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

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Summary

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.

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 30-46% of individuals made retreat movements, and between 5-100% 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 prior to 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.

5. Anthropogenic barriers can thus 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.

INTRODUCTION

Migration is a life history strategy that enables animals to exploit spatially discrete habitats at different life stages (Dingle & Drake, 2007; Bauer & Hoye, 2014). 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 (Smith & Moore, 2005; Jensen et al., 2020), 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 (Castro-Santos & Letcher, 2010; Nyqvist et al., 2017; Benoit et al., 2020). 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) (Rolls et al., 2014; Kirk & Caudill, 2017). Population-level diversity in migration phenology can potentially 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). Further, understanding the responses of animals to impediments along their migratory routes may inform conservation strategies aimed at improving connectivity or aiding passage of impediments (Sawyer et al., 2013; Kirk & Caudill, 2017).

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, Crouzet & Rochard, 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, Andreou & Britton, 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 (Harbicht et al., 2018; Alcott et al., 2021). 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 (Waldman, Grunwald & Wirgin, 2008; Buchinger et al., 2015). They are also 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. 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.

METHODS

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 11420 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 on each of the lower reaches of the River Teme and River 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). While 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).

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 x 9 mm, 4.7-g weight in air, 69 kHz; www.innovasea.com) surgically implanted. The transmitters featured a randomized 60 second pulse interval (minimum interval between acoustic pulses of 30 seconds, maximum interval of 90 seconds). 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 surgical procedures were completed under UK Home Office project licence PD6C17B56. 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 less than 0.1% of lamprey movements between receivers.

Data analyses

The hypothesis testing used an information theoretic approach (Burnham & Anderson 1998) 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 7 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. Hansen et al., 2016; Guo et al., 2017). The candidate model that minimised Akaike information criterion values (AICc) was used to determine the best fitting model (Burnham and 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).

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

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 on the receiver immediately downstream of the study weirs, following detection on receivers positioned ~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 ~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 due 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 and 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 sea 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 hours of arrival) or delayed in passage (passed the weir more than 24 hours after arrival).

Testing the effect of phenotypic traits and environmental variables on delayed migration (H1) used logistic regression, 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 being 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.

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 (m^3s^{-1}), daily change in discharge (water temperature (°C) and light (as day/night, based on the time of sunset and sunrise at weir S2); lamprey body length (mm) was also 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, with 4th or subsequent approaches combined into 4th+) to test whether undertaking previous retreats affected retreat rates on subsequent approaches. In addition, individual ID was included as a random effect to account for multiple retreat observations from the same individual. Lamprey that passed the weir were censored 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 was then carried out as previously described. 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 m^3s^{-1} 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).

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

To test the subsequent consequences for the migration of the lampreys of delayed passage and retreat movements (H3), data were used from S2, the first weir encountered. Generalised linear models (GLMs) were used to assess how passage and retreat movements 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: (i) a retreat was detected (movement recorded during delay > 0 km, *n* individuals = 26) and (ii) no retreat was detected (movement recorded during delay = 0 km, *n* = 24). Delay length was also 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. Due 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).

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 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: (i) the onset of upstream movement from S1 (the release site), S2 and S3 to their arrival downstream of S2 (journey distance: 16 rkm), S3 (42 rkm) and S4 (49 rkm), respectively; and (ii) 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.

RESULTS

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 time, as median (LQ-UQ) at S2, S3, S4 and T1, was 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 hours of the first approach (i.e. non-delayed), while 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 hours 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 hours 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* individuals = 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', Figure 2 and Figure 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 from Weir S2 (Figure 4b). The median total retreat distance moved by retreating individuals at S2 (50.0 km (6.6-83.0), *n* individuals = 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 (two-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 hours 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.

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 was 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 passage time at S2, total retreat distance and body size were not significant predictors of either (i) the upstream extent of migration (Table S3) or (ii) 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 (Table S3, S4).

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 = 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; Spearman's rho = 0.23, $p = 0.11$) (Figure 6A). Arrival at S3 was also strongly correlated with passage time at S2 (Spearman's rho = 0.82, $p < 0.01$) (Figure 6B), and the rank order of approach and passage at S3 was also significantly correlated (Spearman's rho = 0.61, $p = 0.01$) (Figure 6B). The order of arrival of lampreys at S4 was strongly correlated with passage time at S3 (Spearman's rho = 0.99, $p < 0.01$) (Figure 6C), as was the order of arrival and passage at S4 (Spearman's rho = 0.98, $p = 0.01$) (Figure 6C).

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, with potentially related to the physical characteristics of the barrier and prevailing river discharge conditions when the barriers were first approached, but they were not related to lamprey body sizes (contrary to H1). When the 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 due to 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, Shi & Haro, 2017; Kirk & Caudill, 2017; Newton et al., 2018; Goerig et al., 2020). 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, where 32% of individuals passed within 24 hours of the first approach but with the remainder passing after a median delay of more than 2 weeks. Testing the influences of body length and environmental variables on this distribution was unable to determine the causal factors of this bimodal distribution - contrary to H1 - but it may have been a consequence of several factors that we 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 may also 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 (Rooney et al., 2015; Kirk & Caudill, 2017). 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 greater than 100m, we cannot rule out the possibility that some upstream movements towards weirs, defined here as approaches did not culminate in an attempt to pass a weirs, but resulted in halting for another reason such as individuals locating spawning conspecifics (Pinder *et al.*, 2016). More fine-scale studies, potentially incorporating fine scale radio or acoustic telemetry, are needed to truly determine behaviour immediately downstream of weirs.

Individuals that are unable to pass migration barriers can potentially locate alternative, unimpeded, routes to favourable spawning grounds (Rooney et al., 2015; Holbrook et al., 2016). 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 sea 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 is often driven by variations in environmental conditions (Shaw, 2020). For example, in migratory fish attempting to pass barriers, there are generally increased attempt rates at passage in periods of elevated river discharge, emphasising behaviour can be plastic with regard to environmental conditions (Newton et al., 2018; Goerig et al., 2020). 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. While 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). Further, while we considered the retreat behaviours of individual sea lamprey, there may have been important influences of conspecifics on these behaviours (Okasaki *et al.*, 2020), which we were unable to test due to a lack of information on the number and timing of sea 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 freshwater, 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, such as was observed in 16 of the 26 individuals that retreated from S2 and incurred additional migration delays during re-ascent of S1. While previous studies of migratory animal species have found associations between migratory strategy and fitness and productivity (Ely & Meixell, 2015; Abrahms et al., 2018; Cheng et al., 2019), there was little evidence here that downstream movements resulted in a reduction in migration extent in sea 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 sea 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 then 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; Tibblin et al., 2016; Jensen et al., 2020) and buffer populations from environmental stochasticity (Freshwater et al., 2019). In this study, barriers disrupted variation in upstream progress in sea 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 sea 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; it is unknown the extent to which individual variation drives the initiation of upstream migration to spawning sites, but males are generally 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 can also 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.

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Authors 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.

References

Abrahms B., Hazen E.L., Bograd S.J., Brashares J.S., Robinson P.W., Scales K.L., *et al.* (2018). Climate mediates the success of migration strategies in a marine predator. *Ecology Letters* **21**, 63–71

Alcott D.J., Goerig E., Rillahan C., He P. & Castro-Santos T. (2021). Tide gates form physical and ecological obstacles to river herring (Alosa spp.) spawning migrations. *Canadian Journal of Fisheries and Aquatic Sciences*. https://doi.org/10.1139/cjfas-2020-0347

Araújo M.J., Ozório R.O.A., Bessa R.J.B., Kijjoa A., Gonçalves J.F.M. & Antunes C. (2013). Nutritional status of adult sea lamprey (*Petromyzon marinus* Linnaeus, 1758) during spawning migration in the Minho River, NW Iberian Peninsula. *Journal of Applied Ichthyology* **29**, 808–814. https://doi.org/10.1111/jai.12192

Bauer S. & Hoye B.J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**

Belletti B., Garcia de Leaniz C., Jones J., Bizzi S., Börger L., Segura G., *et al.* (2020). More than one million barriers fragment Europe’s rivers. *Nature* **588**, 436–441. https://doi.org/10.1038/s41586-020-3005-2

Benoit L., Hewison A.J.M., Coulon A., Debeffe L., Grémillet D., Ducros D., *et al.* (2020). Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore. *Journal of Animal Ecology* **89**, 173–185. https://doi.org/10.1111/1365-2656.13098

Brodersen J., Nilsson P.A., Chapman B.B., Skov C., Hansson L.A. & Brönmark C. (2012). Variable individual consistency in timing and destination of winter migrating fish. *Biology Letters* **8**, 21–23. https://doi.org/10.1098/rsbl.2011.0634

Brown J.M. & Taylor P.D. (2017). Migratory blackpoll warblers (Setophaga striata) make regional-scale movements that are not oriented toward their migratory goal during fall. *Movement Ecology* **5**, 15. https://doi.org/10.1186/s40462-017-0106-0

Buchinger T.J., Siefkes M.J., Zielinski B.S., Brant C.O. & Li W. (2015). Chemical cues and pheromones in the sea lamprey (Petromyzon marinus). *Frontiers in Zoology* **12**, 32. https://doi.org/10.1186/s12983-015-0126-9

Carpenter-Bundhoo L., Butler G.L., Bond N.R., Bunn S.E., Reinfelds I. V. & Kennard M.J. (2020). Effects of a low-head weir on multi-scaled movement and behavior of three riverine fish species. *Scientific Reports* **10**. https://doi.org/10.1038/s41598-020-63005-8

Castro-Santos T. & Haro A. (2003). Quantifying migratory delay: a new application of survival analysis methods. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 986–996. https://doi.org/10.1139/f03-086

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**, 806–830. https://doi.org/10.1139/F10-026

Castro-Santos T., Shi X. & Haro A. (2017). Migratory behavior of adult sea lamprey and cumulative passage performance through four fishways. *Canadian Journal of Fisheries and Aquatic Sciences* **74**, 790–800. https://doi.org/10.1139/cjfas-2016-0089

Cheng Y., Fiedler W., Wikelski M. & Flack A. (2019). “Closer-to-home” strategy benefits juvenile survival in a long-distance migratory bird. *Ecology and Evolution*, ece3.5395. https://doi.org/10.1002/ece3.5395

Clemens B.J., Binder T.R., Docker M.F., Moser M.L. & Sower S.A. (2010). Similarities, Differences, and Unknowns in Biology and Management of Three Parasitic Lampreys of North America. *Fisheries* **35**, 580–594.

https://doi.org/10.1577/1548-8446-35.12.580

Dingle H. & Drake V.A. (2007). What Is Migration? *BioScience* **57**, 113–121

Durand M., Neal J., Rodríguez E., Andreadis K.M., Smith L.C. & Yoon Y. (2014). Estimating reach-averaged discharge for the River Severn from measurements of river water surface elevation and slope. *Journal of Hydrology* **511**, 92–104. https://doi.org/10.1016/J.JHYDROL.2013.12.050

Eldøy S.H., Bordeleau X., Crossin G.T. & Davidsen J.G. (2019). Individual Repeatability in Marine Migratory Behavior: A Multi-Population Assessment of Anadromous Brown Trout Tracked Through Consecutive Feeding Migrations. *Frontiers in Ecology and Evolution* **7**, 420. https://doi.org/10.3389/fevo.2019.00420

Ely C.R. & Meixell B.W. (2015). Demographic outcomes of diverse migration strategies assessed in a metapopulation of tundra swans. *Movement Ecology* **4**, 10. https://doi.org/10.1186/s40462-016-0075-8

Freshwater C., Trudel M., Beacham T.D., Gauthier S., Johnson S.C., Neville C.E., *et al.* (2019). Individual variation, population-specific behaviours and stochastic processes shape marine migration phenologies. *Journal of Animal Ecology* **88**, 67–78. https://doi.org/10.1111/1365-2656.12852

Goerig E., Wasserman B.A., Castro-Santos T. & Palkovacs E.P. (2020). Body shape is related to the attempt rate and passage success of brook trout at in-stream barriers. *Journal of Applied Ecology* **57**, 91–100. https://doi.org/10.1111/1365-2664.13497

Grill G., Lehner B., Thieme M., Geenen B., Tickner D., Antonelli F., *et al.* (2019). Mapping the world’s free-flowing rivers. *Nature* **569**, 215–221.

https://doi.org/10.1038/s41586-019-1111-9

Guo Z., Andreou D. & Britton J.R. (2017). Sea Lamprey *Petromyzon marinus* Biology and Management Across Their Native and Invasive Ranges: Promoting Conservation by Knowledge Transfer. *Reviews in Fisheries Science & Aquaculture* **25**, 84–99. https://doi.org/10.1080/23308249.2016.1233166

Gurarie E., Bracis C., Delgado M., Meckley T.D., Kojola I. & Wagner C.M. (2016). What is the animal doing? Tools for exploring behavioural structure in animal movements. *Journal of Animal Ecology* **85**, 69–84. https://doi.org/10.1111/1365-2656.12379

Hansen M.J., Madenjian C.P., Slade J.W., Steeves T.B., Almeida P.R. & Quintella B.R. (2016). Population ecology of the sea lamprey (Petromyzon marinus) as an invasive species in the Laurentian Great Lakes and an imperiled species in Europe. *Reviews in Fish Biology and Fisheries* **26**, 509–535. https://doi.org/10.1007/s11160-016-9440-3

Harbicht A.B., Castro-Santos T., Gorsky D., Hand D.M., Fraser D.J. & Ardren W.R. (2018). Environmental, anthropogenic, and dietary influences on fine-scale movement patterns of atlantic salmon through challenging waters. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 2198–2210. https://doi.org/10.1139/cjfas-2017-0476

Holbrook C.M., Jubar A.K., Barber J.M., Tallon K. & Hondorp D.W. (2016). Telemetry narrows the search for sea lamprey spawning locations in the St. Clair-Detroit River System. *Journal of Great Lakes Research* **42**, 1084–1091. https://doi.org/10.1016/J.JGLR.2016.07.010

Jensen A.J., Finstad B., Fiske P., Diserud O.H. & Thorstad E.B. (2020). Repeatable individual variation in migration timing in two anadromous salmonids and ecological consequences. *Ecology and Evolution*. https://doi.org/10.1002/ece3.6808

Kirk M.A. & Caudill C.C. (2017). Network analyses reveal intra- and interspecific differences in behaviour when passing a complex migration obstacle. *Journal of Applied Ecology* **54**, 836–845. https://doi.org/10.1111/1365-2664.12786

Lassalle G., Crouzet P. & Rochard E. (2009). Modelling the current distribution of European diadromous fishes: an approach integrating regional anthropogenic pressures. *Freshwater Biology* **54**, 587–606. https://doi.org/10.1111/j.1365-2427.2008.02135.x

Limburg K.E. & Waldman J.R. (2009). Dramatic Declines in North Atlantic Diadromous Fishes. *BioScience* **59**, 955–965. https://doi.org/10.1525/bio.2009.59.11.7

Newton M., Dodd J.A., Barry J., Boylan P. & Adams C.E. (2018). The impact of a small-scale riverine obstacle on the upstream migration of Atlantic Salmon. *Hydrobiologia* **806**, 251–264. https://doi.org/10.1007/s10750-017-3364-3

Nyqvist D., Greenberg L.A., Goerig E., Calles O., Bergman E., Ardren W.R., *et al.* (2017). Migratory delay leads to reduced passage success of Atlantic salmon smolts at a hydroelectric dam. *Ecology of Freshwater Fish* **26**, 707–718. https://doi.org/10.1111/eff.12318

Okasaki C., Keefer M.L., Westley P.A.H. & Berdahl A.M. (2020). Collective navigation can facilitate passage through human-made barriers by homeward migrating Pacific salmon. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20202137. https://doi.org/10.1098/rspb.2020.2137

Paterson J.E., Baxter-Gilbert J., Beaudry F., Carstairs S., Chow-Fraser P., Edge C.B., *et al.* (2019). Road avoidance and its energetic consequences for reptiles. *Ecology and Evolution* **9**, 9794–9803. https://doi.org/10.1002/ece3.5515

Pinder A.C., Hopkins E., Scott L.J. & Britton J.R. (2016). Rapid visual assessment of spawning activity and associated habitat utilisation of sea lamprey (*Petromyzon marinus* Linnaeus, 1758) in a chalk stream: implications for conservation monitoring. *Journal of Applied Ichthyology* **32**, 364–368. https://doi.org/10.1111/jai.13010

R Core Team (2020). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Rolls R.J., Stewart-Koster B., Ellison T., Faggotter S. & Roberts D.T. (2014). Multiple factors determine the effect of anthropogenic barriers to connectivity on riverine fish. *Biodiversity and Conservation* **23**, 2201–2220. https://doi.org/10.1007/s10531-014-0715-5

Rooney S.M., Wightman G., Ó'Conchúir R. & King J.J. (2015). Behaviour of sea lamprey (Petromyzon marinus L.) at man-made obstacles during upriver spawning migration: use of telemetry to assess efficacy of weir modifications for improved passage. *Biology and Environment: Proceedings of the Royal Irish Academy* **115B**, 125. https://doi.org/10.3318/bioe.2015.14

Sanz-Aguilar A., Béchet A., Germain C., Johnson A.R. & Pradel R. (2012). To leave or not to leave: survival trade-offs between different migratory strategies in the greater flamingo. *Journal of Animal Ecology* **81**, 1171–1182. https://doi.org/10.1111/j.1365-2656.2012.01997.x

Sawyer H., Kauffman M.J., Middleton A.D., Morrison T.A., Nielson R.M. & Wyckoff

T.B. (2013). A framework for understanding semi-permeable barrier effects on migratory ungulates. *Journal of Applied Ecology* **50**, 68–78. https://doi.org/10.1111/1365-2664.12013

Schmaljohann H. (2019). The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: A cross-continental analysis. *Movement Ecology* **7**, 1–18. https://doi.org/10.1186/s40462-019-0169-1

Schoenfeld D. (1982). Partial Residuals for The Proportional Hazards Regression Model. *Biometrika* **69**, 239–241

Shaw A.K. (2020). Causes and consequences of individual variation in animal movement. *Movement Ecology* **8**, 12. https://doi.org/10.1186/s40462-020-0197-x

Silva A.T., Lucas M.C., Castro-Santos T., Katopodis C., Baumgartner L.J., Thiem J.D., *et al.* (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries* **19**, 340–362. https://doi.org/10.1111/faf.12258

Silva S., Barca S., Vieira-Lanero R. & Cobo F. (2019). Upstream migration of the anadromous sea lamprey (*Petromyzon marinus* Linnaeus, 1758) in a highly impounded river: Impact of low-head obstacles and fisheries. *Aquatic Conservation: Marine and Freshwater Ecosystems* **29**, 389–396. https://doi.org/10.1002/aqc.3059

Smith R.J. & Moore F.R. (2005). Arrival Timing and Seasonal Reproductive Performance in a Long-Distance Migratory Landbird. *Behavioral Ecology and Sociobiology* **57**, 231–239. https://doi.org/10.1007/s00265-004-0855-9

Therneau T.M. (2020). coxme: Mixed Effects Cox Models. R package version 2.2-16.

Tibblin P., Forsman A., Borger T. & Larsson P. (2016). Causes and consequences of repeatability, flexibility and individual fine-tuning of migratory timing in pike. *Journal of Animal Ecology* **85**, 136–145. https://doi.org/10.1111/1365-2656.12439

Udyawer V., Dwyer R.G., Hoenner X., Babcock R.C., Brodie S., Campbell H.A., *et al.* (2018). A standardised framework for analysing animal detections from automated tracking arrays. *Animal Biotelemetry* **6**, 17. https://doi.org/10.1186/s40317-018-0162-2

Waldman J., Grunwald C. & Wirgin I. (2008). Sea lamprey *Petromyzon marinus*: an exception to the rule of homing in anadromous fishes. *Biology Letters* **4**, 659–662. https://doi.org/10.1098/rsbl.2008.0341

Wickham H., Averick M., Bryan J., Chang W., McGowan L., François R., *et al.* (2019). Welcome to the Tidyverse. *Journal of Open Source Software* **4**, 1686. https://doi.org/10.21105/joss.01686

William F. & Beamish H. (1979). Migration and spawning energetics of the anadromous sea lamprey, Petromyzon marinus. *Environmental Biology of Fishes* **4**, 3–7. https://doi.org/10.1007/BF00005922

Zeigler S.L. & Fagan W.F. (2014). Transient windows for connectivity in a changing world. *Movement Ecology* **2**, 1

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 Fig. 2.

Metric	Definition	Quantified at
Per cent passage	Per cent of individuals detected on the receiver immediately downstream of the weir that are subsequently 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	Per cent of individuals detected retreating for the weir	S2, S3, T1
Retreat extent	The most 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

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

Weir	*n* approached	*n* passed (%)	Passage time, days	*n* retreaters (%)	Retreat outcome (% of 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)

Table 3: summary of candidate cox proportional hazards models of sea lamprey time-to-retreat from weir S2

Model name	Model structure	df	LogLikelihood	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

Table 4: Summary of covariate effects from best-fitting cox proportional hazards model of sea lamprey time-to-retreat from weir S2

Covariate	Hazard ratio	S.E.	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^3s^{-1})	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 captions

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, UK. 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.

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

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.

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 movements tracks denote detections on acoustic receivers. Black arrows represent passage of S2 for each individual. Y-axis units are river kilometres (rkm), 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

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

Figure 6: (A) Rank order of departure and arrival for acoustic tagged 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 lamprey moving upstream between weir S2 and weir 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 lamprey moving upstream between weir S3 and weir S4 (black); Rank order of first arrival and passage for acoustic tagged lamprey at weir S4 (red).

Figure 1

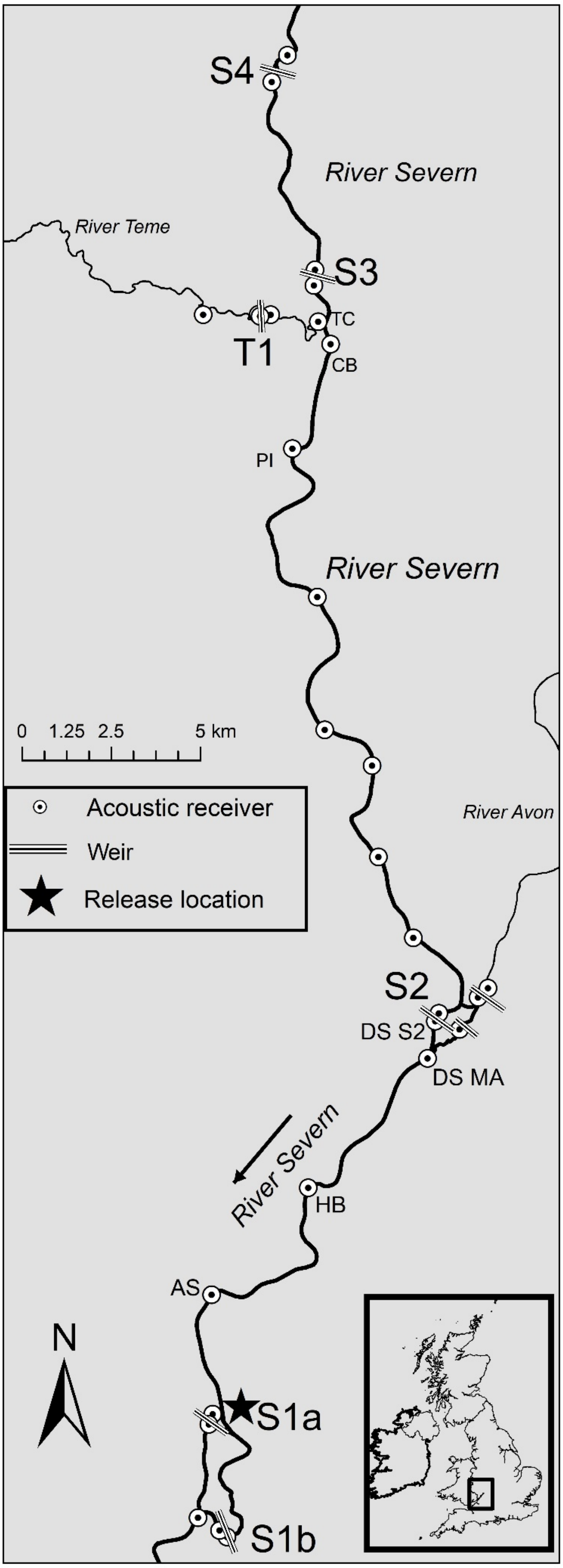
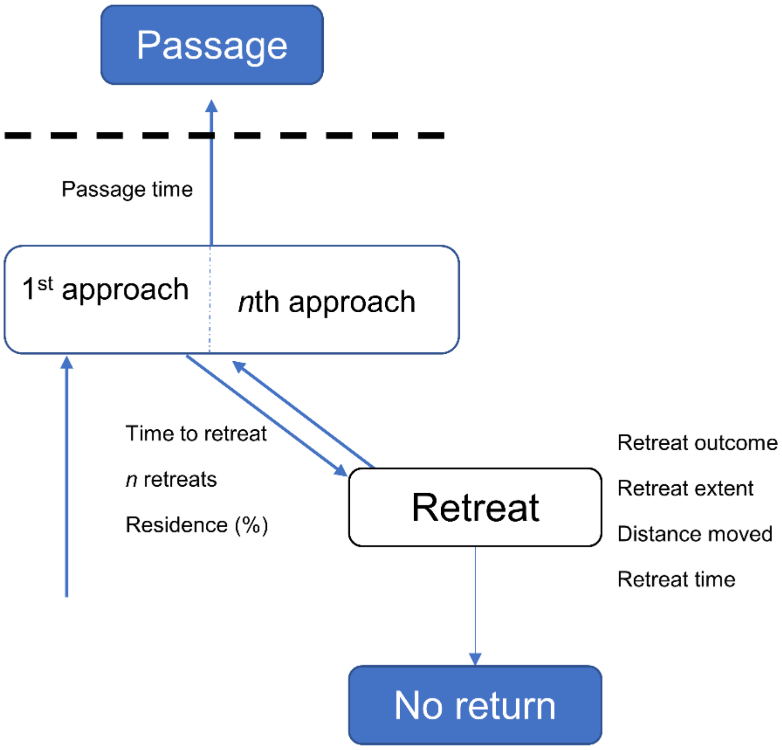
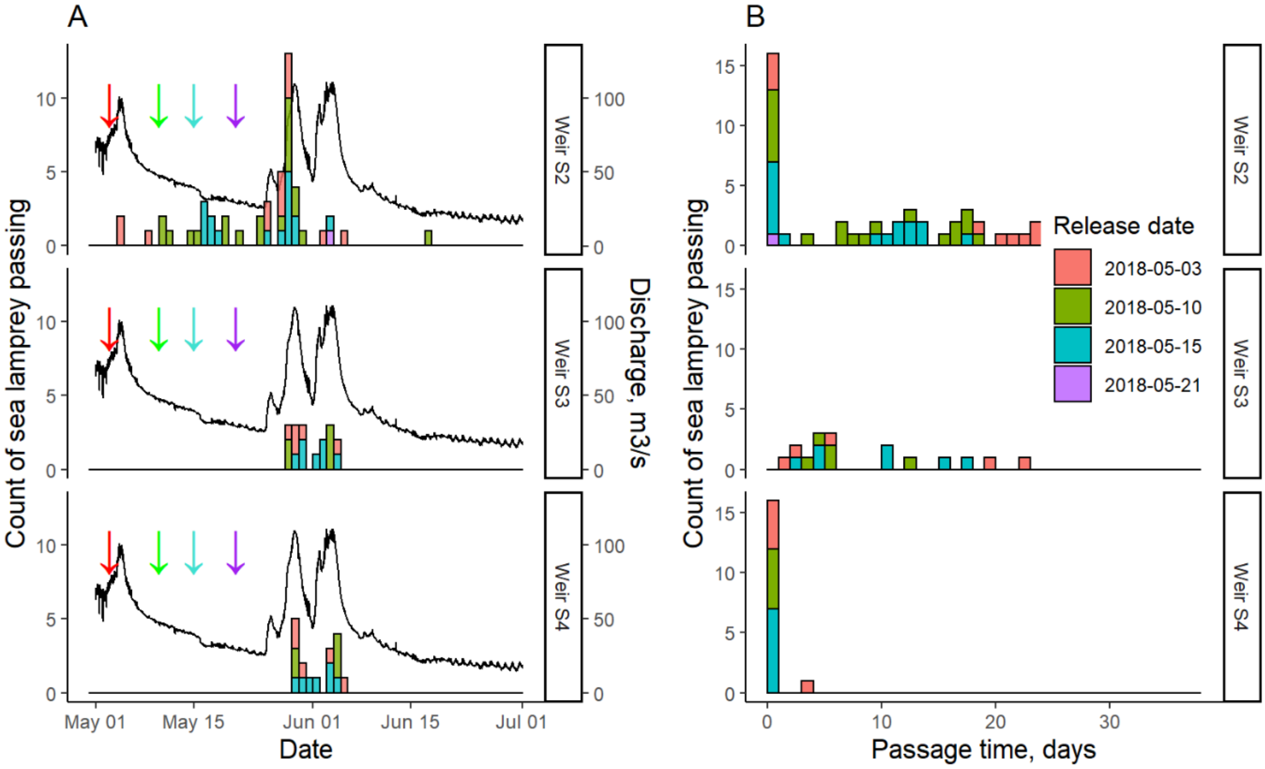

S4
River Severn
River Teme
S3
TC
T1
CB
PI
River Severn
0 1.25 2.5 5 km
Acoustic receiver
Weir
Release location
River Avon
S2
DS S2
DS MA
River Severn
HB
AS
N
S1a
S1b

Figure 2


Passage
Passage time
1st approach
nth approach
Time to retreat
n retreats
Residence (%)
Retreat
Retreat outcome
Retreat extent
Distance moved
Retreat time
No return

846 Figure 3

847



848

Figure 4

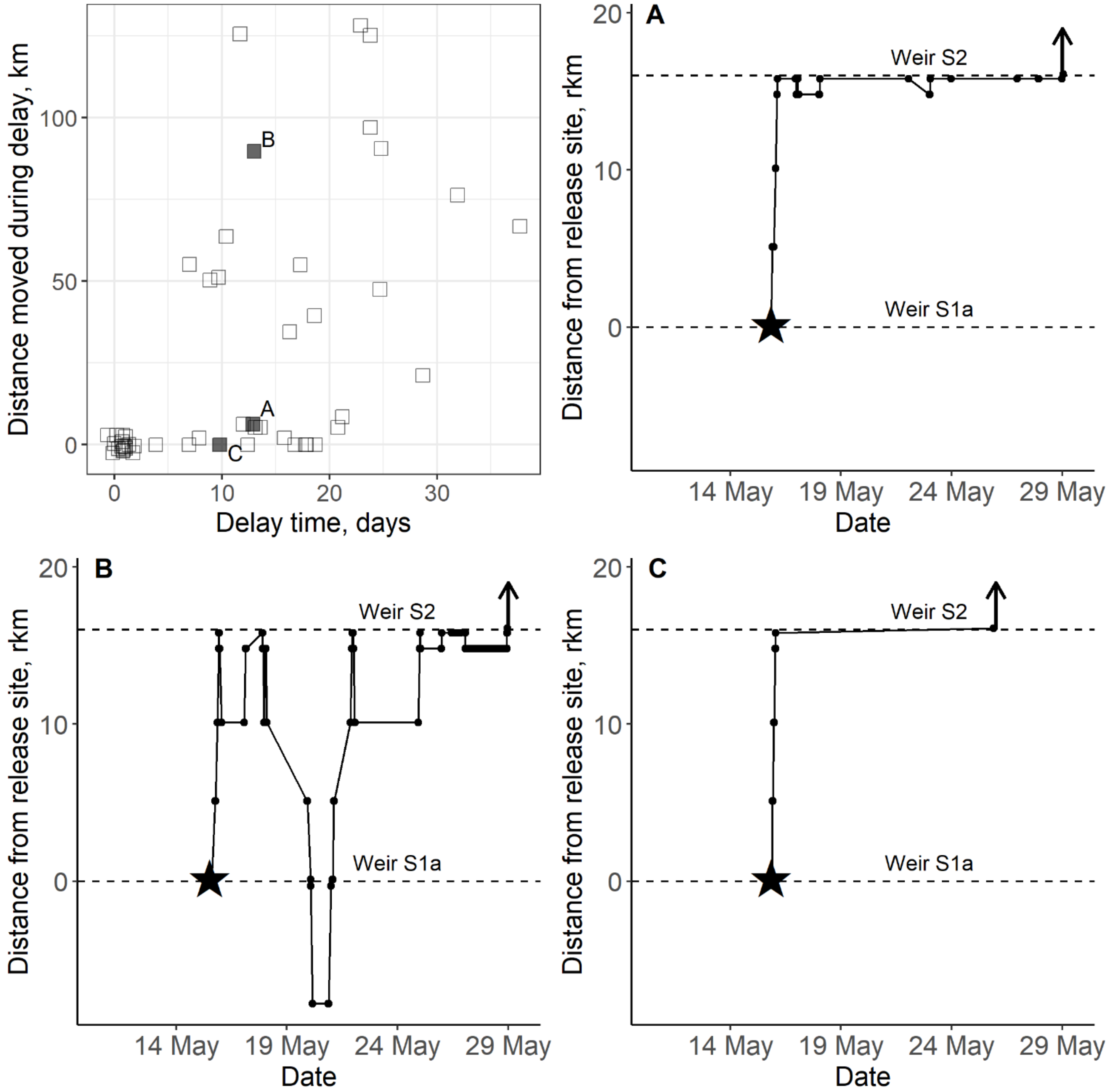
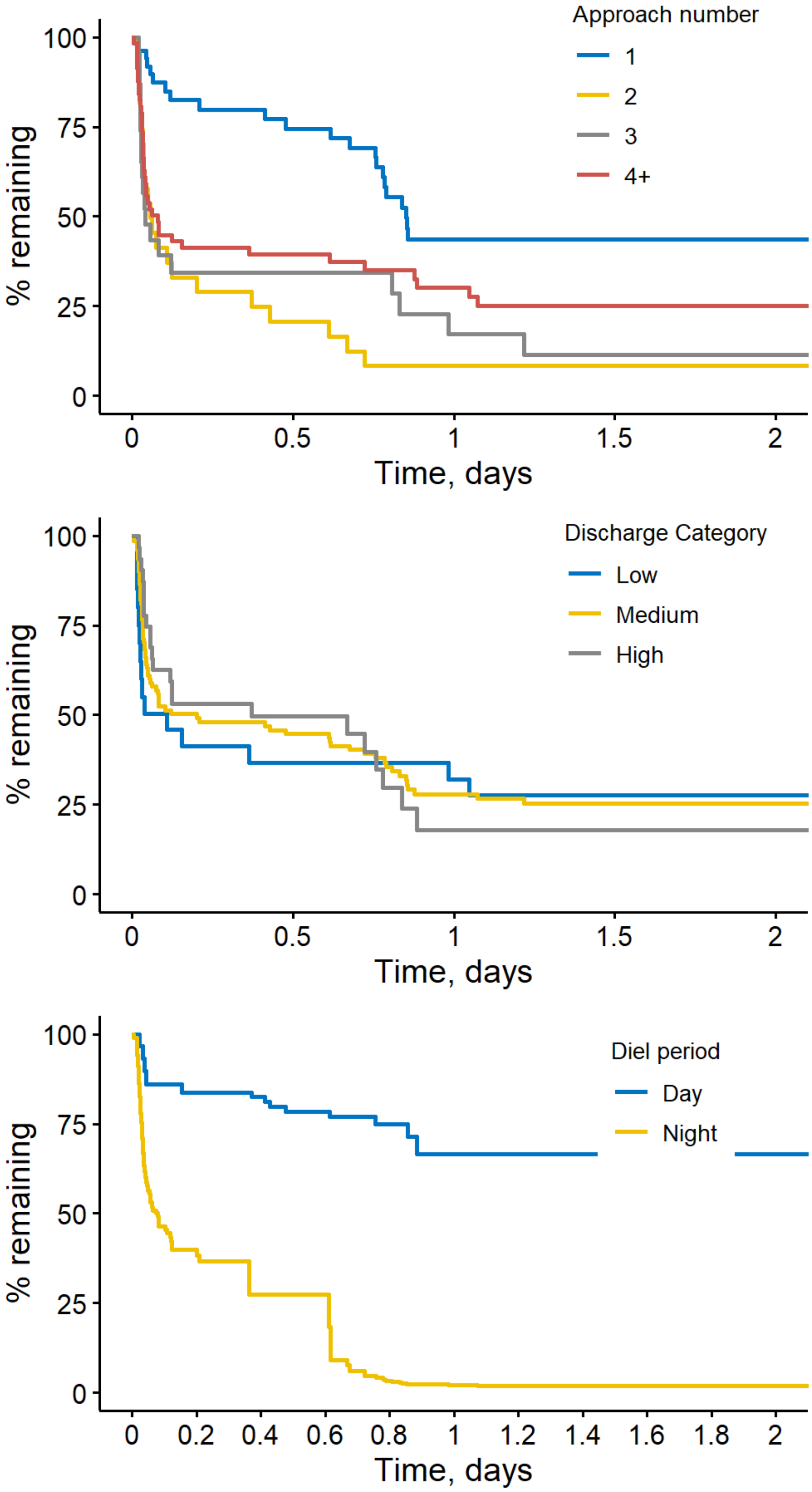

Distance moved during delay, km
0
50
100
Delay time, days
0
10
20
30
A
B
C
Distance from release site, rkm
20
10
0
Weir S2
Weir S1a
14 May
19 May
24 May
29 May
Date

Figure 5


Approach number
1
2
3
4+
% remaining
100
75
50
25
0
Time, days
0
0.5
1
1.5
2
Discharge Category
Low
Medium
High
% remaining
100
75
50
25
0
Time, days
0
0.5
1
1.5
2
Diel period
Day
Night
% remaining
100
75
50
25
0
Time, days
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2