Received: 9 May 2023 | Revised: 21 December 2023 | Accepted: 18 February 2024

DOI: 10.1111/jfb.15713

REGULAR ARTICLE

JOURNAL OF FISH BIOLOGY fsbi

Emigration of post-spawned twaite shad *Alosa fallax*, an anadromous and iteroparous fish, in a highly fragmented river

Mark I. A. Yeldham[1,2] | J. Robert Britton[1] | Charles Crundwell[3] | Peter Davies[1,2,4] | Jamie R. Dodd[2] | Andrew D. Nunn[2] | Randolph Velterop[5] | Jonathan D. Bolland[2]

[1]Department of Life and Environmental Sciences, Bournemouth University, Poole, UK

[2]Hull International Fisheries Institute, University of Hull, Hull, UK

[3]Environment Agency, Riversmeet House, Tewkesbury, UK

[4]School of Biological and Marine Sciences, University of Plymouth, Plymouth, UK

[5]Natural England, Sterling House, Dix's Field, Exeter, UK

Correspondence
Mark I. A. Yeldham, Department of Life and Environmental Sciences, Bournemouth University, Poole, UK.
Email: myeldham@bournemouth.ac.uk

Jonathan D. Bolland, Hull International Fisheries Institute, University of Hull, UK.
Email: j.bolland@hull.ac.uk

Funding information
EU LIFE Programme, Grant/Award Number: LIFE15/NAT/UK/000219; National Lottery Heritage Fund, Grant/Award Number: HG/15/04573; UK Department of Food and Rural Affairs; Natural England; The Fishmongers' Company

Abstract

Anthropogenic barriers are widely known to negatively impact the spawning migrations of anadromous fishes, by delaying or preventing passage upstream. Although the impacts of barriers on emigrating post-spawned adults are less well studied, they could potentially impact the fitness and subsequent return rates of iteroparous species. In this study, passive acoustic telemetry was used to track the emigrations of 53 twaite shad *Alosa fallax* in the River Severn basin in their first spawning migration a year after being tagged, giving insights into their emigration movements and the impacts of anthropogenic weirs on these movements. *A. fallax* began their emigrations after spending varying amounts of time and migrating various distances within the river, with late-emigrating individuals moving fastest and most directly. Emigrations became faster and more direct the further downstream individuals were from their furthest upstream extent. Downstream passage delays at weirs increased emigration times by a median of 61%, with environmental conditions (i.e., temperature, flow, and tidal influence on river level) having little influence on downstream passage at weirs with no modifications to facilitate fish passage. As weir-induced emigration delays are suggested to deplete energy reserves (when energy levels are already depleted post-spawning), limit spawning opportunities (by preventing access to downstream spawning habitat), and expose individuals to increased predation risk and suboptimal conditions (e.g., high temperatures), these delays can potentially diminish the benefits of iteroparity. The evidence presented here suggests that more consideration should be given to the potential impacts of anthropogenic barriers on the emigrations of iteroparous species when assessing river connectivity or undertaking barrier mitigation.

KEYWORDS
acoustic telemetry, barrier delay, diadromous, downstream migration, downstream passage, fish tracking

1 | INTRODUCTION

Anadromous fishes spend the majority of their adult lives in marine environments, only migrating back into fresh water to spawn in habitats that might be far inland, with iteroparous species potentially doing this on multiple occasions (Aprahamian et al., 2003; Birnie-Gauvin et al., 2021; Davies et al., 2020). Centuries of human modifications of rivers have resulted in altered flow regimes and fragmentation due to barriers (Belletti et al., 2020), which have contributed to long-term declines in anadromous fish populations (Aprahamian & Aprahamian, 1990; Le Pichon et al., 2020), with all 16 long- or mid-distance European anadromous species adversely impacted by barriers (van Puijenbroek et al., 2019). Population declines of migratory species have been severe in recent decades, with reductions of up to 93% in European migratory freshwater fish populations between 1970 and 2016 (Deinet et al., 2020).

Whether a species exhibits a semelparous or iteroparous life history can depend on the inter-annual variability in spawning success and survival, with low variability favoring a semelparous life history, whereas high variability favors an iteroparous strategy (Ranta et al., 2002). These two strategies can coexist within a single species, as exhibited by two North Atlantic anadromous *Alosa* species: twaite shad *Alosa fallax* (Lacépède 1803) and American shad *Alosa sapidissima* Wilson 1811 (Aprahamian et al., 2003; Hasselman et al., 2013). High variability in environmental conditions in their spawning rivers at higher latitudes results in iteroparous populations, whereas more stable conditions at lower latitudes result in semelparous populations (Hasselman et al., 2013; Ranta et al., 2002). The benefits of iteroparity include higher lifetime fecundity for iteroparous individuals compared to semelparous individuals. Despite having lower reproductive success in their first spawning season, as observed in steelhead *Oncorhynchus mykiss* Walbaum 1792 (Christie et al., 2018), iteroparous individuals can compensate for poor reproductive success in their first spawning season in future spawning seasons, whereas semelparous individuals cannot (Hasselman et al., 2013; Ranta et al., 2002). The spawning migrations of semelparous anadromous fishes are generally upstream only, whereas iteroparous species that survive spawning must then emigrate downstream to return to marine feeding grounds (Aprahamian et al., 2003; Walter & Olney, 2003). These emigrations from fresh water may require individuals to pass multiple barriers in a downstream direction, despite already having passed them during their upstream migration. Emigration occurs post-spawning, at which point body condition is likely to be poor (Walter & Olney, 2003), which can have important carryover consequences for survival and fitness (Baktoft et al., 2020; Boe et al., 2022). For example, in post-spawned Atlantic salmon *Salmo salar* L. 1758, emigrating fish with relatively high lipid densities had higher subsequent river return rates than those with low lipid densities (Boe et al., 2022). Where the fitness impacts of encountering barriers during these downstream migrations are high, there is the potential for them to diminish the benefits of iteroparity, for example, by causing high mortality rates in delayed individuals (Baktoft et al., 2020; Castro-Santos & Letcher, 2010).

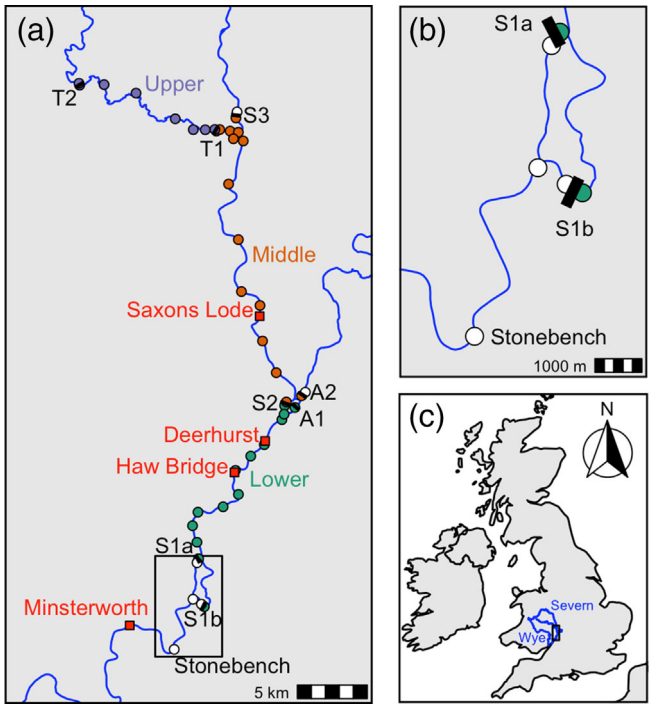

FIGURE 1 Map showing the River Severn study area, featuring the (a) weir locations (black rectangles) and acoustic receivers (circles), where point color relates to Upper (purple), Middle (orange), and Lower (green) "unobstructed reach" (as defined in Table 2), and outside of named reaches (white). Environment Agency gauging station locations (red square) are also marked. The normal tidal limit (NTL) is located at weirs S1a and S1b. (b) The locations of acoustic receivers in the context of weirs S1a and S1b located on the bifurcated channel; and (c) the location of the study area in the context of Great Britain and Ireland and the neighboring River Wye.

Studies on the riverine emigrations of diadromous fishes have focused mainly on juvenile anadromous species, such as salmonid smolts, and silver eel forms of catadromous European eel *Anguilla anguilla* L. 1758. In *S. salar*, where smolts have to pass through novel environments, such as standing bodies of water located within river systems, high mortality rates are often incurred through predation, as individuals struggle to navigate downstream (Hanssen et al., 2022; Lilly et al., 2022). Anthropogenic barriers can severely impede the riverine emigration of the silver form of *A. anguilla*, with the presence of multiple passage routes at the Bois Joli Dam on the Frémur River, France, resulting in migration delays of varying duration (median delays: 1.1–16 days) (Trancart et al., 2020). In a hydropower regulated river, *S. salar* kelt survival was reduced by approximately 20% by dam presence, where emigration delays were of approximately 6 days (Babin et al., 2021). For post-spawned *S. salar* kelts passing freshwater hydropower plants, the consequent migration delays depleted their remaining energy reserves (Baktoft et al., 2020).

Although large dams are strongly associated with causing substantial fragmentation, low-head barriers (<5 m) also represent a major barrier to fish migration (Jones et al., 2019) and account for most in-river barriers globally (Grill et al., 2019). Where downstream migrating

fish approach these low-head barriers, they can encounter relatively high hydraulic head (height difference of water level upstream and downstream), high velocity gradients, and shallow head of water above weir crests (Trancart et al., 2020; Vallazza et al., 2021; Vowles et al., 2014). Reductions in the hydraulic head across weirs have increased the passage probability of bighead carps *Hypophthalmichthys* spp. Bleeker 1860 (Vallazza et al., 2021). When high-velocity gradients are encountered at weirs, fish often express avoidance behaviors, such as positive rheotaxis (facing against flow) and swimming upstream against the flow (Haro et al., 1998; Russon & Kemp, 2011; Vowles et al., 2014). For example, fish passage has been measured as significantly slower over weirs than passive particles, suggesting avoidance, with *S. salar* smolts' passage delays at weirs being significantly related to the velocity gradient of water across the structure, with longer delays occurring at higher velocities (Haro et al., 1998).

The River Severn, Western Britain, is an important population stronghold for *A. fallax*, an iteroparous fish species that is increasingly threatened across its range (north-eastern Atlantic and Mediterranean) (Aprahamian et al., 2003; Mota et al., 2016; Rambonilaza et al., 2023). Substantial declines are apparent in their populations, driven at least in part by river fragmentation and overexploitation (Aprahamian et al., 2003; Degroot, 1990). Their population declines have resulted in the species having international conservation designations (e.g., on Annex II and V of the European Union Habitats Directive [Council of the European Communities, 1992]). As previous-spawned fish can represent over 50% of the spawning run in the northern part of their range (Aprahamian et al., 2003), successful emigration is important for population sustainability. The lower River Severn is highly fragmented by a series of low-head navigation weirs (Figure 1), and upstream migrants must pass at least one weir to reach suitable spawning habitat. The weirs located furthest downstream have high upstream passage efficiencies (~100% of returners in 2019 and 2020), with a high proportion of migrating shad passing upstream of at least two weirs (64% and 82% of returners in 2019 and 2020, respectively) (Davies et al., 2023). Despite this relatively high passage rate, the weirs do incur delays in the upstream passage of both *A. fallax* (Davies et al., 2023) and semelparous sea lamprey *Petromyzon marinus* L. 1758 (Davies et al., 2021, 2022). The effects of these weirs on the emigration of post-spawned *A. fallax* are, however, unknown. Although these weirs can be drowned out during periods of elevated flow and, for weirs located in tidal areas, during periods of high tidal influence, emigrating *A. fallax* must pass these weirs in early summer (primarily in May and June) when river flows are reduced and water temperatures increase. Moreover, these emigrating fish are post-spawned, and as a result, their energy levels are likely to be highly depleted due to the interaction of spawning activities and fasting while in fresh water (Bayse et al., 2018; Leonard & McCormick, 1999; Walter & Olney, 2003).

As weirs may compromise the ability of *A. fallax* to emigrate from the lower River Severn post-spawning, the aim here was to assess how these low-head weirs influenced the downstream migrations of these fish through the application of a series of acoustic-telemetry-derived migration metrics. We examined how emigrating *A. fallax* moved downstream through the river, how this was influenced by characteristics of their upstream spawning migrations, and how their emigration was impacted by weir presence and environmental conditions. We posit that some emigrating *A. fallax* incur considerable passage delays as they pass weirs, but that weir passage will be facilitated by periods of elevated river levels that result from increased flows and/or high tidal influence.

2 | MATERIALS AND METHODS

2.1 | Study river

This study in the River Severn basin occurred between 2018 and 2022. The study area began at the most downstream acoustic receiver, which is located in the upper estuary at "Stonebench" (Figure 1), and primarily covered eight artificial in-river barriers ("weirs"): four on the Severn (S1a, S1b, S2, and S3), two on the Teme (T1 and T2), and two on the Avon (A1 and A2). There were no modifications to facilitate fish passage at weirs S1a or S1b that are located at the normal tidal limit (Figure 1). However, both weirs on the Teme were modified prior to the 2019 spawning migration (T1: lowered and partially removed; T2: rock ramp installed to reduce approach gradient), and there was a "notch" fish easement present on the upstream end of S2 for the entirety of the study period (Figure 1). Weir S2 was also occasionally drowned out during large spring tides that resulted in the reversal of freshwater flows. Also, there were no modifications at either A1 or A2 to facilitate fish passage, with no fish known to approach A1 or pass upstream of A1 or A2 in any year.

The study area upstream of S1a and S1b was divided into three "unobstructed reaches": upstream of S1a/b, but downstream of S2 and A1 (Lower); upstream of S2, but downstream of T1, A2, and S3 (Middle); and upstream of T1 (no returning fish passed upstream of S3 during the study period) (Upper) (Figure 1). River temperature (Deerhurst), flow (Saxons Lode), and river level (Minsterworth and Haw Bridge) were obtained as 15-min interval data from Environment Agency gauging stations (Figure 1). River level at S1a/b and S2 was calculated by adjusting levels recorded at Minsterworth and Haw Bridge by 30 and 45 min, respectively, to account for the observed delay in tidal influence.

2.2 | Fish sampling and tracking

A. fallax capture and transmitter implantation took place in May 2018 and 2019, as well as in April–June 2021 (Table 1a). No fish could be captured in spring 2020 due to the COVID-19 lockdown in England. The capture methods involved rod and line angling downstream of S1a ($n = 70$) and S2 ($n = 77$), and the use of a manually operated trap positioned at the upstream exit of the notch in S2 ($n = 123$). Fish were captured between day of the year 129 and 144 (median: 136) in

TABLE 1 Summary of (a) the number of *Alosa fallax* (*n*) surgically implanted with acoustic transmitters and the minimum (Min), maximum (Max), and median (25th–75th percentiles) day of year of tagging in each year. (b) The number of *Alosa fallax* completing full emigrations in the year after tagging (*n*), grouped by the year this migration occurred in (Year) and the migration group these individuals were assigned to (Migration Group), with metrics summarized using the minimum (Min), maximum (Max), and median (25th–75th percentiles) for day of the year of river entry, day of the year of emigration, furthest upstream extent, total emigration time, net speed of emigration, and tortuosity of emigration; and minimum, maximum, and mean (±95% C.I.) for total time in river and time in river prior to the start of emigration.

Year	*n*	Day of year of transmitter implantation: Min–Max	Median
a			
2018	73	129–144	136 (130–142)
2019	100	122–136	133 (128–135)
2021	47	117–158	117 (117–118)

	Year						Migration group					
	2019 (*n* = 23)		2020 (*n* = 25)		2022 (*n* = 5)		Lower (*n* = 15)		Middle (*n* = 33)		Upper (*n* = 5)	
Metric	Min–Max	Median/Mean	Min–Max	Median/Mean	Min–Max	Median/Mean	Min–Max	Median/Mean	Min–Max	Median/Mean	Min–Max	Median/Mean
b												
Day of the year of river entry	109–143	127 (114.5–134)	107–143	119 (111–124)	105–119	106 (105–106)	106–143	115 (110–122)	105–143	119 (112–130)	117–141	134 (127–135)
Day of the year of emigration	131–187	158 (150–171.5)	139–167	151 (148–154)	142–165	145 (144–149)	137–167	151 (146–161.5)	131–187	152 (148–158)	150–183	169 (153–181)
Total time in river/days	9.2–55.7	33.5 (±4.7)	15.8–48.4	31.5 (±3.0)	36.7–44.3	40.4 (±2.7)	18.2–48.4	33.1 (±4.7)	9.2–52.1	32.8 (±3.1)	18.7–55.7	36.2 (±11.8)
Time in river prior to the start of emigration/days	4.5–51.0	25.1 (±5.1)	3.8–42.5	24.9 (±3.8)	26.2–38.1	31.4 (±4.6)	3.8–42.5	24.7 (±5.9)	4.5–51.0	26.4 (±3.7)	14.1–32.8	22.7 (±7.6)
Furthest upstream extent/km	23.6–67.9	49.9 (48.3–51.6)	23.6–59.8	38.8 (23.6–49.9)	23.6–49.9	49.9 (23.6–49.9)	23.6–23.6	23.6 (23.6–23.6)	27.1–51.6	49.9 (48.6–49.9)	52.7–67.9	55.8 (53.8–59.8)
Total emigration time/days	0.9–34.3	8.0 (2.6–14.8)	0.8–26.8	4.5 (2.7–12.9)	2.0–16.9	8.7 (8.0–12.5)	0.8–29.1	6.8 (2.1–17.2)	1.0–21.3	6.7 (2.9–12.9)	0.9–34.3	10.0 (4.9–18.9)
Net speed of emigration/km day^{-1}	0.8–54.1	5.3 (3.4–19.4)	0.9–29.7	9.2 (3.5–14.3)	1.4–25.6	5.7 (1.9–6.2)	0.8–29.7	3.5 (1.4–11.2)	2.0–50.0	7.2 (3.9–16.8)	1.6–54.1	5.3 (3.2–14.0)
Tortuosity of emigration	0.09–1.00	0.66 (0.45–0.95)	0.11–1.00	0.64 (0.51–0.87)	0.30–0.86	0.45 (0.44–0.86)	0.09–1.00	0.51 (0.24–0.73)	0.20–1.00	0.75 (0.51–0.91)	0.23–0.96	0.89 (0.47–0.96)

2018, 122 and 136 (median: 133) in 2019, and 117 and 158 (median: 117) in 2021 (Table 1a).

Following their capture, individuals were anaesthetized (ethyl 3-aminobenzoate methanesulfonate; MS-222; 0.4 g per 10 L of water), measured (fork length, nearest millimeter; mass, to 5 g), and internally (peritoneal cavity) implanted with a V9 acoustic transmitter (29 × 9 mm, 4.7 g in weight in air, 69 kHz; www.innovasea.com) using the protocol of Bolland et al. (2019), with 220 individuals tagged across all seasons. The transmitters were programmed with a randomized 1-min pulse interval (minimum–maximum interval between signals 30–90 s) during their spawning period (April–July), before switching to a 10-min pulse interval until reverting to their randomized 1-min pulse interval the following April. The rationale for this programming was that it extended transmitter battery life to approximately 3 years, enabling the spawning migrations of these individuals to be measured for up to three consecutive spawning migrations (Davies et al., 2020). At the time of transmitter implantation, a uniquely coded passive integrated transponder (PIT tag; 23-mm) was also inserted to enable recaptured fish to be identified (and to avoid retagging of recaptured fish in subsequent years), as well as for use in associated fish pass efficiency studies (unpublished data). Sexing was possible only where gametes were incidentally observed during the tagging process, which allowed for the identification of 53 female, and 58 male individuals, with sex remained undetermined for the remaining 109 fish. Once tagged, fish were recovered in the river and were released when they were able to orientate themselves in the water and exhibit normal swimming behaviors (Bolland et al., 2019). Individuals were released either upstream or downstream of the weir where they were captured (supporting information: Table S1a), with release sites (upstream or downstream of a weir) determined by the requirements of a complementary study (Davies et al., 2023). Movements were then tracked on an array of acoustic receivers (VR2W; www.innovasea.com; Figure 1).

2.3 | Data analyses

A total of 79 individual *A. fallax* reached spawning habitats upstream of weirs S1a/b in the year after they were implanted with an acoustic receiver (33 in 2019, 37 in 2020, and 9 in 2022), with a series of migration metrics (cf. Table 2) calculated for individuals that survived to complete a full spawning migration and emigrate from the river ($n = 57$: 24 in 2019, 28 in 2020, and 5 in 2022; 72% riverine survival). These returning migrants were used to avoid including tagging effects on emigration in the year of tagging and enabled the entire spawning migration to be tracked (i.e., entry to and exit from the acoustic array). Four fish were removed from analyses as they either entered the River Wye (Figure 1) or reentered the Severn after exiting the array (i.e., their spawning migration was incomplete). Mortality during emigration was not investigated due to the complex nature of identifying whether an individual was emigrating when it died. For the purposes of these emigration analyses, the fish were categorized into three different migration groups based on the reach where their emigration commenced (i.e., their furthest upstream extent; Table 2), where the groups were "Upper" ($n = 5$), "Middle" ($n = 33$), and "Lower" ($n = 15$). Summary information for individuals that emigrated in each year and migration group (Table 1b) is provided, with means reported for metrics with normally distributed data and medians reported for metrics with non-normally distributed data. Error around the mean represents 95% confidence limits, and variation around median values represents the interquartile range (25th–75th percentiles), unless otherwise stated.

Differences in migration metrics between the migration groups, years, and unobstructed reaches were assessed using parametric tests (i.e., *t*-tests) for normally distributed data and nonparametric tests (i.e., Kruskal-Wallis χ^2tests and Wilcoxon rank sum tests) for non-normally distributed data. Migration metrics were compared between sexes using these same tests, but sex was excluded from further analyses due to the relatively low proportion of sexed individuals and non-significant differences between sexes for all migration metrics tested (Wilcoxon rank sum tests and *t*-tests: $p > 0.05$; Table S1b,c). Speed through the unobstructed reach and tortuosity of downstream movements in unobstructed reaches (cf. Table 2) were compared between reaches for individuals using Wilcoxon signed-rank tests due to the non-normal distribution of data. Statistical tests were conducted only when the minimum sample size of each group in the analysis was $n = 5$. However, sample sizes of below 5 are still reported in tables and figures for illustrative purposes, and when the data are also used to calculate ungrouped summary statistics.

The influence of time spent in the river prior to the start of emigration and the furthest upstream extent on the net speed of emigration (cf. Table 2) were tested using generalized linear models (GLM: gamma distribution [log-link]; lme4 in R [Bates et al., 2015]), to assess whether downstream emigrations of individuals were influenced by their upstream migrations. The influence of the day of the year of river entry on the net speed of emigration was also tested to assess whether individuals behaved differently during emigration depending on whether they arrived earlier or later into their spawning river. The influence of the tortuosity of emigration (cf. Table 2) on the net speed of emigration was also tested to determine how the net speed of emigration was influenced by individuals making upstream movements during their emigrations. The significance of the influence of fixed predictors on the net speed of emigration was assessed by comparing models to their null (intercept only) model using the AIC (corrected for small sample size; AICc [Mazerolle, 2020]). The fixed predictor was determined to significantly influence the net speed of emigration when the AICc of the null model was ≥2 higher than the model retaining the fixed predictor.

To assess how the weirs influenced emigration, individuals' weir passage speeds were compared to their speeds through the unobstructed reach (cf. Table 2) immediately upstream of each weir, using Wilcoxon signed-rank tests. Weir passage delays (cf. Table 2) at each weir were compared between fish from different migration groups (i.e., Upper, Middle, Lower) using Wilcoxon rank sum tests and between weirs for individuals using Wilcoxon signed-rank tests. To assess how delays impacted shad movements, correlations between

TABLE 2 Summary of *Alosa fallax* migration metrics, method of calculation, and whether each metric was considered to be included in the full generalized linear mixed effects models (GLMMs) for downstream passage success at weirs.

Migration metric	Calculation	Included in GLMMs
Furthest upstream extent	River distance (from Stonebench receiver) of the most upstream acoustic receiver with a detection, except for fish recorded in both the Severn and the Teme upstream of their confluence, when the most upstream detection during the last movement upstream of the confluence was used.	Yes
Last time at furthest upstream extent	Time of last detection at "furthest upstream extent."	No
Time in river prior to the start of emigration	Time between entry into the receiver array (first detection on Stonebench receiver) and "last time at furthest upstream extent."	No
Total emigration time	Time between "last time at furthest upstream extent" and leaving the receiver array (last detection on Stonebench receiver).	No
Net speed of emigration	"Furthest upstream extent" divided by "total emigration time."	No
Tortuosity of emigration	"Furthest upstream extent" divided by total distance moved (regardless of direction) during emigration.	No
Speed through the unobstructed reach	Distance between most upstream and downstream receivers in each unobstructed reach (e.g., Upper, Middle, and Lower) divided by time between last detection on the former and first detection on the latter.	Yes
Tortuosity through the unobstructed reach	Distance between most upstream and downstream receivers in reach (e.g., Upper, Middle, and Lower) divided by total distance moved between last detection on the former and first detection on the latter.	Yes
Observed weir passage time	Time difference between first detections at closest receivers upstream and downstream of weir during downstream passage.	No
Weir passage speed	Distance between closest receivers upstream and downstream of weir divided by "observed weir passage time." Passage speed was used for analysis, rather than time, as distances between receivers were not equal between the weirs.	No
Expected weir passage time	Distance between closest receivers upstream and downstream of weir divided by "speed through the unobstructed reach" immediately upstream of weir.	No
Weir passage delay	"Observed weir passage time" minus "expected weir passage time."	No
Cumulative downstream passage delay	Sum of "weir passage delays" at all significant barriers.	No
Expected emigration time	"Total emigration time" minus "cumulative downstream passage delay."	No
Percentage increase in total emigration time	"Cumulative downstream passage delay" divided by "expected emigration time" times by 100.	No
Days since arrival into array	Number of days since the first detection at the Stonebench receiver.	Yes
Days since last at furthest upstream extent	Number of days since "last time at furthest upstream extent."	Yes

length of delay and distance moved during delay were assessed at each weir using Pearson's correlation coefficient. In 2019, due to a receiver lost at S2 during a major flood event, no data were available to calculate weir passage speeds or weir passage delays at this weir for individuals approaching after day 149 of the year ($n = 13$). To assess the overall impact of weirs on emigration, cumulative downstream passage delay, as well as the associated percentage increase in total emigration time (cf. Table 2), was calculated for all individuals where downstream passage delays at S2 and S1a/b were known and compared between migration groups using Wilcoxon rank sum tests. χ^2 tests were used to assess whether shad were more likely to both first approach and pass a particular weir (i.e., S1a or S1b; Figure 1) during emigration through the Lower reach.

To test the factors influencing downstream weir passage, a total of 73, 86, and 75 generalized linear mixed effects models (GLMM: binomial distribution; lme4 [Bates et al., 2015]) were built for weirs S1a, S1b, and S2, respectively. The response variable was a binary representation of daily downstream passage success at a weir (days with a downstream passage = 1, days with a weir approach but no downstream passage = 0, with days having upstream passage and no downstream passage removed). Individual fish ID was the random predictor variable, with mean daily environmental conditions (flow, temperature, and tidal influence on river level) as fixed predictors, as were day of the year, fish length at tagging, and certain individual migration metrics (Table 2), with no interactions between predictors tested. Model selection used backward selection, with AICc compared between models as per GLMs; the best fitting model was identified based on the lowest AICc, and models with ΔAICc <2 were also considered to have strong support if they were parsimonious. At S1a, furthest upstream extent and speed through the unobstructed reach

directly upstream of the weir were identified as colinear (Pearson's correlation coefficient: $r \geq 0.7$) (Figure S1b) and at S2, mean daily temperature was colinear with day of the year and mean daily flow (Figure S1). The colinear predictors retained in full models were determined based on their significance in predicting passage at S1b, where no predictors were identified as colinear.

2.4 | Ethical statement

The care and use of experimental animals complied with UK Home Office animal welfare laws, guidelines and policies as approved by UK Home Office project license PD6C17B56.

3 | RESULTS

3.1 | Migration metrics

The immigrating *A. fallax* entered the acoustic array between days 105 and 143 of the year, emigrated between days 131 and 187, and spent between 9.2 and 55.8 days in the river (Table 1b,c). Furthest upstream extent varied between 23.6 and 67.9 km, with individuals beginning their emigrations between 3.8 and 51.0 days after entering the river and taking 0.8–34.3 days to complete this emigration at net speeds of 0.8–54.1 km day^{-1}, at a tortuosity ranging between 0.09 and 1.00 (Table 1b,c). Differences between migration groups for day of the year of emigration, total emigration time, net speed of emigration, and tortuosity of emigration were not significant (Kruskal-Wallis χ^2tests, $p > 0.05$; Figure S2; Table S2a). Day of the year of emigration did differ significantly between years ($\chi^2 = 6.22$, $df = 2$, $p = 0.045$), with individuals emigrating earlier in 2020 versus 2019 (Wilcoxon rank sum test: $W = 383.5$, $p = 0.048$) (Figure S2; Table S2b). Total emigration time, net speed of emigration, and tortuosity of emigration did not differ significantly between any years (Kruskal-Wallis χ^2 tests, $p > 0.05$) (Figure S2; Table S2a).

Individuals that spent longer in the river prior to the start of their emigration had significantly faster net speeds of emigration (GLM; Figure 2a; Table S3), but neither furthest upstream extent (GLM; Figure 2b; Table S4a) nor day of the year of river entry (GLM; Figure 2c; Table S4b) significantly influenced net speed of emigration. Tortuosity of emigration was a significant and positive predictor of net speed of emigration, with more direct emigrations having faster net speeds (GLM; Figure 2d; Table S5).

3.2 | Emigrations through unobstructed reaches

Speed through the unobstructed Middle reach was not significantly different between migration groups (Wilcoxon rank sum test: $W = 40$, $p = 0.07$) (Figure 3a; Table S6d). However, there were significant differences between all migration groups in the Lower river reach (Kruskal-Wallis χ^2 test: $\chi^2 = 19.9$, $df = 2$, $p < 0.01$), with individuals from the Upper reach moving fastest and the those from the Lower reach moving slowest (Figure 3a, Table S6e). Individuals migrating through multiple reaches were faster in the Lower river reach compared to the Middle river reach (Wilcoxon signed-rank test: $V = 11$, $p < 0.001$) (Figure S3a; Table S6f).

Tortuosity through the unobstructed reach was always 1.00 in the Upper reach (Figure 3b; Table S6a), but it varied between 0.12 and 1.00 in the Middle reach (Figure 3b; Table S6b), with no significant differences observed between individuals emigrating from the Upper and Middle reaches ($W = 54$, $p = 0.21$) (Figure 3b; Table S6d). Tortuosity in the Lower reach varied between 0.09 and 1.00 (Figure 3b; Table S6c), with movements of fish emigrating from the Lower reach being significantly less direct than those from the Middle reach ($W = 177.5$, $p = 0.04$; Figure 3b; Table S6e). Individuals emigrating through multiple reaches were significantly more direct in the Lower reach compared to the Middle reach ($V = 26$, $p < 0.001$) (Figure S3b; Table S6f).

3.3 | Influence of weirs on emigrations

Weir passage speeds were highly variable between weirs and migration groups (Figure 4a; Table S7). Fish emigrating from the Upper reach were significantly faster compared to those emigrating from the Middle reach when passing S2 ($W = 33$, $p = 0.03$; Figure 4a). Weir passage speed at S1a/b was also significantly different between migration groups ($\chi^2 = 8.53$, $df = 2$, $p = 0.014$; Figure 4a), with fish emigrating from the Lower reach moving significantly slower than those emigrating from both the Middle and Upper reaches ($W = 144$, $p = 0.02$; $W = 12$, $p = 0.03$ respectively), whereas fish from Middle and Upper reaches showed similar speeds ($W = 45$, $p = 0.11$) (Figure 4a; Table S7). Although weir passage speeds at T1 did not differ significantly from speeds through the unobstructed Upper reach (Wilcoxon signed-rank test: $V = 5$, $p = 0.63$) (Figure 4a), weir passage speeds at both S2 and S1a/b were significantly slower than speeds through the unobstructed Middle and Lower reaches, respectively ($V = 300$, $p < 0.001$; $V = 1170$, $p < 0.001$, respectively) (Figure 4a; Table S7). Consequently, T1 was not identified as a significant barrier to downstream passage, with weir passage delays being minimal (<0.1 day), whereas S2 and S1a/b were significant barriers, resulting in longer, more variable delays (Figure 4b; Table S7). At S1a/b, individuals emigrating from the Lower reach experienced longer delays compared to those emigrating from the Middle reach (Wilcoxon rank sum test: $W = 329$, $p < 0.01$) (Figure 4b), with the distance moved during weir passage delays being positively correlated with the length of delay at both S2 and S1a/b (Pearson's correlation coefficient: $r = 0.78$, $df = 22$, $p < 0.001$; $r = 0.87$, $df = 47$, $p < 0.001$, respectively; Figure 4c).

Fish with known weir passage speeds at both S2 and S1a/b ($n = 22$) had weir passage delays between <0.1 and 18.4 days (median: 0.4 [0.2–1.9] days) at S2 and between <0.1 and 4.4 days (median 0.5 [0.3–1.1] days) at S1a/b, with the differences between weirs not being significant (Wilcoxon signed-rank test: $V = 117$,

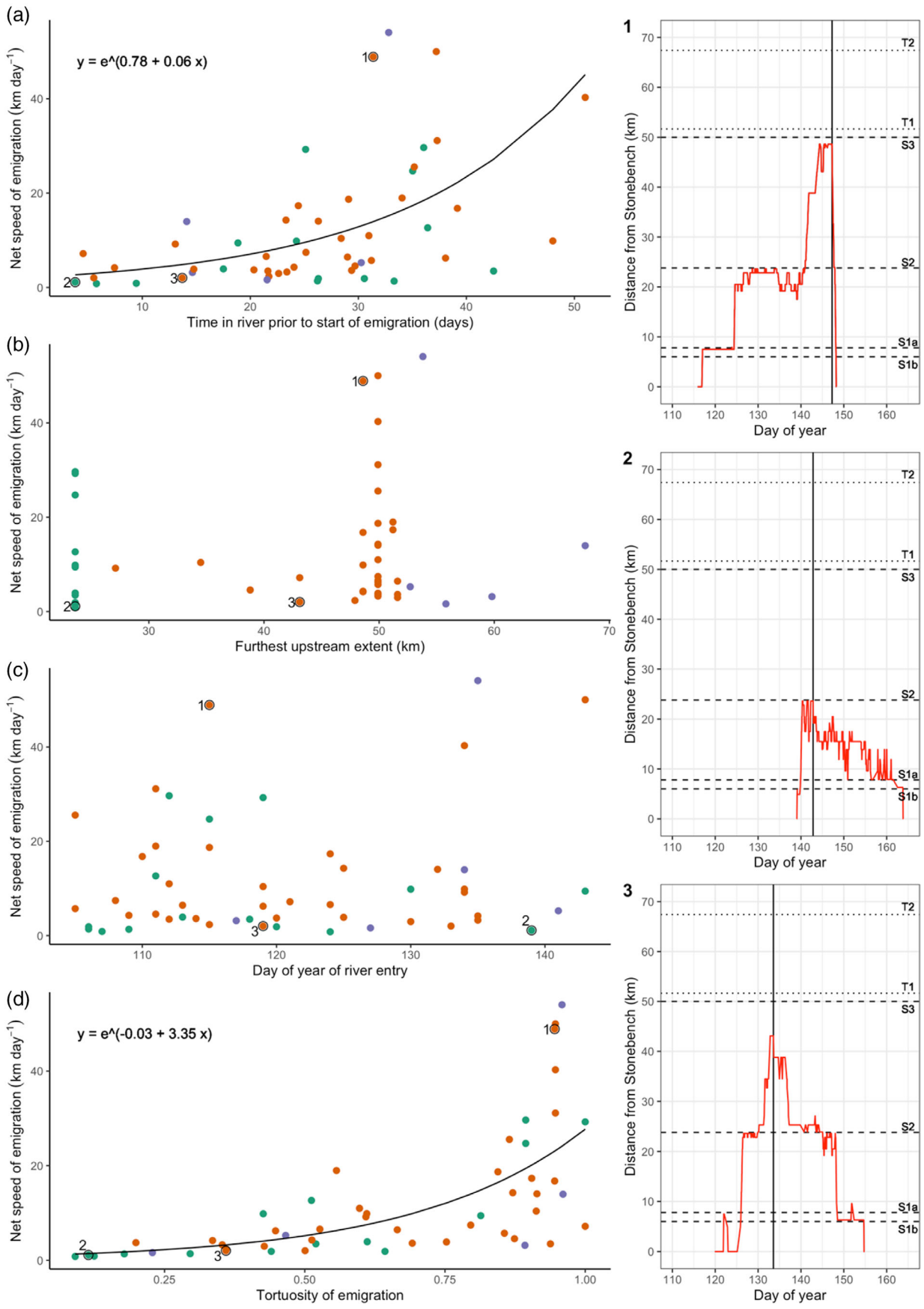

FIGURE 2 Legend on next page.

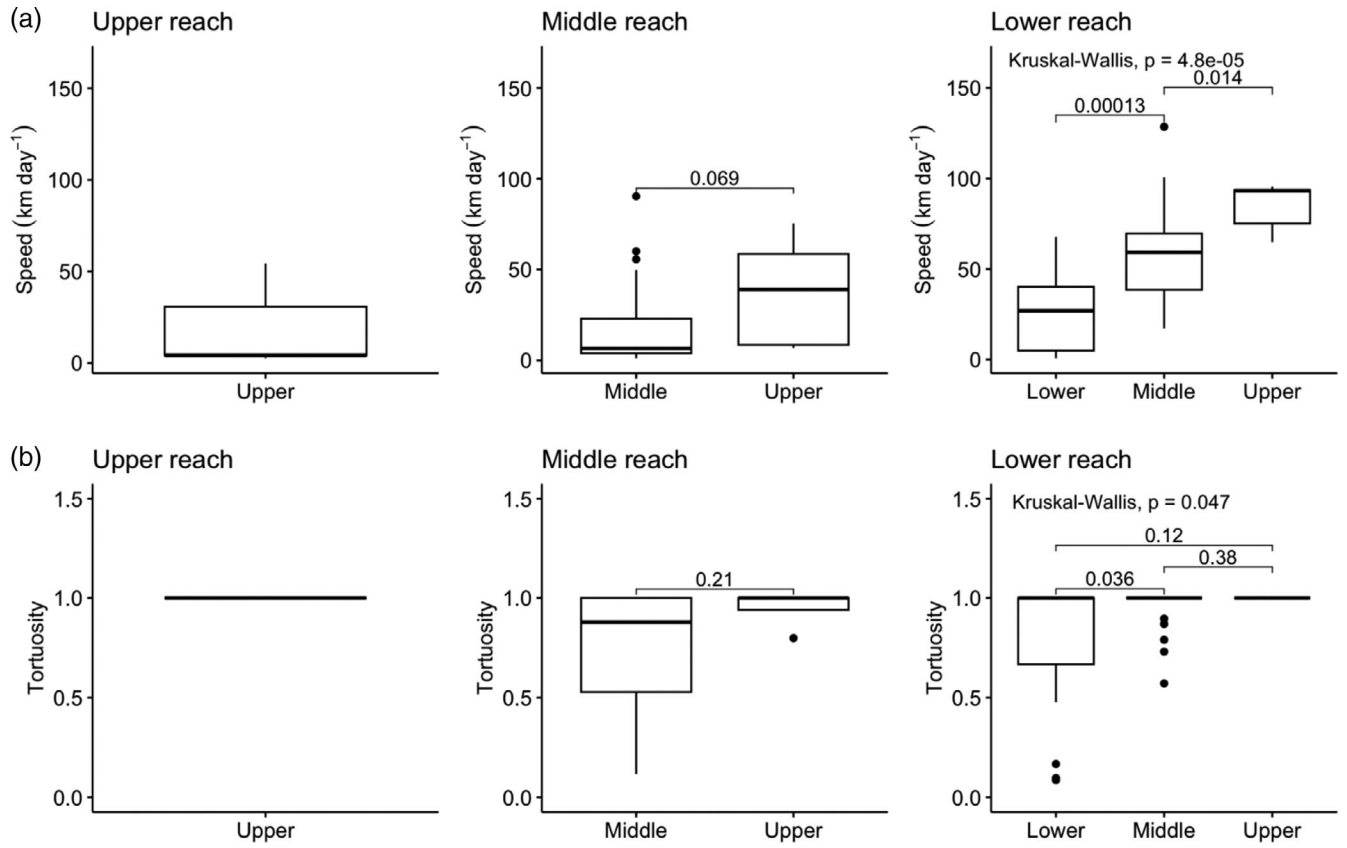

FIGURE 3 Boxplots comparing differences between *Alosa fallax* migration groups in (a) speed and (b) tortuosity through the unobstructed reach in the Upper, Middle, and Lower reaches (left to right). Horizontal lines indicate the 25th, 50th, and 75th percentiles; vertical lines indicate the minimum and maximum values within 1.5 times the interquartile range of the 25th percentile and the 75th percentile, respectively; and points indicate values outside of this range.

$p = 0.77$). The cumulative downstream passage delay varied between <0.1 and 19.6 days (median: 1.4 [0.6–6.5] days), with the median increase in emigration time due to these delays being 61% (23%–166%) (Table 3). There were no significant differences in cumulative downstream passage delay (Wilcoxon rank sum test: $W = 165$, $p = 0.56$) or percentage increase in emigration time ($W = 180$, $p = 0.28$) between fish emigrating from the Middle and Lower reaches. The sample size of fish emigrating from the Upper reach was too low for statistical analysis ($n = 1$). In the Lower reach, the proportion of fish that first approached S1a ($n = 25$) and S1b ($n = 28$) during their emigration did not significantly differ from equality (χ^2 goodness of fit: $\chi^2 = 0.17$, $df = 1$, $N = 53$, $p = 0.68$). All 28 fish that initially approached S1b subsequently passed S1b (100%). However, among the 25 that first approached S1a, only 12 subsequently passed S1a (48%), whereas the remaining 13 passed S1b (52%). This resulted in a significant difference between the proportions passing S1a ($n = 12$) and S1b ($n = 41$), indicating that fish were more likely to pass S1b than S1a during their emigration ($\chi^2 = 15.9$, $df = 1$, $N = 53$, $p < 0.001$).

There was one GLMM with strong support predicting the successful downstream passage at each of weirs S2 and S1a, with three models with strong support at S1b (Table S8). The best-fitting GLMM for the successful downstream passage at S2 retained a significant positive influence of day of the year, days since first arrival into the array, and mean daily flow on probability of downstream passage (Figure 5a; Table 4a). For S1a, the only significant predictor retained

FIGURE 2 Scatterplots indicating the relationship between the net speed of emigration of *Alosa fallax* versus (a) time in river prior to start of emigration, (b) furthest upstream extent, (c) day of the year of river entry, and (d) tortuosity of emigration. Black lines indicate a significant generalized linear regression (gamma distribution [log-link]). Migration group is indicated by color (purple = Upper, orange = Middle, and green = Lower). Numbered points (1–3) refer to individuals with: (1) a high furthest upstream extent, long time in river prior to start of emigration and fast net speed of emigration; (2) a low furthest upstream extent, short time in river prior to start of emigration, and a slow net speed of emigration; and (3) an intermediate individual, with these spawning migrations represented as tracks (panels 1–3, respectively), where red lines indicate the distance upstream of the Stonebench receiver against time, the vertical lines indicate last time at furthest upstream extent, and horizontal lines represent weirs on the Severn (dashed) and Teme (dotted).

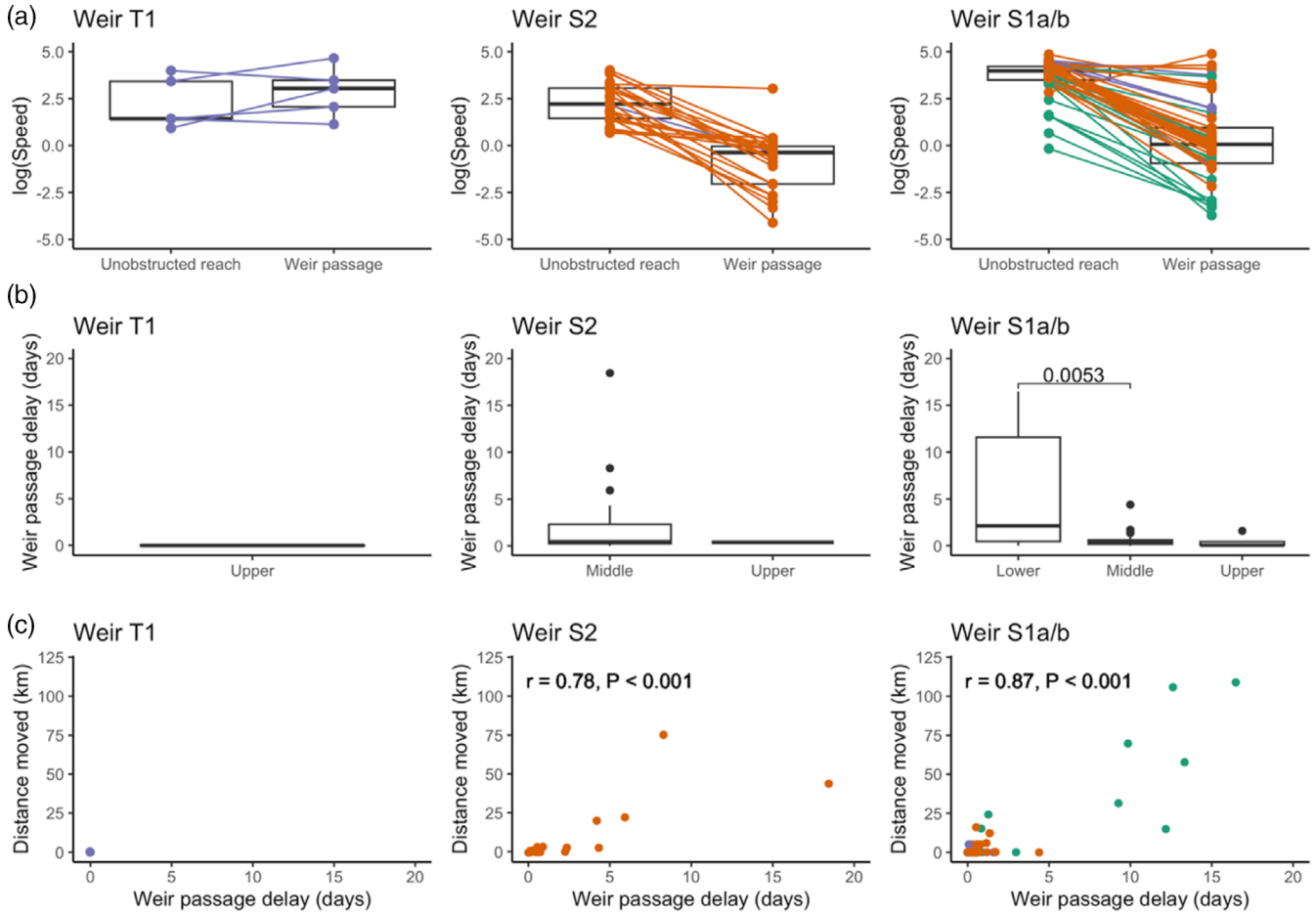

FIGURE 4 Boxplots indicating (a) difference between the logarithm of weir passage speed and speed through the unobstructed reach immediately upstream of the weir for individual *Alosa fallax*. (b) Difference in weir passage delay between migration groups, where horizontal lines indicate the 25th, 50th, and 75th percentiles; vertical lines indicate the minimum and maximum values within 1.5 times the interquartile range of the 25th percentile and the 75th percentile, respectively; and points indicate values outside of this range. (c) Scatterplots indicating the relationship between weir passage delay and distance moved during delay, where "r" is the Pearson's correlation coefficient. Panels represent weirs T1, S2, and S1a/b (left to right). In plots (a) and (c), migration group is indicated by color (purple = Upper, orange = Middle, and green = Lower).

was the negative influence of days since last at furthest upstream extent (Figure 5b; Table 4b). At S1b, furthest upstream extent was retained in all three models with strong support as a significant positive predictor of downstream passage; year was also a significant predictor of passage, with passage probability significantly lower in 2020 versus 2019 (Figure 5c; Table 4c, Table S9). All other predictors retained in these models were non-significant (Table 4, Table S9), with a non-significant positive influence of mean daily flow and mean daily tidal influence on river level retained in the best-fitting model for the successful downstream passage at S1a (Table 4b), and no environmental variables retained in any of the three models with strong support for passage at S1b (Table 4c; Table S9).

4 | DISCUSSION

There was high individual variability in time spent in the river and furthest upstream extent reached by individual *A. fallax* prior to starting their emigration, with fish that spent considerably longer in the river before emigrating tending to undertake faster, more direct emigrations. These results suggest that *A. fallax* were not simply entering the river and then moving upstream as far as possible to spawn before then emigrating. Indeed, as fractional spawners, female *A. fallax* produce multiple batches of eggs across a spawning season (Pina et al., 2003), with individuals in the River Severn identified as occupying areas of varying spatial size in which they may have spawned (Davies, 2021). Thus, across this population, it appears that individuals use a range of different migration and spawning strategies, similar to those already observed in alewife *Alosa pseudoharengus* Wilson 1811, which can make multiple movements between the estuary and upstream spawning grounds during their spawning migrations (McCartin et al., 2019).

For individual *A. fallax* that reach their furthest upstream extent relatively slowly but then emigrate quickly, it is speculated that some spawning occurs during their upstream migrations, with fish emigrating when spent or having depleted their energy reserves below a

TABLE 3 Summary of the number of *Alosa fallax* (*n* Fish) in each migration group emigrating from the River Severn in their second tracked spawning season, the number of weirs they were required to pass (*n* Weirs) during this emigration, their minimum (Min), maximum (Max), and median (25th–75th percentiles) cumulative downstream passage delay, and percentage increase in emigration time resulting from these delays.

			Cumulative downstream passage delay (days)		Percentage increase in emigration time (%)	
Migration group	***n* Fish**	***n* Weirs**	**Min–max**	**Median**	**Min–max**	**Median**
Lower	14	1	<0.1–16.5	2.1 (0.5–11.6)	<0.1–3386.8	70.0 (53.4–265.5)
Middle	21	2	0.2–19.6	1.1 (0.6–2.3)	3.5–1215.8	60.2 (22.7–97.5)
Upper	1	>2	NA	2.0	NA	11.7
All	36		<0.1–19.6	1.4 (0.6–6.5)	<0.1–3386.8	61.1 (23.0–165.9)

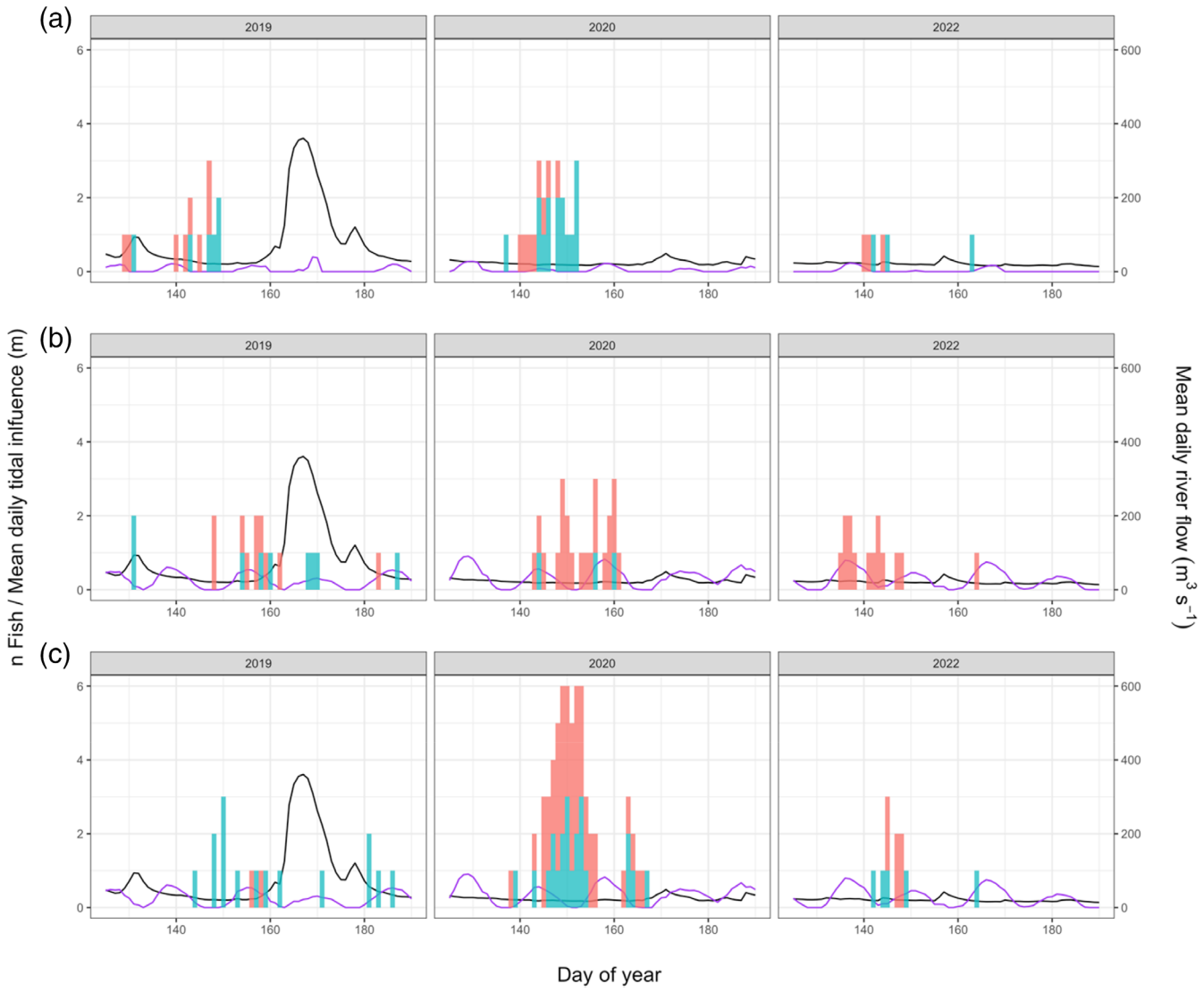

FIGURE 5 Daily downstream passage summaries of *Alosa fallax* at (a) Weir S2, (b) Weir S1a, and (c) Weir S1b in years 2019, 2020, and 2022 (left to right). Size of each bar represents the number of emigrating individuals (*n* Fish) detected upstream of the weir on that day, and the proportion of the bar colored blue represents the proportion of those detected individuals to successfully pass the weir in a downstream direction on that day. Black lines represent the mean daily river flow, and purple lines represent the mean daily tidal influence on river level in the reach downstream of the weir.

threshold level (Castro-Santos & Letcher, 2010). However, for those reaching their furthest extent quickly before then emigrating slowly, it is speculated that some spawning activity is likely to also occur during this downstream emigration. This is supported by *A. sapidissima*, which are thought to spawn during their downstream migration, which is suggested as an energetically favorable strategy, with

TABLE 4 Summary of the fixed predictors in the best-fitting generalized linear mixed effects models (GLMMs; binary distribution) predicting probability of successful downstream passage of *Alosa fallax* at weirs (a) S2, (b) S1a, and (c) S1b, with fish ID as the random predictor and 2019 as the reference year where year is retained as a predictor. Fixed predictors include Day of year (DOY); mean daily flow (flow); mean daily tidal influence on river level (tidal influence); days since river entry, days since last at furthest upstream extent (days since FUE), furthest upstream extent (FUE), and year.

Fixed predictors	Estimate ± SE	z value	*p*
a			
(Intercept)	0.50 ± 0.44	1.14	0.25
DOY	2.48 ± 0.91	2.73	0.006
Flow	1.88 ± 0.73	2.60	0.009
Days since river entry	1.55 ± 0.57	2.70	0.007
b			
(Intercept)	−2.11 ± 1.52	−1.38	0.17
Flow	3.88 ± 3.08	1.26	0.21
Tidal influence	8.07 ± 4.65	1.74	0.08
Year: 2020	−3.45 ± 1.88	−1.84	0.07
Year: 2022	$-3.73 \pm 6.47e^{6}$	0.00	1.00
Days since FUE	−1.33 ± 0.66	−2.03	0.04
c			
(Intercept)	2.04 ± 0.97	2.11	0.04
FUE	1.08 ± 0.32	3.37	<0.001
DOY	0.80 ± 0.45	1.80	0.07
Days since FUE	−0.51 ± 0.31	−1.67	0.10
Year: 2020	−2.67 ± 1.03	−2.58	0.0099
Year: 2022	−0.99 ± 1.22	−0.81	0.42

upstream movement less energetically costly in the lower temperatures at the beginning of the spawning migration (Castro-Santos & Letcher, 2010). There is also evidence in *A. sapidissima* that the spatial extent of spawning moves downstream over the course of the spawning season (Maltais et al., 2010) and that high proportions of emigrating females are only partially spent (Olney et al., 2001). The finding that *A. fallax* emigrating from more upstream reaches were faster and more direct when moving through the Lower river reach compared to fish emigrating from more downstream reaches could therefore relate to them having differing spawning status. For example, individuals emigrating from upstream reaches may have been fully spawned once they had passed weir S2, whereas those spending their entire spawning migration downstream of S2 may still have been exploring and/or spawning in the river after reaching their furthest upstream extent. This must, however, remain speculative here, as acoustic telemetry only provides information on the spatial and temporal movements of the fish, not their actual behavior (e.g., when and where individuals spawned).

Previous research on immigrating *A. fallax* in the River Severn found that weirs delayed upstream migrations by a median of 4.6 days (Davies et al., 2023), which is longer than the 1.4 days observed for the downstream passage of emigrating fish in this study. However, these downstream delays still accounted for a substantial increase (median: 61%) in emigration time. This is consistent with *Alosa* spp. in North America, where cumulative delays at culverts were found to increase upstream migration times of *A. pseudoharengus* and blueback herring *Alosa aestivalis* Mitchill 1814 by 119%–149% and downstream migration times by 63%–83% (Alcott et al., 2021). These delays during emigration could have important implications on individual fitness, as emigrating *A. fallax* are likely to be in relatively poor body condition compared to their pre-spawned condition, as also observed in *A. sapidissima* (Walter & Olney, 2003). Indeed, delays to downstream migration further deplete energy reserves, which can potentially result in mortality or the curtailment of any further spawning downstream (Castro-Santos & Letcher, 2010). Even short-term passage delays at barriers may have energetic costs that could potentially lead to reduced survival and return rates, as detected in *S. salar* kelts (Baktoft et al., 2020). The risk of mortality can also increase due to the delayed emigration being completed in suboptimal conditions. For example, delays in *S. salar* smolt emigration increased their likelihood of moving through river stretches of potentially lethal water temperatures (Marschall et al., 2011). When downstream passage delays result in significant fitness costs, through reduced survival or future fecundity, these can diminish the benefits of an iteroparous life history (Baktoft et al., 2020; Castro-Santos & Letcher, 2010). Therefore, the impacts of these delays on survival and future reproductive effort warrant further investigation.

Increased river flows elevate river levels, which reduces the hydraulic head across weirs and increases the head of water above weir crests (El-Belasy, 2013). Reduced hydraulic head can facilitate downstream passage, as observed in *Hypophthalmichthys* spp. in the upper Mississippi River, USA (Vallazza et al., 2021), and increased head of water above a spillway crest was found to increase *A. anguilla* passage on the Frémur River, France (Trancart et al., 2020). Further, when river levels are elevated such that the weir crest becomes submerged, velocity gradients across the weir can be reduced (Fleit et al., 2018). This is potentially important, as high-velocity gradients at weirs can elicit avoidance behaviors and delay weir passage in various species (Haro et al., 1998; Russon & Kemp, 2011; Vowles et al., 2014). Nevertheless, we detected that increased flow only significantly influenced the probability of downstream passage of individuals at the most upstream (S2) of the three significant barriers to downstream passage, despite this being the only significant barrier modified to facilitate fish passage (with the presence of a notch fish easement). Further, the only weir studied that did not significantly delay passage was T1, which had been lowered and partially removed, suggesting that downstream passage of *A. fallax* can be better facilitated through barrier remediation rather than mitigation.

Downstream passage rate varied between the two weirs at the tidal limit, with 41 fish passing over S1b compared to just 12 passing over S1a, despite similar numbers first approaching each weir (S1a: 25; S1b: 28), with neither flow nor tidal influence on river level significantly influencing passage at either weir. This suggests that differences between weir characteristics allowed them to be passed with

differing ease by emigrating *A. fallax*. Although the hydraulic head at S1a is known to be ~0.1 m greater than S1b at Q95 (Davies et al., 2023), little information is available regarding the construction or dimensions of these weirs. Therefore, further research is required to identify the drivers of these differences in passage rate. These drivers could include whether avoidance behaviors differ at each weir, with emigrating fish exposed to different velocity gradients (Haro et al., 1998; Russon & Kemp, 2011; Vowles et al., 2014).

Individuals emigrating from the Lower reach experienced significantly more delays at S1a/b compared to those emigrating from the Middle reach. Additionally, various aspects of individuals' spawning migrations (i.e., furthest upstream extent, days since last being at the furthest upstream extent, and days since arrival into the array) had significant influences on downstream passage probability at the weirs. As a result, there is the potential that some delays at these weirs may not relate to a delay to a post-spawned emigration and instead relate to a delay to accessing downstream spawning habitat (Castro-Santos & Letcher, 2010) and/or returning to estuarine feeding grounds between spawning events (McCartin et al., 2019). Each of these scenarios is likely to incur fitness costs. It is arguably not essential to (and not possible with the methods used here) identify the exact motivation for every approach to a weir by downstream migrating individuals to conclude that delays to downstream passage, irrespective of motivation for passage, are likely to have associated fitness costs.

In summary, the emigrations of *A. fallax* from their spawning grounds in the River Severn comprise not only relatively fast, unidirectional downstream movements but also a range of different emigration patterns, including slower and less-direct downstream movements of individuals. Emigrations were significantly delayed by the presence of weirs, with these delays potentially affecting survival rates at sea as well as future reproduction. As a result, it is argued that the impacts of anthropogenic barriers on the downstream passage of *A. fallax*, specifically, and iteroparous diadromous fishes more generally, always need consideration when assessing both river connectivity and barrier mitigation schemes.

AUTHOR CONTRIBUTIONS

Conceived and designed the field experiments: Jonathan D. Bolland, Andrew D. Nunn, Jamie R. Dodd, Charles Crundwell, Randolph Veltero, J. Robert Britton, and Peter Davies. Conducted fieldwork: Jonathan D. Bolland, Andrew D. Nunn, Jamie R. Dodd, Charles Crundwell, J. Robert Britton, Peter Davies, and Mark I. A. Yeldham. Conducted telemetry analysis: Mark I. A. Yeldham, with advice from Peter Davies. Wrote the article: Mark I. A. Yeldham. Edited the article: Jonathan D. Bolland, Peter Davies, J. Robert Britton, Andrew D. Nunn, Jamie R. Dodd, Charles Crundwell, and Randolph Veltero.

ACKNOWLEDGMENTS

The authors acknowledge funding for the purchase of acoustic tags from the UK Department of Food and Rural Affairs (DEFRA) and Natural England. MIAY was supported by a match-funded PhD grant from the Fishmongers' Company and Bournemouth University, with support from the "Unlocking the Severn" project (Heritage Lottery Fund Grant/Award Number: HG/15/04573, LIFE Nature Programme Grant/Award Number: LIFE15/NAT/UK/000219). The authors thank staff of the Environment Agency, Natural England, Severn Rivers Trust, and Canal and Rivers Trust for their contributions, and permission from the landowner at Maisemore Weir.

CONFLICT OF INTEREST STATEMENT

The authors have no competing interests to declare.

ORCID

Mark I. A. Yeldham https://orcid.org/0000-0001-6323-4021
J. Robert Britton https://orcid.org/0000-0003-1853-3086
Peter Davies https://orcid.org/0000-0003-3739-5352
Jamie R. Dodd https://orcid.org/0000-0001-5528-4141
Andrew D. Nunn https://orcid.org/0000-0001-8370-1221
Jonathan D. Bolland https://orcid.org/0000-0001-7326-5075

REFERENCES

Alcott, D., Goerig, E., & Castro-Santos, T. (2021). Culverts delay upstream and downstream migrations of river herring (Alosa spp.). *River Research and Applications*, *37*(10), 1400–1412.

Aprahamian, M. W., & Aprahamian, C. D. (1990). Status of the genus *Alosa* in the British Isles; past and present. *Journal of Fish Biology*, *37*, 257–258.

Aprahamian, N. W., Bagliniere, J. L., Sabatie, M. R., Alexandrino, P., Thiel, R., & Aprahamian, C. D. (2003). Biology, status, and conservation of the anadromous Atlantic twaite shad Alosa fallax fallax. *Biodiversity, Status, and Conservation of the World's Shads*, *35*, 103–124.

Babin, A. B., Ndong, M., Haralampides, K., Peake, S., Jones, R., Curry, R. A., & Linnansaari, T. (2021). Overwintering and migration behaviour of post-spawned Atlantic salmon Salmo salar in a large hydropower-regulated river and reservoir. *Journal of Fish Biology*, *99*(3), 856–874.

Baktoft, H., Gjelland, K. O., Szabo-Meszaros, M., Silva, A. T., Riha, M., Okland, F., Alfredsen, K., & Forseth, T. (2020). Can energy depletion of wild Atlantic Salmon Kelts negotiating hydropower facilities Lead to reduced survival? *Sustainability*, *12*(18), 7341.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Bayse, S. M., Regish, A. M., & McCormick, S. D. (2018). Proximate composition, lipid utilization and validation of a non-lethal method to determine lipid content in migrating American shad Alosa sapidissima. *Journal of Fish Biology*, *92*(6), 1832–1848.

Belletti, B., de Leaniz, C. G., Jones, J., Bizzi, S., Borger, 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., Fernandez, S., … Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*(7838), 436–441.

Birnie-Gauvin, K., Koed, A., & Aarestrup, K. (2021). Repeatability of migratory behaviour suggests trade-off between size and survival in a wild iteroparous salmonid. *Functional Ecology*, *35*, 2717–2727.

Boe, K., Power, M., Robertson, M. J., Dempson, J. B., & Fleming, I. A. (2022). Life history contrasts in nutritional state and return probability of post-spawned Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *79*(4), 548–557.

Bolland, J. D., Nunn, A. D., Angelopoulos, N. V., Dodd, J. R., Davies, P., Roberts, C. G., Britton, J. R., & Cowx, I. G. (2019). Refinement of acoustic-tagging protocol for twaite shad Alosa fallax (Lacepede), a species sensitive to handling and sedation. *Fisheries Research*, *212*, 183–187.

Castro-Santos, T., & Letcher, B. H. (2010). Modeling migratory energetics of Connecticut River American shad (Alosa sapidissima): Implications for the conservation of an iteroparous anadromous fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(5), 806–830.

Christie, M. R., McNickle, G. G., French, R. A., & Blouin, M. S. (2018). Life history variation is maintained by fitness trade-offs and negative frequency-dependent selection. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(17), 4441–4446.

Davies, P. (2021). *Movement ecology of two threatened anadromous species, twaite shad Alosa fallax and sealamprey Petromyzon marinus, revealed by acoustic telemetry', PhD thesis*. Bournemouth University.

Davies, P., Britton, J., Castro-Santos, T., Crundwell, C., Dodd, J., Nunn, A., Velterop, R., & Bolland, J. D. (2023). Tracking anadromous fish over successive freshwater migrations reveals the influence of tagging effect, previous success, and abiotic factors on upstream passage over barriers. *Canadian Journal of Fisheries and Aquatic Sciences*., *80*, 1110–1125.

Davies, P., Britton, J. R., Nunn, A. D., Dodd, J. R., Bainger, C., Velterop, R., & Bolland, J. D. (2021). Cumulative impacts of habitat fragmentation and the environmental factors affecting upstream migration in the threatened sea lamprey, Petromyzon marinus. *Aquatic Conservation-Marine and Freshwater Ecosystems*, *31*(9), 2560–2574.

Davies, P., Britton, J. R., Nunn, A. D., Dodd, J. R., Bainger, C., Velterop, R., & Bolland, J. D. (2022). Individual movement variation in upstream-migrating sea lamprey Petromyzon marinus in a highly fragmented river. *Freshwater Biology*, *67*(4), 643–656.

Davies, P., Britton, R. J., Nunn, A. D., Dodd, J. R., Crundwell, C., Velterop, R., O'Maoileidigh, N., O'Neill, R., Sheehan, E. V., Stamp, T., & Bolland, J. D. (2020). Novel insights into the marine phase and river fidelity of anadromous twaite shad Alosa fallax in the UK and Ireland. *Aquatic Conservation-Marine and Freshwater Ecosystems*, *30*(7), 1291–1298.

Degroot, S. J. (1990). The former allis and twaite shad fisheries of the lower Rhine, The Netherlands. *Journal of Applied Ichthyology-Zeitschrift Fur Angewandte Ichthyologie*, *6*(4), 252–256.

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W. M., Marconi, V., McRae, L., Baumgartner, L. J., Brink, K., Claussen, J. E., Cooke, S. J., Darwall, W., Eriksson, B. K., de Garcia Leaniz, C., Hogan, Z., Royte, J., Silva, L. G. M., Thieme, L. M., Tickner, D., Waldman, J., … Berkhuysen, A. (2020). *The living planet index (LPI) for migratory freshwater fish – technical report*. World Fish Migration Foundation.

El-Belasy, A. (2013). Developing formulae for combined weir and orifice (case study: El-Fayoum weirs). *Alexandria Engineering Journal*, *52*, 763–768.

Fleit, G., Baranya, S., & Bihs, H. (2018). CFD modeling of varied flow conditions over an ogee-weir. *Periodica Polytechnica-Civil Engineering*, *62*(1), 26–32.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Macedo, H. E., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M. E., Meng, J., Mulligan, M., … Zarfl, C. (2019). Mapping the world's free-flowing rivers. *Nature*, *569*(7755), 215–221.

Hanssen, E. M., Vollset, K. W., Salvanes, A. G. V., Barlaup, B., Whoriskey, K., Isaksen, T. E., Normann, E. S., Hulbak, M., & Lennox, R. J. (2022). Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (Salmo salar) smolts migrating through lakes. *Ecology of Freshwater Fish*, *31*(2), 424–437.

Haro, A., Odeh, M., Noreika, J., & Castro-Santos, T. (1998). Effect of water acceleration on downstream migratory behavior and passage of Atlantic salmon smolts and juvenile American shad at surface bypasses. *Transactions of the American Fisheries Society*, *127*(1), 118–127.

Hasselman, D. J., Ricard, D., & Bentzen, P. (2013). Genetic diversity and differentiation in a wide ranging anadromous fish, American shad (Alosa sapidissima), is correlated with latitude. *Molecular Ecology*, *22*(6), 1558–1573.

Jones, J., Borger, L., Tummers, J., Jones, P., Lucas, M., Kerr, J., Kemp, P., Bizzi, S., Consuegra, S., Marcello, L., Vowles, A., Belletti, B., Verspoor, E., Van de Bund, W., Gough, P., & de Leaniz, C. G. (2019). A comprehensive assessment of stream fragmentation in Great Britain. *Science of the Total Environment*, *673*, 756–762.

Le Pichon, C., Lestel, L., Courson, E., Merg, M. L., Tales, E., & Belliard, J. (2020). Historical changes in the ecological connectivity of the Seine River for fish: A focus on physical and chemical barriers since the mid-19th century. *Water*, *12*(5), 1352.

Leonard, J. B. K., & McCormick, S. D. (1999). The effect of migration distance and timing on metabolic enzyme activity in an anadromous clupeid, the American shad (Alosa sapidissima). *Fish Physiology and Biochemistry*, *20*(2), 163–179.

Lilly, J., Honkanen, H. M., McCallum, J. M., Newton, M., Bailey, D. M., & Adams, C. E. (2022). Combining acoustic telemetry with a mechanistic model to investigate characteristics unique to successful Atlantic salmon smolt migrants through a standing body of water. *Environmental Biology of Fishes*, *105*(12), 2045–2063.

Maltais, E., Daigle, G., Colbeck, G., & Dodson, J. J. (2010). Spawning dynamics of American shad (Alosa sapidissima) in the St. Lawrence River, Canada-USA. *Ecology of Freshwater Fish*, *19*(4), 586–594.

Marschall, E. A., Mather, M. E., Parrish, D. L., Allison, G. W., & McMenemy, J. R. (2011). Migration delays caused by anthropogenic barriers: Modeling dams, temperature, and success of migrating salmon smolts. *Ecological Applications*, *21*(8), 3014–3031.

Mazerolle, M. J. (2020). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1.

McCartin, K., Jordaan, A., Sclafani, M., Cerrato, R., & Frisk, M. G. (2019). A new paradigm in alewife migration: Oscillations between spawning grounds and estuarine habitats. *Transactions of the American Fisheries Society*, *148*(3), 605–619.

Mota, M., Rochard, E., & Antunes, C. (2016). Status of the diadromous fish of the Iberian Peninsula: Past, present and trends. *Limnetica*, *35*(1), 1–18.

Olney, J. E., Denny, S. C., & Hoenig, J. M. (2001). Criteria for determining maturity stage in female American shad, Alosa sapidissima, and a proposed reproductive cycle. *Bulletin Francais de la Peche et de la Pisciculture*, *362-63*, 881–901.

Pina, T., Esteves, E., & Andrade, J. P. (2003). Gross and histological observations of ovarian development in twaite shad, Alosa fallax fallax, from the Rivers Mira and Guadiana (Portugal). *Scientia Marina*, *67*(3), 313–322.

Rambonilaza, T., Kerouaz, F., & Boschet, C. (2023). Recreational anglers? Preferences about harvest regulations to protect a threatened freshwater fish in France. *Journal of Environmental Management*, *332*, 117356.

Ranta, E., Tesar, D., & Kaitala, A. (2002). Environmental variability and semelparity vs. iteroparity as life histories. *Journal of Theoretical Biology*, *217*(3), 391–396.

Russon, I. J., & Kemp, P. S. (2011). Advancing provision of multi-species fish passage: Behaviour of adult European eel (Anguilla Anguilla) and brown trout (Salmo trutta) in response to accelerating flow. *Ecological Engineering*, *37*(12), 2018–2024.

Trancart, T., Carpentier, A., Acou, A., Danet, V., Elliott, S., & Feunteun, E. (2020). Behaviour of endangered European eels in proximity to a dam during downstream migration: Novel insights using high accuracy 3D acoustic telemetry. *Ecology of Freshwater Fish*, *29*(2), 266–279.

Vallazza, J. M., Mosel, K. J., Reineke, D. M., Runstrom, A. L., Larson, J. H., & Knights, B. C. (2021). Timing and hydrological conditions associated with bigheaded carp movement past navigation dams on the upper Mississippi river. *Biological Invasions*, *23*(11), 3409–3425.

van Puijenbroek, P., Buijse, A. D., Kraak, M. H. S., & Verdonschot, P. F. M. (2019). Species and river specific effects of river fragmentation on European anadromous fish species. *River Research and Applications*, *35*(1), 68–77.

Vowles, A. S., Anderson, J. J., Gessel, M. H., Williams, J. G., & Kemp, P. S. (2014). Effects of avoidance behaviour on downstream fish passage

through areas of accelerating flow when light and dark. *Animal Behaviour*, *92*, 101–109.

Walter, J. F., & Olney, J. E. (2003). Feeding behavior of American shad during spawning migration in the York river, Virginia. *Biodiversity, Status, and Conservation of the World's Shads*, *35*, 201–209.

SUPPORTING INFORMATION

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

How to cite this article: Yeldham, M. I. A., Britton, J. R., Crundwell, C., Davies, P., Dodd, J. R., Nunn, A. D., Velterop, R., & Bolland, J. D. (2024). Emigration of post-spawned twaite shad *Alosa fallax*, an anadromous and iteroparous fish, in a highly fragmented river. *Journal of Fish Biology*, 1–15. https://doi.org/10.1111/jfb.15713