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Individual movement variation in upstream-migrating sea lamprey *Petromyzon marinus* in a highly fragmented river

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Abstract

1. Anthropogenic reductions in riverine connectivity can severely impede the migrations of anadromous species. In fragmented rivers, successful migrations depend on the ability of migrants to negotiate barriers or locate alternative passage routes. However, individual variation in the specific aspects of movement that determine migration success in fragmented rivers, is poorly characterised.

2. Here, individual variation was investigated in the spawning migrations of 56 adult sea lamprey *Petromyzon marinus*, an anadromous, semelparous species that does not show fidelity to natal rivers. The variability and consequences of two key aspects of fish migration within fragmented rivers were tested: passage time (total time taken to pass a barrier) and retreats (exploratory downstream movements after unsuccessful passage attempts). These were tested using acoustic telemetry in the highly fragmented River Severn catchment, western England, U.K.

3. Distinct unimodal, bimodal, and multimodal patterns of variation in passage times were displayed across the different barriers, potentially related to the physical characteristics of the barrier and prevailing river discharge conditions when the barriers were first approached, but were not related to lamprey body sizes. At the first three barriers encountered by upstream-migrating sea lamprey in the study, between 30% and 46% of individuals made retreat movements, and between 5% and 100% of retreating individuals were able to locate alternative tributaries. Retreating individuals were highly variable in their distance and frequency of retreats; overall, retreat movements comprised 11% (lower-upper quartiles 0%–52%, range 0%–76%) of the total distance moved before reaching spawning areas. Time-to-event analysis indicated that retreat rates reduced as river discharge increased.

4. There was no evidence indicating that individual variation in passage time, or presence of retreat movements at barriers, influenced the subsequent upstream migration speed or final upstream extent of lampreys. While predictability in rank arrival timing was high within three unobstructed reaches, this predictability was disrupted at barriers due to individual variation in passage times.

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5. Anthropogenic barriers thus can both disrupt and reveal individual variation in the migration dynamics of anadromous species. Substantial variability in retreat behaviours can be displayed by anadromous species facing delays at barriers, with these behaviours also associated with environmental conditions and the availability of alternative migration routes. Individual variation in exploration and passage time of migrants strongly influence their eventual spawning distribution.

KEYWORDS
acoustic telemetry, barriers, individual variation, migration, rivers

1 | INTRODUCTION

Migration is a life history strategy that enables animals to exploit spatially discrete habitats at different life stages (Bauer & Hoye, 2014; Dingle & Drake, 2007). Within populations, however, there can be considerable variations in the timing, distance, and route of migrations, which might partly reflect differences in the responses of individuals to environmental cues (Brown & Taylor, 2017; Eldøy et al., 2019). Variations in the timing of individual migrations can have consequences for fitness (Jensen et al., 2020; Smith & Moore, 2005), but may be an important buffer against environmental stochasticity at the population level (Freshwater et al., 2019; Shaw, 2020). The advancement of biotelemetry technology, techniques, and analytical methods is increasing our ability to identify the patterns and proximate causes and consequences of individual variation in migratory movements (Shaw, 2020).

Anthropogenic activities can greatly reduce habitat connectivity (Carpenter-Bundhoo et al., 2020). This can impact the fitness of migrating animals by preventing access to optimal reproductive or feeding sites, and/or incurring additional energetic costs as migrants attempt to overcome obstacles along their migratory path (Benoit et al., 2020; Castro-Santos & Letcher, 2010; Nyqvist et al., 2017). The ability of individuals to overcome barriers, and hence the persistence of populations within fragmented ecosystems, can be determined by their phenotypic traits (e.g., physical and behavioural traits) and the barrier characteristics (e.g., head height) (Kirk & Caudill, 2017; Rolls et al., 2014). Population-level diversity in migration phenology potentially can be reduced or disrupted by barriers, where passage by migrants relies on episodic environmental events which may be unpredictable/stochastic in nature (Zeigler & Fagan, 2014). Consequently, it is important to understand the extent to which barriers disrupt the passage of migrants, and how they potentially disrupt the predictable relationships between departure and arrival timing typical of migration along unfragmented routes (Schmaljohann, 2019). Furthermore, understanding the responses of animals to impediments along their migratory routes may inform conservation strategies aimed at improving connectivity or aiding passage of impediments (Kirk & Caudill, 2017; Sawyer et al., 2013).

There are now few rivers in the world that remain free-flowing over their entire length (Grill et al., 2019), especially in developed regions (Belletti et al., 2020). The consequences of this connectivity loss have been especially severe for diadromous species, which have experienced global population declines and extirpations (Lassalle et al., 2009; Limburg & Waldman, 2009). An anadromous species whose upstream migration to spawning grounds has been severely impacted by anthropogenic structures is the sea lamprey *Petromyzon marinus* L. (Guo et al., 2017). Upstream-migrating adults can experience substantial delays at man-made barriers (Silva et al., 2019), and individuals failing to pass have been recorded moving downstream, possibly in search of alternative passage routes (Rooney et al., 2015). In other anadromous species, individual variation in movements away from barriers following an approach ("retreats") have been linked to environmental conditions, phenotypic traits, and predator avoidance (Alcott et al., 2021; Harbicht et al., 2018). However, the drivers of variation in the behavioural responses of adult sea lamprey to delayed migration, and how barriers influence individual variation in migration dynamics, including retreat behaviours, are poorly understood.

There are several factors that make the sea lamprey a strong candidate species for studying migration processes within fragmented ecosystems. Globally, lampreys are unusual amongst anadromous species in their absence of fidelity to natal sites; suitable spawning habitats are located by a range of hydrological and olfactory cues, including pheromones released by larvae and spawning adults (Buchinger et al., 2015; Waldman et al., 2008). They also are semelparous, and cease feeding once they have entered fresh water (Araújo et al., 2013), so it can be assumed that all movements made during their spawning migration relate primarily to locating spawning habitat, and that individual movements are focused on achieving optimal spawning habitat rather than reaching a specific location.

Here, the individual variation in sea lamprey movements was quantified within a fragmented river ecosystem that featured multiple anthropogenic barriers of differing permeability in its lower reaches, the lower River Severn basin, western England, U.K. Sea lamprey that were acoustic-tagged during their upstream spawning migration were used to test the following hypotheses (H): H1, the distribution of passage times over barriers is related to lamprey body length, and the prevailing environmental conditions when a barrier is first approached; H2, individual body lengths and prevailing environmental conditions significantly influence the rate at which sea lamprey make downstream retreat movements away from barriers; H3,

individuals that incur longer delays at barriers, and move more during these delays, do not achieve the same upstream distance as those lampreys that successfully pass barriers without delay; and H4, in unobstructed reaches, there are predictable relationships between the time that individuals reach a new location and their departure timing from a known point, but this relationship is lost at barriers.

2 | METHODS

2.1 | Study system

The River Severn rises in mid-Wales before flowing for 354 km and discharging into the Bristol Channel, forming a drainage area of 11,420 km^2 (Durand et al., 2014). In the study area within the lower catchment, there are confluences with two major tributaries, the River Teme and River Avon, and there are eight major weirs (four on the main river channel, plus two each on the lower reaches of the rivers Teme and Avon) that result in the river being highly fragmented (Figure 1). The normal tidal limit is at Maisemore (Weir S1a) and Llanthony Weirs (S1b) on the western and eastern branches of the river, respectively (Figure 1). With the exception of S2 and Powick Weir on the River Teme (T1), which had notch and Larinier fish passes, respectively, there were no fish-passage structures on the weirs at the time of study. Weirs S2 to S4, and T1, were the main river barriers under investigation here (Figure 1). Although they were all passable at high discharge levels, their permeability varied at other times; S3 and T1 were impassable at low discharge, S2 was passable at all discharge levels recorded during the study, and S4 was only approached/passed at high discharge (Davies et al., 2021).

2.2 | Capture, tagging, and tracking

The study was completed from May to July 2018, covering the peak sea lamprey ("lamprey") spawning migration period in western Britain (Maitland, 2003). The lampreys were captured approximately 200 m downstream of S1a (Figure 1) in un-baited two-funnel eel pots (Lucas et al., 2009). Following their removal, they were held in water-filled containers before being anaesthetised (MS-222), having their biometric data recorded (mass to 10 g, length to 10 mm), and a Vemco V9 acoustic transmitter (29 × 9 mm, 4.7 g weight in air, 69 kHz; www.
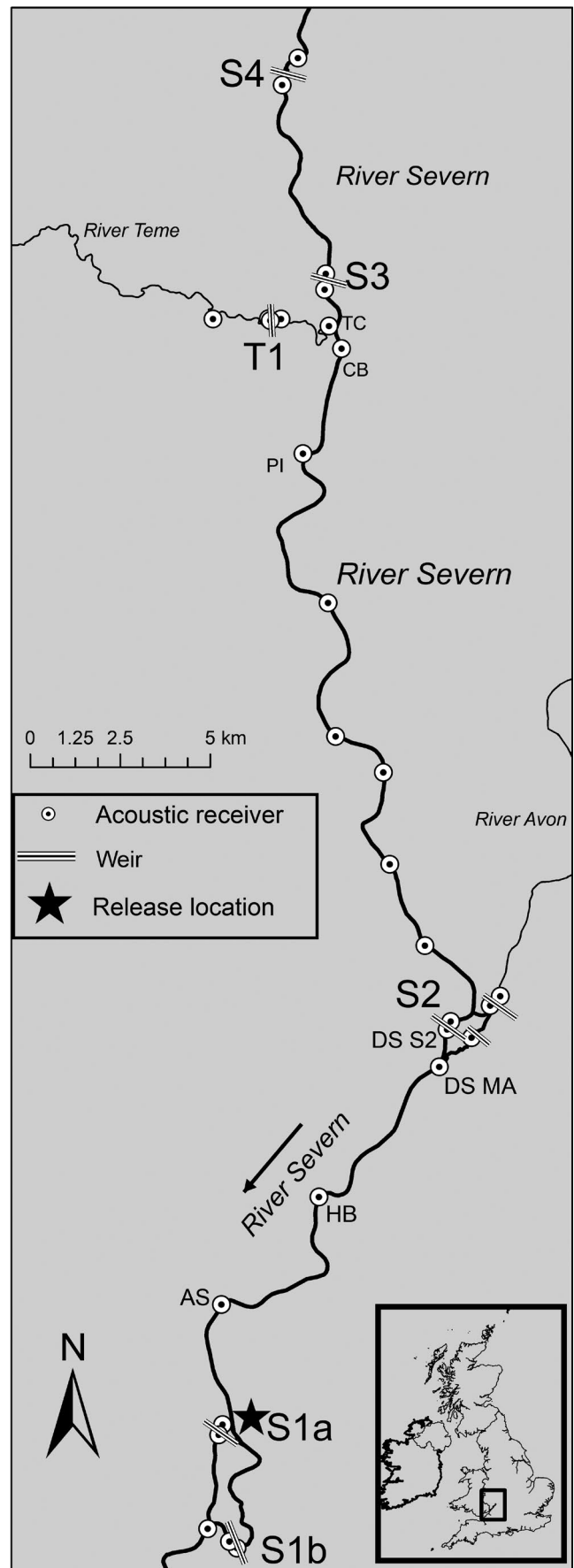

FIGURE 1 The River Severn catchment study area, including: location of capture and release of acoustic-tagged sea lamprey at the normal tidal limit of the river (black star); weirs (bars); and acoustic receivers (circles) in the rivers Severn, Teme, and Avon, U.K. The black arrow denotes the direction of flow. Receivers DS MA, TC, CB, and OB were used to confirm the retreat of sea lamprey from weirs. Receiver AS was used to estimate the timing of the first upstream movement of tagged sea lamprey following release

innovasea.com) surgically implanted. The transmitters featured a randomised 60-s pulse interval (minimum interval between acoustic pulses 30 s, maximum interval 90 s). In all cases, tag weight in air was less than 2% of body mass. In total, 60 lamprey were tagged and released on four occasions over the course of three weeks (Table S1). All lampreys were released upstream of weir S1a. Four individuals did not move upstream after release, so were removed from the dataset.

Lamprey were tracked using an array of 36 acoustic receivers (VR2-W and VR2-Tx; www.innovasea.com) deployed upstream and downstream of each navigation weir on the main channel of the River Severn and the flow-regulation weirs on the rivers Teme, Avon, and Mill Avon, with additional receivers deployed in unobstructed reaches between weirs (Figure 1). Receivers were anchored on steel fencing pins driven into the river bed. In the River Teme, which featured sections of relatively fast-flowing riffle, the receivers were located in slower-flowing pools to maximise their detection distances. Data were downloaded from receivers every 2 weeks until no further movements were detected. Range tests showed that 100% of test tag transmissions were detected a minimum of 100 m away from receivers in the River Severn, and a minimum of 50 m away from receivers in the River Teme. In all cases, the detection range was greater than the river width at the receiver deployment location. Detection efficiency calculations (using three sequential receivers to determine the efficiency of the middle receiver) indicated that missed detections accounted for <0.1% of lamprey movements between receivers.

2.3 | Data analyses

The hypothesis testing used an information theoretic approach (Burnham & Anderson, 2002) to select the most appropriate model from a set of a priori candidate models. For each hypothesis, we started with the most complex model that included data on all of the available predictor variables for testing, without interactions; a set of up to seven other candidate models were then selected a priori through a combination of simplifying this initial model whilst maintaining biological relevance from existing knowledge (e.g., Guo et al., 2017; Hansen et al., 2016). The candidate model that minimised Akaike information criterion values (AICc) was used to determine the best-fitting model (Burnham & Anderson, 2002). Candidate models were considered well-supported if they were within two ΔAICc of the best-fitting model, and improved on the null model by greater than two ΔAICc, and were not more complex versions of nested models with better support (Richards et al., 2011).

2.3.1 | Individual variability in passage time (H1) and retreat rates (H2)

In order to test H1 and H2, an "Approach → Passage/Retreat" framework was adopted (Figure 2), which incorporated the tendential, temporal, and spatial aspects of movement variation (Shaw, 2020). Approaches were upstream movements, characterised by detection
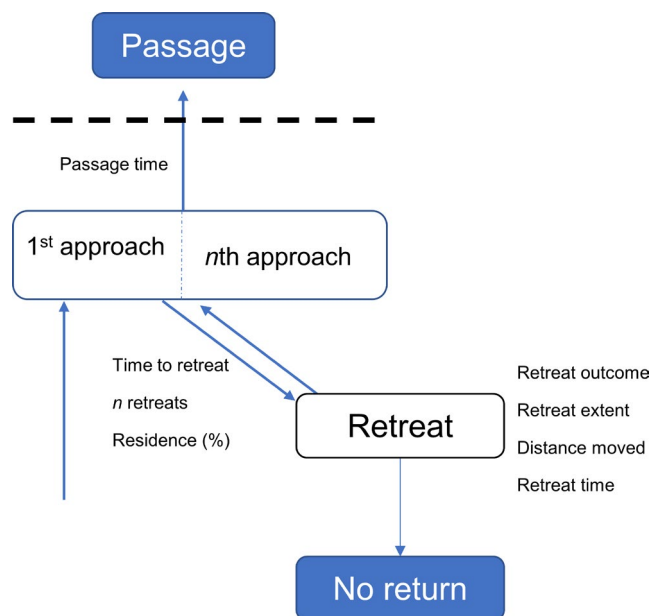

FIGURE 2 Framework used to analyse individual variation in movement by acoustic-tagged sea lamprey in relation to anthropogenic barriers in the River Severn catchment

on the receiver immediately downstream of the study weirs, following detection on receivers positioned c. 0.5–1 km further downstream (receivers DS MA [S2; Figure 1], TC/CB [S3; Figure 1], OB [T1; Figure 1]); passage was defined as subsequent detection on a receiver upstream of the weirs following an approach, and retreats were defined as downstream movements away from the weirs following an upstream approach, confirmed by subsequent detection on receivers positioned c. 0.5–1 km downstream (Figure 1). The timing of approach, passage, and retreat was defined as the time of first detection on the destination receiver. Terminal downstream movements (i.e., not followed by a subsequent approach) were not included in the analysis of retreats owing to uncertainty over the status of the individual (i.e., whether the movements were by pre-spawning, post-spawning, or dead individuals). Metrics within the framework (Table 1) were quantified for each individual at four weirs upstream of the release site (S2, S3, S4, and T1; Figure 1). Continuous metrics are presented as median values with lower (25%) and upper (75%) quartiles ("LQ-UQ"). The detection data were analysed in R (R Core Team, 2020), with use of the packages Vtrack for classifying movement events (Udyawer et al., 2018), and dplyr and ggplot2 for data manipulation and visualisation (Wickham et al., 2019).

To then decouple the causes of variation in passage times and retreat rates between intrinsic (body length) and extrinsic (environmental) factors, data from weir S2 were used as these provided the largest sample size of lamprey approach ($n = 56$) and passage ($n = 50$), with passage rates at this weir already established as being positively correlated with environmental variables, particularly increased river discharge (Davies et al., 2021). Lampreys that passed the weir were categorised as having been non-delayed (passed the weir within 24 hr of arrival) or delayed in passage (passed the weir over 24 hr after arrival).

TABLE 1 Glossary of metrics used to explore variation in catchment-scale movement behaviour by sea lamprey associated with man-made barriers. Weir codes as in Figure 2

Metric	Definition	Quantified at
Per cent passage	% of individuals detected on the receiver immediately downstream of the weir that subsequently are detected upstream	S2, S3, S4, T1
Passage time	Time elapsed from first detection on receiver immediately downstream of the weir to first detection upstream	S2, S3, S4, T1
Per cent retreated	% of individuals detected retreating for the weir	S2, S3, T1
Retreat extent	Greatest downstream distance moved during a retreat by retreating individuals	S2, S3, T1
Retreat outcome	Whether an individual returned to the same weir or explored an alternative tributary during retreat movements	S2, S3, T1
Total retreat distance	Distance moved during all retreats at each weir	S2, S3/T1
Cumulative retreat distance	Distance moved during all retreats at all weirs	All weirs
Time-to-retreat	Time elapsed from detection on receiver immediately downstream of weir until first detection further downstream	S2
n retreats	Number of downstream movements away from weir	S2
Duration of retreat	Time elapsed from start of retreat to next approach of same or different weir	S2
Total retreat time	Total time spent in retreat from weir	S2
Residence %	% of time spent immediately downstream of weir between first approach and passage	S2

In order to test the effect of phenotypic traits and environmental variables on delayed migration (H1) logistic regression was used where body length was used as the phenotypic trait. To assess its effect on delayed migration, the initial model also used movement speed of first approach (speed of movement between the release site and first approach, chosen as a proxy for swimming ability), with the abiotic variables capture date, river discharge at first approach (as recorded at Saxon's Lode gauging station, 3 km upstream of weir S2), and water temperature at first approach (recorded by a logger immediately downstream of weir S2). Best-fitting and well-supported models were selected from the candidate models by the process outlined above.

In order to test H2 on how body length and environmental conditions influenced the retreat rate of lampreys from Weir S2 (Figure 1), a mixed-effects Cox proportional hazards model was used (Castro-Santos & Haro, 2003; Goerig et al., 2020). Individuals were considered available to retreat if they were last detected at the receiver DS S2 during an upstream approach (Figure 1). Individuals remained in the "risk set" (i.e., the set of individuals available to retreat) until their retreat downstream or passage over the weir; the time of retreat was recorded as the time of first detection at receiver DS MA, and passage was classified as the time of first detection on any receiver upstream of S2 (Figure 1). In the initial model, the time-varying covariates were river discharge (m³/s), daily change in discharge (m³/s), water temperature (°C) and diel period (day/night, based on the time of sunset and sunrise at weir S2); lamprey body length (mm) also was included as a covariate. All retreats by individuals that retreated multiple times were included. Approach number was included as a

categorical effect (1st, 2nd, or 3rd approaches, with 4th or subsequent approaches combined into 4th+) to test whether undertaking previous retreats affected retreat rates on subsequent approaches. In addition, individual identification number (ID) was included as a random effect to account for multiple retreat observations from the same individual. Lamprey that passed the weir were censored (removed) from the model dataset at the time of passage, but individuals that made no retreats remained in the risk set until passage. Other candidate models, model-fitting, and selection then were carried out as described previously. The assumptions of proportional hazards in the top-ranked Cox models were assessed by visual inspection of Schoenfeld residuals to confirm a horizontal slope for each covariate (Schoenfeld, 1982). Covariate effects from the final model were presented as hazard ratios, which represent the impact on the retreat rate of increasing the value of continuous covariates by one unit (e.g., by 1 m³/s for river discharge) or by changing the value of a categorical covariate. The analysis was conducted in the coxme package (Therneau, 2020) in R (R Core Team, 2020).

2.3.2 | Onward migration consequences of delay and movement at barriers (H3)

In order to test the subsequent consequences of delayed passage and retreat movements (H3) for the migration of the lampreys, data were used from S2, the first weir encountered. Generalised linear models (GLMs) were used to assess how passage and retreat movements

TABLE 2 Summary of variation in passage, retreats, and extent of retreats by acoustic-tagged sea lamprey at three weirs in the River Severn catchment

Weir	n Approached	n Passed (%)	Passage time (days)	n Retreaters (%)	Retreat outcome (% retreaters exploring alternative tributary during retreat)	Retreat extent (km)	Total retreat distance (km)
S2	56	50 (89%)	10.4 (0.4–18.6)	26 (46%)	1 (4%)	21.1 (1.0–23.6)	50 (6.6–83)
S3	41	17 (41%)	5.3 (4.1–13.0)	16 (40%)	8 (50%)	1.3 (1.0–5.6)	8 (1–14)
S4	17	17 (100%)	0.2 (0.1–0.3)	NA	NA	NA	NA
T1	10	4 (40%)	0.1 (0.0–0.1)	3 (30%)	3 (100%)	3.0 (3.0 –3.0)	8 (1–14)

Notes: Weir codes as in Figure 1. Continuous metrics presented as median values alongside lower (25%) and upper (75%) quartiles (LQ, UQ). *n*, number of individual sea lamprey. Refer to Table 1 for definition of column headings.
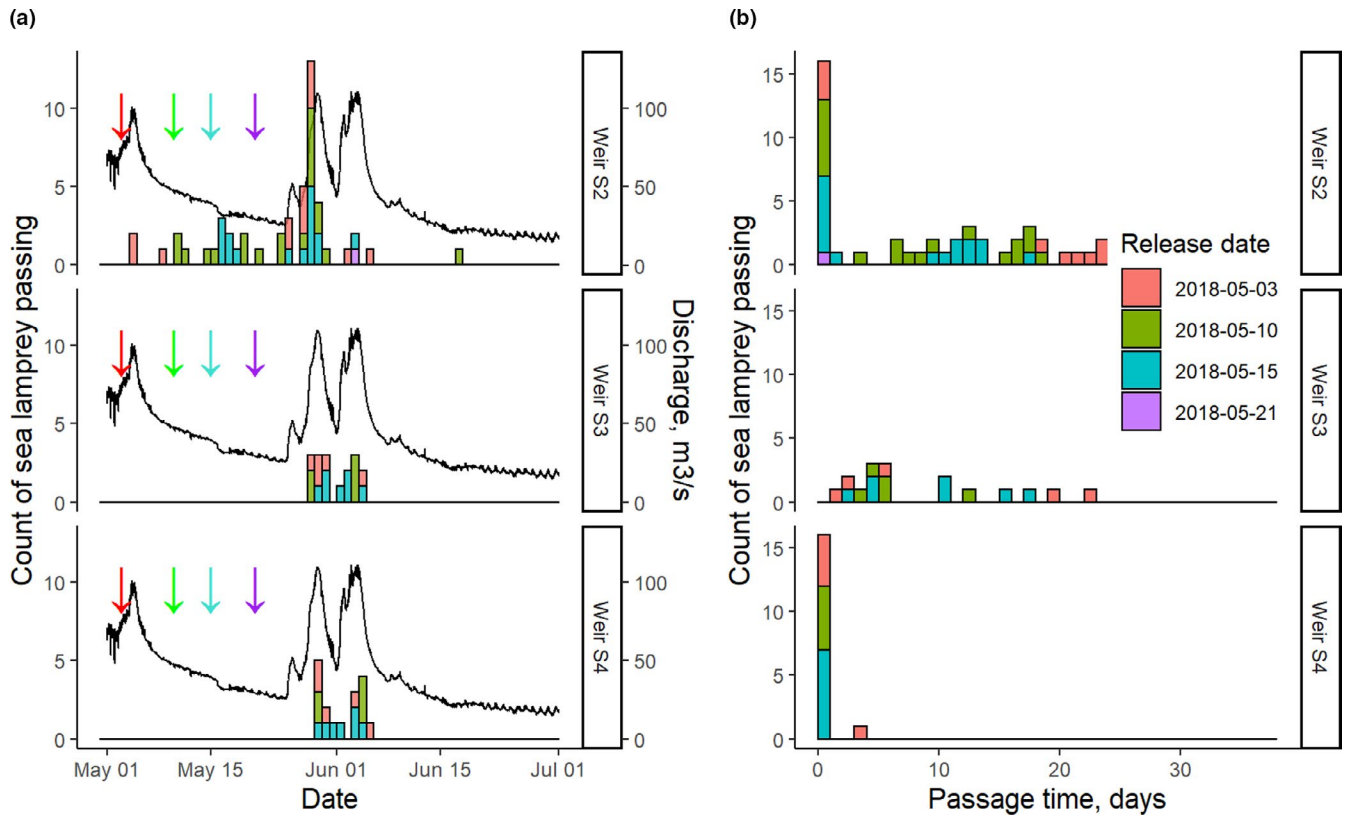

FIGURE 3 (a) Distribution of passage for acoustic-tagged sea lamprey at weirs S2, S3, and S4. Black line (secondary axis) is discharge recorded at Saxon's Lode gauging station, located approximately 3 km upstream from S2. Bar colours correspond to individuals from four release dates (arrows) of four batches of tagged sea lamprey (b) Distribution of passage times for acoustic-tagged sea lamprey at weirs S2, S3, and S4

influenced the overall migration extent of individual lampreys (measured as the furthest upstream location achieved relative to S2), and their upstream movement speed (measured as the movement speed recorded between passage of S2 and the Severn/Teme confluence). As the movement distance of lampreys during delay at S2 was multimodally distributed (zero-inflated), it was not included as a continuous variable in GLMs but instead categorised into two groups: (a) a retreat was detected (movement recorded during delay >0 km, *n* individuals = 26) and (b) no retreat was detected (movement recorded during delay = 0 km, *n* = 24). Delay length also was treated as a categorical variable (delayed/non-delayed). Upstream movement speed was log-transformed to account for positive-skew. Individual body length was retained as an explanatory factor in the models. Owing to

logical linkage between delay length and retreat movements, these variables were not included in the same model sets. Delay length and retreat movements were individually combined with body length in candidate GLM model sets, and compared to model sets containing body length only and the intercept only (null model).

2.3.3 | Barriers disrupt predictable timings of movement in unfragmented reaches (H4)

To then test H4 on how individual variation in passage time at the weirs influenced the intrinsic variation in the timing of upstream migration within the tagged sample (measured as the timing of

first upstream movement of each lamprey from the release site), the tagged lampreys were put into rank order and compared in unobstructed versus obstructed reaches of river as they progressed upstream through the river. Rank order testing was chosen to explore the impacts of barriers on between-individual variation in upstream movement timing; the timing of first upstream movement by individuals in this study was determined by the timing of capture, and thus the upstream-moving individuals were not a representative sample of individual variation in run timing. The individual rank orders of the timings of the start and finish of movement through reaches of river were determined for: (a) the onset of upstream movement from S1 (the release site), S2, and S3 to their arrival downstream of S2 (journey distance: 16 river [r] km), S3 (42 rkm), and S4 (49 rkm), respectively; and (b) the arrival and passage times at S2 (0.8 rkm), S3 (0.7 rkm), and S4 (0.8 rkm) (Figure 1). The strength of correlation between departure and arrival in movements through free-flowing reaches and passage of weirs was tested and compared using Spearman's rank correlation coefficient (rho, ρ).

3 | RESULTS

3.1 | Overview of passage times and rates, and time to retreat

The metrics of the "Approach → Passage/Retreat" framework (Table 1; Figure 2) revealed patterns of individual movement variation at weirs, as well as variation between weirs (Table 2). Passage times, as median (LQ-UQ) at S2, S3, S4, and T1, were 10.4 (0.4–18.6), 5.3 (4.1–13.0), 0.2 (0.1–0.3), and 0.1 (0.0–0.1) days, respectively. Of the 50 sea lamprey that passed weir S2, passage times were bimodal, with 16 (32%) passing within 24 hr of the first approach (i.e., non-delayed), whereas the remainder ($n = 34$; 68%) passed during episodic high-flow events after 17.1 (6–24) days (Figure 3). At S3, passage times were multimodal; no individuals passed within 24 hr of the first approach, and all passages were associated with episodic high flow events (Figure 3). At S4, all approaches and passages were associated with episodic high flow events and passage times were unimodal, with 94% of passage occurring within 24 hr of the first approach (Figure 3).

The proportions of individuals undertaking downstream retreats at weirs were similar (S2 = 46% [n approached = 56], S3 = 40% [n = 41], and T1 = 30% [n = 10]). The median retreat extent at S2 (21.1 km [1.0–23.6], n = 26) was generally greater than at S3 (1.3 km [1.0–5.6], n = 16), and T1 (3.0 km [1.0–4.8], n = 3) (Table 2). There was inter-individual variation in the downstream extent of retreats; of the 26 retreating individuals at S2, eight (31%) were detected 1 km downstream of S2 (DS MA; Figures 2 and 4a), two (8%) were detected 6 km downstream (HB; Figure 2), and the remainder (n = 16; 62%) were detected retreating downstream of the normal tidal limit of the river, more than 16 km downstream of Weir S2 (Figure 4b). The median total retreat distance moved by retreating

individuals at S2 (50.0 km [6.6–83.0], n = 26) was generally greater than that moved by individuals retreating from S3 and/or T1 (8.0 km [1.0–14.0], n = 19) (Table 2). The median cumulative retreat distance moved by all lamprey at all weirs was 5.8 km (LQ-UQ 0–51.0 km, range 0–144 km). Retreat movements represented 11% (LQ-UQ 0%–52%, range 0%–76%) of the total distance travelled by the lampreys between the release site and the upstream extent of their migration.

For individuals retreating from weir S2 after their first approach (n = 26), the median (LQ-UQ) time-to-retreat for the first retreat was 0.6 (0.1–0.9) days. The median number of retreats by these individuals was four (range two to five) and the most retreats by one individual was 11. The median per-individual duration of retreat was 2.3 (1.3–4.5) days, and total retreat time was 9.2 (4.2–14.3) days for retreating individuals. Of the 34 individuals with delayed passage (>24 hr after their first approach) at S2, nine (27%) individuals performed no retreats (100% residency immediately downstream of S2; Figure 4c). For retreating individuals, median residency in the section immediately (i.e., <1 km) downstream was 26% (10%–78%). For the 16 individuals that retreated from S2 to areas downstream of S1, their upstream return necessitated re-passage of S1, incurring an additional delay of 2.3 ± 1.5 days.

3.2 | Hypothesis testing

In testing the effect of variation on body length on the bimodal distribution of passage times at Weir S2, and in relation to abiotic variables (H1), none of the candidate models of the logistic regression were well-supported (Table S2). These results suggest that neither lamprey body length, upstream movement speed, nor the abiotic variables were driving the bimodal pattern of passage times at this weir.

In testing the influences on retreat rates (H2), the best-supported model was the full model (Table 3). In this model, higher discharge significantly reduced retreat rates, with retreat rates also significantly lower at night than during the day. Second and third approaches were associated with significantly reduced retreat rates compared to the first approach (Table 4; Figure 5). Although body length and Δdischarge were included in this model as covariates, they did not have significant effects ($p > 0.05$; Table 4). The standard deviation in per-individual random effects coefficients of 0.56 indicated substantial individual variation in retreat rates. Retreat rates were not constant in time; between 0 and 1 days, retreats occurred with relatively high likelihood, after which the retreat rate for remaining individuals decreased, as evidenced by a plateau in the Kaplan Meier survival curves (Figure 5). The GLMs testing the consequences of delayed passage and retreat behaviours (H3) then indicated that neither passage time at S2, total retreat distance, nor body size were not significant predictors of either (a) the upstream extent of migration (Table S3) or (b) upstream movement speed after passage ($p > 0.05$; Table S4). In both sets of GLMs, all of the model sets received lower AIC support than the intercept-only model (Tables S3 and S4).
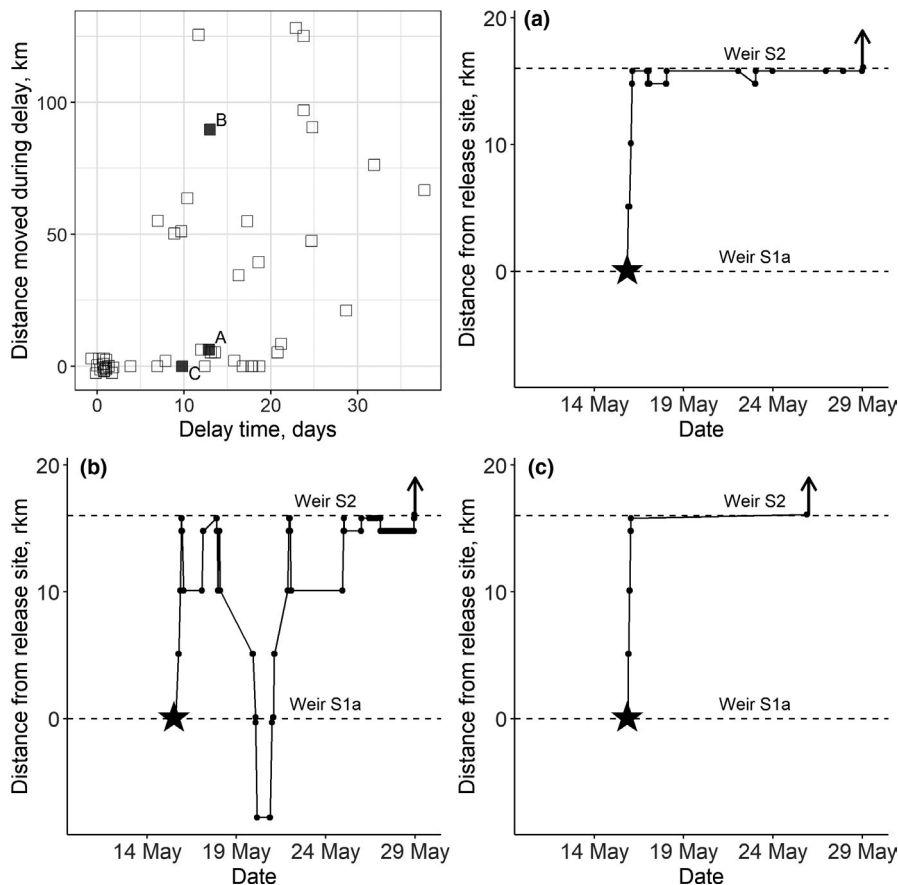
FIGURE 4 Main panel; delay and distance moved during delay by 50 upstream – migrating acoustic-tagged sea lamprey that passed weir S2 (see Figure 1) in the River Severn. Panels a–c: movement tracks for three sea lamprey illustrating the diversity of catchment-scale movements made during delays of similar duration at weir S2. Black points within movement tracks denote detections on acoustic receivers. Black arrows represent passage of S2 for each individual. Y-axis units are river (r)km, representing the circuitous distance of each location on the track from the release site. Horizontal dashed lines represent the location of weirs. Black stars indicate the location and time of release. (a) Individual displaying no detectable movements downstream during delay. (b) Individual displaying short distance movements, detected 1 km downstream during delay at receiver MA. (c) Individual displaying long-distance movement, including return downstream to tidal area downstream of the release site

TABLE 3 Summary of candidate Cox proportional hazard models of sea lamprey time-to-retreat from weir S2

Model name	Model structure	df	Log-likelihood	ΔAIC	Weight
Full model	Body length + light + Δdischarge + discharge + water temperature + attempt group	24	−412	0	0.99
Environmental conditions only	Light + Δdischarge + discharge + water temperature	24.4	−416	9.3	0.01
Individual characteristics only	Body length + attempt group	15.5	−454	66.5	0.00
Hydraulic conditions only	Discharge + Δdischarge	17.8	−455	73.3	0.00
Null model	Intercept only	14	−461	77.1	0.00
Body length only	Body length	14.4	−461	78.3	0.00

The relationships between individual departure from the release site and arrival timings (H4) revealed a significant correlation for the time taken to move upstream from their release site to S2, indicating that the rank order of variation in upstream progress was maintained during this 16 km reach (Spearman's rho [ρ] = 0.98, $p < 0.01$) (Figure 6a). However, there was no significant correlation between the rank order of first detection downstream and upstream of weir S2 (0.6 rkm upstream movement; $\rho = 0.23$, $p = 0.11$) (Figure 6a). Arrival at S3 also was strongly correlated with passage time at S2 ($\rho = 0.82$, $p < 0.01$) (Figure 6b), and the rank order of approach and passage at S3 also was significantly correlated ($\rho = 0.61$, $p = 0.01$) (Figure 6b). The order of arrival of lampreys at S4 was strongly correlated with passage time at S3 ($\rho = 0.99$, $p < 0.01$) (Figure 6c), as was the order of arrival and passage at S4 ($\rho = 0.98$, $p = 0.01$) (Figure 6c).

4 | DISCUSSION

Characterising movement behaviours of animals in fragmented ecosystems is critical to understanding, predicting, and mitigating the consequences of fragmentation. In a highly fragmented river catchment, we revealed here that the individual variation in the movements of migratory sea lamprey was expressed in their ability to pass anthropogenic barriers and where this was not achieved, then in the subsequent movements of those individuals. There were distinct unimodal, bimodal, and multimodal patterns of variation in passage times evident at the different barriers, which potentially were related to the physical characteristics of the barrier and prevailing river discharge conditions when the barriers were first approached, but not related to lamprey body sizes (contrary to H1). When the

TABLE 4 Summary of covariate effects from best-fitting Cox proportional hazards model of sea lamprey time-to-retreat from weir S2. Significant p-values (p < 0.05) are displayed in bold

Covariate	Hazard ratio	SE	z	p
Body length (m)	0.8	2.34	−0.08	0.94
Approach 2	3.60	0.33	3.92	**<0.01**
Approach 3	2.29	0.33	2.48	**0.01**
Approach 4+	1.25	0.30	0.74	0.46
Light:night	10.61	0.36	6.6	**<0.01**
River discharge (m^3/s)	0.41	0.39	−2.25	**0.02**
Δdischarge	0.96	0.16	−0.24	0.81
Water temperature	0.92	0.08	−0.91	0.36

FIGURE 5 Kaplan–Meir survival distributions of acoustic-tagged sea lamprey time-to-retreat at Weir S2. Lines represent percentage of sea lamprey that are yet to retreat, by approach number

lampreys were delayed at weirs, their consequent exploratory movements comprised a substantial proportion of the total distance moved during their spawning migration, with evidence that retreat rates were positively affected by higher river discharge (as per H2), but not lamprey body length (contrary to H2). There was no evidence of a negative consequence of increased delay or movement during delay of these movements on upstream migration extent or speed (contrary to H3). The predictability in rank arrival timing of the lampreys was high in unobstructed reaches but was strongly disrupted at barriers as a consequence of individual variation in passage times (as per H4).

Passage time is a key metric for assessing the impact of barriers on upstream migration in fish (Silva et al., 2018), and numerous studies have identified the abiotic, individual, and behavioural factors affecting passage rates at barriers (Castro-Santos et al., 2017; Goerig et al., 2020; Kirk & Caudill, 2017; Newton et al., 2018). A previous study on these lampreys indicated that their passage over Weir S2 was increased during periods of elevated river discharge (Davies et al., 2021). Here, we revealed that across all of the lampreys passing Weir S2, there was a strong bimodal distribution in their passage times, whereby 32% of individuals passed within 24 hr of the first approach but the remainder passed after a median delay of over 2 weeks. Testing the influences of body length and environmental variables on this distribution did not determine the causal factors of this bimodal distribution – contrary to H1 – but it may have been a consequence of several factors that could not be tested here. For example, passage probability may have decreased sharply if initial attempts to pass the barrier resulted in exhaustion in unsuccessful individuals. Unsuccessful attempts to pass also may have resulted in lamprey switching behavioural states (Gurarie et al., 2016) to search for alternative passage routes or spawning habitats (retreat) or adopt a sedentary sit-and-wait (for favourable passage conditions) strategy (Kirk & Caudill, 2017; Rooney et al., 2015). Although we show evidence of large-scale exploratory behaviour, understanding these apparent sit-and-wait strategies requires finer-scale telemetry/biologging studies to assess the behaviour of individuals that were delayed but remained in the immediate vicinity of migration barriers
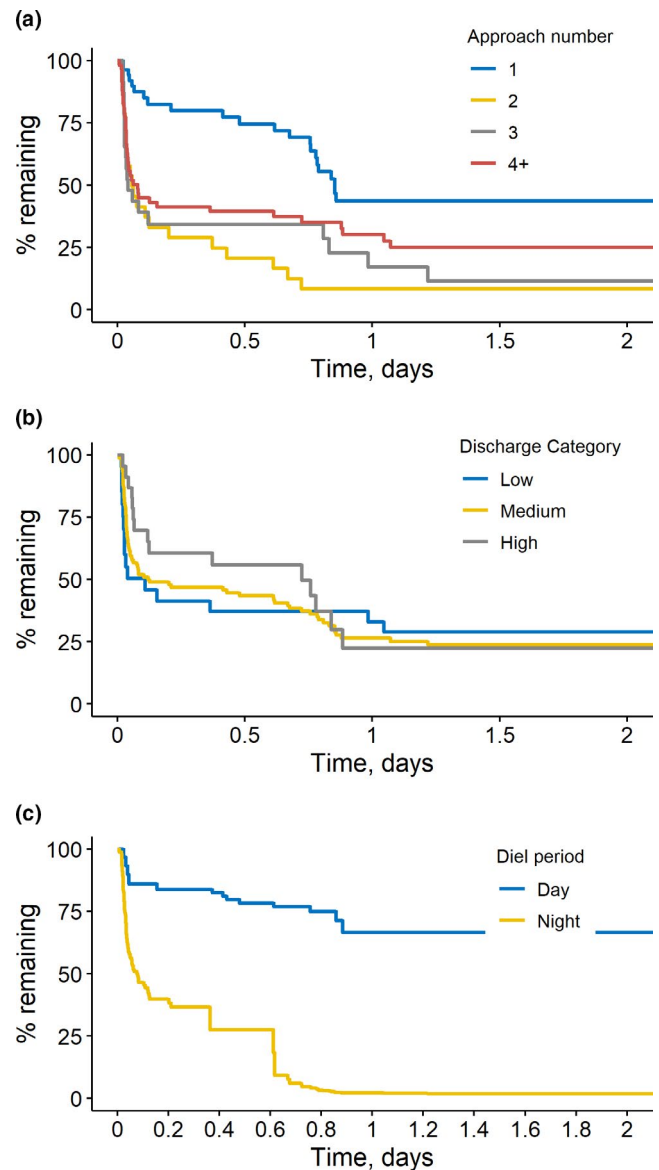
(Harbicht et al., 2018). Moreover, the multimodal passage times at S3, where passage was only possible during high flows, illustrate how migratory delays can be determined from arrival times with respect to episodic environmental events (Zeigler & Fagan, 2014), which in this case manifested in the early arrivals experiencing the longest delays. Finally, given the relatively coarse positioning of individuals inherent in the use of omnidirectional acoustic receivers with a detection range >100 m, we cannot rule out the possibility that some upstream movements towards weirs, defined here as approaches that did not culminate in an attempt to pass a weir, but resulted in halting for another reason such as individuals locating spawning conspecifics (Pinder et al., 2016). More detailed studies, potentially incorporating fine-scale radio or acoustic telemetry, are needed to truly determine behaviour immediately downstream of weirs.
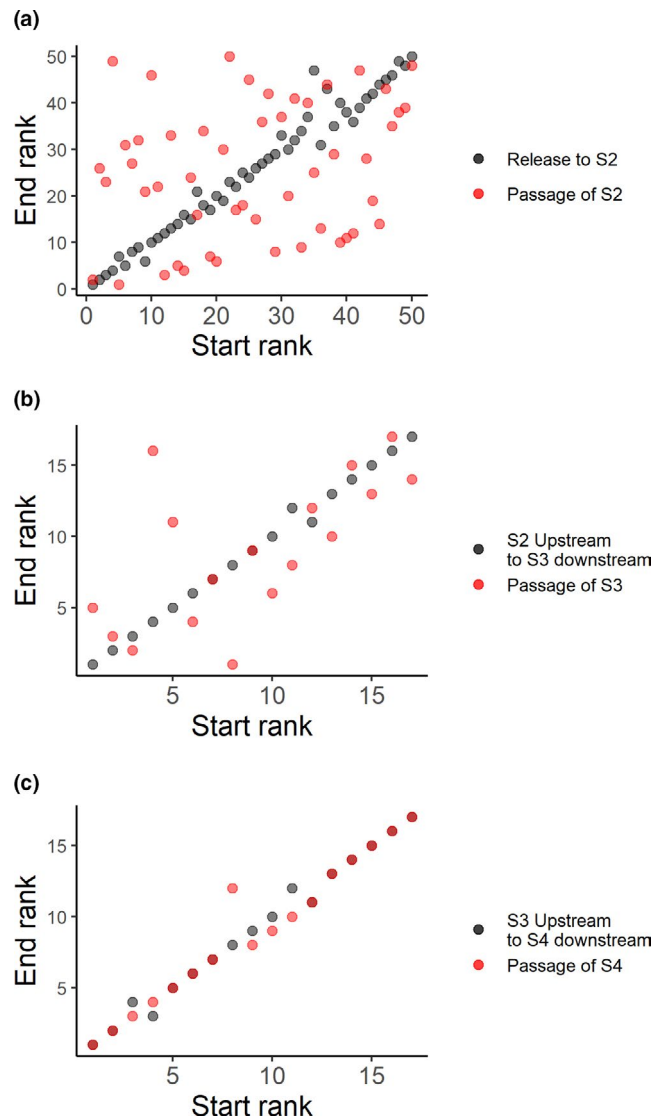
(a)

(b)

(c)

FIGURE 6 (a) Rank order of departure and arrival for acoustic-tagged sea lamprey moving upstream between release and weir S2 (black); rank order of first arrival and passage for acoustic-tagged lamprey at weir S2 (red). (b) Rank order of departure and arrival for acoustic-tagged sea lamprey moving upstream between weirs S2 and S3 (black); rank order of first arrival and passage for acoustic-tagged lamprey at weir S3 (red). (c) Rank order of departure and arrival for acoustic-tagged sea lamprey moving upstream between weirs S3 and S4 (black); rank order of first arrival and passage for acoustic-tagged lamprey at weir S4 (red)

Individuals that are unable to pass migration barriers potentially can locate alternative, unimpeded, routes to favourable spawning grounds (Holbrook et al., 2016; Rooney et al., 2015). Here, we revealed that the retreat movements made by some sea lamprey in response to weirs comprised a substantial proportion of their total distance moved, but varied significantly in tendential, temporal and spatial ways (Shaw, 2020). For example, at the first three weirs encountered by upstream-migrating lamprey, more than 30% of individuals made downstream (>1 km) movements, whereas others displayed a high degree of residency to the area immediately

downstream of the barriers. This variation in movement tendency may reflect different strategies with respect to passage at barriers (Kirk & Caudill, 2017), with some individual lampreys searching for alternative routes and others awaiting favourable passage conditions. For example, the downstream extent of retreats from S2 (median 21.1 km) were substantially greater than at S3 (1.3 km) and T1 (3 km), potentially reflecting the varying suitability of alternative tributaries as spawning sites. At S3 and T1, 50% and 100% of retreating individuals explored alternative routes upstream in the River Teme and River Severn, respectively, whereas only one individual (4%) of those retreating from S2 explored an alternative upstream route (Mill Avon).

By testing the retreat rate data against abiotic data, we revealed that increased river discharge reduced retreat rates and the likelihood of exploratory behaviours, with this consistent with H2. Thus, this suggests that retreats, as a behavioural response to impeded passage, occurred at higher rates during low flow conditions that were not conducive to passage of the barrier in question. This behavioural plasticity is consistent with other studies of animal movement behaviours, where variability in individual behaviours often is driven by variations in environmental conditions (Shaw, 2020). For example, in migratory fish attempting to pass barriers, generally there are increased attempt rates at passage in periods of elevated river discharge, emphasising how behaviour can be plastic with regard to environmental conditions (Goerig et al., 2020; Newton et al., 2018). Similar to the distribution of passage times at S2, the temporal distribution of retreats suggest there are time "windows" during which retreat was likely to occur following an approach, after which retreat became less likely, potentially due to a behavioural switch from an active "searching" state to a sedentary "waiting" state (Kirk & Caudill, 2017). Overall, testing data on retreat indicated the existence of substantial inter-individual variation in retreat rates, although the underlying causes of this remain uncertain. Although intrinsic variation in migration strategy may play a role, other untested factors include sex, which was not determined here, and the reproductive/nutritional state of individuals, which have been shown in other species to influence movement tendencies (Harbicht et al., 2018). Furthermore, although we considered the retreat behaviours of individual lamprey, there may have been important influences of conspecifics on these behaviours (Okasaki et al., 2020), which we were unable to test owing to a lack of information on the number and timing of lamprey entering the river; while challenging to collect, this information may inform future studies on passage and retreat behaviour.

When faced with barriers to migration, exploring alternative routes may represent a trade-off (Sanz-Aguilar et al., 2012) between the probability of locating suitable spawning habitat and the probability of favourable passage conditions occurring. In sea lamprey, the energetic costs of retreat movements may be particularly significant given that the species is semelparous and that individuals cease feeding after entering fresh water, so rely on stored energy reserves for upstream migration and spawning (Araújo et al., 2013).

Such costs may be considered a cryptic impact of anthropogenic barriers on migratory fish species. In highly fragmented systems, the negative effect of performing downstream movements may be amplified by having to re-ascend barriers, as was observed in 16 of the 26 individuals that retreated from S2 and incurred additional migration delays during re-ascent of S1. Previous studies of migratory animal species have found associations between migratory strategy and fitness and productivity (Abrahms et al., 2018; Cheng et al., 2019; Ely & Meixell, 2015), yet there was little evidence here that downstream movements resulted in a reduction in migration extent in lampreys, contrary to H3. Previous studies have reported that the energetic costs of unobstructed upstream migration in sea lamprey may be low relative to energy expended during spawning (William & Beamish, 1979). This is consistent with energetic studies of terrestrial animals, which suggest that additional movements caused by habitat fragmentation may be negligible relative to the cost of reproduction (Paterson et al., 2019). However, the majority of lamprey examined in this study achieved an upstream extent of migration that was immediately downstream of a barrier (Davies et al., 2021). Thus, the permeability of upstream barriers, rather than energy expended during exploratory movements, was suggested as being the primary driver of their upstream extent. As identifying spawning sites or quantifying the reproductive success of tagged individuals was beyond the scope of this study, it is suggested that there is a need to develop a more complete understanding of the spatial factors driving their spawning success if the consequences of catchment-scale movement behaviours are to be better understood.

Inter-individual variation in migration timing might reflect variations in their responses to environmental cues, and may influence fitness (Brodersen et al., 2012; Jensen et al., 2020; Tibblin et al., 2016) and buffer populations from environmental stochasticity (Freshwater et al., 2019). In this study, barriers disrupted variation in upstream progress in lamprey and increased the influence of environmental variability on upstream progress rates, as per H4. In unobstructed sections of river, the ranked individual departure time (start of journey) was highly correlated with arrival time (end of journey), indicating that relative variation in upstream progress was preserved in free-flowing sections. By contrast, at the first two barriers encountered by upstream-migrating lamprey, the correlation between the individual rank of departure timing (first approach) and arrival (passage) was non-significant or reduced; the overall effect was that timing arrival at upstream sites was unpredictable based on the timing of release. Sea lamprey are believed to respond to environmental cues (temperature, flow) in estuaries or transitional waters to commence the spawning migration from "holding" zones into fresh water; the extent to which individual variation drives the initiation of upstream migration to spawning sites is unknown, but males generally are thought to migrate earlier than females (Clemens et al., 2010). In fragmented ecosystems, a population consequence of individual variation in barrier passage time may be a dilution of this phenological variation, whereby early- and late-migrating individuals are effectively "mixed" during the upstream migration, potentially disrupting sex-linked structuring of phenologies and reproductive processes such as nest building.

In summary, anthropogenic barriers can both disrupt and reveal individual movement variation in anadromous species. For example, barriers can disrupt the predictability of individual upstream progress, in comparison to unobstructed river sections, but the degree of disruption is likely to be dependent on environmental conditions and the characteristics of the barriers. Barriers also can reveal individual variation in the tendential, temporal, and spatial aspects of retreats, a behaviour that constituted a substantial proportion of the total distance moved during the spawning migration of some of the sea lamprey in this study. These results suggest that fish passage studies should consider catchment-scale exploratory movements as a mechanism by which individuals optimise spawning success in fragmented systems, and the individual drivers and consequences of these movements warrant further study across a range of contexts.

CONFLICTS OF INTEREST
The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS
Conceived and designed the field experiments: JDB, ADN, JRD, CB, RV, JRB, PD. Conducted fieldwork: JDB, ADN, JRD, PD. Conducted analysis: PD. Wrote the paper: PD. Edited the Paper: JDB, JRB, ADN, JRD, CB, RV. Revised the Paper: PD, JDB, RDB.

DATA AVAILABILITY STATEMENT
Data used in this study will be made available by the authors upon reasonable request.

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