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RESEARCH ARTICLE

Contrasting responses to riverine barrier modification and fish pass provision in two anadromous non-salmonid species during their spawning migrations

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Abstract

1. Anthropogenic in-river structures represent barriers to migrating fishes. Fish pass designs usually focus on passing anadromous salmonids, and fish pass studies usually focus on site-scale metrics, failing to consider the wider effects.
2. Weir passage metrics and spawning distributions of anadromous iteroparous twaite shad *Alosa fallax* and semelparous sea lamprey *Petromyzon marinus* were assessed using acoustic telemetry between 2018 and 2023, within a catchment-scale reconnection programme on the River Severn ('Unlocking the Severn' [UtS]). Reconnection was by fish pass installation (Severn mainstem; 3 deep-vertical slot (DVS), 1 column bypass) and weir modification (Teme tributary; 1 partial removal/reduced head height, 1 reduced gradient).
3. Time-to-event analysis revealed reconnection increased the probability of lamprey passing both the most downstream DVS and modified weir, and virgin shad were more likely than previous spawners to pass the DVS, but not the modified weir. Improvements in the proportion of tagged shad (to 7%) and lamprey (to 48%) passing the most downstream DVS were modest, but shad passage times were significantly reduced (by 20 days). Weir modification resulted in greater improvements in shad (to 58%) and lamprey (to 78%) passage. Reconnection also enabled passage on substantially lower flows; shad passed the most downstream Severn weir (via the DVS) at Q89 versus Q3 prior to construction, and lampreys at Q86 versus Q45.
4. At catchment scales, reconnection significantly increased the proportion of shad passing the pre-reconnection migration limit. However, the upstream extent of both species in the mainstem was not significantly increased. This was attributed

to the limited motivations of individuals to access previously fragmented reaches; returning shad expressed fidelity to previous spawning sites and lamprey lacked pheromone cues from ammocoetes upstream. Passage motivations are predicted to increase subsequently as more individuals' spawn in these reaches.

5. *Synthesis and applications*. UtS succeeded in facilitating both species to pass weirs under lower flow conditions than before. Weir modification improved passage rates more than fish pass installation, although catchment-scale benefits currently remain limited. Project legacies include identifying long-term monitoring needs to measure accumulating catchment-scale benefits, and information on the suitability of reconnection methods to inform similar reconnection programmes.

KEYWORDS

acoustic telemetry, fish pass, fish tracking, lamprey, multi-species, river restoration, shad

1 | INTRODUCTION

Anthropogenic riverine structures can be significant barriers to migratory fishes, with even low head barriers impeding their upstream passage (Meixler et al., 2009; Newton et al., 2018). Sequences of barriers can have cumulative energetic impacts on upstream migrating species, including salmonids (*Salmo*, *Oncorhynchus* spp.; Kemp & O'Hanley, 2010), shads (*Alosa* spp.; Alcott et al., 2021; Davies et al., 2023; Zydlewski et al., 2021) and Petromyzontidae lampreys (Davies et al., 2021; Jubb et al., 2023). Although riverine barriers are now increasingly being removed to restore free-flowing conditions (Watson et al., 2018), when the barrier retains a functional purpose or has heritage value, then an alternative reconnection method is to install a fish pass. However, fish pass designs tend to be biased towards providing an easier, alternative passage route around the barrier for anadromous salmonids (*Salmo*, *Oncorhynchus* spp.) (Noonan et al., 2012). Accordingly, shad and lamprey passage efficiencies through fish passes (e.g. pool-and-weir and vertical slot designs) tend to be low (Belo et al., 2021; Pereira et al., 2017; Weaver et al., 2019), with optimal pass designs not yet established and with real-world performance assessments urgently needed.

Delivering catchment-scale reconnection for anadromous species in severely fragmented rivers requires improving passage rates at multiple barriers (van Puijenbroek et al., 2019), potentially deploying differing measures at each barrier due to local technical and logistical considerations. Passage efficiencies across individual barriers and through fish passes are then often a function of environmental conditions, where elevated river levels facilitate twaite shad *Alosa fallax* and sea lamprey *Petromyzon marinus* passage over weirs (Davies et al., 2021, 2023), and relatively low flows and higher temperatures improve fish pass efficiencies (Belo et al., 2021; Pereira et al., 2019). In contrast to anadromous salmonids, shad and lamprey spawning migrations remain poorly understood. However, it has recently been established that iteroparous twaite shad express fidelity to previous spawning locations, including in areas downstream of barriers (Davies et al., 2020, 2024). Semelparous sea lampreys are non-homing, relying on pheromone cues from ammocoetes to move upstream (Li et al., 2018; Wagner et al., 2009). Consequently, the motivation of these species to pass upstream barriers and use fish passes might be limited and influenced by a range of environmental and biotic cues (Dodd et al., 2023; Sullivan et al., 2023), including the previous in-river experiences of shad (Davies et al., 2024).

The lower River Severn in western Britain became severely fragmented when navigation weirs were constructed in the 1850s, with two weirs already present before then on its major tributary, the River Teme (Day, 1890; Unlocking the Severn, 2024). Historical evidence suggested that prior to Severn weir construction, the river hosted abundant twaite shad and Allis shad *Alosa alosa* spawning populations that could previously move over 100 km further upstream to spawn each spring (Day, 1890). Since the weir construction in the 1850s, Allis shad have been limited to straying individuals, and the twaite shad population is much reduced, with some hybridisation between the species having also occurred due to their sharing of spawning areas downstream of weirs (Antognazza et al., 2022). As these shads have high conservation designations (e.g. Annex II, V, European Union Habitats Directive [Council of the European Communities, 1992]), the Unlocking the Severn project ('UtS') was implemented in 2017/2018 to reconnect the river through weir modifications and fish pass installation (approximate overall cost: 26 M€). The aim of UtS was to restore the access of shad to their former spawning areas upstream of the weirs and thus provide catchment-scale benefits. Accordingly, fish passes (three deep-vertical slot [DVS], one column bypass) were installed on four sequential Severn mainstem weirs (completed by 2022), with substantial modifications made to two weirs in the lower Teme (by 2019) (Figure 1; Table S1; Unlocking the Severn, 2024).

The aim here was to assess the success of the UtS in providing catchment-scale benefits to twaite shad ('shad') by enabling them to access former upstream spawning areas, with sea lamprey ('lamprey') migrations also assessed to identify the response to

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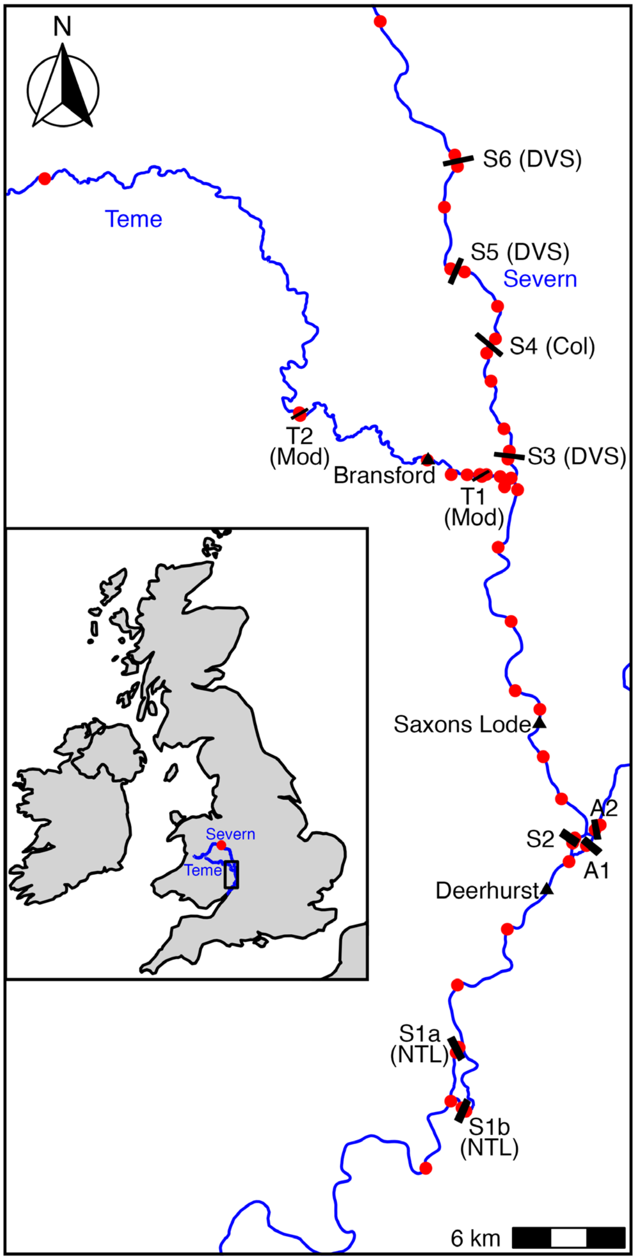

FIGURE 1 Map of rivers Severn and Teme, showing acoustic receiver locations (red points), weirs (black lines), and gauging stations (black triangles), and (inset) the location of the study area in the wider context of the islands of Great Britain and Ireland. The pre-reconnection migration limit was at S3 and T1 and Normal Tidal Limit (NTL) was at S1a and S1b. Project weirs are coded by reconnection method: Col, column bypass; DVS, deep-vertical slot fish pass; Mod, weir modification.

reconnection in another anadromous species. Through application of passive acoustic telemetry before and after reconnection, objectives were to assess how reconnection affected the upstream extent of spawning shad and lamprey across the catchment, identify how the proportions passing barriers and their passage times were altered, and assess the biotic and abiotic factors influencing passage. Key learnings that arose during the UtS project are then discussed in relation to these results.

2 | METHODS

2.1 | Study area

This study was completed between 2018 and 2023, covering both pre-reconnection and post-reconnection periods. The study area covered 11 artificial in-river barriers ('weirs'); seven on the Severn mainstem (S1a, S1b, S2, S3, S4, S5 and S6), two on its River Teme tributary (T1 and T2), and two on its River Avon tributary (A1 and A2) (Figure 1). Weirs S1a (Maisemore), S1b (Llanthony) and S2 (Upper Lode) were not modified in UtS as they are influenced by tide and considered passable by shad at high tides. Four weirs further upstream on the Severn mainstem had fish passes installed (S3 [Diglis], S4 [Bevere], S5 [Holt] and S6 [Lincomb]) and two on the River Teme were modified (T1 [Powick] and T2 [Knightwick]) (Table S1). Prior to reconnection, the most downstream of these weirs on both rivers (S3 and T1; Figure 1) were largely impassable to shad (Antognazza et al., 2021; Davies et al., 2023), and only passable by lamprey under relatively high flows (above Q_{45} at S3 and Q_{17} at T1; Davies et al., 2021). These weirs were thus considered the 'pre-reconnection migration limit' under normal river conditions.

On the Severn mainstem, DVS fish passes were constructed at S3 (opened in 2021), S5 (2022) and S6 (2021), with a column bypass constructed at S4 (2021) (Figure 1; Table S1). Both Teme weirs were modified prior to the 2019 spawning season; T1 was lowered and partially removed with a rock ramp installed within the removed section, and T2 had a low gradient rock ramp constructed up to the original weir crest (Figure 1; Table S1). For brevity, weirs with a fish pass installed are referred to hereafter as 'mitigated' (weir remained but its impact on passage was potentially reduced) and modified weirs are referred to as 'remediated' (as passage impacts were potentially removed). 'Reconnected' refers to both remediated and mitigated weirs.

Data on river temperature (Severn: Deerhurst; Teme: Bransford), flow (Severn: Saxons Lode) and level (Teme: Bransford) for the tracking period (13 April to 8 July) were obtained from the Environment Agency (EA) gauging stations (15-min intervals) (Figure 1). Missing temperature data for the River Teme (12 May 23 to 24 May 23) was estimated from Severn temperature (0.5 × DeerhurstTemperature + 7°C) and river level was estimated from similar trends in previous years ((2018 level + 0.022 + 2019 level + 0.093)/2 m). Environmental conditions differed significantly between years (Figure S1; Table S2). Diel period (day/night) was identified through the suncalc R package (Thieurmel & Elmarhraoui, 2022). Flow and level exceedance (Q) values were provided by the EA for Saxons Lode and Bransford, respectively.

2.2 | Capture and tagging

Shad were captured using angling downstream of S1a and S2, and in a bespoke trap positioned upstream of a 'notch' fish easement at S2 (Figure 1; Table S3a). Individual shad were anaesthetised (ethyl

3-aminobenzoate methanesulfonate; MS-222; 0.4 g/L), measured (fork length [FL], nearest mm), three scales taken (Baglinière et al., 2001) and internally implanted (peritoneal cavity) with a Vemco V9 acoustic transmitter (www.innovasea.com) and a passive integrated transponder (PIT) tag, using protocols outlined in Bolland et al. (2019), with the incision closed using a single absorbable monofilament suture (2–0). Acoustic transmitter programming was a randomised 1-min pulse interval (minimum-maximum interval 30–90 s) in the spawning period (April–July), switching to a 10-min pulse interval, before reverting to the randomised 1-min pulse interval the following April. This extended transmitter battery life, enabling tracking of spawning migrations across three seasons (Table S3b; Davies et al., 2020; Yeldham et al., 2023). Exceptions were 11 individuals tagged in 2018 with short (~145 day) battery life transmitters and in 2023, when Vemco V9 sensor tags (pressure and temperature) on a consistent randomised 1-min pulse interval were used. Following recovery to normal behaviour, shad were released upstream of the weir where they were captured, as their capture location was interpreted as either being motivated to pass or attempting to pass the weir (Figure 1; Table S3a). The exceptions were 18 shad in 2018 released downstream of S2 for the purposes of a related study (Davies et al., 2023). Sexing was possible when gametes were observed during tagging, identifying 114 females and 130 males (137 undetermined). Scales were analysed on a projecting microscope to assess spawning history, with fish identified as virgins (no spawning marks) or previous spawners (spawning marks present) (Table S3c; Baglinière et al., 2001).

Sea lampreys were captured using un-baited two-funnel eel pots downstream of S1a (Figure 1; Table S3a). Captured individuals were anaesthetised using MS-222 (0.8 g/L) as described above, measured (total length [TL], nearest mm) and internally implanted (peritoneal cavity) with a PIT tag and V9 acoustic transmitter programmed with a randomised 1-min pulse interval, with the incision closed as above. They were recovered in aerated river water and released upstream of S1a (Figure 1; Table S3a). Lampreys were not sexed.

All tagging was conducted after ethical review and in accordance with UK Animals (Scientific Procedures) Act 1986, with surgical procedures completed under UK Home Office project licences PPL 60/4400, PD6C17B56 and PP9326830.

2.3 | Acoustic receivers

Acoustic receivers were primarily deployed at 46 locations between the upper Severn Estuary and downstream of Shrewsbury Weir on the River Severn, and Tenbury Wells on the River Teme (Figure 1). Minor variation in receiver placement occurred across the study due to refinement of receiver locations to optimise detection probabilities, plus some receivers were lost during floods. Nevertheless, receivers were maintained upstream and downstream of the key weirs in all years (except 2019 and 2020 when no receivers were at weirs S4, S5 or S6), to detect tagged individuals during weir approach and passage. Inter-array, multi-way efficiencies were calculated in the residency function of the actel R package (Flávio & Baktoft, 2021), with minimum receiver efficiencies reported. Efficiencies were generally >90% at Severn weirs and upstream of Teme weirs, but were more variable downstream of Teme weirs (55.6%–100%; Table S4), where detection ranges were lower due to placement in shallow, narrow channels (Davies et al., 2023). The detection efficiency upstream of T2 may be overestimated due to the large distance to the next receiver upstream (33 km), where no individuals were detected.

2.4 | Sample sizes, passage rates and upstream extent

Tagged individuals that either passed S2 of their own volition or were released upstream and subsequently detected moving upstream were used in this study, resulting in 315 shad (387 separate spawning migrations) (Table S3b) and 86 lampreys (Table S3d) for analyses. The numbers and proportions of shad and lamprey that approached S3 or T1 (as the pre-reconnection migration limits) were calculated for the entire study period, along with the proportions of first approaches to each of these weirs and the proportion of individuals that approached one or both weirs.

The proportion of individuals reaching the pre-reconnection migration limit (S3/T1) that accessed upstream habitat was calculated. Passage efficiencies were calculated for all reconnected weirs (proportion of individuals detected directly downstream of a weir that were then detected upstream) and compared between pre- and post-reconnection (chi-squared), with passing individuals then considered as available to approach the next weir upstream. Passage time (the duration between first detections downstream and upstream of a weir) was compared pre- and post-reconnection using Wilcoxon rank sum tests. Seven transmitters (2019: 6; 2021: 1) were detected simultaneously at receivers up and downstream of T1 due to elevated river levels between 20:38UTC on 12 June 2019 and 04:17UTC on 21 June 2019, and 15:21UTC and 15:45UTC on 24 May 2021. Thus, passage of T1 was only considered to have occurred in those periods if the individual was subsequently detected further upstream.

Upstream extents in the Severn and Teme were described as the maximum distance individuals were detected upstream of the Normal Tidal Limit (NTL; Weir S1a), and compared between pre- and post-reconnection periods for individuals reaching S3 and T1 (Wilcoxon rank sum test). For individual shad that emigrated, the proportion of their total time in the river spent upstream of S3 or T1 was compared between pre- and post-reconnection (Wilcoxon rank sum test).

2.5 | Biotic and abiotic influences on weir passage

To identify the lowest flows/river levels that shad and lamprey passed S3 and T1 pre- and post-reconnection, mean daily flow/river level (and corresponding percentage flow/level exceedance: Q) was calculated for days that shad and lamprey passed each weir. Time-to-event analysis (mixed-effects Cox models) assessed the relative influence of biotic and abiotic factors on weir passage (as 'risk' [probability] of passing) (coxme R package; Therneau, 2022). Individuals entered the risk set (i.e. available to pass) when first detected on the receiver directly downstream of the weir (or last detected at the previous receiver if missed at this receiver), and remained in the risk set until either passing or retreating downstream. Individual biotic and time-varying environmental conditions were fixed predictors. Environmental conditions were summarised at 15-min intervals between first approach and passage/retreat. At S3, Severn flow and temperature data were used; at T1, Teme level and temperature data were used; with day/night included as a binary categorical variable. Environmental conditions were checked for collinearity (Pearson's correlation coefficient, all $r<0.7$; Wei & Simko, 2021). Biotic variables were spawning history and FL at tagging for shad (sex omitted due to high proportions of unsexed individuals), and TL for lamprey. At each 15-min interval, an individual was assigned a binary outcome representing whether it passed before the next time interval (passage = 1, no passage = 0). Models assessed the influence of the fixed predictors on passage risk for shad post-reconnection (insufficient passages pre-reconnection for testing) and for lamprey for the entire study period. For lampreys, reconnection status (pre-/post-) was a fixed predictor, and because the influence of flow/river level on passage over barriers and through fish passes can differ (Davies et al., 2021; Pereira et al., 2017), the interaction between reconnection status and flow/river level was tested by comparing Akaike's information criterion (corrected for small sample size; AICc) between models with and without the interaction in the R package AICcmodavg (Mazerolle, 2020). The final model was that with lowest AICc. Individual fish ID was a random effect to control for individuals making multiple approaches.

All analyses were conducted in R (R Core Team, 2023). Mean values (±95% confidence intervals) were reported for normally distributed data; with median values (inter-quartile range) reported for non-normal data. For shad tracked in multiple years, each spawning migration was considered as independent.

3 | RESULTS

3.1 | Upstream extent

A total of 71% of available shad and 87% of available lamprey reached the pre-reconnection migration limit across all years (Figure 2). Most individuals first approached S3 (95% shad; 89% lamprey), with 25% of shad and 16% of lampreys approaching both S3 and T1. Pre-reconnection (2018), no shad and 48% of lampreys reaching the

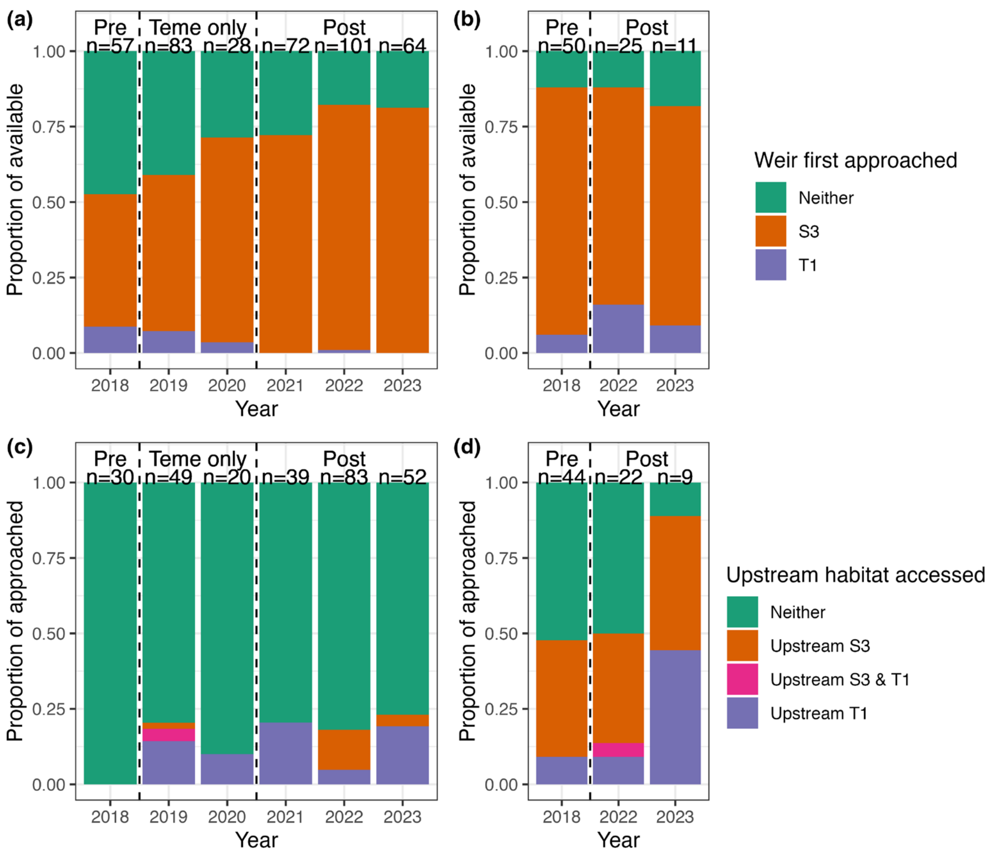

FIGURE 2 Proportion of available (a) shad and (b) lamprey that first approached each of the two weirs at the pre-reconnection migration limit; and the proportion of (c) shad and (d) sea lamprey to reach the pre-reconnection migration limit that then accessed habitat upstream of each weir. Data are separated by year, with sample size and period of reconnection (pre/Teme only/post) indicated above bars.

pre-reconnection migration limits then accessed habitat upstream (Figure 2). After full reconnection (2021–2023), 20% of shad and 61% of lampreys that reached the pre-reconnection migration limit then accessed upstream habitat (Figure 2). For lamprey, these proportions did not differ significantly pre- and post-reconnection ($\chi^2(1, N=85)=0.85$, $p=0.36$; Figure 2), but did for shad, with significantly higher proportions post-reconnection ($\chi^2(2, N=273)=7.27$, $p=0.03$; Figure 2; Table S5).

Upstream extent in the Severn did not increase significantly following mitigation for either species (Wilcoxon rank sum test; shad: $W=7728$, $p=0.14$; lamprey: $W=548$, $p=0.94$; Figure 3; Table S6a), although the most upstream detection location increased by 18.8 km for shad and 16.1 km for lamprey (Table S6a). In the post-remediation period in the Teme, the upstream extent of shad increased significantly ($W=810$, $p<0.001$), but not for lamprey ($W=50$, $p=0.70$; Figure 4; Table S6b), with the most upstream detection location

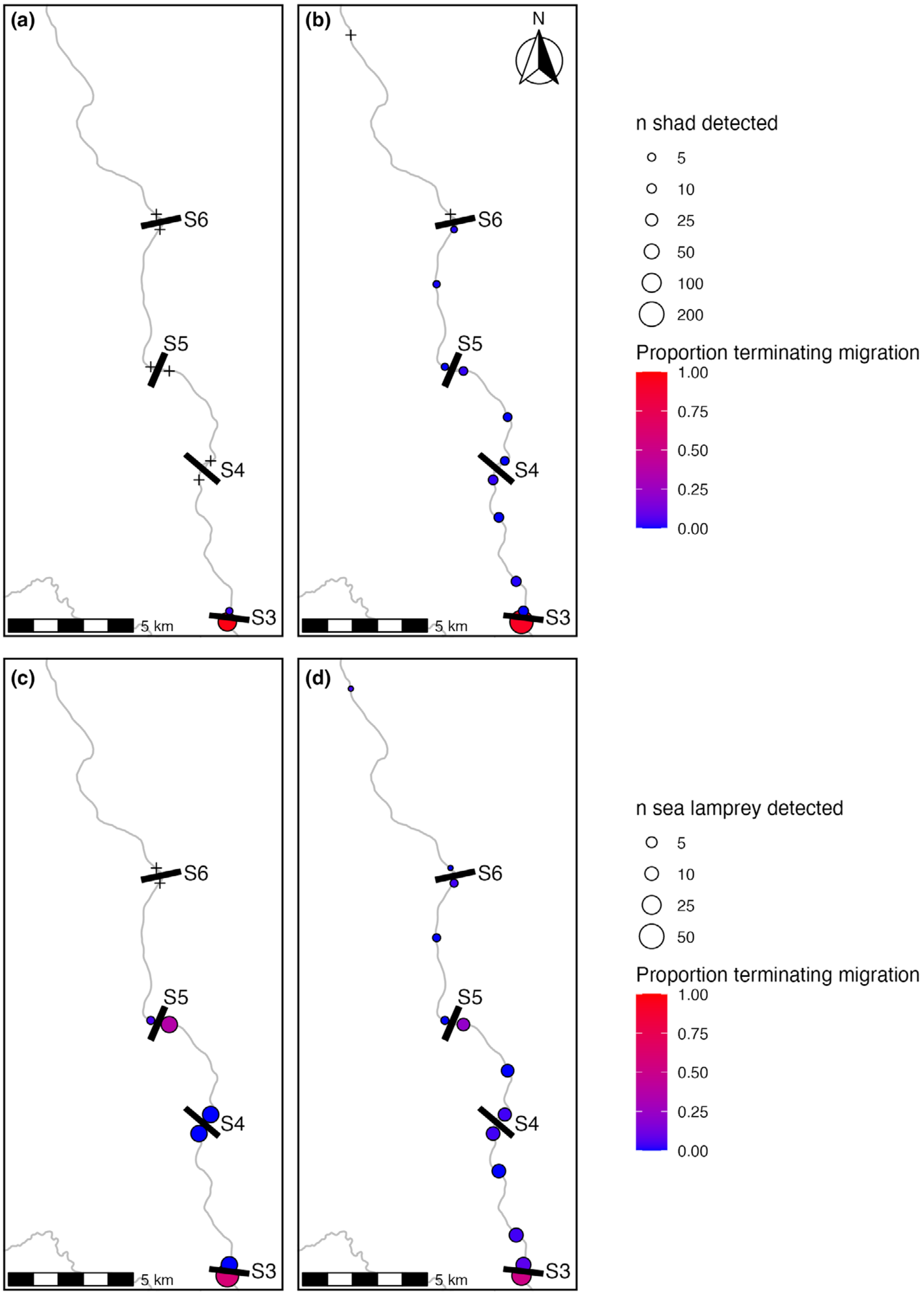

FIGURE 3 Number of individuals to approach S3 detected at each subsequent station (point size), with shading indicating the proportion of these individuals terminating their migration at each station (i.e. they reached their upstream extent), for shad: (a) pre- (2018–2020) and (b) post-mitigation (2021–2023), and for sea lamprey: (c) pre- and (d) post-mitigation. Crosses (+) indicate receivers where no individuals were detected.

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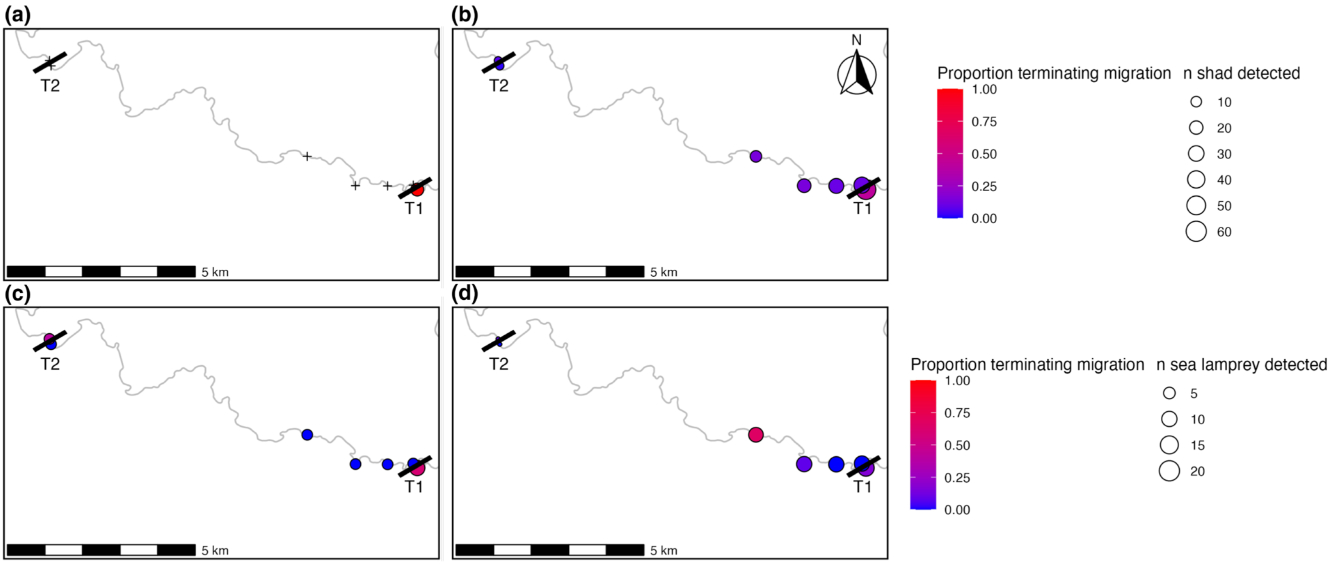

FIGURE 4 Number of individuals to approach T1 detected at each subsequent station (point size), with shading indicating the proportion of these individuals terminating their migration at each station (i.e. they reached their upstream extent), for shad: (a) pre- (2018) and (b) post-remediation (2019–2023), and for sea lamprey: (c) pre- and (d) post-remediation. Crosses (+) indicate receivers where no individuals were detected.

in the Teme increasing by 16.3 km for shad and with no change in lamprey (Table S6b). Post-mitigation, shad that passed S3 and subsequently emigrated ($n=8$) spent a median of 10.5 (3.8–16.3) days upstream of S3 (37% (15.4%–51.5%) of their time in the river). Shad passing T1 post-remediation that subsequently emigrated ($n=22$) spent a median of 8.5 (0.6–14.2) days upstream of T1 (33% (2.5%–45.7%) of their time in the river).

3.2 | Weir passage

Passage efficiency at S3 was low in both pre- and post-mitigation periods for shad (3 ± 4% versus 7 ± 4%; Table 1). Post-mitigation, shad passage efficiencies were 64 ± 32% at S4 and 43 ± 46% at S5, but with only two shad approaching S6 (and not passing) (Table 1). In the Teme, shad passage efficiency at T1 was 0% pre-remediation, and 58 ± 13% post-remediation and 80 ± 50% at T2 post-remediation. Passage efficiencies of lamprey at S3 were similar pre- and post-mitigation (41 ± 15% versus 48 ± 20%; Table 1), with passage efficiency at S4 always high (100% pre- versus 90 ± 21% post-mitigation), but lower at S5 (12 ± 17% versus 25 ± 36%; Table 1). Only two lampreys approached S6, both post-mitigation, with one passing (Table 1). At T1, lamprey passage efficiency was 40 ± 35% pre-remediation, and was 78 ± 32% post-remediation, and was always 100% at T2 (Table 1).

Shad passage times at S3 were much reduced post-mitigation (23.3 (22.1–25.8) to 3.3 (2.2–8.2) days; Table 1), with post-mitigation passage times shorter at S4 and S5 than S3 (Table 1). Passage times for lamprey at S3 were slightly reduced post-mitigation (5.3 (4.1–13.0) to 2.2 (0.1–12.0) days; Table 1). Passage times at T1 and T2 for shad and lampreys in both periods were always relatively short (Table 1).

3.3 | Influences on weir passage

Pre-mitigation, shad only passed S3 when mean daily flows exceeded 349 $m^3 s^{-1}$ (Q_3), but post-mitigation, passage occurred at flows down to 18.8 $m^3 s^{-1}$ (Q_{89}) (Figure 5a). Mean daily flows above 349 $m^3 s^{-1}$ only occurred in 2019, whilst flows above 18.8 $m^3 s^{-1}$ occurred in all study years (Figure 5a; Figure S1a). There was no passage of T1 at any river level pre-remediation, whereas post-remediation, passage occurred at mean daily river levels down to 0.47 m (Q_{78}) (Figure 5b), a level that occurred in all six study years (Figure 5b; Figure S1c). For lampreys, pre-mitigation passage of S3 only occurred at flows exceeding 63.6 $m^3 s^{-1}$ (Q_{45}) versus 19.7 $m^3 s^{-1}$ (Q_{86}) post-mitigation (Figure 6a), with flows exceeding 63.6 $m^3 s^{-1}$ not occurring in 2022, and for only 1 day in 2020, whilst flows exceeding 19.7 $m^3 s^{-1}$ occurred in all six study years (Figure 5a; Figure S1a). Lamprey passage of T1 occurred at levels above 0.48 m (Q_{78}) post-remediation, versus ≥1.30 m (Q_{17}) pre-remediation (Figure 6b), with levels above 0.48 m occurring in all six study years, whilst levels above 1.30 m did not occur at all in 2020 or 2022, and occurred for only 1 day in 2021 (Figure 5b; Figure S1c).

Mixed-effects Cox models indicated that post-mitigation, the only significant predictor of shad passing S3 was spawning history, with virgin fish having a higher probability (risk) of passing than previous spawners (Table 2). The most influential environmental variable was temperature, which was a non-significant positive predictor of passage risk ($p=0.08$; Figure 5; Table 2). At T1, river level and temperature significantly and positively influenced shad passage (Figure 5; Table S8). For lamprey at S3, flow significantly and positively influenced the probability of passing, and the probability of passing was significantly greater at night and post-mitigation (Figure 6; Table 3). At T1, river level significantly

TABLE 1 Summary of the numbers of shad and sea lamprey (Lamp.) that were available to approach (*n* available), approached (*n* approached) and passed (*n* passed) each weir and their median (25th–75th percentile) passage time pre- and post-reconnection.

		Pre-reconnection				Post-reconnection			
Spp.	Weir	*n* available	*n* approached (% of available)	*n* passed (% of approached)	Median passage time (days)	*n* available	*n* approached (% of available)	*n* passed (% of approached)	Median passage time (days)
Shad	S3	168	93 (55.4%)	3 (3.2%)	23.3 (22.1–25.8)	219	174 (79.5%)	13 (7.5%)	3.3 (2.2–8.2)
	S4	3	NA	NA	NA	13	11 (84.6%)	7 (63.6%)	2.2 (1.6–2.6)
	S5	NA	NA	NA	NA	7	7 (100%)	3 (42.9%)	1.9 (1.1–3.0)
	S6	NA	NA	NA	NA	3	2 (66.7%)	0 (0%)	NA
	T1	57	18 (31.6%)	0 (0%)	NA	330	57 (17.3%)	33 (57.9%)	0.08 (0.02–1.05)
	T2	0	0 (NA)	0 (NA)	NA	33	5 (15.2%)	4 (80%)	0.21 (0.06–0.73)
Lamp.	S3	50	41 (82%)	17 (41.5%)	5.3 (4.1–13.0)	36	27 (75%)	13 (48.1%)	2.2 (0.1–12.0)
	S4	17	17 (100%)	17 (100%)	0.2 (0.1–0.3)	13	10 (76.9%)	9 (90%)	3.0 (0.1–7.1)
	S5	17	17 (100%)	2 (11.8%)	6.1 (4.9–7.3)	9	8 (88.9%)	2 (25%)	11.5 (7.7–15.2)
	S6	2	0 (0%)	0 (NA)	NA	2	2 (100%)	1 (50%)	16.9
	T1	50	10 (20%)	4 (40%)	0.04 (0.03–0.07)	36	9 (25%)	7 (77.8%)	0.01 (0.01–0.03)
	T2	4	4 (100%)	4 (100%)	0.6 (0.5–0.7)	7	1 (14.3%)	1 (100%)	0.004

positively influenced the probability of lamprey passing, and the probability of passing was significantly greater post-remediation (Figure 6; Table S9).

4 | DISCUSSION

The UtS reconnection programme resulted in more shad and lamprey migrating upstream of weirs in the Severn mainstem and Teme tributary, and accessing areas that were previously only accessible under high flows. However, the proportion of tagged shad that accessed reconnected reaches was relatively low (20% of those reaching the pre-reconnection migration limit), and the increased river distance accessed was limited for both species (generally <20 km). Compared with fish pass installation, weir remediation (i.e. reducing weir head height and gradient) was more successful at improving passage. However, most tagged shad remained downstream of the most downstream mitigated Severn weir (DVS fish pass; S3), with the few that passed mainly being virgins.

The results here support other work, suggesting that weir mitigation using fish passes is generally less successful at improving fish passage than weir remediation (Watson et al., 2018; Whittum et al., 2023). This was considered due to weir modifications applying across the entire weir face, with no requirement to attract fish into a relatively small area where the pass entrance is located (Noonan et al., 2012). Indeed, fish pass efficiencies are often low for *Alosa* spp. (Gahagan & Bailey, 2020; Weaver et al., 2019) and sea lamprey (Castro-Santos et al., 2017; Pereira et al., 2017). The limited success of UtS in increasing upstream spawning extent was considered to relate strongly to the migration biology and spawning behaviours of both species, rather than issues solely associated with the reconnection methods. Shad have highly repeatable individual migration behaviours, with previous spawners in the post-reconnection period using spawning areas in reaches they used in the pre-reconnection period (Davies et al., 2023, 2024). As virgin shad were more likely than previous spawners to pass the mitigated weir S3, this suggests virgin spawners were more motivated to pass and are likely to drive range expansion in future. Accordingly, fish pass construction as a reconnection tool may result in a delayed response by shad, as observed on the Penobscot River (USA), where the abundance of *Alosa* spp. upstream of mitigated barriers was considerably higher after 8 years post-reconnection compared with the initial 3 years (Whittum et al., 2023).

Sea lamprey are semelparous and non-homing, relying on pheromone cues from ammocoetes to locate spawning rivers and access spawning areas (Guo et al., 2017; Li et al., 2018; Wagner et al., 2009). In the Rivers Wye and Usk, western Britain, river fragmentation resulted in lower ammocoete abundance upstream of obstacles, with fewer year classes present when compared with downstream areas (Nunn et al., 2017). In the Mondego River, Portugal, there was increased ammocoete abundance upstream of a dam following installation of a vertical slot fish pass, despite the pass having a relatively low passage

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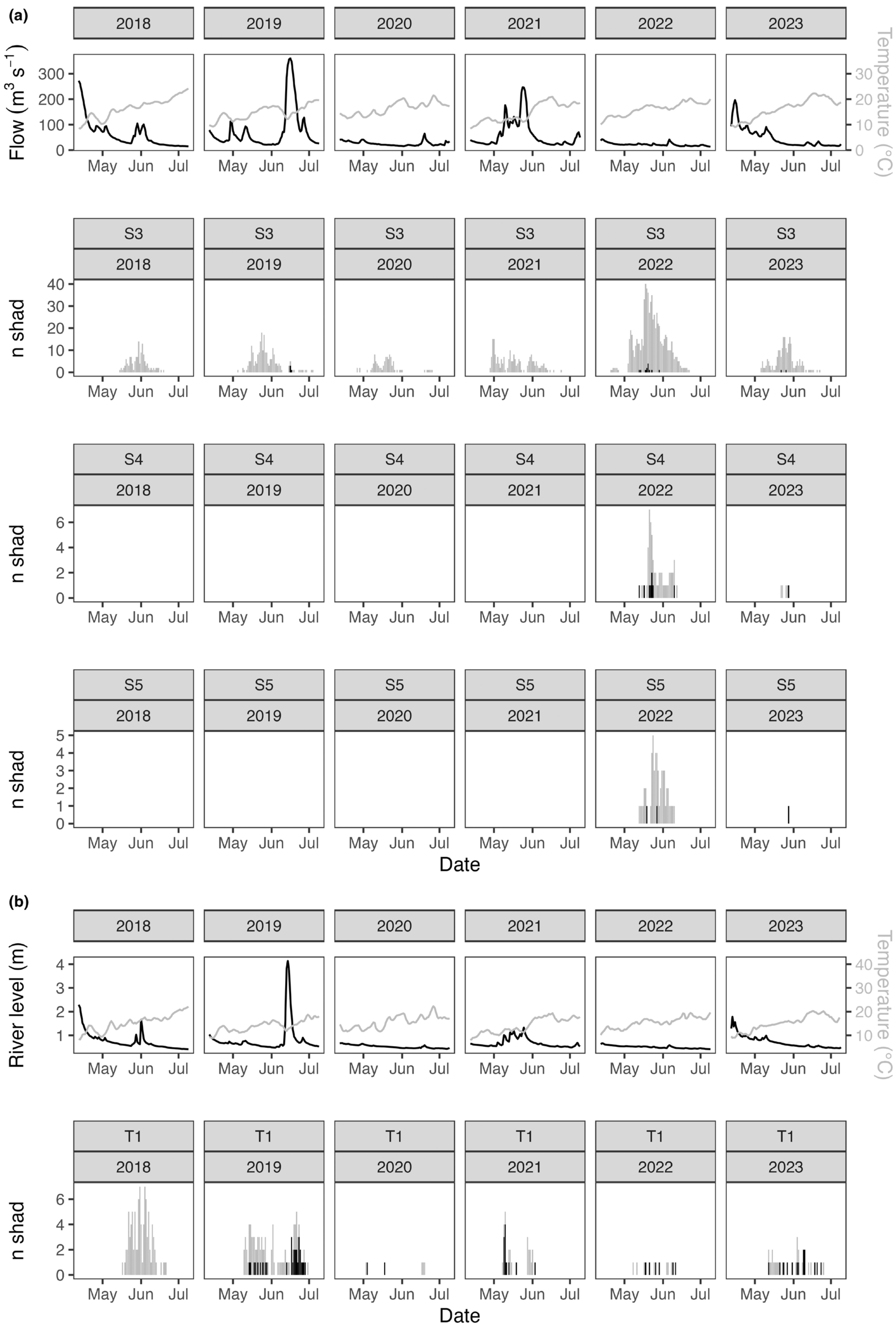

FIGURE 5 Environmental conditions on: (a) the River Severn; and (b) River Teme, in each year, and histograms of the number of shad available to pass each of S3, S4, S5 and T1 (bar height) and the proportion of available shad to successfully pass the weir (proportion of bar coloured black) per day.

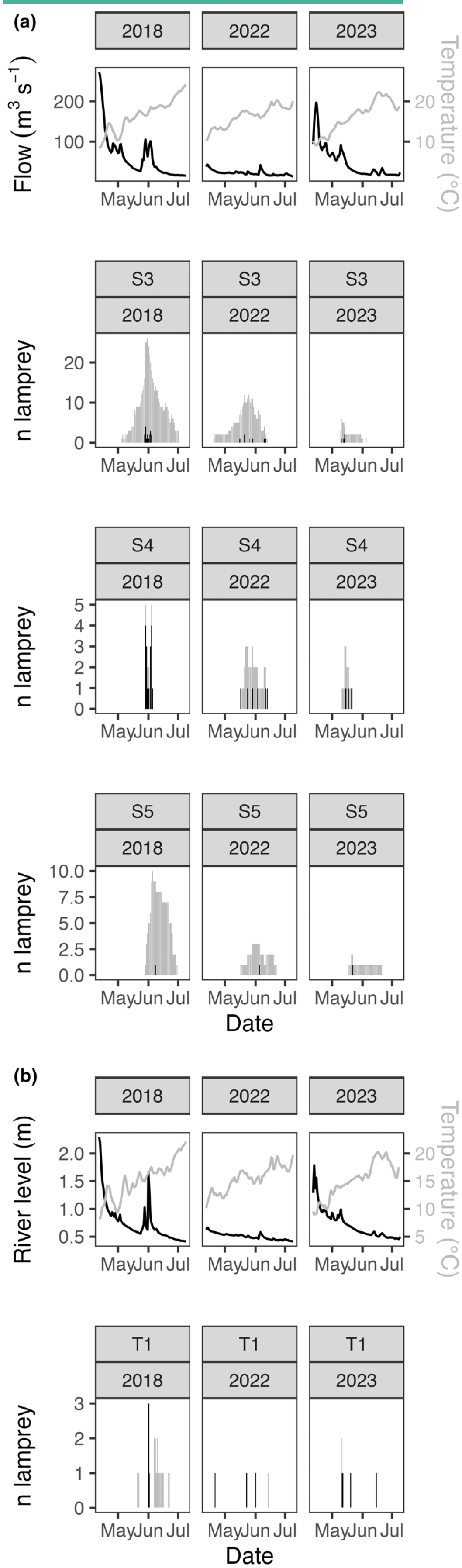

FIGURE 6 Environmental conditions on: (a) the River Severn; and (b) River Teme, in each year, and histograms of the number of sea lamprey available to pass each of S3, S4, S5 and T1 (bar height) and the proportion of available lamprey to successfully pass the weir (proportion of bar coloured black) per day.

efficiency (33%) (Pereira et al., 2017). In the River Severn, whilst similar proportions of lamprey passed S3 in the pre- and post-reconnection periods, the only pre-reconnection year studied (2018) had a period of high flows when individuals passed S3 and the weirs further upstream. Post-mitigation, lampreys were detected as passing S3 in both low and high flows. Importantly, river reconnection enabled lamprey passage at S3 and T1 at flows occurring in all six study years, whereas without reconnection, passage during the tracking period (13 April to 08 July) would not have been possible for more than 1 day in two (S3) and three (T1) years. Accordingly, we expect ammocoete abundances to increase over time upstream of the reconnected weirs, with their increased pheromone concentrations then elevating the migration cues for adult lampreys, so potentially resulting in higher motivations to pass the weirs and spawn upstream (Moser et al., 2021; Wagner et al., 2009).

The delay in catchment-wide benefits being realised here, particularly for shad, provides the opportunity to assess key learnings from UtS, thereby enabling it to inform catchment-wide reconnection programmes elsewhere. Fish passes were installed on weirs on the Severn mainstem as the River Severn Navigation Act (1843) prevented their removal. Given weir remediation in the Teme tributary was more successful in facilitating upstream passage of both species, stronger efforts could have been pursued to repeal legislation for weirs S4 to S6, where boat traffic is considerably reduced from historic industrial levels. The fish passes were designed for shad using expert opinion from across Europe (given the general lack of published information on shad passes, but see Groux et al., 2015; Belo et al., 2021). Nevertheless, the DVS designs appeared to provide sub-optimal passage solutions for shad from these initial results. Although alternative pass designs might have delivered higher passage rates, site constraints meant alternative designs were only feasible at S4 (column bypass).

Despite 26 M€ funding for UtS, there was relatively limited resource allocated for legacy monitoring for shad and none for other species, limiting measurement of inter-annual variability in fish pass performance and longer-term recolonisation. It is now clear this continued monitoring is required for the long-term evaluation of this reconnection project and to inform other programmes seeking to achieve similar catchment-level restorations where barrier removals are not an option. Also, for sea lamprey, a short pre-reconnection monitoring period (1 year) prevented a more rigorous evaluation of their reconnection benefits, further emphasising the importance of multi-year pre-reconnection baselines where feasible, potentially with complementary methods, such as ammocoete surveys (Baltazar-Soares et al., 2022).

TABLE 2 Summary of: (a) the fixed predictors in the final mixed-effects Cox model describing the effects of biotic and abiotic variables on the relative risk (Hazard ratio) of passage at S3 for shad, post-mitigation; and (b) the AICc and log-likelihood of the final and null models.

(a)

Predictor	Coefficient	Standard error	Hazard ratio	z	p
Flow	−0.03	0.09	0.97	−0.31	0.75
Temperature	0.85	0.48	2.33	1.75	0.08
Diel period: day	—	—	—	—	—
Diel period: night	−1.58	1.06	0.21	−1.48	0.14
Spawning history: previous spawner	—	—	—	—	—
Spawning history: virgin	3.83	1.19	46.00	3.23	0.0013
Fork length	0.02	0.01	1.02	1.35	0.18

(b)

Model	K	AICc	Log-likelihood
Final	6	233.99	−111.00
Null	1	250.25	−124.13

Note: Biotic variables were spawning history (virgin or previous spawner) and fork length (mm). Abiotic variables were flow ($m^3 s^{-1}$), temperature (°C) and diel period (day/night). Individual fish ID was the random predictor.

TABLE 3 Summary of: (a) the fixed predictors in the final mixed-effects Cox model describing the effects of biotic and abiotic variables on the relative risk (Hazard ratio) of passage at S3 for sea lamprey; and (b) the AICc and log-likelihood of the final, interaction and null models.

(a)

Predictor	Coefficient	Standard error	Hazard ratio	z	p
Post-mitigation	—	—	—	—	—
Pre-mitigation	−4.64	1.49	0.01	−3.12	0.002
Flow	0.08	0.02	1.08	4.99	<0.001
Temperature	−0.26	0.31	0.77	−0.85	0.40
Diel period: day	—	—	—	—	—
Diel period: night	2.24	0.50	9.38	4.51	<0.001
Total length	0.01	0.01	1.01	0.86	0.39

(b)

Model	K	AICc	Log-likelihood
Final (no interaction)	6	483.78	−235.89
Interaction	7	495.44	−240.72
Null	1	530.63	−264.32

Note: Biotic variables were total length (mm). Abiotic variables were flow ($m^3 s^{-1}$), temperature (°C) and diel period (day/night). Reconnection status (pre-/post-mitigation) was a fixed predictor. Individual fish ID was the random predictor.

In the UtS programme, the three most downstream weirs (S1a, S1b and S2) were not reconnected as these were considered as relatively minor obstacles to upstream migration during project planning, given they can be flooded out during high spring tides, and thus improving passage at other weirs was prioritised. However, telemetry studies have since indicated these weirs present much greater obstacles to migrating shad and lamprey than previously thought (Davies et al., 2021, 2023). Thus, if UtS was able to be done again, the revised project plan would include: (i) application of remediation or mitigation efforts on the most downstream tidal weirs to improve passage in the lower river; (ii) greater efforts to remove or lower the Severn mainstem weirs, removing the need to install fish passes; (iii) where fish passes still require installation then consider revision of the DVS design (accepting that quantitative evidence for alternative designs remains lacking); and (iv) include more resource for long-term monitoring of fish pass performance and catchment-wide movements for shad and other species, including potamodromous species.

In conclusion, the partial removal and lowering of Teme tributary weirs was more successful in facilitating the upstream passage of twaite shad than the most downstream DVS fish pass on the Severn mainstem, the principal migration route, where passing shad were primarily virgins. For sea lamprey, passage at mitigated and remediated barriers is now possible in low-flow years, whereas it was previously only possible under high flows. Thus, whilst the catchment-scale UtS reconnection project has yet to realise substantial benefits for both species, likely influenced by their contrasting ecologies, we consider these benefits should accrue in future years.

AUTHOR CONTRIBUTIONS

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

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Animal metadata and data relating to weir approaches, passages and retreats are available via the Bournemouth Online Research Data Repository (BORDaR), https://doi.org/10.18746/bmth.data.00000453 (Yeldham et al., 2025). Due to political sensitivity around the spawning migrations of the protected twaite shad in the River Severn, and as the tracking project has not yet been completed, a partial data waiver has been granted, with detailed tracking data not publicly available at the time of publishing. However, it is intended that detailed tracking data will become available in the future, along with animal metadata, in the European Tracking Network (ETN), https://marineinfo.org/doc/dataset/6052 (Davies et al., 2018).

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SUPPORTING INFORMATION

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

Table S1: Locations and head drops of the study weirs, and the river reconnection method used at each weir.

Table S2: Kruskal–Wallis test results comparing environmental conditions of the River Severn and River Teme between years over the course of the study period.

Table S3: Summary of (a) the number of shad (*n* shad) and sea lamprey (*n* sea lamprey) tagged with acoustic transmitters in each year, the weir at which they were captured, the method used to capture them (angling, trap, or eel pot), and whether they were released upstream (US) or downstream (DS) of that weir; summary of the number of shad available to approach weirs S3 and T1 in each year (Total) and the split of individuals by (b) tracking season and (c) spawning history (virgin or previous spawner); and (d) number of sea lamprey available to approach weirs S3 and T1 in each year.

Table S4: Summary of the minimum detection efficiencies (%) of the acoustic receivers directly downstream (DS) and upstream (US) of each study weir in each of the study years, where '-' corresponds to no deployment, and 'NA' to no tagged individuals detected at, or upstream of that station in that year.

Table S5: Contingency table indicating the observed numbers of shad (*n*) that accessed (1) and did not access (0) habitat upstream of the most downstream mitigated/remediated weir (S3 or T1) having approached at least one of the two weirs during each period of reconnection (pre/Teme only/post).

Table S6: Summary of the number of shad and lamprey (*n*) to approach each of weirs: (a) S3, and (b) T1, and the median (25th–75th percentile) and maximum upstream extent, from the Normal Tidal Limit, they reached in the (a) Severn mainstem and (b) Teme tributary.

Table S7: Summary of the numbers of (a) shad, and (b) sea lamprey that were available to approach (*n* available), did approach (*n* approached) and passed (*n* passed) each weir and their median (25th–75th percentile) passage time at each weir.

Table S8: Summary of the predictors in the final mixed-effects Cox model describing the effects of biotic and abiotic variables on the relative risk (Hazard ratio) of passage at T1 for shad, post-remediation (a), and comparison of AICc and log-likelihood between the final and null models (b).

Table S9: Summary of the predictors in the final mixed-effect Cox model describing the effects of biotic and abiotic variables on the relative risk (Hazard ratio) of passage at T1 sea lamprey across the entire study period (a), and comparison of AICc and log-likelihood between the final, interaction and null models (b).

Figure S1: Boxplots indicating mean daily: (a) flow and (b) temperature on the Severn mainstem; and: (c) river level and (d) temperature on its Teme tributary, between mid-April and early July (days 103–189 of the year) in each year, where horizontal lines indicate the 25th percentile, median and 75th percentile and vertical lines indicate the minimum and maximum values.

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