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RESEARCH ARTICLE

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# Cumulative impacts of habitat fragmentation and the environmental factors affecting upstream migration in the threatened sea lamprey, *Petromyzon marinus*

**Peter Davies[1,2] | J. Robert Britton[1] | Andrew D. Nunn[2] | Jamie R. Dodd[2] | Chris Bainger[3] | Randolph Velterop[4] | Jonathan D. Bolland[2]**

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

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

[3]Environment Agency, Tewkesbury, UK

[4]Natural England, Exeter, UK

**Correspondence**
Peter Davies, Department of Life and Environmental Sciences, Bournemouth University, Christchurch House, Talbot Campus, Poole, BH12 5BB, UK.
Email: daviesp92@gmail.com

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## Abstract

1. River ecosystems are often fragmented by artificial structures, such as weirs. For anadromous species, these structures can impede access to upstream spawning sites and ultimately lead to severe population declines.
2. This study focused on the freshwater spawning migration of the sea lamprey, *Petromyzon marinus*, an anadromous species threatened by habitat fragmentation across its native range. To quantify the cumulative impacts of multiple weirs on upstream-migrating adults, and to explore the environmental factors affecting migratory movements, passive acoustic telemetry was applied to 56 individuals during their spawning migration in the heavily fragmented River Severn basin, UK.
3. While 89% of tagged sea lamprey passed the first weir upstream of the release site on the main river, only 4% passed the fifth weir. For 85% of migrants, the upstream extent of migration was immediately downstream of a weir. Individuals that passed weirs upstream of the release site ($n = 50$) took 21.6 ± 2.8 days to reach their most upstream location, experiencing cumulative passage times at weirs of 15.7 ± 2.8 days; these delays constituted a median of 84% of total upstream movement times.
4. Multistate models showed that the weir passage rates of sea lamprey in tidal and non-tidal areas increased significantly when downstream river level and discharge were elevated. Upstream-to-downstream changes in direction were frequent downstream of weirs, but rare in unobstructed river sections.
5. The results provided evidence for a cumulative effect of multiple weirs on sea lamprey movements, substantially delaying upstream migrants and limiting their spawning to atypical habitat. The results also demonstrated the crucial roles of high tides and elevated discharge events in enabling weir passage. Although the

Severn Estuary features conservation designations for sea lamprey, this study reveals that barriers are inhibiting their upstream migration, a problem that should be addressed to assist sea lamprey conservation.

**KEYWORDS**
catchment, engineering, fish, impoundment, migration, protected species, river, tracking

## 1 | INTRODUCTION

Dams and weirs are major artificial disturbances on rivers that interrupt longitudinal connectivity, inhibit fish migrations across ecosystem boundaries (marine–freshwater), modify gene flow, and affect population sustainability (Dudgeon et al., 2006). The effects of these structures on populations of anadromous fishes can be particularly severe as they impede or inhibit access to spawning sites in the upper reaches of rivers (Lucas & Baras, 2001; Rolls et al., 2014). Population declines in anadromous species attributable to artificial structures have had considerable adverse ecological, economic, and cultural impacts (Limburg & Waldman, 2009; van Puijenbroek et al., 2019).

Anadromous species threatened by disrupted river connectivity include the sea lamprey (*Petromyzon marinus* L.), which has protected status in Europe but is highly invasive in the Great Lakes of North America (Hansen et al., 2016). Adults of this jawless vertebrate, native to the northern Atlantic and Mediterranean (Guo, Andreou & Britton, 2017), feed parasitically on large marine vertebrates before migrating into fresh water to spawn in shallow, fast-flowing river habitats (Maitland, 2003; Rooney et al., 2015). Concerns over sea lamprey population declines, attributed primarily to overharvesting, pollution, habitat loss, and artificially constructed barriers to migration (Guo, Andreou & Britton, 2017; Silva et al., 2019; Moser et al., 2020), are reflected in international conservation legislation. The species is listed in the European Habitats Directive, both in Annex II, which requires European Union member states to designate high-quality sites that contain listed species as Special Areas of Conservation (SACs), and in Annex V, which ensures that any exploitation of listed species is sustainable (Council of the European Communities, 1992). In addition, the sea lamprey is listed on Appendix III of the Bern Convention, a treaty that aims to ensure protection for vulnerable migratory species and their habitats across Europe.

Traditional monitoring of anadromous sea lamprey populations has focused on quantifying densities of their larvae (ammocoetes), a key indicator of spawning success, and has shown that the spatial distribution of ammocoetes is limited by weirs (Andrade et al., 2007; Nunn et al., 2008; Nunn et al., 2017). Visual spawning surveys (nest counts) have also documented areas of high spawning activity immediately downstream of structures that were assumed to inhibit migration (Pinder et al., 2016). Modern telemetry techniques (e.g. radio, passive integrated transponder (PIT), and acoustic) are increasingly being used to quantify the riverine movements of migrating adult sea lamprey. Much of the knowledge on sea lamprey migration ecology derives from studies completed in the North American Great Lakes, where the species is invasive and threatens economically important populations of freshwater fish through parasitism (Hansen et al., 2016). Consequently, telemetry studies have informed sea lamprey control efforts by identifying spawning areas (Holbrook et al., 2016) and characterizing migration strategies (Meckley, Wagner & Gurarie, 2014; McLean & McLaughlin, 2018). In their native range, telemetry studies have identified diel behavioural patterns, upstream movement rates, resting sites, and potential spawning grounds, and have demonstrated the influence of environmental conditions on upstream passage (Almeida, Silva & Quintella, 2000; Andrade et al., 2007; Rooney et al., 2015). Several authors have quantified the adverse spatial impacts that barriers can have on sea lamprey spawning migrations, including delaying upstream migration and preventing access to optimum spawning grounds (Almeida, Quintella & Dias, 2002; Castro-Santos, Shi & Haro, 2017; Silva et al., 2019).

In Great Britain, more than 99% of catchments contain artificial barriers and it has been estimated that there is one barrier for every 1.5 km of watercourse length (Jones et al., 2019). Understanding the movements of sea lamprey through the highly fragmented river catchments typical of such areas is important, as the cumulative effects of multiple barriers can be considerable (Castro-Santos, Shi & Haro, 2017; van Puijenbroek et al., 2019). The aim of this study was to quantify the spatial and temporal impacts of a series of artificial structures on the migratory movements of sea lamprey in the heavily fragmented River Severn basin in western England. Sea lamprey are known to use this river system for spawning (Bird et al., 1994), with historical evidence suggesting that the construction of navigation weirs in the 19th century resulted in rapid reductions in spawning populations of anadromous fishes upstream of the weirs, including sea lamprey (Buffery, 2018). Today, the Severn Estuary has been designated as an SAC, with the sea lamprey as a primary reason for this designation (sac.jncc.gov.uk/site/UK0013030). Sea lamprey are also a feature of the Severn Estuary Site of Special Scientific Interest (SSSI) under the Wildlife and Countryside Act (designatedsites.naturalengland.org.uk), and further upstream in the catchment the River Teme SSSI is noted as featuring sea lamprey spawning habitat (APEM, 2014). Here, through the application of passive acoustic telemetry, the objectives were: (i) to determine the passage and passage time, as well as cumulative spatial and temporal effects, of 11 weirs for upstream-migrating sea lamprey in the River Severn catchment; and (ii) to identify the environmental and human drivers of migratory movements in obstructed and unobstructed river sections.

## 2 | METHODS

### 2.1 | Study area

The River Severn is the longest river in Great Britain, rising in mid-Wales and flowing for 354 km before discharging into the Bristol Channel, and has a drainage area of 11,420 km$^2$ (Durand et al., 2014). The lower river catchment is characterized by confluences with two major tributaries, the River Teme and the River Avon, and by 10 major weirs (six on the main river channel, and two on each of the lower reaches of the River Teme and the River Avon) that result in high fragmentation (Figure 1; Table 1). The normal tidal limit is at Maisemore (hereafter S1a) and Llanthony (S1b) weirs on the western and eastern branches of the river, respectively (Figure 1). Spring tides penetrate the river up to Upper Lode Weir (hereafter S2). 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.

### 2.2 | Sea lamprey sampling, tagging, and tracking

The study was performed between May and July 2018 to coincide with the peak sea lamprey migration period in western Britain

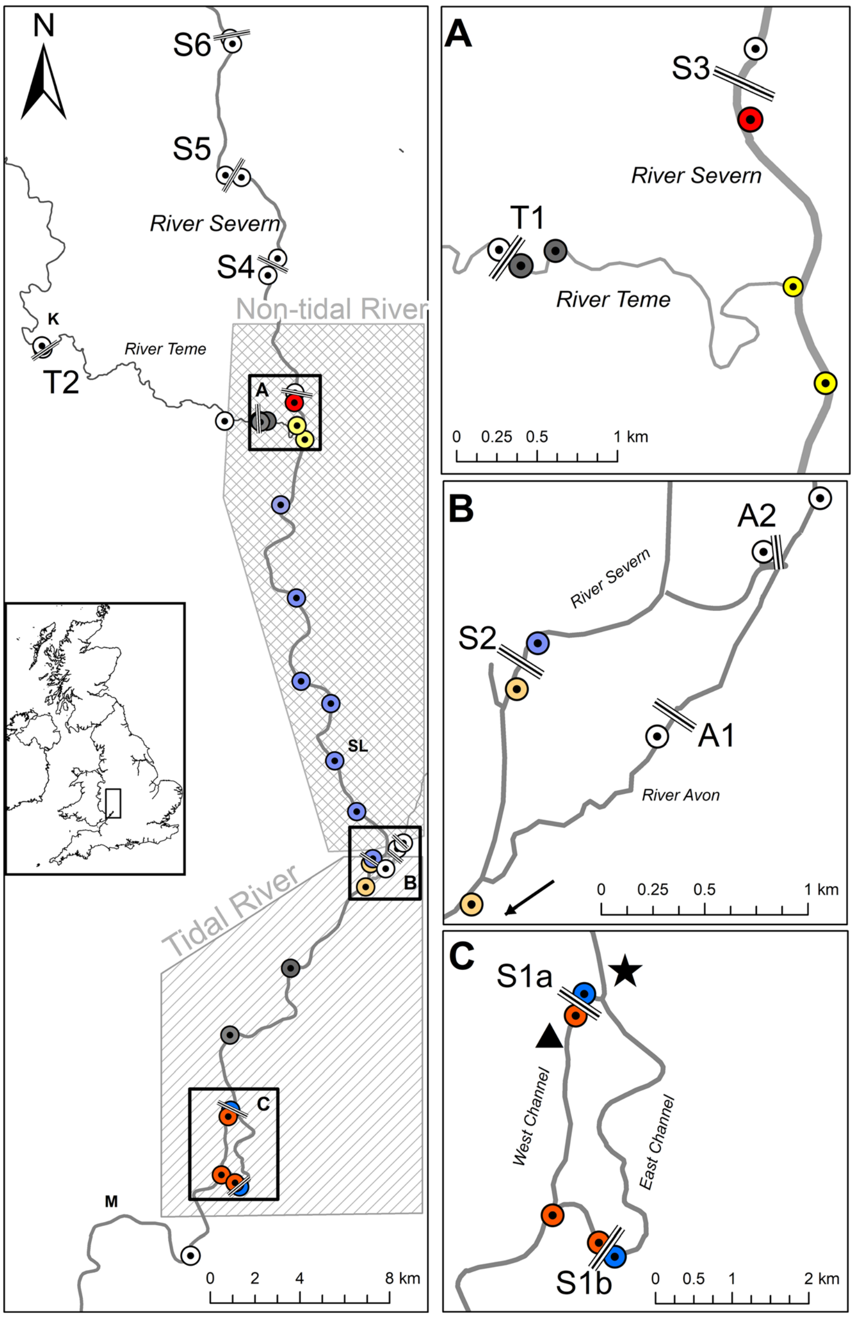


**FIGURE 1** The River Severn catchment study area, including the locations of capture (black triangle) and release (black star) of acoustic-tagged sea lamprey, weirs (bars), and acoustic receivers (circles) in the rivers Severn, Teme, and Avon, UK. The weir codes are listed in Table 1. Colour groupings of the receivers represent the river sections used in the modelling of sea lamprey movements; white receivers were not included. The dashed area (tidal river area) was used to model sea lamprey movements between the furthest downstream receiver and S2, and comprised four sections: downstream S1a/S1b (three receivers, red); upstream S1a/S1b (two receivers, blue); middle reach (two receivers, grey); and downstream S2 (two receivers, orange). The hatched area (non-tidal river area) was used to model movements in the river sections bounded by S2, S3, and T1, and comprised four sections: upstream S2 (seven receivers, blue); Severn/Teme confluence (two receivers, yellow); downstream S3 (one receiver, red); and downstream T1 (two receivers, grey). The black arrow denotes the direction of flow. M (Minsterworth), SL (Saxon's Lode), and K (Knightsford Bridge) denote the positions of gauging stations from which discharge and river level data were derived

**TABLE 1** Locations of study weirs in the River Severn, which were used to assess the cumulative impacts of multiple weirs on the 2018 upstream migration of acoustic-tagged sea lamprey, *Petromyzon marinus*

| Weir code | Name | River | Location, decimal degrees[a] | Distance from normal tidal limit, rkm[b] | Original function |
|---|---|---|---|---|---|
| S1a | Maisemore Weir | Severn (West Channel) | 51.89318, −2.26574 | 0 | Navigation |
| S1b | Llanthony Weir | Severn (East Channel) | 51.86227 −2.26028 | 0 | Navigation |
| S2 | Upper Lode Weir | Severn | 51.99346, −2.17407 | 16 | Navigation |
| S3 | Diglis Weir | Severn | 52.17926, −2.22597 | 42 | Navigation |
| S4 | Bevere Weir | Severn | 52.23256, −2.24027 | 49 | Navigation |
| S5 | Holt Weir | Severn | 52.26812, −2.26576 | 54 | Navigation |
| S6 | Lincomb Weir | Severn | 52.32290, −2.26596 | 61 | Navigation |
| T1 | Powick Weir | Teme | 52.16975, −2.24712 | 44 | Flow regulation |
| T2 | Knightwick Weir | Teme | 52.19908, −2.38940 | 60 | Flow regulation |
| A1 | Abbey Mill Weir | Avon | 51.99133, −2.16325 | 16 | Flow regulation |
| A2 | Stanchards Pit Weir | Avon | 51.99837, −2.15561 | 18 | Flow regulation |

[a]The coordinates provided use the World Geodetic System (WGS) 1984 geographical coordinate system.
[b]rkm, river kilometres.

**TABLE 2** Lengths and weights of sea lamprey tagged in the lower River Severn in 2018

| Date | *n* | Mean ± SE length, mm (range) | Mean ± SE weightg (range) |
|---|---|---|---|
| 3 May 2018 | 14 | 866 ± 35 (760–960) | 1268 ± 144 (875–1700) |
| 10 May 2018 | 26 | 835 ± 19 (710–920) | 1186 ± 95 (800–1650) |
| 15 May 2018 | 18 | 817 ± 25 (740–910) | 1130 ± 105 (775–1650) |
| 21 May 2018 | 2 | 840 ± 254 (820–860) | 1337 ± 158 (1325–1350) |

(Maitland, 2003). Migrating sea lamprey (hereafter 'lamprey') were captured approximately 200 m downstream of S1a (Figure 1), using unbaited two-funnel eel pots (Lucas et al., 2009), and held in water-filled containers (100 L) prior to general anaesthesia (MS-222), weighing and measuring (to the nearest g and cm), and surgical implantation with a V9 acoustic transmitter (29 × 9 mm, 4.7 g in weight in air, 69 kHz; www.innovasea.com). The transmitters featured a randomized 1-min pulse interval (with minimum and maximum intervals between acoustic pulses of 30 and 90 s, respectively). In all cases, the tag weight in air was less than 2% of the lamprey mass. In total, 60 adult lamprey were tagged and released over a 3-week period (Table 2). All surgical procedures were completed under UK Home Office project licence PPL 60/4400. A summary of the lamprey biometric data and movement metrics is provided in Table S1. Four individuals did not move upstream after release so were removed from the dataset; thus, the analyses in this study focused on the movements of the 56 remaining individuals.

Lamprey were tracked using an array of 36 acoustic receivers (VR2-W, www.innovasea.com) (Figure 1) deployed upstream and downstream of each navigation weir on the main channel and the flow-regulation weirs on the rivers Teme, Avon, and Mill Avon, with additional receivers deployed in unobstructed reaches between the weirs. Receivers were anchored on steel fencing pins driven into the river bed. In the River Teme, which featured sections of fast-flowing riffle, receivers were deployed in slower-flowing pools to maximize detection performance. 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) revealed that missed detections accounted for less than 0.1% of lamprey movements between receivers.

## 2.3 | Environmental data

Environmental data were obtained by request from the Environment Agency gauging stations at Saxon's Lode ('SL'; discharge, River Severn) and Knightsford Bridge ('K'; discharge, River Teme) (Figure 1). River levels for the tidal reaches downstream of S1a and S1b were determined by adjusting the levels at Minsterworth gauging station ('M' in Figure 1) forward by 30 min (visually calibrated), to account for the observed delay between high tide at Minsterworth and S1a/S1b. All environmental data were collected at 15-min intervals. In addition, water level and temperature data were collected by a logger immediately downstream of S2. To assess the representativeness of the hydraulic conditions encountered by tagged lamprey during the study period, daily mean discharge values occurring during the study period (May–June 2018) measured at the SL gauging station were converted to exceedance percentiles and compared with the equivalent time period during the 10 previous years (2008–2017), using data obtained from the National River Flow Archive (https://nrfa.ceh.ac.uk). This showed that the discharge during May–June 2018 did not significantly differ from that of the previous 10-year period (Wilcoxon rank sum, $W = 87{,}630$, $P = 0.96$) (Figure 2).

## 2.4 | Analyses of lamprey movements

### 2.4.1 | Percentage passage and passage time at weirs

For each weir in the study (Table 1) the number of lamprey that approached was calculated as a proportion of the number *n* available to approach, with available individuals defined as those that ascended the previous weir downstream. Then, percentage passage was calculated as the proportion of individuals detected at the downstream receiver (*n* approached) that were subsequently detected at the upstream receiver (*n* passed). To quantify the migratory delay for individuals that passed each weir, passage time was calculated as the time between the first detection at the downstream receiver and the first detection at the upstream receiver; for comparison, passage times between successive receivers in unobstructed reaches upstream of the release site were also calculated.

### 2.4.2 | Upstream extent, cumulative passage time, and delay proportion

To understand the cumulative impact of successive weirs on movement, the proportion of the original cohort of 56 acoustic-tagged lamprey that passed each weir was calculated. To understand the upstream spatial distribution of migrants in the study area (and so the overall impact of the structures on the upstream migration of all tagged individuals), the furthest upstream extent for each individual lamprey was estimated as its location of furthest upstream detection in the receiver array. To quantify the cumulative time spent by lamprey between their first approach and passage of weirs, total passage time was calculated for each individual as the sum of passage times recorded at all weirs. To quantify the temporal impact of weir passage on the total migration times, delay proportion (%) was calculated for each individual as the total passage time of weirs, as a proportion of the time between first upstream movement from the release site and upstream extent of migration. Delays incurred at S1a/S1b by lamprey that moved downstream of the release site immediately after release (interpreted as fallback related to capture and tagging) were not included in the calculations of the total passage time, but delays incurred by individuals that returned downstream of these structures after an initial upstream movement were included.

### 2.4.3 | Continuous-time multistate Markov models

Continuous-time multistate Markov models (CTMMs) treat animal movements as a series of transitions between discrete states in continuous time (Miller & Andersen, 2008), and enable testing of the effects of time-dependent variables on the instantaneous rates of movements between different states (referred to as 'transition rates') (Nakayama, Ojanguren & Fuiman, 2011; Bravener & McLaughlin, 2013). Here, CTMMs were used to analyse the effects of time-dependent environmental variables (river discharge, river level, water temperature, and day/night) and individual variables (body length and capture date) on upstream transition rates through sections of river that were either obstructed or unobstructed by weirs. Explanations of the terms used in the description and results of the CTMM process are provided in Table 3.

In the model design, acoustic receivers were grouped into defined sections of river and into two section categories: obstructed and unobstructed. Obstructed sections encompassed between one and three receivers, and upstream exit by a lamprey from the section required passage of a weir. Unobstructed sections encompassed between two and seven receivers and contained no weirs at their upper boundary. These groupings were used to compare upstream transition rates and the probability of downstream

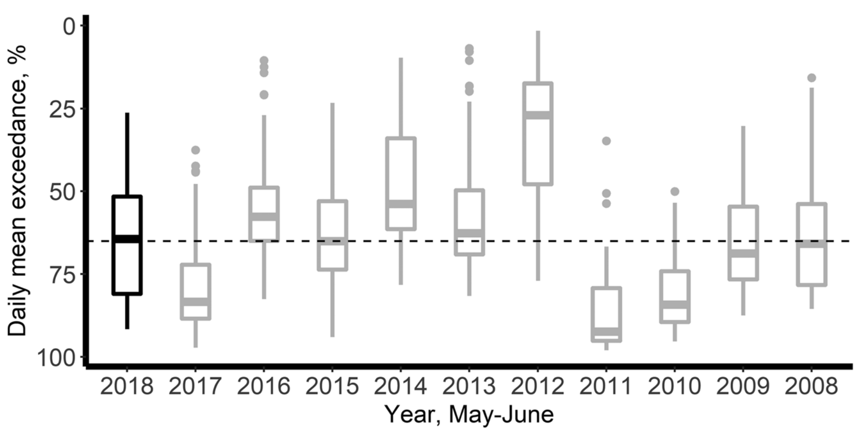


**FIGURE 2** Box plot of mean daily river discharge (exceedance, %) measured at Saxon's Lode gauging station on the River Severn during the study period (May–June 2018) and during the same time period for the previous 10 years (2008–2017). The horizontal dashed line represents the median daily discharge during May–June for 2008–2017

**TABLE 3** Definitions of terms used in the continuous-time multistate Markov models of sea lamprey movements in the River Severn catchment, measured in 2018

| Term | Definition |
|---|---|
| Section | Contiguous length of river either unobstructed (no weir at upstream boundary) or obstructed (weir at upstream boundary) |
| Area | Tidal or non-tidal portions of the river |
| Transition rate | Modelled daily rate of movement from one section to another, i.e. transitions day$^{-1}$, which can take any non-negative value. Baseline transition rates were modelled with covariates set to their mean value within the dataset |
| Downstream reversal | Upstream to downstream change in direction (not including final downstream movements) |
| Hazard ratio | Estimates of the effect on transition rates of increasing the value of a covariate by one unit, e.g. increasing river discharge by 1 m$^3$ s$^{-1}$ |

movements in obstructed versus unobstructed sections. In addition, they allowed the effects of environmental variables on upstream transition rates to be tested. To minimize the number of sections and thus avoid issues with non-convergence during modelling, the tidal (downstream of S2) and non-tidal (upstream of S2) areas of the river were modelled separately (Figure 1). S2 was used as the tidal limit as it is the upstream extent of most spring tides. The tidal river and non-tidal river both comprised four sections, with receivers in each section grouped by colour in Figure 1. In the tidal river, the three receivers downstream of S1a (West Channel) and S1b (East Channel) were pooled (downstream S1a/S1b) to reduce complexity and because the weirs are similar in altitude, head height, and hydraulic conditions (Figure 1).

Correspondingly, lamprey left the tidal river at the time of their upstream passage of S2 and left the modelled area of the non-tidal river at the time of passage at either S3 or T1. Individuals were conservatively removed from the dataset after their final upstream movement, after which time it was uncertain whether they remained motivated to migrate upstream, and their status could not be determined. Lamprey that moved downstream immediately after release, which was interpreted as capture-related fallback, were included in the model dataset at the point of their first upstream movement. Areas upstream of S3 and T1 were not included in the models as the number of lamprey entering these areas was considered too low and the range of environmental conditions experienced was too narrow.

During data preparation, raw detection data for each lamprey were converted into hourly observations of location (section) and observations of transitions between sections, i.e. observations occurring at the exact time of the first detection on a receiver in the destination section. Observations were classified as occurring during the day or the night using the R package MAPTOOLS (Bivand & Lewin-Koh, 2019), according to sunrise and sunset at the release site. Observations were then associated with individual metadata (body length and capture date) and hourly mean environmental data in the two datasets representing movements in the tidal and non-tidal river.

The CTMM models were parameterized in the R package MSM (Jackson, 2011). Upstream transition rates out of each section were modelled separately according to whether a lamprey had entered the section from a downstream or an upstream direction. This was to avoid violating the Markov assumption that transitions depend only on the identity of the current section, since downstream-moving lamprey may have been more likely to leave in a downstream direction than upstream-moving lamprey. Model fitting was then conducted according to an information-theoretic approach (Burnham & Anderson, 2002); the model selection procedure is further described in Appendix SM1. Following the derivation of the best-fitting model in the tidal and non-tidal river areas, the daily transition rates of upstream-migrating lamprey were calculated for each transition between the river sections. Transition rates were considered significantly different if there was no overlap between their 95% confidence intervals (Nakayama, Ojanguren & Fuiman, 2011). For each section, the probability of upstream to downstream direction changes by upstream-migrating lamprey ('downstream reversals') were also derived. The effects of environmental covariates on upstream transition rates from each section were calculated and expressed as hazard ratios. A covariate effect was considered significant if the 95% confidence interval of its hazard ratio did not overlap with 1 (Nakayama, Ojanguren & Fuiman, 2011). All data analyses were completed in the R statistical software (version 3.5.1; R Core Team, 2018).

## 3 | RESULTS

### 3.1 | Approach, percentage passage, and passage time at weirs

At the nine weirs upstream of the release site (Figure 1), the numbers of approaching lamprey and the percentage passage were highly variable (Table 4). The lowest percentage passage where at least 10 individuals approached was 12% at S5 (*n* approached = 17, *n* passed = 2) and 40% at T1 (*n* approached = 10, *n* passed = 4), and the highest was 100% at S4 (*n* approached and passed = 17). Approach rates at weirs in the River Avon were low: one individual approached A1 (2% of available), two approached A2 (4% of available), and no lamprey passed these structures. The greatest passage times occurred at S2 (median passage time lower quartile - upper quartile (LQ–UQ) = 10.4 days (0.4–18.6 days), *n* approached = 56, *n* passed = 50) and at S3 (5.3 days (4.1–13.0 days), *n* approached = 40, *n* passed = 17) (Table 4). Passage times at these weirs were substantially greater than unobstructed passage times between receivers in the River Severn, where median passage times for upstream-migrating individuals were all less than 0.2 days (Figure 3).

There were 13 lamprey detected in the River Teme, four of which had moved into this tributary during their first upstream movement

**TABLE 4** Approach, percentage passage, passage time, and cumulative impact of sea lamprey at weirs in the River Severn catchment during their 2018 spawning period

| Weir | *n* available[a] | *n* approached[b] (% of *n* available) | *n* passed (% passage) | Median passage time, days (25% quartile–75% quartile) | % of tagged cohort passing |
|---|---|---|---|---|---|
| S1a | 18 | 15 (83%) | 15 (100%) | 1.6 (0.1–2.8) | N/A[c] |
| S1b | 18 | 3 (17%) | 3 (100%) | N/A[d] | N/A[c] |
| S2 | 56 | 56 (100%) | 50 (89%) | 10.4 (0.4–18.6) | 89% |
| S3 | 50 | 41 (82%)[e] | 17 (41%) | 5.3 (4.1–13.0) | 30% |
| S4 | 17 | 17 (100%) | 17 (100%) | 0.2 (0.1–0.3) | 30% |
| S5 | 17 | 17(100%) | 2 (12%) | 6.1 (4.9–7.2) | 4% |
| S6 | 2 | 0 (0%) | N/A | N/A | 0% |
| T1 | 50 | 10 (20%)[e] | 4 (40%) | 0.1 (0.0–0.1) | 7% |
| T2 | 4 | 4 (100%) | 4 (100%) | N/A[d] | 7% |
| A1 | 56 | 1 (2%) | 0 (0%) | N/A | 0% |
| A2 | 50 | 2 (4%) | 0 (0%) | N/A | 0% |

[a]Individuals moving upstream through the unobstructed reach of river downstream of the weir.
[b]Individuals detected immediately downstream of the weir.
[c]Tagged sea lamprey were released upstream of S1a and S1b.
[d]Passage times unavailable owing to missed detections at the downstream acoustic receivers.
[e]Includes three individuals (S3, $n = 1$; T1, $n = 2$) missed by the downstream receiver but detected upstream.

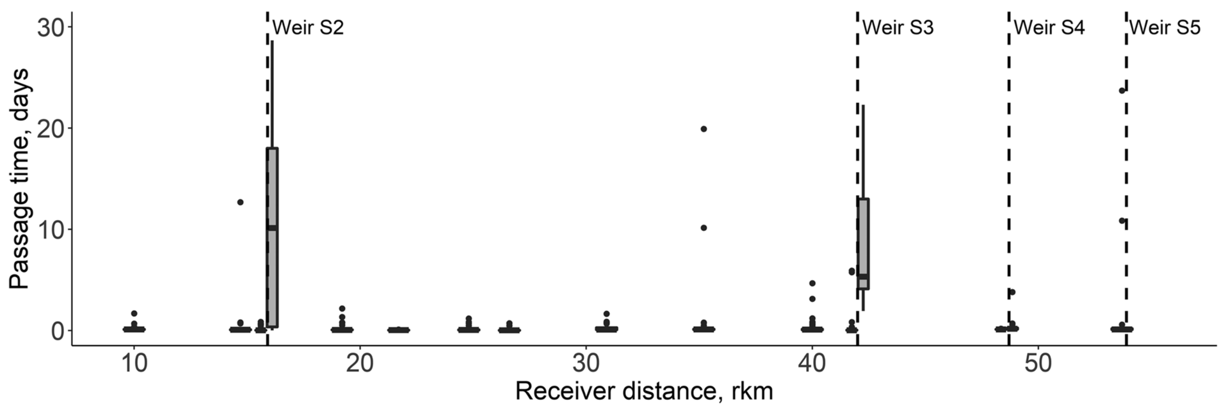


**FIGURE 3** Net upstream passage time of sea lamprey recorded between receivers in the River Severn during their 2018 spawning migration. Passage time was calculated as the difference in time between the last detection at the downstream receiver and the first detection at the upstream receiver. Passage times are displayed at the location (rkm, river kilometres) of the upstream receiver in each pair. Vertical dashed lines represent the location of weirs lying between receivers

from S2. The remaining nine moved upstream in the Severn, past the Teme confluence, and approached S3, before returning downstream and entering the River Teme. Eighteen lamprey moved downstream of the release site at S1a before returning upstream and passing either weir S1a (*n* approached and passed = 15, 100%) or weir S1b (*n* approached and passed = 3, 100%).

## 3.2 | Upstream extent, cumulative passage time, and final location

The mean (±95% CI) distance moved upstream by lamprey relative to the release site was 50.0 ± 3.4 river kilometres (rkm) (Figure 3). Four lamprey passed T2 into an area outside of the receiver array, so the upstream extent of their movements could not be determined. Of the remaining 52 lamprey, 44 (85%) reached the upstream extent of their migration immediately downstream of a weir: S3 = 17 (33% of remaining individuals), S5 = 15 (29%), S2 = six (12%), and T1 = six (12%) (Figure 4). Six (12%) lamprey that passed S2 did not approach S3 or T1, with the most upstream detection occurring at the confluence of the Teme and the Severn (2 rkm downstream of S3) ($n = 2$), Severn Stoke (11 rkm downstream of S3) ($n = 2$), or immediately upstream of S2 ($n = 2$) (Figure 4). The two lamprey that passed S5 did not approach S6. Individuals that passed weirs upstream of the release site took 21.6 ± 2.8 days to reach their upstream extent after their first upstream movement ($n = 50$), and experienced cumulative passage times at weirs of 15.7 ± 2.8 days. The cumulative passage time at

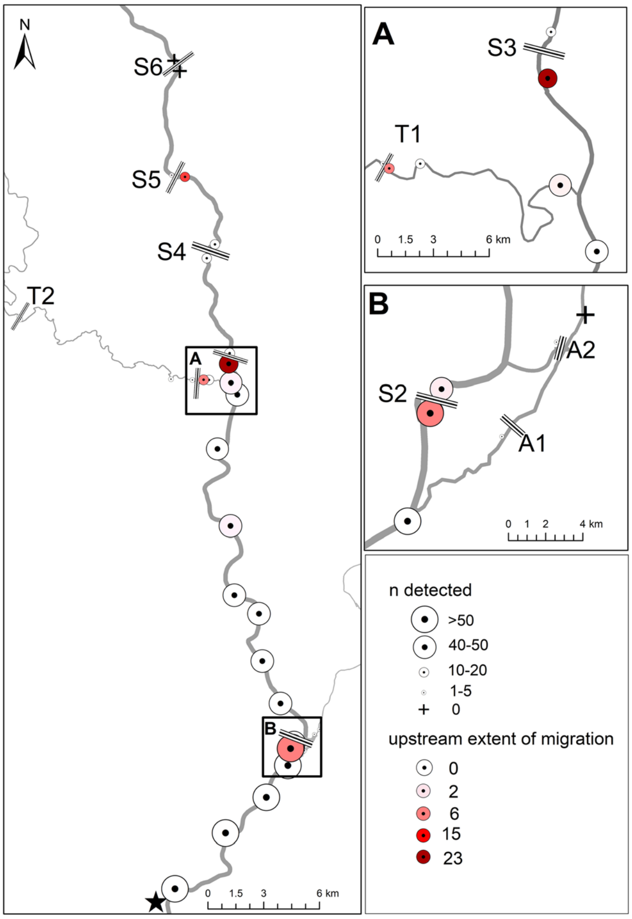


**FIGURE 4** The upstream extent of 56 acoustic-tagged sea lamprey in the River Severn catchment during the 2018 spawning migration. The number of sea lamprey reaching each receiver, and the number of upstream extents of migration by individual sea lamprey at each receiver, are represented by the size and colour intensity of the circles, respectively. The release site (upstream of Weir S1a) is denoted by the black star. The weir codes are listed in Table 1

weirs constituted a median of 84% of the time taken to reach the upstream extent of migration (mean proportion = 68 ± 9%). For 13 lamprey (23%) the upstream extent of their migration was also their final detection location, whereas 43 lamprey (67%) made downstream movements after reaching their most upstream location. Of these, 31 were last detected at a receiver within the array and 12 were last detected at the most downstream receiver, with their approximate final location undetermined.

### 3.3 | Continuous-time multistate Markov modelling of lamprey movements

The best-fitting CTMM describing the movements of lamprey between river sections in the tidal and non-tidal areas of the river are presented in Tables 5 and 6, respectively. The full ranked suite of tested models is provided in Table S2.

In the tidal river, the rate of upstream passage by lamprey at weirs S1a/S1b was positively affected by river level, associated with spring tide periods, and the rate of upstream passage at S2 was positively affected by river discharge during an elevated discharge event (Figure 5; Table 5). The effect of discharge was non-significant for upstream movements through unobstructed sections, and upstream transition rates were significantly higher at night than during the day for all sections (Table 5). The probability of downstream reversal during upstream migration was significantly greater in downstream S2, where approximately half of the upstream movements resulted in a downstream reversal (probability = 0.51, 95% CI 0.40–0.62), than in the two unobstructed sections, where downstream reversals were relatively unlikely (middle reach, 0.02, 95% CI 0.00–0.15; upstream S1a/S1b, 0.01, 95% CI 0.00–0.10) (Table 5).

In the non-tidal river, increasing river discharge had a significantly positive effect on the passage rates of S3 and T1 (Table 6), with weir presence/passage data showing that lamprey passed these structures exclusively during elevated discharge events when the mean daily discharge exceeded 60 $m^3\ s^{-1}/Q_{45}$ in the River Severn and 30 $m^3\ s^{-1}/Q_{17}$ in the River Teme (Figure 6). Discharge also had a positive effect on most unobstructed transition rates (Table 6). For all sections, upstream transition rates were greater at night, although uncertainty around the hazard ratios was high and non-significant for passage at S3 and T1. The best-fitting model in the non-tidal river included an interaction term between river discharge and day/night. This interaction was significant for upstream transitions from upstream S2 to the Severn/Teme confluence, with a hazard ratio of less than 1 indicating that the positive effect of night on transition rates between these sections decreased as discharge increased. The section-specific probability of downstream reversal was significantly greater in downstream S3 (probability = 0.66, 95% CI 0.47–0.74) and downstream T1 (0.55, 95% CI 0.25–0.83) than in the Severn/Teme confluence (0.02, 95% CI 0.00–0.12) (Table 6).

## 4 | DISCUSSION

Knowledge of animal movements in fragmented ecosystems is essential for understanding, predicting, and mitigating the impacts of fragmentation. Here, passive acoustic telemetry provided strong evidence that weirs consistently acted as impediments to the upstream migration of adult sea lamprey in the River Severn catchment. The impacts of these impediments on sea lamprey migration were both spatial (inhibiting access to favourable spawning areas upstream and inducing downstream exploratory movements) and temporal (delaying passage and restricting the opportunity for upstream migration to episodic environmental events).

### 4.1 | Cumulative impacts of artificial structures on upstream-migrating sea lamprey

Low-head weirs and other structures (<2 m head loss), which are estimated to represent approximately 99.5% of artificial impediments globally (Lehner et al., 2011), can negatively affect the ability of

**TABLE 5** Best-fitting continuous-time multistate Markov model for the tidal River Severn describing the upstream movements of 56 sea lamprey between four sections of the River Severn in 2018 and including passage at S1a/S1b and S2 (Figure 1)

| Transition | Length km | Obstructed | *N* transitions | Baseline transition rate (transitions day$^{-1}$) | Coefficient hazard ratios (95% CI) | | | Probability of downstream reversal |
|---|---|---|---|---|---|---|---|---|
| | | | | | Discharge m$^3$ s$^{-1}$ | River level m | Light: night | |
| Downstream S1a/1b → upstream S1a/S1b | 3.0 | Yes | 30 | 0.11 (0.06–0.19) | NA | **4.1 (2.6–6.6)** | **4.5 (2.0–10)** | NA |
| Upstream S1a/S1b → middle reach | 4.0 | No | 74 | 0.75 (0.56–1.06) | 1.1 (1.0–1.2) | NA | **5.1 (3.1–8.5)** | 0.01 (0.00–0.10) |
| Middle reach → downstream S2 | 11 | No | 76 | 1.54 (1.10–2.10) | 1.0 (0.9–1.1) | NA | **4.2 (2.5–7.2)** | 0.02 (0.00–0.15) |
| Downstream S2 → upstream S2 | 1.3 | Yes | 50 | 0.05 (0.03–0.08) | **1.5 (1.4–1.6)** | NA | **6.1 (3.3–11)** | 0.51 (0.40–0.62) |

*Note:* Baseline transition rates with covariates set to their mean values. Coefficients with a hazard ratio not overlapping 1 (set in bold) were considered significant for each transition.

**TABLE 6** Best-fitting continuous-time multistate Markov model describing the upstream movements of 50 sea lamprey between four sections of the rivers Severn and Teme during their 2018 spawning migration, and including passage at S3 and T1

| Transition | Length km | Obstructed | *N* transitions | Baseline transition rate(transitions day$^{-1}$) | Coefficient hazard ratios (95% CI) | | | | Probability of downstream reversal |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | Discharge Severn m$^3$ s$^{-1}$ | Discharge Teme m$^3$ s$^{-1}$ | Light: night | Discharge: light (night) | |
| Upstream S2 → Severn Teme confluence | 24 | No | 46 | 0.34 (0.19–0.37) | **1.2 (1.1–1.4)** | NA | **13 (2.8–61)** | **0.7 (0.6–0.9)** | NA |
| Severn/Teme confluence → downstream S3 | 1.8 | No | 45 | 1.04 (0.46–1.48) | **1.4 (1.3–1.5)** | NA | **20 (4.0–96)** | **0.8 (0.7–1.0)** | 0.02 (0.00–0.12) |
| Downstream S3 → upstream S3 | 1 | Yes | 17 | 0.01 (0.00–0.02) | **1.7 (1.4–2.1)** | NA | 13 (0.03–585) | 1.0 (0.7–1.6) | 0.62 (0.47–0.74) |
| Severn/Teme confluence → downstream T1 | 3.3 | No | 12 | 0.11 (0.04–0.20) | NA | 2.3 (0.9–5.5) | 34 (0.2–460) | 1.2 (0.7–2.1) | 0.02 (0.00–0.12) |
| Downstream T1 → upstream T1 | 1 | Yes | 4 | 0.08 (0.00–0.30) | NA | **1.2 (1.0–1.4)** | 188 (0.1–300) | 0.4 (0.2–1.2) | 0.55 (0.25–0.83) |

*Note:* Baseline transition rates with covariates set to their mean values. Coefficients with a hazard ratio not overlapping 1 (bold) were considered significant for each transition.

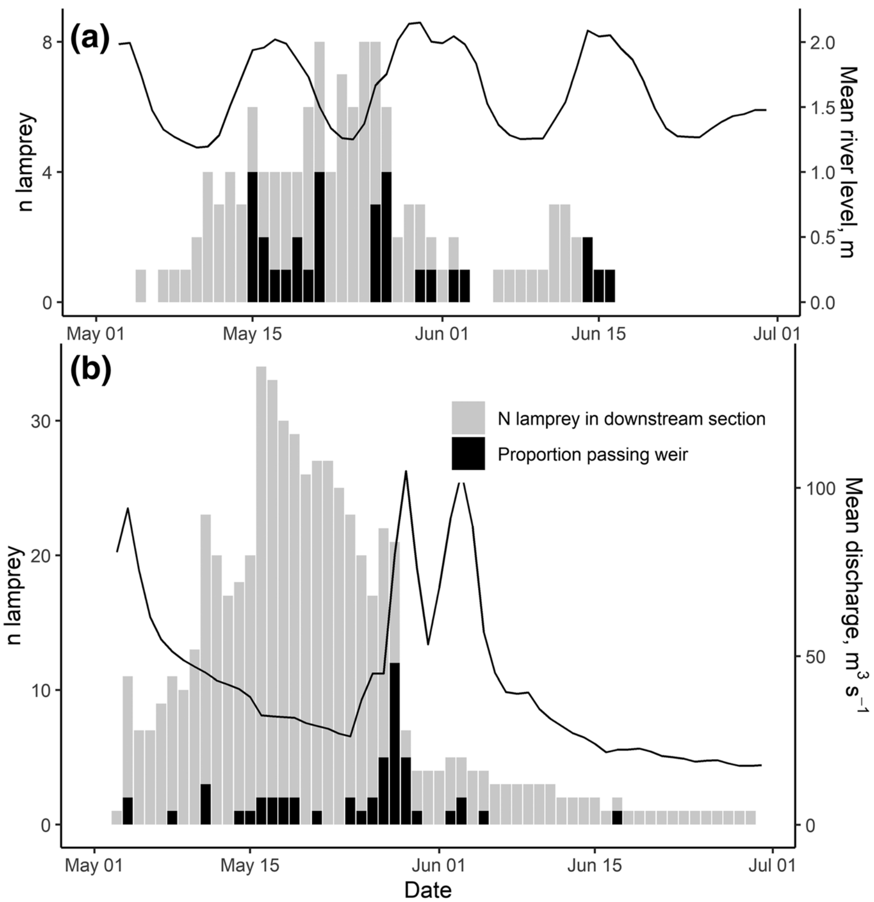


**FIGURE 5** (a) Daily presence of acoustic-tagged sea lamprey (grey bars) in the 'downstream S1a/S1b' section of the River Severn and the proportion passing the weirs (black bars) into the 'upstream S1a/S1b' section during May–June 2018. (b) Daily presence of acoustic-tagged sea lamprey (grey bars) in the 'downstream S2' river section and the proportion passing the weir (black bars) into the 'upstream S2' section. Daily mean river level (Minsterworth gauging station) and river discharge (Saxon's Lode gauging station) are presented as black lines

anadromous aquatic species to complete their spawning migrations as a result of physical impediment and habitat loss (Gibson, Haedrich & Wernerheim, 2005; Lucas et al., 2009; Birnie-Gauvin et al., 2017). The consequences of river habitat fragmentation on anadromous populations can be severe (Limburg & Waldman, 2009; Hall, Jordaan & Frisk, 2011). For sea lamprey, the adverse impacts of barriers on their migration have now been observed in telemetry studies across their native range (Andrade et al., 2007; Castro-Santos, Shi & Haro, 2017; Silva et al., 2019), with historical evidence suggesting that access to available spawning habitat is drastically reduced (Mateus et al., 2012). Here, the impacts of multiple structures on upstream sea lamprey migration appeared to be cumulative; although no weir on the Severn or Teme was a complete barrier to upstream migration, the majority of structures inhibited a proportion of the upstream-migrating cohort, to the extent that no individuals migrated as far as the most upstream navigation weir on the River Severn. This cumulative effect of low-head weirs on lamprey migration has been apparent elsewhere, where low percentage passage across multiple weirs has resulted in only a small fraction of upstream migrants passing all weirs (Keefer et al., 2009; Castro-Santos, Shi & Haro, 2017). The temporal effects of weirs on individuals were also cumulative, with median total passage times of 16.2 days, constituting 84% of the time taken to reach the most upstream location. In other migratory species, temporal delay to migration has been linked to multiple impacts on fitness, including loss of condition and increased risk of predation (Nyqvist et al., 2017; Newton et al., 2018); here, temporal and spatial effects were likely to be interlinked, with sexual maturation and energetic consequences of delay reducing the ability of individuals to pass weirs.

## 4.2 | Downstream movements during upstream migration

Overall counts or percentages of animals that pass artificial structures are important metrics for describing the impacts of barriers on migration, but further temporal, behavioural, and energetic impacts should be considered to provide a comprehensive impact assessment (Castro-Santos, Shi & Haro, 2017; Silva et al., 2018; Birnie-Gauvin et al., 2019). In addition to the temporal delays experienced by sea lamprey at weirs, this study showed that downstream reversals occurred with substantially higher probabilities in obstructed sections compared with unobstructed sections during upstream migration. These downstream movements, a rarely considered consequence of barriers, might represent a behavioural mechanism to locate alternative passage routes and spawning grounds when upstream access is impeded; however, when this exploration is unsuccessful, the energetic costs incurred may be a further impact of habitat fragmentation on their migration. The energetic impacts of such

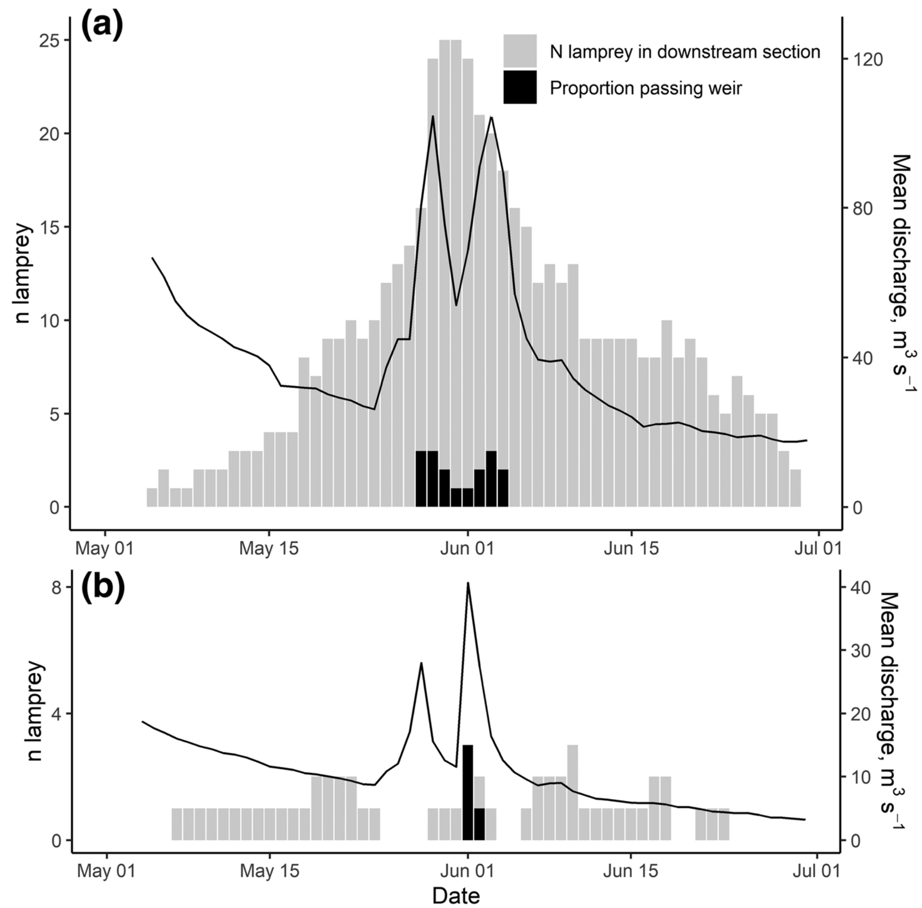


**FIGURE 6** (a) Daily presence of acoustic-tagged sea lamprey (grey bars) in the 'downstream S3' section of the River Severn and the proportion passing the weir (black bars) into the 'upstream S3' section during May–June 2018. (b) Daily presence of acoustic-tagged sea lamprey (grey bars) in the 'downstream T1' river section and the proportion passing the weir (black bars) into the 'upstream T1' section. Daily mean river discharges (Saxon's Lode gauging station, River Severn, and Knightsford Bridge gauging station, River Teme) are presented as black lines

movements in sea lamprey remain poorly understood but may be particularly significant given that the species is semelparous, ceasing feeding after entering fresh water, and relying on stored energy reserves to migrate upstream and spawn (Araújo et al., 2013). Although the section-specific probabilities of downstream movements presented here are a simplistic descriptor and did not account for temporal variation, the biotic and abiotic factors affecting downstream movements, and the impacts of exploratory movements on individual migration success, are recommended as requiring further exploration.

### 4.3 | Impact of weirs on probable spawning areas of sea lamprey

Of the 52 individuals that did not leave the array, 44 (85%) achieved a maximum upstream extent that was immediately downstream of an artificial structure. Sea lamprey are known to aggregate and spawn downstream of weirs (Smith & Marsden, 2009; Pinder et al., 2016), but the reaches downstream of the weirs in the River Severn did not feature the 'typical' sea lamprey spawning characteristics of shallow riffle areas with gravel and cobble (Maitland, 2003; Andrade et al., 2007; Rooney et al., 2015). It was thus assumed that a high proportion of sea lamprey in this study spawned in atypical habitat, which has potential implications for subsequent recruitment. For the 14% of individuals that achieved an upstream extent that was not immediately downstream of a weir, their fate was unknown, including whether they located spawning habitat within the impounded reaches of the lower River Severn or suffered predation during their upstream migration (Boulêtreau et al., 2020). Although some studies have visually quantified lamprey spawning habitat in relation to the location of tagged individuals (Andrade et al., 2007; Lucas et al., 2009), this was not possible in the lower River Severn owing to its relatively high turbidity and depth. A study in the Connecticut River, where high-quality sea lamprey spawning habitat exists in the reaches of river between artificial structures, found that between 36 and 75% of lamprey that passed weirs did not then approach the next weir (Castro-Santos, Shi & Haro, 2017), although non-approaching individuals were subject to substantial delays that reduced their ability to approach the next structure. Here, relatively few individuals (14%) reached an upstream extent in the unobstructed areas between weirs, potentially suggesting a relative lack of suitable spawning habitat. Notably, the final detection location for the majority of sea lamprey was downstream of their most upstream location, which was potentially indicative of an abandonment of the upstream migratory effort and an attempt to locate the most suitable spawning habitat further downstream. Although it was beyond the scope of this study to attempt to identify exact spawning locations, it was also notable that some of these terminal downstream movements were extensive, including a proportion of individuals that returned to the estuary downstream of the receiver array. However, such long-distance movements are difficult to interpret, and have been interpreted elsewhere as post-spawning movements (Holbrook et al., 2016) or even the movements of dead or dying individuals being carried downstream (Havn et al., 2017).

## 4.4 | Influence of environmental conditions on weir passage

Several studies have observed inconsistent distributions of ammocoete length in areas upstream of weirs: weak annual length classes are often coincident with low discharge during the corresponding spawning periods, implying that upstream passage by adult sea lamprey at structures may only be possible during favourable environmental conditions (Andrade et al., 2007; Nunn et al., 2008; Nunn et al., 2017). Here, rates of upstream passage at weirs S2, S3, and T1 increased during episodic periods of elevated river discharge. Indeed, upstream passage at the last two of these structures occurred exclusively during two periods of elevated discharge following heavy rain at the end of May and in early June. The results indicate that the prevailing flow conditions during the migration season may strongly affect the ultimate distance achieved upstream. For example, passage of S3 by tagged individuals occurred exclusively during periods when river discharge was above $Q_{45}$; historical discharge data for the previous 10 years (Figure 2) thus indicates that certain years (2017, 2011, and 2010) would have provided few opportunities for passage of S3 during the typical sea lamprey migration, and in other years (2012 and 2014) upstream migration may have been aided by higher than normal discharge. The results also suggest that passage times during high discharge periods may be short; indeed, at S4, approach and passage occurred exclusively during the same high flow event that enabled passage at S3, and resulted in 100% passage over a median of 0.2 days. The results show that under certain flow conditions barriers become ‘passable’, potentially owing to the weir being inundated and thus reducing the flow velocities experienced by sea lamprey attempting to ascend the weir face. In highly tidal areas downstream of the release site, CTMM indicated that the river level significantly increased upstream passage rates at the tidally affected S1a/S1b weirs. Spring tides overwhelming these two weirs appeared to be an enabling factor for sea lamprey passage, and probably contributed to the relatively high percentage passage and upstream transition rates of sea lamprey at these structures compared with less tidally influenced weirs further upstream.

## 4.5 | Movements in unobstructed reaches

In the non-tidal river area, the upstream passage rates in unobstructed sections increased significantly with increasing river discharge, suggesting that elevated flow events may act as a stimulus to upstream migration. Previous studies have shown that sea lamprey may halt migration away from weirs, with episodic flow pulses stimulating further upstream movements (Almeida, Quintella & Dias, 2002), and this effect is widely reported in other migratory species (Lucas & Baras, 2001; Thorstad et al., 2008). Here, sea lamprey movements were generally highly nocturnal, but during elevated flow periods there was evidence that this nocturnality decreased in the unobstructed sections upstream of S2, but not for weir passages. Consistent with these findings, other studies have found that nocturnality in the Pacific lamprey, *Entosphenus tridentatus* may be context dependent, and can be affected by reach type, with nocturnality strongest around weirs and weakest in unfragmented reaches (Keefer et al., 2013).

Sea lamprey are unusual among anadromous species in that they do not exhibit homing behaviour to natal rivers, but rather select rivers based on innate physiochemical cues (Bergstedt & Seelye, 1995; Waldman, Grunwald & Wirgin, 2008), with tributary selection positively influenced by the presence of pheromones released by ammocoetes, as well as nesting males (Buchinger et al., 2015). In the present study, sea lamprey displayed a preference for certain migration paths when presented with tributary choices; only one entered the Mill Avon (i.e. A1) and two entered the Warwickshire Avon (i.e. A2), with all three ultimately returning to continue up the River Severn. For upstream-migrating sea lamprey at the Severn/Teme confluence, transition rates were significantly higher towards S3 on the River Severn than T1 in the Teme, suggesting that the Severn was the preferred upstream migration route. Indeed, of the 13 sea lamprey that were detected in the River Teme, nine were first detected at the receiver downstream of S3 (1.3 km upstream of the confluence with the River Teme), and were subsequently detected in the River Teme after a downstream movement away from S3.

## 4.6 | Implications for conservation and management of sea lamprey

The River Severn once supported extensive fisheries for sea lamprey that declined following the construction of the navigation weirs in the 19th century (Buffery, 2018). Today, the sea lamprey is a designated feature of the Severn Estuary SAC under the European Union Habitats Directive and is also a feature of the Severn Estuary SSSI under the Wildlife and Countryside Act (Joint Nature Conservation Committee, 2015). The condition of the sea lamprey population in the Severn Estuary SAC is currently assessed as ‘unfavourable’, and the unimpeded passage of adults within spawning tributaries in the catchment is recognized as being required in order to achieve favourable status (Natural England & the Countryside Council for Wales, 2009; Natural Resources Wales, 2018). Although the persistence of sea lamprey within the fragmented Severn catchment is ultimately reliant on the ability of adults to spawn and the larvae to then survive in suboptimal habitats (Almeida & Quintella, 2002; Dawson et al., 2015), this study highlights the issue of migration blockages that inhibit the access of adults to optimal spawning areas in the upper catchment. Generally, physical barriers that limit access to historical river habitat, combined with poor water quality, are thought to be responsible for the low numbers of sea lamprey within rivers in the UK, with improvements required to maintain the species at ‘favourable conservation status’ (Joint Nature

Conservation Committee, 2019). Consequently, the results emphasize the need for barrier removal or the retrofitting of fish passes on structures in the Severn catchment that inhibit passage but that cannot be removed. Previous studies have demonstrated that such actions, when well implemented, have the potential to allow the rapid colonization of upstream areas (Moser et al., 2020). Fish passage improvement works in the Severn should incorporate the needs of sea lamprey, as well as other species, in their design if target passage rates are to be achieved (Silva et al., 2018), and the species-specific knowledge base (Hume et al., 2020) should be integrated within fish-pass designs.

More widely, the results presented here are relevant for the restoration and conservation of sea lamprey populations across their native range and illustrate how knowledge of river connectivity for sea lamprey can present managers with alternative remediation strategies to consider. For example, based on the cumulative impact of multiple weirs in this study, it could be argued that passage remediation efforts should focus initially on improving passage at the furthest downstream structures before working on structures further upstream. An alternative strategy would be to improve passage in the tributaries that provide the greatest area of available upstream spawning habitat, provided that mainstem barriers further downstream allow a proportion of adults to reach such tributaries. As Moser et al. (2020) summarize, multiple studies indicate that when an opportunity to exploit reopened habitat is presented, rapid colonization can occur by pioneering individuals, establishing new core areas of larval production that promotes the further attraction of adults in future years. This point is especially relevant given the finding here that sea lamprey can move downstream to locate alternative spawning tributaries when their primary route is inhibited; the majority of sea lamprey that moved into the River Teme tributary only did so having first moved upstream in the Severn. Therefore, barrier remediation at T1 would open an important spawning tributary for sea lamprey that were unable to pass S3. In other rivers that have channels that are more braided or have more tributaries than the Severn, greater consideration might be needed on deciding which channels and tributaries are the most appropriate for these remediation efforts. These decisions should be underpinned by an intimate knowledge of barrier permeability (Moser et al., 2020), which, as demonstrated here, has the potential to vary substantially depending on environmental conditions within and between years.

### 4.7 | Further research

The results indicated that weirs limit the upstream distribution of sea lamprey spawning in the catchment to impounded sections, but the impacts of habitat fragmentation on ultimate spawning success remain unknown and require further investigation. In particular, the importance of areas immediately downstream of weirs as spawning habitat needs more consideration, and quantifying habitat availability, spawning activity, and reproductive success in these areas should be prioritized in fragmented river catchments (Pinder et al., 2016). Further investigations, potentially coupling telemetry in adults with assessments of ammocoete distribution, are required to study the effects of interannual variation and trends in environmental conditions during the migration season on catchment-wide distributions of sea lamprey, especially in the context of changing climatic patterns. Given the emphasis here on fish passes having high potential for increasing passage connectivity, further work is also needed to find optimal designs that maximize sea lamprey passage rates. Although challenging, this work will be essential to ensure that sea lamprey populations are to remain sustainable in fragmented lowland rivers.

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## CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest associated with this work.

## AUTHOR CONTRIBUTIONS

Conceived and designed the field experiments: JDB, ADN, JRD, CB, RV, JRB, and PD. Conducted fieldwork: JDB, ADN, JRD, and PD. Conducted analysis: PD. Wrote the article: PD. Edited the article: JDB, JRB, ADN, JRD, CB, and RV.

## ORCID

*Peter Davies* https://orcid.org/0000-0003-3739-5352
*J. Robert Britton* https://orcid.org/0000-0003-1853-3086
*Andrew D. Nunn* https://orcid.org/0000-0001-8370-1221
*Jamie R. Dodd* https://orcid.org/0000-0001-5528-4141

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## SUPPORTING INFORMATION

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

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