seasons using long-life acoustic transmitters (Bolland et al., 2019; Davies et al., 2023; Yeldham et al., 2023) and so their passage over these weirs can be tested using fish implanted with transmitters in previous years, eliminating the need to capture fish in areas downstream. With the two head-of-tide weirs present in the study area being located on a bifurcated channel, there is also the opportunity to analyse weir-specific approach rates and passage efficiencies. The aim here was to thus quantify how these head-of-tide weirs impede twaite shad migrations through assessments of the biotic and abiotic factors influencing: (i) migration route choice on the bifurcated channel; (ii) passage probability during approaches to the two head-of-tide weirs; and (iii) total passage time.

Methods

Study Site and Fish Tracking

The River Severn is Britain's longest river, rising in the Welsh Cambrian Mountains and flowing for 290 km before reaching its tidal waters, where the Severn estuary stretches for a further 64 km before draining into the Atlantic Ocean via the Bristol Channel. The river drains a catchment of 11,266 km^2, with its major tributaries being the rivers Teme and Avon (Britannica, 2024). The Severn estuary has one of the highest tidal ranges of rivers globally at ~ 14 m (Binnie, 2016). The river's NTL is located at two weirs on separate arms of a bifurcated channel in the upper estuary at Maisemore (S1a; 1.8 m high) and Llanthony (S1b; 1.7 m high) weirs, which drown out during spring high tides, but downstream river levels are not influenced by the smaller neap high tides (Fig. 1; Online Resource: Fig. S1). The focus area for this study was from downstream of the bifurcated channel confluence, upstream to the two head-of-tide weirs, S1a and S1b, which are 2.9 km and 1.1 km upstream of the confluence on the west and east channels, respectively (Fig. 1). The flow split between the two channels is not uniform across all flows; while the flow is split evenly at Q77 (the flow exceeded 77% of the time), when flows are lower than this, then the dominant flow is through the east channel (S1b), while at higher flows, the dominant flow is through the west channel (S1a). Known spawning areas are located in freshwater reaches upstream of these head-of-tide weirs (Fig. 1; Davies et al., 2024).

Twaite shad were captured in May 2018 and 2019, and April and June 2021 (with no fish captured in 2020 due to Covid- 19 lockdown measures) (n = 220; Table S1a). Capture methods combined rod and line angling downstream of weirs S1a and S2 (Upper Lode Weir; Fig. 1; Fig. S2), and a bespoke manually operated fish trap positioned upstream of a 'notch' fish passage easement at Weir S2 (Fig. 1, Fig. S2; Table S1a). Following their capture, individual twaite shad were anaesthetised (ethyl 3-aminobenzoate methanesulfonate; MS- 222), measured (fork length to nearest mm; mass rounded to 5 g) and internally implanted (peritoneal cavity) with a V9 acoustic transmitter (frequency = 69 kHz; www.innovasea.com), according to the protocol of Bolland et al. (2019). The transmitters were programmed with a randomised 1-min pulse interval (minimum–maximum interval between signals 30–90 s) in the spawning period (April to July) before switching to a 10-min pulse interval until reverting to their randomised 1-min pulse interval the following April. The rationale for this programming was that it extended transmitter battery life to enable tracking the spawning migrations back to the river in subsequent years (Davies et al., 2020; Yeldham et al., 2023) while also enabling movements at sea to be elucidated (Davies et al., 2020). At the time of transmitter implantation, a uniquely coded passive integrated transponder tag (PIT tag; 12 mm) was also inserted to enable recaptured individuals to be identified (and so avoid re-tagging).

Twaite shad are recognised as being a highly sensitive species to capture, air exposure, handling and anaesthesia (Breine et al., 2017). Accordingly, the focus during the tagging procedure outlined above was to optimise the survival of tagged fish by reducing air exposure time and handling to a minimum (Bolland et al., 2019). This focus meant that sexing of the fish was only undertaken when gametes were observed incidentally during the tag implantation process, with further pre- or post-procedure manipulation of the fish to identify running milt or eggs not undertaken on welfare grounds. Identification of the sex of the tagged fish through

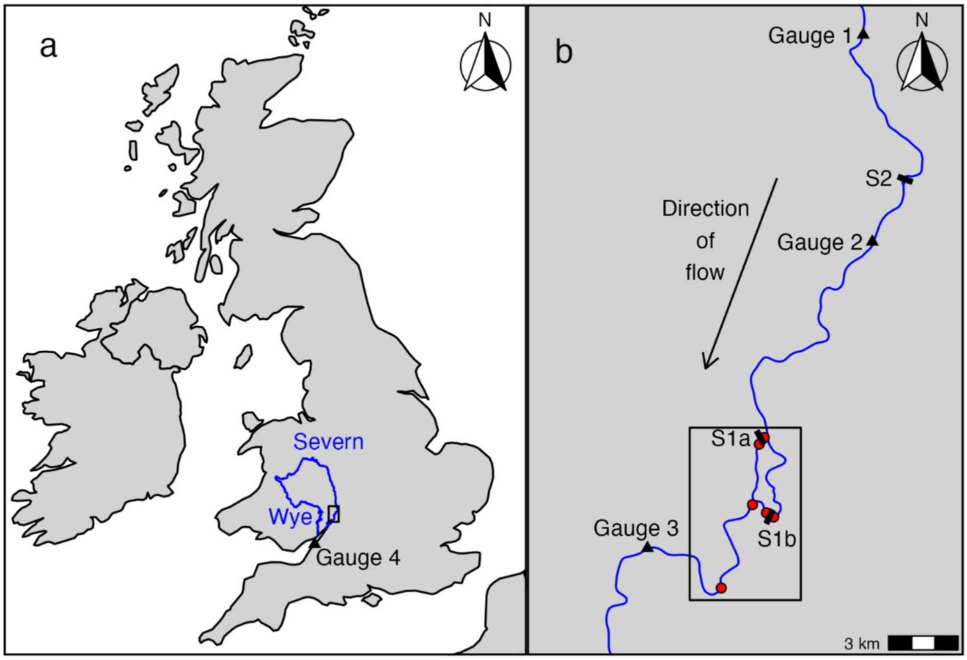


Fig. 1 Map of study area, showing: **a** the study area in relation to the islands of Great Britain and Ireland, the wider River Severn and neighbouring River Wye; and **b** the locations of acoustic receivers (red circles) within the study area (inset), weirs (black rectangles; S1a, S1b, S2) and environmental data gauges (black triangles: gauge 1 = flow; gauge 2 = flow, temperature; gauge 3 = river level; gauge 4 = river level). The position of weirs S1a and S1b corresponds with the normal tidal limit, with the highest spring tides impacting river levels up to Weir S2

genetic analyses was beyond the scope of this study. In its entirety, this meant that 53 female and 58 males were identified, but with sex undetermined for the remaining 109 fish. Following their recovery to normal behaviour, individuals were released either upstream or downstream of the weir where they were captured (Table S1b). All surgical procedures were completed under UK Home Office project licence PD6 C17B56.

Movements of these twaite shad in the year they were tagged are not reported here, as the fish had already passed the two study weirs (Fig. 1). Instead, the fish studied here were those that had returned to sea, where they were able to recondition (Davies et al., 2020), and then were detected as returning to the river to spawn in the year following their tagging ($n = 80$). All analyses focused on fish returning in this second tracking year, as the numbers of fish that returned for a third tracking year were much reduced ($n = 21$). With no individuals tagged in 2020 (Covid- 19 lockdown), no data for 2021 were available for analyses.

An array of six acoustic receivers (VR2W; www.innovasea.com) was deployed in the study area: one receiver located directly upstream and downstream of each weir (S1a and S1b), and two located downstream of the confluence of the bifurcated channel (Fig. 1, Table S2). All receivers were identified as having at least a 100-m detection range during range testing (Davies et al., 2023), although detection range can vary with environmental conditions, including turbidity (Winter et al., 2021), which can be high in the Severn estuary. Detection efficiencies were calculated for the period between the deployment of the last receiver in the array and midnight after the last weir passage in each year, using the residency function in the R package 'actel' (Flávio & Baktoft, 2021), with maximum detection efficiencies calculated using known missed detections, and minimum detection efficiencies calculated using known and potential missed detections (Table S2). Understanding the performance of the receiver array in detecting acoustic-tagged fish is important for data interpretation (Kessel et al., 2014; Winter et al., 2021). The most variable detection efficiency was at the receiver directly downstream of S1b. Given the high performance of the receiver directly upstream of S1b, the data relating to passage at S1b weir were robust, but there was the potential for some approaches to S1b not to have been identified. However, missed detections during non-passage approaches would have involved the fish failing to be detected on both their approach and retreat from the weir, reducing the probability of non-detection. Due to a lost receiver directly downstream of the confluence in 2019, the duration of some approaches may have been overestimated, and the number of approaches made may have been underestimated in that year. However, as the environmental conditions predicting total passage time were also found to influence the probability of passage during individual weir approaches, we are confident that the impact this had on the overall conclusions was minimal.

Environmental Data

To test the environmental variables influencing passage at both head-of-tide weirs, flow at Saxons lode (gauge 1; 52.049661, −2.200744), temperature at Deerhurst (gauge 2; 51.969211, −2.1950057) and river level at Minsterworth (gauge 3; 51.850206, −2.336612) (Fig. 1b) were provided as 15-min interval data, whilst flow at Deerhurst was provided as daily interval data by the Environment Agency (EA). River level directly downstream of S1a and S1b was estimated by adjusting the data from the Minsterworth gauge by 30 min to account for the observed delay in river level change at the head-of-tide weirs caused by tidal influence. The tidal influence on river level was estimated by calculating the difference between the estimated river level at S1a and S1b and the minimum river level on that day. Mean daily flow at Deerhurst was used to estimate the flow split between the bifurcated channels on each day, with the equation for calculating the flow split provided by the EA, whilst the 15-min interval flow at Saxons lode was used for all other analyses, as the reversal of freshwater flows during spring tides had the potential to influence flow at Deerhurst at the 15-min resolution. The point in the lunar tidal cycle was determined through identification of peaks of spring and neap tides using river level data for Portbury (gauge 4; 51.492687, −2.7565905) (Fig. 1a), the closest available location to the River Severn where river levels were influenced by neap tides, from www.bodc.ac.uk (data downloaded on 06/07/2022), with the days with minimum tidal amplitude (neap tide) given a value of 0/1 (start and end of the lunar tidal cycle, respectively), and the days with peaks of amplitude (spring tide) given a value of 0.5 (middle of the cycle). Due to the circular nature of these data, the point in the lunar tidal cycle was split into its sine and cosine components to be included in linear models, with sine relating to the direction of change in tidal amplitude (positive value = increasing amplitude, negative value = decreasing amplitude) and cosine relating to the actual tidal amplitude (1 = neap tide (minimum tidal amplitude), −1 = spring tide (maximum tidal amplitude)) (Yeldham et al., 2023).

Weir Approach and Passage

Twaite shad movements were analysed in relation to their approach to and subsequent passage at head-of-tide weirs S1a or S1b. A weir approach was considered to have been made when an individual was recorded at the receiver directly downstream of a weir, or if they were detected at the receiver directly upstream, when the previous detection was downstream of the confluence (S1a: 0 of 97 approaches; S1b: 10 of 51 approaches). They were considered to have passed a weir when detected on the receiver directly upstream, or when detected further upstream, at a receiver from a wider array described by Davies et al. (2021), when the detection prior to passage was directly downstream of the weir (S1a: 6 of 46 passages; S1b: 1 of 27 passages). Retreats were defined as downstream movements away from a head-of-tide weir following an approach, confirmed by subsequent detection on a receiver downstream of the confluence or downstream of the alternative head-of-tide weir.

Circumstances that arose during the study period meant that some movements could not be identified, and thus these fish were excluded from some analyses, with sample sizes and reasons for exclusions for each analysis summarised in Table S3. In 2019, retreats could not be identified unless the fish retreated as far as the most downstream receiver or subsequently approached the alternative weir. For context, across 2020 and 2022, of the 33 retreats that were followed by subsequent re-approach to the same weir, 19 were only as far as the receiver not recovered in 2019, whilst six retreats that resulted in subsequent re-approach to the same weir were identified in 2019.

Statistical Analysis

Statistical analyses were carried out in base R (R Core Team, 2023). In all results, medians were reported due to non-normally distributed data, with variation around median values representing the interquartile range (25 th-75 th percentiles).

A chi square goodness-of-fit test assessed whether twaite shad were more likely to approach a particular weir on their first approach and whether the proportion of shad passing each weir differed for the proportion first approaching each weir. To assess whether the flow split between the two channels influenced route choice, mixed-effects binary logistic regression (‘lme4’ package; Bates et al., 2015) was used for all weir approaches. The probability of approaching S1a (rather than S1b) was the dependent variable (1: approached S1a; 0: approached S1b), the proportion of total flow down the west channel was the fixed predictor and fish ID was the random predictor. This model was compared to the intercept-only model using Akaike’s information criterion (corrected for small sample size; AICc; ‘AICcmodavg’ (Mazerolle, 2020)), with flow split considered to influence route choice when the intercept-only model had a ΔAICc value of ≥ 2.

Wilcoxon rank sum tests were used to compare the environmental conditions during first approaches that resulted in either passage or retreat at that weir and between weirs (maximum tidal influence on river level, change in tidal influence on river level and mean flow and water temperature). Mixed-effects binary logistic regression then assessed the overall impact of these environmental conditions on passage probability during all weir approaches (1: successful; 0: unsuccessful). Predictors in the full model included all environmental variables used in the comparison of first weir approaches, plus individual data considered to potentially relate to the swimming capacity of individuals (i.e. fish length, and speed of first weir approach). Year and weir approached (S1a or S1b) were categorical predictors (Table 1a). As the head difference across the weirs had the potential to be influenced by both flow (from upstream) and tide (from downstream), and differed between weirs, all possible interactions (including no interaction) between the weir approached, maximum tidal influence on river level and mean flow were explored in separate models, with models compared using AICc. The best-fitting model was considered as that of lowest AICc, whilst models within 2 AICc of this model (ΔAICc < 2) were considered candidates for the final model when they were not a more complex version of a nested model with lower AICc. Predictors in the best fitting model were then considered as the variables with the greatest potential to explain passage probability. There were 138 weir approaches (43 in 2019, 72 in 2020 and 23 in 2022) from 69 individuals used for this modelling (Table S3).

Generalised linear models (GLMs; gamma distribution (log-link)) investigated whether conditions at first weir approach influenced total passage time (as time difference between first approach and passage). The fixed predictors were the environmental conditions at the time of first weir approach and the same individual data as outlined above, with year and first weir approached included as categorical predictors (Table 1b). The sine and cosine components of the point in the lunar tidal cycle at first weir approach (and their interaction) were included due to their relationship to current and future tidal influences on river levels (Table 1b). Backward model selection was used, with AICc used to select the best-fitting model. The total passage time of 68 individuals was used for this modelling (Table S3).

In models used to assess passage probability and total passage time, continuous predictors were scaled by z-score standardisation to ensure numerical stability, optimise model convergence and allow for the interpretation of the relative contributions of predictors and interaction terms in the best-fitting model. Best-fitting models conformed to their model assumptions. Predictors were checked for co-linearity (Pearson’s correlation coefficient) in the R package ‘corrplot’ (Wei & Simko, 2021), with no predictors highly correlated (all $r < 0.7$). The mixed-effects binary logistic regression testing passage probability had a linear relationship between its continuous predictors and the log-odds of the response; there were no extreme outliers (Cook’s distance < 0.5 for all residuals), and binned residual plots indicated good model fit in the R package ‘arm’ (Gelman & Su, 2024). The model fit of the GLM testing passage time was assessed in

Table 1 Predictor variables included within **(a)** the mixed effects binary logistic regression predicting probability of passage during all weir approaches, and **(b)** the generalised linear models (gamma distribution (log-link)) predicting total passage time

Predictor	*Explanation*
(a)	
Maximum tidal influence on river level	The maximum river level (m) directly attributed to tidal intrusion rather than freshwater discharge whilst the individual was available to pass the weir
Mean flow	The mean river flow (discharge; m^3s^{-1}) whilst the individual was available to pass the weir
Mean water temperature	The mean water temperature (°C) of the river whilst the individual was available to pass the weir
Change in tidal influence on river level	The cumulative change in river level (m) directly attributed to tidal intrusion rather than freshwater discharge whilst the individual was available to pass the weir
Fish length	The length of the fish (mm) when captured in the previous year, measured to the tail fork
Speed of first weir approach	The speed of upstream movement (ms^{-1}) of an individual twaite shad immediately prior to their first weir approach, measured between the receiver last detected at downstream of the channel bifurcation and the receiver associated with first weir approach
Year	The year the weir approach occurred in
Weir approached	The weir (S1a or S1b) that was approached
(b)	
Tidal influence on river level	The river level (m) directly attributed to tidal intrusion rather than freshwater discharge at time of first approach
Flow	The river flow (discharge; m^3s^{-1}) at time of first approach
Water temperature	The temperature (°C) of the river at time of first approach
Sine component of point in lunar tidal cycle	The component of the point in the lunar tidal cycle associated the direction of change in tidal amplitude, on day of first weir approach
Cosine component of point in lunar tidal cycle	The component of the point in the lunar tidal cycle associated with the proximity to the spring and neap tide, on day of first weir approach
Fish length	The length of the fish (mm) when captured in the previous year, measured to the tail fork
Speed of first weir approach	The speed of upstream movement (ms^{-1}) of an individual twaite shad immediately prior to their first weir approach, measured between the receiver last detected at downstream of the channel bifurcation and the receiver associated with first weir approach
Year	The year the weir approach occurred in
Weir approached	The weir (S1a or S1b) that was first approached

the R package 'DHARMa' (Hartig, 2024), which compared observed and expected residuals, confirming uniformity of residuals, no over/under dispersion and no outliers, suggesting a good-fitting model.

Results

The first anthropogenic barrier encountered by twaite shad during their spawning migration in the River Severn is one of two head-of-tide weirs located on separate arms of a bifurcated channel (S1a and S1b; Fig. 1). A total of 80 of the 220 tagged twaite shad were detected returning to the River Severn in the year after they were tagged (33 in 2019, 38 in 2020, 9 in 2022), with all individuals reaching at least as far as these head-of-tide weirs (Fig. 1). Moreover, 79 of 80 twaite shad passed these weirs (98.8% passage efficiency), with one individual retreating downstream from S1a in 2020 and subsequently being detected in the nearby River Wye (Fig. 1).

The split of the flow between the channels influenced route choice, with the proportion of flow over S1a being greater during approaches to S1a (median: 57.9% (54.0–60.1%)) than S1b (median: 54.0% (47.8–56.1%)) (Fig. 2, Table S4). Of the 70 individuals that were certain not to have made a weir approach prior to full array deployment, more individuals made their first approach to S1a than S1b ($n = 52$ vs. 18; chi square goodness-of-fit: $\chi^2 = 16.51$, df $= 1$, $p < 0.001$) and more passed that weir ($n = 42$ vs. 27; chi square goodness-of-fit: $\chi^2 = 3.26$, df $= 1$, $p = 0.07$; Fig. 3). However, more individuals passed S1b and fewer passed S1a than expected, based on the proportion of individuals first approaching each weir (n expected: S1a $= 51$, S1b $= 18$; $\chi^2 = 6.50$, df $= 1$, $p = 0.011$). Although 55% of twaite shad that passed the weirs did so on their first approach, some individuals were recorded making multiple approaches, with one recorded making nine separate approaches prior to passage (Fig. 4). A further four individuals were known to pass S1a in 2020; although, their weir of first approach and number of approaches prior to passage was unknown as they potentially made weir approaches prior to full deployment of the array (Table S3).

For twaite shad that successfully passed on their first weir approach ($n = 38$), the time spent downstream of the

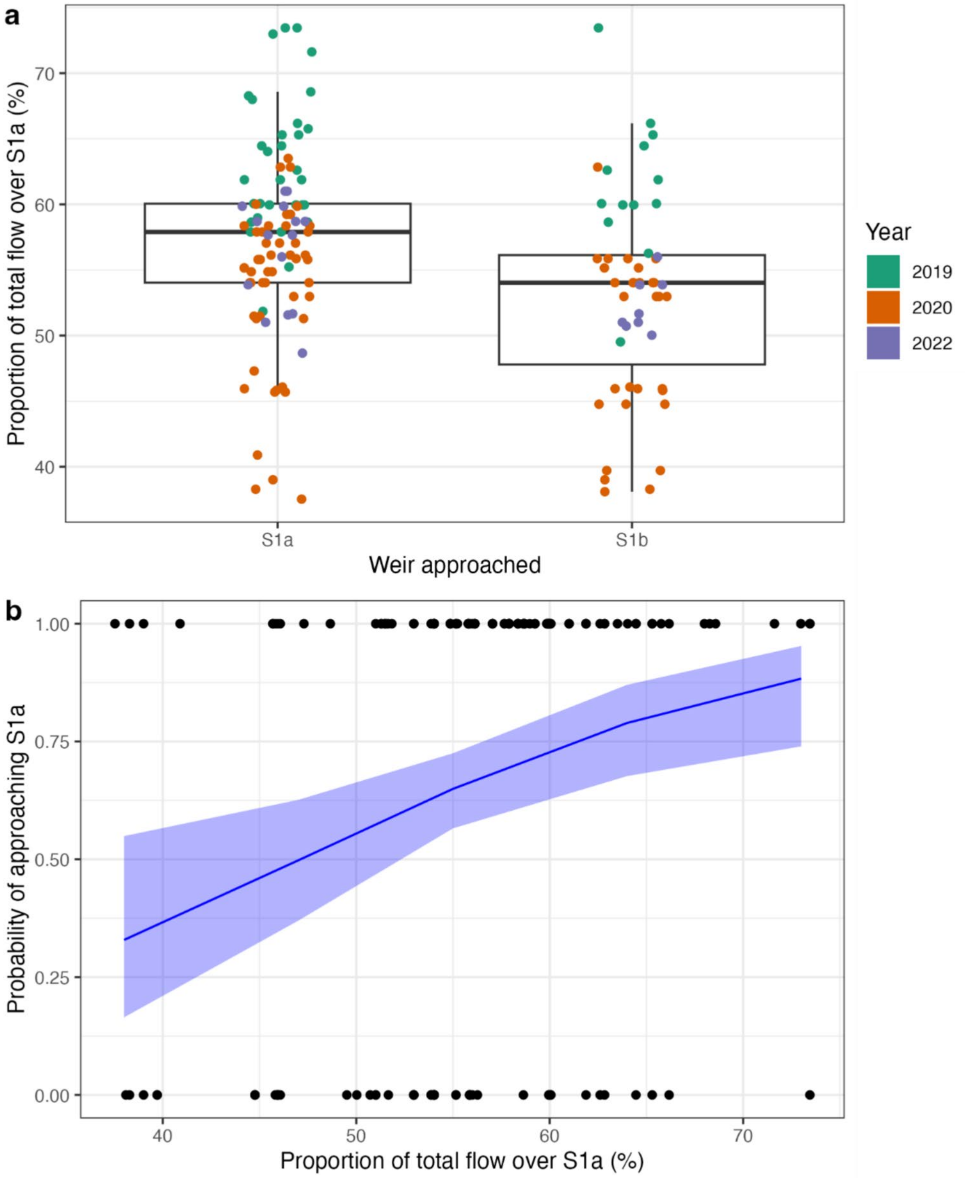


Fig. 2 **a** Summary of the proportion of the total flow being directed down the west channel, and thus over Weir S1a, during approaches to S1a and S1b. Horizontal lines indicate the 25th, 50th and 75th percentile, whilst vertical lines indicate the minimum and maximum value within 1.5 times the interquartile range. **b** Predictor effects plot for the mixed effects binary logistic regression indicating how the probability of approaching Weir S1a is influenced by the proportion of total flow directed over S1a

weir (i.e. the time available to pass the weir) was between 13 min and 6.8 days (median: 6.3 h (1.5–17.9 h)); for those retreating on this first approach ($n = 32$), this time was not significantly longer, being between 26 min and 3.3 days (median: 9 h (2.5–24.4 h)) (Wilcoxon rank sum test: $W = 559$, $p = 0.57$). At S1a, first approaches that resulted in passage rather than retreat coincided with higher tidal influence and change in tidal influence, with these values also greater during passages at S1a versus S1b (Fig. 5, Table 2); although, differences between years were apparent (Fig. S3, Table S5). The difference in mean flow between passages and retreats also varied between years at S1a, with the greatest difference in 2019 ($W = 87$, $p = 0.003$; Fig. S3, Table S5).

Three mixed-effects binary logistic regression models testing passage probability during all weir approaches were candidates for the final model (Table S6). In the best-fitting model, maximum tidal influence, change in tidal influence and mean flow were positive predictors of weir passage, and passage probability was greater during approaches to S1b rather than S1a. The interaction between weir approached and maximum tidal influence indicated that passage probability was less influenced by maximum tidal influence at S1b compared to S1a (Table 3).

Total passage time at the head-of-tide weirs was between 13 min and 16.8 days (median: 19.8 h (4.8–82.7 h), and was lower for fish first approaching S1b than S1a (S1a: 13 min to 16.8 days (median: 28.1 h (9.3–83 h); S1b: 13 min

Fig. 3 Summary of the number of twaite shad: **a** approaching each of the weirs S1a and S1b on their first weir approach and **b** passing each of the weirs S1a and S1b

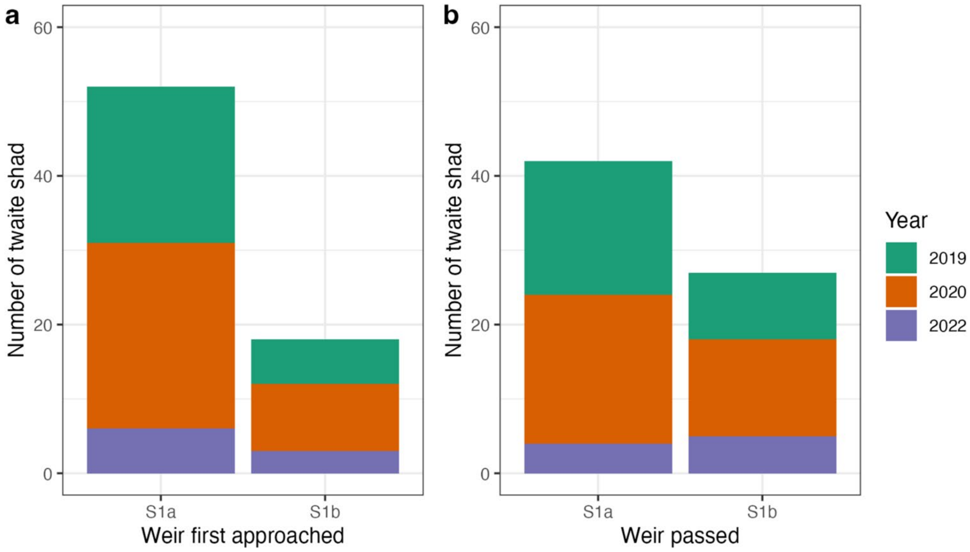
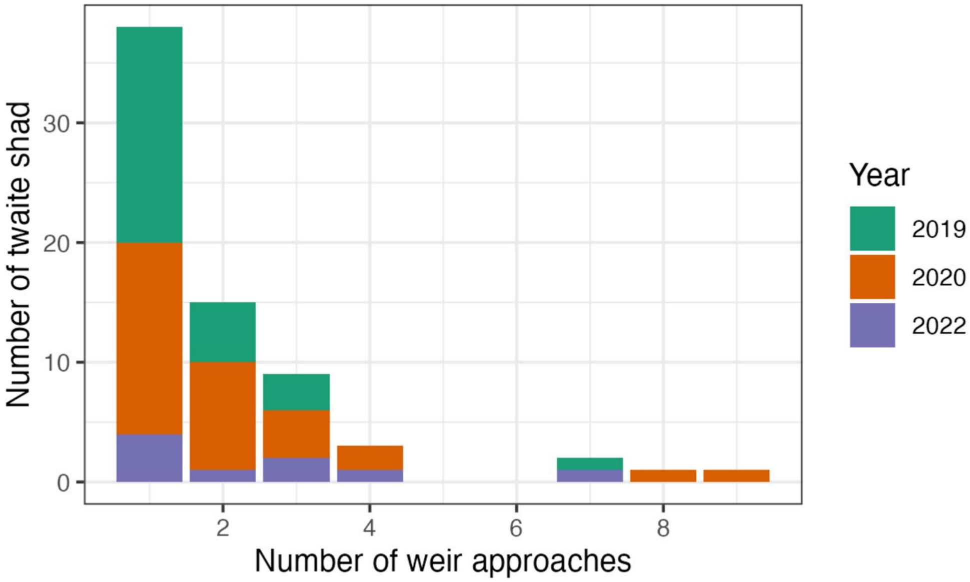


Fig. 4 Summary of the number of approaches to head-of-tide weirs by individual twaite shad prior to successful passage



to 6.3 days (median: 9 h (1.5–19.3 h); $W = 628.5$, $p = 0.02$). There were two GLMs considered as candidates for the final model testing total passage time (Table S7). In the best-fitting model, tidal influence on river level, flow, fish length and speed of first approach had negative effects on total passage time, with delayed passage also occurring when the first approach was to S1a and when it was during a period of neap tides (Table 4).

Discussion

In this study, we identified that twaite shad route choice at a river bifurcation in the upper Severn estuary was influenced by the flow split between the channels, resulting in different proportions of twaite shad approaching the head-of-tide weirs located on these channels. Environmental conditions differentially influenced passage at these two weirs, resulting in individuals following the more common migratory route having increased passage times, particularly when arriving during periods of low tidal influence.

With greater numbers of twaite shad approaching S1a than S1b, and with route choice predicted by flow split, it is likely that dominant flow had a great influence on route choice at the confluence of the two channels. Dominant flow was seen as a major influence on the route choices of migratory brown trout *Salmo trutta* L. 1758 in the Rhine delta, although other local conditions also influenced route choice at some confluences (Bij de Vaate et al., 2003). River flow was also found to have an influence on the route choice of Chinook salmon *Oncorhynchus tshawytscha* Walbaum 1792 in the Columbia River, although olfactory cues had the

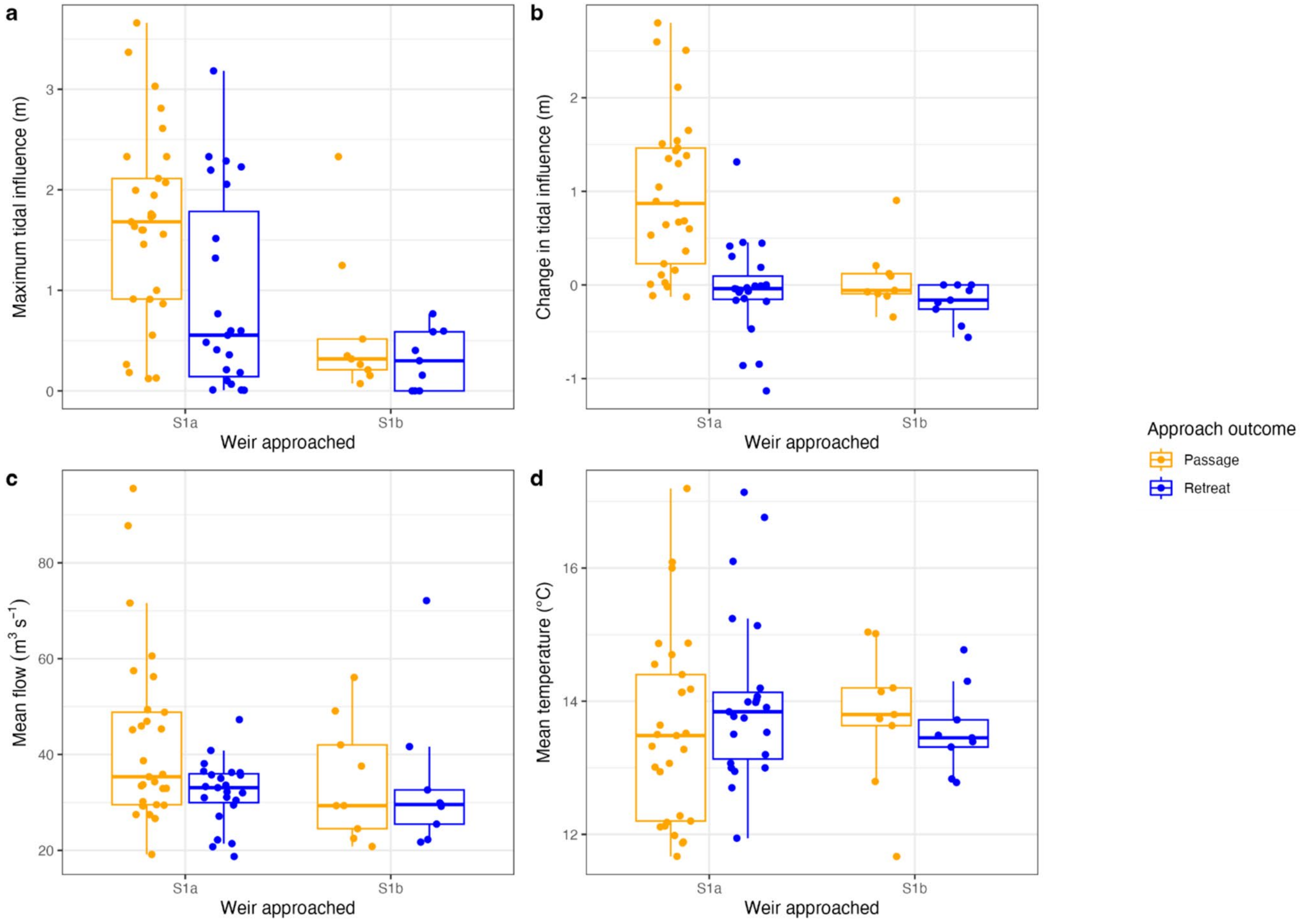


Fig. 5 Summary of the environmental conditions during first weir approaches that resulted in passage (orange) and retreat (blue) at each of S1a and S1b. Environmental variables summarised are: **a** maximum tidal influence; **b** change in tidal influence; **c** mean flow; and **d** mean temperature during first approach. Horizontal lines indicate the 25th, 50th and 75th percentiles, whilst vertical lines indicate the minimum and maximum values within 1.5 times the interquartile range

greatest influence, with individuals homing to natal tributaries (Keefer et al., 2006). In this study, other factors (e.g. channel width, confluence angle) may have had an influence on route choice; however, olfactory cues are less likely, as although twaite shad show high fidelity to the spawning river (Davies et al., 2020) and reach (Davies et al., 2024), the channels bifurcate downstream of known spawning areas; thus, olfactory cues are likely to be similar in both channels.

With more twaite shad approaching and passing S1a than S1b, S1a was considered the primary route to access freshwater spawning areas. Yet, passage probability was less influenced by environmental conditions at S1b than S1a, with individuals first approaching S1b having shorter passage times. Barrier characteristics influence the extent to which they are passable by fish, with height, crest width, slope, and length of the ramp all being important (Amaral et al., 2018, 2019; Doehring et al., 2011). For example, Atlantic salmon *Salmo salar* L. 1758 were more attracted to, and more able to pass, specific sections of a weir that varied greatly in its ramp dimensions (Newton et al., 2018). Accordingly, the differing dimensions of S1a and S1b might have affected their differential passage efficiency, with S1a having a greater head height than S1b, and S1a having damaged/missing sections of its ramp (Fig. S1).

Upstream passage at in-river barriers is often positively influenced by increasing river levels, as seen in Australian bass *Macquaria novemaculeata* Steindachner 1866 at natural barriers in the Hawkesbury-Nepean River, Australia (Reinfelds et al., 2020), sea lamprey *Petromyzon marinus* L. 1758 at weirs in the River Severn (Davies et al., 2022) and by European river lamprey *Lampetra fluviatilis* L. 1758 at weirs in the River Trent (Jubb et al., 2023; Lothian et al., 2024). Elevated flow facilitates upstream passage as barriers are either drowned out (Keller et al., 2012) or the head difference across the barrier is reduced as the downstream river level increases (El-Belasy, 2013). The predominant abiotic influence on the passage of twaite shad at weirs in freshwater reaches

Table 2 Summary of the median (25 th–75 th percentile) environmental variables and the Wilcoxon rank sum test statistics comparing first weir approaches that resulted in passages and retreats at: (**a**) S1a, and (**b**) S1b; and (**c**) Wilcoxon rank sum test statistics comparing first weir approaches resulting in the same outcome between S1a and S1b

a

Environmental variable	*n* passed	Median of passages	*n* retreated	Median of retreats	Test statistic
Maximum tidal influence	29	1.68 (0.91–2.11)	23	0.55 (0.14–1.79)	$W = 475.5, p = 0.009$
Change in tidal influence	29	0.87 (0.23–1.46)	23	-0.04 (-0.16–0.09)	$W = 583, p < 0.001$
Mean flow	29	35.4 (29.5–48.8)	23	33.1 (30.0–36.0)	$W = 430, p = 0.08$
Mean temperature	29	13.5 (12.2–14.4)	23	13.8 (13.1–14.1)	$W = 268, p = 0.23$

b

Environmental variable	*n* passed	Median of passages	*n* retreated	Median of retreats	Test statistic
Maximum tidal influence	9	0.32 (0.21–0.52)	9	0.30 (0.00–0.59)	$W = 48, p = 0.54$
Change in tidal influence	9	-0.06 (-0.09–0.12)	9	-0.16 (-0.26 – 0.00)	$W = 59, p = 0.11$
Mean flow	9	29.3 (24.5–42.0)	9	29.6 (25.5–32.6)	$W = 43, p = 0.86$
Mean temperature	9	13.8 (13.6–14.2)	9	13.4 (13.3–13.7)	$W = 53, p = 0.30$

c

Environmental variable	Test statistic comparing passages	Test statistic comparing retreats
Maximum tidal influence	$W = 52.5, p = 0.008$	$W = 61.5, p = 0.08$
Change in tidal influence	$W = 41, p = 0.0013$	$W = 78, p = 0.29$
Mean flow	$W = 93, p = 0.21$	$W = 84, p = 0.43$
Mean temperature	$W = 155, p = 0.42$	$W = 77, p = 0.28$

of the River Severn is the river level downstream of the weir being passed (Davies et al., 2023). Although both tide and river flow influence river level in the Severn estuary, tidal influence was the most influential environmental variable facilitating passage at the head-of-tide weirs studied here, with spring and high tides occurring on a cyclical basis, whilst high river flows were more stochastic.

Importantly, the combined passage efficiency at the two head-of-tide weirs was high, with the only individual failing to pass during the study period subsequently entering the River Wye, a known twaite shad spawning river (Aprahamian et al., 2003). Thus, all tracked twaite shad accessed reaches of river containing identified spawning areas (Davies et al., 2023). However, this high passage efficiency does not necessarily equate to no negative effects from these weirs, given that total passage time was delayed by up to 16.8 days, and that median time spent in the River Severn is 33 days (Davies et al., 2024). The longest delays occurred when individuals arrived at the weirs during unfavourable passage conditions, i.e. low tidal influence (from downstream) and low flows (from upstream). Weir delays have the potential to impact fitness and survival of *Alosa* spp. (Alcott et al., 2020; Castro-Santos & Letcher, 2010); although, there was no mortality detected at these barriers during upstream migrations. Larger individuals had shorter passage times, and such size selection has the potential to exert population-level selective pressures (Goerig et al., 2020; Volpato et al., 2009). As twaite shad size is sexually dimorphic, with females larger than males (Aprahamian et al., 2003), then passage selectivity on size has the potential to indicate differential passage between sexes. There is evidence of differing swimming capacities identified between male and female American shad *Alosa sapidissima* Wilson 1811 attempting to pass migration barriers (Bayse et al., 2019). Although it was not possible to sex all fish during this study, this should be an area of further study in the future, potentially using genetic methods to sex fish (Hsu & Gwo, 2010; Mascali et al., 2022; Zheng et al., 2024).

Where anthropogenic barriers are impassable for a proportion of a population of *Alosa* spp., their removal can be effective in restoring their access to historical upstream spawning grounds (Beasley & Hightower, 2000; Burdick & Hightower, 2006; Raabe & Hightower, 2014). As weir characteristics influence passage (Amaral et al., 2018, 2019; Doehring et al., 2011), altering these, such as by lowering or reducing the weir gradient, might improve passage. Where barrier removal or altering a weir is not possible, due to, for example, compromising the primary function of the weir, the provision of fish passes has the potential to allow *Alosa* spp. to move upstream over otherwise impassable barriers (Belo et al., 2021). In the context of this study system, these methods may reduce migration delays and associated energetic costs for twaite shad approaching these head-of-tide weirs (particularly S1a) during periods of low tidal influence and low

Table 3 Summary of the fixed predictors retained in the best fitting mixed effects binary logistic regression model predicting probability of passage during all approaches to the head-of-tide weirs (S1a and S1b)

Predictor	*Estimate ± SE*	*z value*	*p value*
(Intercept)	-0.31 ± 0.59	-0.52	0.60
Year (2019)	–	–	–
Year (2020)	-0.30 ± 0.77	-0.39	0.70
Year (2022)	-0.42 ± 1.03	-0.41	0.68
Fish length	0.53 ± 0.27	1.98	0.048
Speed of first weir approach	0.45 ± 0.26	1.71	0.09
Weir approached (S1a)	–	–	–
Weir approached (S1b)	1.66 ± 0.61	2.73	0.006
Maximum tidal influence on river level	1.57 ± 0.43	3.66	< 0.001
Change in river level due to tidal influence	1.51 ± 0.39	3.93	< 0.001
Mean flow	1.74 ± 0.78	2.23	0.03
Mean water temperature	0.15 ± 0.35	0.44	0.66
Weir approached (S1a): maximum tidal influence on river level	–	–	–
Weir approached (S1b): maximum tidal influence on river level	-1.37 ± 0.68	-2.01	0.04
Maximum tidal influence: mean flow	1.01 ± 0.65	1.55	0.12

Table 4 Summary of predictors retained in the best fitting generalised linear model (GLM) predicting total passage time at the head-of-tide weirs

Predictor	*Estimate ± SE*	*t value*	*p value*
(Intercept)	0.72 ± 0.15	4.76	< 0.001
Fish length	-0.38 ± 0.13	-2.99	0.004
Speed of first weir approach	-0.37 ± 0.13	-2.79	0.007
First weir approached (S1a)	–	–	–
First weir approached (S1b)	-1.75 ± 0.31	-5.56	< 0.001
Tidal influence on river level	-0.67 ± 0.14	-4.64	< 0.001
Flow	-0.46 ± 0.15	-3.17	0.002
Sine component of point in lunar tidal cycle	-0.03 ± 0.14	-0.22	0.83
Cosine component of point in lunar tidal cycle	0.49 ± 0.216	3.05	0.003
Sine component of point in lunar tidal cycle × cosine component of point in lunar tidal cycle	-0.40 ± 0.18	-2.24	0.03

flow, which may become increasingly prevalent in the River Severn due to climate change (Murgatroyd & Hall, 2020).

In summary, these head-of-tide weirs did not prevent migrating twaite shad from accessing freshwater spawning areas but did incur some considerable passage delays. The cyclical nature of the daily and lunar tidal cycles provided repeated opportunities for twaite shad to pass these barriers on spring tides over the course of the spawning season, but individuals arriving outside of these periods were significantly delayed. We conclude that in-river barriers at head-of-tide can significantly impact the migrations of anadromous fishes, even where they appear to have high passage efficiencies. Accordingly, environmental cues that determine migration decisions, such as photoperiod for river entry (Yeldham et al., 2023) and dominant flow for route choice, may be mismatched with conditions that facilitate upstream weir passage, especially when this relies on tidal influences and river flows.

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Data Availability Data available upon reasonable request.

Declarations

Competing interests The authors have no competing interests to declare.

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