Tracking repeat spawning anadromous fish migrations over multiple years in a fragmented river suggests philopatry and sex-linked variation in space use

Peter Davies[1,2*]; J Robert Britton[1]; Demetra Andreou[1]; Charles Crundwell[3]; Jamie R Dodd[2]; Olivier Lepais[4], Andrew D Nunn[2]; Stephen Sabatino[5]; Randolph Velterop[6]; and Jonathan D Bolland[2*]

[1]Department of Life and Environmental Sciences, Bournemouth University, UK
[2]Hull International Fisheries Institute, University of Hull, UK
[3]Environment Agency, Riversmeet House, Northway Lane, Tewkesbury, UK
[4]INRAE, Univ. Bordeaux, BIOGECO, F-33610 Cestas, France
[5]Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, nº 7, 4485-661 Vairão, Portugal
[6]Natural England, Sterling House, Dix's Field, Exeter, UK

*peter.davies@plymouth.ac.uk
* j.bolland@hull.ac.uk

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Competing Interests

The authors have no competing interests to declare

Data availability

Data from this study will be made available upon reasonable request

Abstract

There is limited knowledge of how philopatry influences the spatial ecology of iteroparous anadromous species during their spawning migrations, but this knowledge is important to understand population responses to interventions such as river reconnection. Here, acoustic telemetry was applied to twaite shad *Alosa fallax* and hybrids (n = 184) during their freshwater spawning migration, enabling quantification of philopatry across spawning migrations, and assessment of the factors affecting space use. Tagged fish moved a median of 7 km d^{-1}. Their migration routes were tortuous (median ratio of total distance moved:upstream extent = 2.8), and included multiple upstream/downstream direction changes (median = 27), over a median freshwater movement distance of 247 km. Females occupied larger core areas than males, but previous spawning experience, body length, tagging status, and introgression with *A. alosa* did not predict core area size. Seventy-one fish returned a year after tagging, with a median freshwater residency of 33 days. Between years, intra-individual similarity in space use was significantly greater than inter-individual, providing strong evidence of philopatry. These results provide insights into how spawning philopatry and phenotype influence riverine space use in a threatened anadromous species, and have implications for river reconnection efforts.

Keywords

telemetry; space-use; anadromy; migration;

Introduction

Iteroparity is a bet-hedging strategy that aims to maximise fitness in relatively unstable environments (Glebe & Leggett, 1981; Stearns, 1992). In anadromous fish species, iteroparity reduces the relative importance of individual spawning migrations by prioritising adult survival to ensure future reproduction. Iteroparous individuals may therefore be relatively risk averse in their migratory behaviours (Warner, 2005). Natal philopatry is also evident in many anadromous species, especially those in the Salmonidae family (Dittman & Quinn, 1996; Thorstad et al., 2021). This brings the advantage of local genetic adaptation, with patterns of local population structuring usually evident within salmonid species (Beacham & Withler, 2017; Sylvester et al., 2018). In iteroparous species, spawning philopatry - the return of adults to a previous spawning site - can also occur (Stepien et al., 2009).

Anadromous members of the herring family Clupeidae are distributed throughout the Northern hemisphere and comprise both iteroparous and semelparous species (Leggett & Carscadden, 1978). Some widely distributed anadromous clupeid species utilise both strategies, with iteroparity prevailing in environmentally variable northern rivers and semelparity prevailing in more stable southern rivers (Leggett & Carscadden, 1978; Aprahamian et al., 2003). In iteroparous clupeids, individuals can generally survive several annual spawning events, with natal philopatry suggested by strong patterns of population structuring; genetic isolation by distance is usually evident between different spawning populations (Hasselman, Bentzen & Bradford, 2010; Jolly et al., 2012; Sabatino, Faria & Alexandrino, 2022). Distinct sub-populations are also often present in specific river tributaries (Carscadden & Leggett, 1975; Jolly et al., 2012). In addition, recent telemetry work has indicated that repeat-spawning adults primarily return to the same catchment, despite sharing marine habitats with individuals from other spawning populations (Davies et al., 2020).

Natal philopatry is likely to increase the likelihood that returning adults will find mates, and favourable spawning and nursery habitats (Hendry et al., 2004; Quinn, 2005). However, whether natal philopatry by virgin spawners leads to spawning philopatry in subsequent migrations is uncertain, especially in rivers where migration routes are potentially impeded by engineered structures. While there is evidence that migration timing can be ‘fine-tuned’ throughout the lifecycle of iteroparous fish (Tibblin et al., 2016), there is high uncertainty on the inter-annual differences in, and the biological and environmental drivers of, riverine space use by individual fish, such as body size and sex, despite being important for impact assessments of spawning movements and behaviours (Pess et al., 2014).

While natal philopatry is a highly adaptive strategy, straying can buffer anadromous populations from environmental perturbations, and enable colonisation of new habitats and recolonisation after local extinctions (Keefer & Caudill, 2014). Increasingly, conservation interventions in impounded rivers, including barrier removals and fish pass installation, are being used to restore aspects of longitudinal connectivity for migratory fishes and provide accessible once more to former reproductive areas (Nunn & Cowx, 2012; Bubb et al., 2021). Reconnection potentially represents a special form of environmental instability where population responses can be influenced by their degree of philopatry to natal sites in the pre-reconnection period (Pess et al., 2012). There are, however, considerable knowledge gaps in how iteroparous, non-salmonid fishes react to river reconnection, including how natal philopatry influences the extent to which individuals alter their selection of spawning areas.

An anadromous and iteroparous clupeid that is becoming increasingly threatened across its range is the twaite shad *Alosa fallax*, which is distributed across the north-eastern Atlantic and Mediterranean (Aprahamian et al., 2003a). River fragmentation and overexploitation have driven substantial declines in their populations (de Groot, 1990; Aprahamian et al., 2003b), resulting in international conservation designations (e.g. listing on Annexes II and V of the European Union Habitats Directive (Council of the European Communities, 1992)). In the northern part of their range, previous-spawned fish often represent over 50% of the spawning run (Aprahamian et al., 2003b). They also readily hybridise with sympatric allis shad *Alosa alosa*, with higher rates of genetic introgression being associated with the anthropogenic fragmentation of their spawning rivers, which results in overlapping spawning ranges (Jolly, Maitland & Genner, 2011; Taillebois et al., 2020; Antognazza et al., 2021; Sabatino, Faria & Alexandrino, 2022). High rates of hybridisation could be important to note given hybrids may use migration routes and spawning destinations that are intermediate between the parental routes, and have higher variability in their migration patterns (Alvarado, Fuller & Smith, 2014; Delmore & Irwin, 2014).

Advances in passive telemetry have facilitated the identification of the spawning migration routes of anadromous fish (e.g. Kirk & Caudill, 2017; Lennox et al., 2019; Mack, White & Rohde, 2021) and individual variability in their movements and habitat choice (e.g. Moore et al., 2017; Davies et al., 2022). For twaite shad, refinements to tagging protocols have enabled internal implantation of acoustic transmitters to track their spawning migrations and marine habitat use (Bolland et al., 2019; Davies et al., 2020), and enabled individuals to be tracked over multiple spawning migrations. This approach has already revealed the negative effect of anthropogenic barriers on twaite shad upstream migrations in the highly engineered River Severn basin, western Britain. In this basin, a series of navigation and flow regulation weirs have already been demonstrated to prevent and delay the upstream movements of returning spawning shad that were tracked over successive spawning migrations (Davies et al., 2023). Here, the focus is on how philopatry among individuals tracked during at least two successive spawning migrations influenced their riverine spatial habitat use, with the influence of sex, body length, genetic introgression, tagging and migratory experience also considered. The objectives were to: i) quantify the movements, extent of freshwater residency and catchment-scale space use of twaite shad and their hybrids during their spawning migrations; ii) test the individual and genetic factors affecting riverine space use during their spawning migrations ('core area size'); and iii) assess the extent of philopatry during their spawning migration in the River Severn basin by returning fish.

Methods

Study duration and area

The study was conducted on the spawning migrations of twaite shad (including their hybrids) in the River Severn in 2018, 2019 and 2020. These migrations tend to commence in late April and are concluded by late June (Antognazza et al., 2019). The study area, was the lower river catchment that includes confluences with two major tributaries, the River Teme and River Avon, and eight major weirs (four on the main river channel, and two on each of the lower reaches of the River Teme and River Avon) that result in high fragmentation (Figure 1). The normal tidal limit is at Maisemore (hereafter Weir S1a) and Llanthony Weirs (S1b) on the western and eastern branches of the river respectively (Figure 1), although large spring tides can penetrate the river up to Upper Lode Weir (hereafter Weir S2). Further description of the study area, including detailed description of anthropogenic structures and fish passage infrastructure, is provided in Davies et al., (2023).

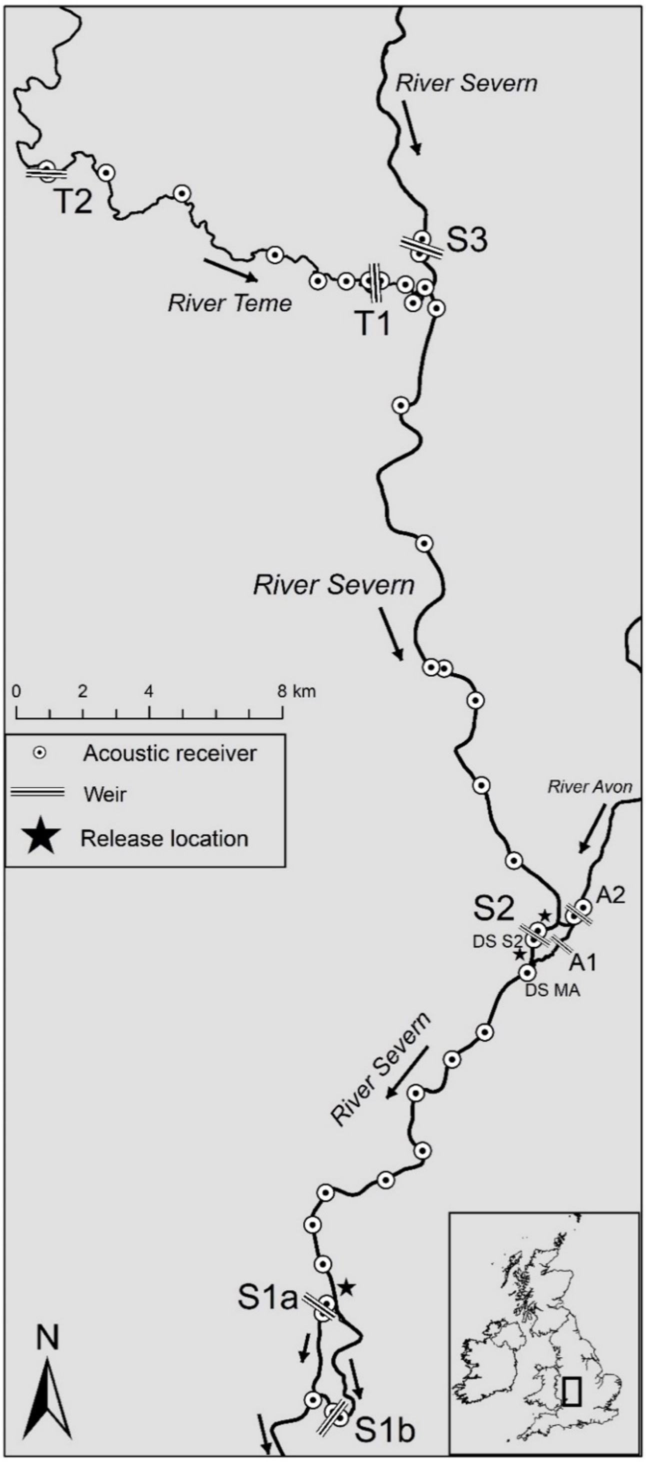

Figure 1: The River Severn catchment study area, including locations of release of acoustic-tagged twaite shad *Alosa fallax* (black stars), weirs (bars) and acoustic receivers (black dots within white circles) in the rivers Severn, Teme and Avon, UK. The black arrows denote the direction of the flow. For full description of weirs and characteristics, see Davies et al. (2023).

Twaite shad capture and tagging

At the commencement of their migration season in May 2018 and 2019, upstream-migrating twaite shad were captured by angling in the weir pools of S1a and S2. In addition, twaite shad were captured at S2 using an aluminium trap featuring a manually operated sliding trapdoor positioned at the upstream exit of the notch fish pass. Fish were captured individually as they exited the pass and immediately removed from the trap via hand net. Following their anaesthesia (ethyl 3-aminobenzoate methanesulfonate; MS-222), all fish were weighed (to nearest 10 g), measured (fork length, nearest mm) and sexed (see subsection '*Assignment of sex and hybrid classes'*), and approximately three scales were removed for analysis of spawning history. These scales were analysed to determine their number of spawning-marks (i.e. their previous spawning history) on a projecting microscope (x48 magnification) (Baglinière et al., 2001). In addition, a tissue sample from a pelvic fin biopsy was taken from each individual for subsequent genetic analysis.

The fish were tagged with 69 kHz Vemco V9 acoustic transmitters (29-mm long x 9-mm diameter, 4.7-g weight in air) (innovasea.com), following the protocol of Bolland et al. (2019), under UK Home Office project licence PD6C17B56. All captured fish were tagged, apart from those (<1%) displaying injury due to possible attack by predators. Following tagging, fish were immediately transferred for recovery in the river by being gently held facing upstream, and released when they were able to swim upstream. A total of 184 twaite shad were tagged with acoustic transmitters over the two years (Table 1). Most transmitters (n = 173) were programmed to transmit randomly between 30-90 seconds in the period April-June inclusive to encompass the freshwater migration period and then every 10 minutes July-March inclusive to encompass their marine phase. This programming increased the battery life of the transmitters to approximately three years, potentially enabling three consecutive spawning migrations to be tracked. The remaining transmitters (*n* = 11) had a battery life extending to one spawning season only (random burst interval 30-90 seconds), with the decision to tag some fish with these shorter life transmitters based on tag availability. All fish captured at S1a were released upstream of this weir in order to study their migration and the impacts of barriers further upstream. Eighteen fish captured at S2 were released downstream in 2018 (Table 1) as part of wider investigations into the factors affecting barrier passage (Davies et al., 2023).

Table 1: Twaite shad *Alosa fallax* (including hybrids) tagged over two years in the River Severn.

	Dates	Capture Location	Method	Release location	*n*	Length ± SE, mm	Weight ± SE, g
2018	9,10, 24 May	S1a	Angling	Upstream S1a	20	365.9 ± 5.6	653.8 ± 33.2
	22,23 May	S2	Angling	Downstream S2	10	375.4 ± 6.5	645.0 ± 33.7
	16,22 May	S2	Angling	Upstream S2	24	339.8 ± 6.5	479.2 ± 29.0
	23 May	S2	Trap	Downstream S2	8	357.6 ± 9.9	559.4 ± 64.6
	14,23 May	S2	Trap	Upstream S2	22	376.4 ± 3.6	736.4 ± 24.0
2019	2-3,13- 15 May	S1a	Angling	Upstream S1a	50	350.9 ± 6.1	617.5 ± 36.1
	7-9, 16 May	S2	Trap	Upstream S2	50	376.9 ± 5.4	776.5 ± 35.3
Total					184	362.8 ± 2.7	659.8 ± 16.8

Acoustic array

An array of Vemco acoustic receivers (VR2-W and VR2-Tx, www.innovasea.com) was installed in the study area (Figure 1), prior to the commencement of the spawning migration period in each study year. Receivers were deployed upstream and downstream of each navigation weir on the main channel of the River Severn and the flow-regulation weirs on the rivers Teme and Avon, with additional receivers deployed between weirs (Figure 1). The furthest downstream receiver in the array (51.8347 N, -2.2901 W; Figure 1) was located in the estuary, 8 km downstream of the tidal limit, and slightly upstream of approximate limit of saltwater incursion into the river (Bassindale, 1943). Although no tagging occurred in 2020, the receiver array was installed to track returning fish tagged in previous years. Receivers were anchored on steel fencing pins driven into the river bed. In the River Teme, which has sections of fast-flowing riffle, receivers were deployed in slower-flowing pools to maximise detection distance. In each tracking year, data were downloaded from receivers every two weeks until no further movements were detected. Basic range tests were conducted on one day in 2019 during normal flow conditions by suspending a range test tag (V9, fixed burst interval 10s) at 1 m depth in the river and moving sequentially away from the receiver. The tag was suspended in the water column for two minutes in 20 m increments, up to a maximum distance from the receiver of 200 m. These tests revealed that 100% of test tag transmissions were detected a minimum of 100 m away from the receivers in the River Severn, and a minimum of 50 m away from the receivers in the River Teme. Individual receiver detection efficiency in each year was calculated using the *actel* R package (Flávio & Baktoft, 2021) and ranged from 43 to 100 %. The two receivers with the lowest detection efficiencies (annual efficiencies = 53 to 93 % and 43 to 91 %) were in narrow channels and/or high turbidity tidal areas. The detection efficiency of receivers in non-tidal areas of the River Severn was generally high (median: 98.9%).

Assignment of sex and hybrid classes

Of the 184 individuals, 77 (42%) were sexed by positive identification of gonads, eggs or milt during tagging by visual inspection of the body cavity through the tagging incision, or by the presence of milt. Since twaite shad display marked sexual polymorphism (Aprahamian et al., 2003), sex was estimated for any unsexed individuals based on the length/weight ratio-at-age distributions of individuals of known sex. Individuals of a given age were conservatively assigned a sex if they fell outside the size range of individuals determined to be of the other sex. After this process, 155 (84%) individuals had a known or estimated sex classification while the remainder fell within the overlapping size range for length/weight ratio-at-age of individuals of known sex, and so remained unsexed. Assignment of hybrid classes between twaite shad and allis shad was conducted using the protocol of Taillebois et al. (2020) on the fin tissues of a subset of 95 individuals, selected on the basis of their recording across successive spawning migrations. In short, 75 species-specific SNPs were genotyped using the MassARRAY system as described in Taillebois et al. (2020). Individual genetic assignment to one of the 15 purebred or hybrid classes up to 3 generations were performed using NewHybrids (Anderson & Thompson, 2002 [https://doi.org/10.1093/genetics/160.3.1217]) jointly with the data from Taillebois et al. (2020) [https://doi.org/10.5061/dryad.ht76hdr9t] to allow for a good representation of allele frequencies from the two species. NewHybrids was run using uniform priors and a burn of 5,000 iterations followed by a record of 10,000 iterations. Each multilocus genotype was assigned to the class that showed more than 50% of membership probability or the most likely hybrid class.

Data processing

All data processing, summaries and analyses were conducted using R statistical software (version 4.0.2, R Core Team, 2020), making particular use of the *dplyr* package for data processing (Wickham et al., 2019). Data were initially processed to identify and remove false detections using the *actel* R package (Flávio & Baktoft, 2021). For individuals that did not emigrate from the river in any given year, detections occurring after the first detection at their final detection location were removed to avoid spatial bias during space use analysis.

Quantifying survival, duration of freshwater residency and movement distances

To estimate the survival rates of newly tagged and returning fish, individuals were classed as surviving or non-surviving depending on whether they emigrated from the river. Fish were classed as having emigrated from the river if their final detection location was the most downstream receiver in the array. Fish that failed to emigrate were assumed to have died within the river (e.g. due to predation (Nolan, Gutmann Roberts & Britton, 2019) or failure to recover from spawning activities).

To provide a general characterisation and comparison of the movements of twaite shad during their spawning migration, summary metrics were calculated for each emigrating individual in each year. First, to estimate the duration of freshwater residency, the time-at-large was calculated as the time between the first and last detections. Then, to estimate the minimum distance moved while in fresh water, total movement distance was calculated as the cumulative distance moved between receivers. Daily movement rate was calculated as the total movement distance standardised by the time-at-large. Tortuosity was calculated as the ratio of total movement distance to the theoretical minimum river distance of an individual’s journey to its upstream extent, followed by emigration. To further explore the broadscale movement characteristics of shad in fresh water, and assess the extent to which changes in migration direction were made in response to weirs, we calculated the number of changes of direction occurring in obstructed versus obstructed reaches by tagged fish. Obstructed changes of direction were those occurring immediately downstream of a weir, while unobstructed changes of direction occurred elsewhere.

Movement metrics (time-at-large, total movement distance, daily movement rate, tortuosity) were summarised for newly tagged and returning individuals in each year as the median, with the range around the median given using the lower (25th) and upper (75th) quartiles (LQ-UQ). Tracking periods lasting less than 10 days were excluded from calculations of distance metrics, to avoid including fish that might have been tagged post-spawning, or ‘fallback’ individuals that emigrated soon after tagging. These individuals were also excluded from quantification of space use (see next section) to avoid potential spatial biases associated with short tracking periods.

Quantifying riverine space use

The space use of individuals during their spawning migration was quantified as a utilisation distribution (UD), a metric representing the relative probability distribution of a tagged fish within the river (Keating & Cherry, 2009). Detection histories were converted to UDs by applying a dynamic Brownian bridge movement model (Horne et al., 2007), which incorporated the time and location of each detection, as well as estimated positions of tagged individuals within the river during movements between receivers.

UDs for each tagged individual in each year were generated using the *dynBBMM* function in the *RSP* R package (Niella et al., 2020).

To visualise and understand the overall distribution of tagged individuals in the study area, a mean UD was generated by calculating mean values of each cell in the UD across all individuals. Mean UDs were calculated separately for (i) individuals tracked upstream of Weir S2 (i.e. individuals released upstream of S2 and individuals that passed S2), and (ii) individuals that did not pass Weir S2 (i.e. individuals released upstream S1 or downstream S2 that did not approach and/or pass S2).

Modelling factors affecting core space use area

The 50% kernel utilisation distribution (KUD50) was estimated for each individual in each year. KUD50 is a widely used metric to quantify the core area or 'home range' of an animal (Campbell et al., 2013; Barry et al., 2020), which represents the spatial area or 'kernel' in which 50% of an animal's time is spent. Here, it was applied to assess the core space use area (CSUA) of fish during their freshwater spawning migration. First, the CSUA (km^2) was calculated from the UD, in the *raster* R package (Hijmans, 2020). The individual factors affecting CSUA were then tested using linear mixed-effects models (LMMs) in the *lme4* R package (Bates et al., 2015). Individual covariates were body length, sex, spawning history (virgin versus previously spawned) and tagging status (newly tagged versus returning individuals). To account for repeated measures occurring from the same individuals, a random effect of individual ID was included in the models. Data exploration was conducted to assess collinearity between covariates. Since sex and spawning history were both collinear with body length, these factors were not included together within the same models. Then, models containing all possible combinations of covariates (body length, sex, spawning history, tagging status) without interactions were tested and ranked according to AICc; models within 2 AICc of the top-ranked model were considered to have strong support (Burnham & Anderson 2002), unless they were a more complex version of a nested model with lower AICc (Richards, Whittingham & Stephens 2011). We considered the risk of obtaining spurious results due to an ‘all possible models’ approach as low, due to the low number of covariates tested (<6); indeed, including all covariates counters the risks of confirmation bias and minimises the risk of excluding unanticipated results (Alcott et al., 2021). In addition, a univariate LMM containing hybrid class as the sole covariate was fitted on a reduced dataset, to assess the effect of hybridisation on CSUA.

Assessing individual similarity in space use

The degree of similarity in space use by returning individuals between their first and second year of tracking was examined by calculating the intra-individual volume of intersection (VI) of individual UDs in consecutive years. VI is calculated as the cumulative sum of the minimum volume of intersection for corresponding cells between two UDs, and is a widely used metric that represents the degree of similarity in space use between UDs (Fieberg & Kochanny, 2005; Dwyer et al., 2020). It is considered superior to area-based indices of overlap between space use polygons or kernels (Millspaugh et al., 2004). To avoid potential biases, two selection criteria were applied to UDs prior to calculation of VI. Firstly, since weirs had the potential to impede the upstream distribution of twaite shad in the river, only individuals that were tracked upstream of Weir S2 in both years, or that were tracked upstream of S2 in neither year, were considered appropriate for calculation of VI. This was to avoid biases in VI calculations that would result in these individuals having low overlap values that did not necessarily reflect a lack of fidelity.

This decision was justified based on results presented in Davies et al, (2023), which clearly demonstrated that successful passage of weir S2 in an individual's first year significantly increased passage likelihood upon return. It was thus assumed that unsuccessful individuals in their return migration were likely to be motivated to pass the weir had they done so previously. Secondly, for individuals that passed Weir S2 in a given year, detections that occurred downstream of this barrier were removed prior calculation of UD, to reduce biases imposed by barrier passage delays on their overall space use distributions.

Inter-individual VI was calculated between the UD of each individual in a given year with the UDs of 10 randomly selected returning fish in the following year. Finally, to test whether intra-individual space use was more similar than inter-individual space use (indicating that individuals displayed fidelity to previously occupied areas), differences in intra-individual VI versus inter-individual VI were assessed using ANOVA.

Modelling factors affecting riverine space use (spawning philopatry)

Factors affecting variation in riverine space use (intra-individual VI) were then tested using binomial generalised linear models GLMs. Covariates were body length and spawning history at the time of tagging, and sex (with sex and body length excluded from the same models). Model selection was conducted as per the LMMs. In addition, a univariate GLM on the reduced dataset (n = 95) containing individuals with a known hybrid class (pure *A. fallax* versus *A. fallax x alosa* backcrosses) was fitted to assess the effect of hybridisation on spawning philopatry.

Results

Hybridisation rates and summary of movement metrics

Of the 95 twaite shad analysed, 75 (79%) were pure *A. fallax* and 20 (21%) were third generation (or greater) backcrosses (*A. fallax* X *A. fallax* backcross hybrids), indicating historical hybridisation with *A. alosa*. Of the 184 twaite shad tagged with acoustic transmitters, 133 (72%) emigrated from the River Severn after concluding their spawning migration. Of those with programmed transmitters allowing the potential for further detection (*n* =125) 71 (57%) returned the following year, of which 53 (75%) emigrated, and seven returned for a third successive spawning migration (representing 10% of the 73 fish tagged in 2018 with long-life transmitters, and 29% of those that emigrated in 2019 (*n* = 24) (Table 2).

Table 2: Summary of movement metrics for twaite shad *Alosa fallax* tracked during their spawning migration in the River Severn in 2018, 2019 and 2020. Time-at-large was calculated for all emigrating individuals. Median values are presented along with 25% and 75% quartiles.

Year	Status	*n* fish tracked	*n* emigrated (%)	Time-at-large, days (LQ-UQ)	Upstream extent, rkm (LQ-UQ)	Distance moved, km (LQ-UQ)	Daily distance moved, km day^{-1} (LQ-UQ)	Track tortuosity, (LQ-UQ)	*n* downstream direction changes (LQ-UQ)
2018	Newly tagged	84	66 (79%)	19 (17-27)	49 (24-52)	134 (97-163)	6 (5-8)	1.6 (1.3-2)	12 (8-19)
2019	Newly tagged	100	67 (67%)	27 (20-35)	49 (24-50)	195 (123-269)	7 (6-9)	2.6 (1.8-3.3)	21 (12-28)
	Returning year 2	33	24 (73%)	35 (28-39)	50 (48-52)	247 (185-292)	6 (6-8)	2.6 (1.9-3)	24 (17-46)
2020	Returning year 2	38	29 (76%)	30 (27-36)	31 (24-50)	245 (189-303)	8 (6-10)	3.3 (2.3-5.5)	30 (20-49)
	Returning year 3	7	4 (57%)	29 (24-34)	42 (33-54)	140 (117-264)	6 (5-9)	1.8 (1.6-2.9)	15 (12-21)
Overall	Newly tagged	184	133 (72%)	24 (18-30)	49 (24-51)	156 (113-223)	7 (5-8)	1.9 (1.4-2.8)	16 (10-24)
	Returning year 2	71	53 (75%)	33 (27-38)	49 (24-50)	247 (188-304)	7 (6-9)	2.8 (2.1-4.2)	27 (18-48)
	Returning year 3	7	4 (57%)	29 (24-34)	42 (33-54)	140 (117-264)	6 (5-9)	1.8 (1.6-2.9)	15 (12-21)

In general, the time-at-large of newly tagged individuals (median (LQ-UQ) = 24 (18-30) days) was less than for individuals returning the subsequent year (33 (27-38) days) (Table 2). During their freshwater migration, the median minimum distance moved between the first and last detections by newly tagged individuals was 156 km (113-223 km), and 247 km (188-304 km) for returning individuals. Distances moved per day by the two groups of fish were highly similar (newly tagged individuals, median 7 km day^{-1} (5-8 km day^{-1}), n = 184; individuals returning the subsequent year, 7 km day^{-1} (6-9 km day^{-1}), n = 71) (Table 2). Fish tended to make multiple upstream and downstream movements; for example, returning individuals in their second year made upstream-downstream changes in direction a median of 27 (18-30) times prior to emigration. Upstream-downstream changes in direction occurred in both obstructed and unobstructed reaches both prior to and following barrier approach (Figure 2); overall a median of 60 % of downstream reversals occurred in unobstructed reaches. These multiple downstream movements were reflected in migration path tortuosity values of 2.8 (2.1-4.2) for returning individuals.

Mean utilisation distribution and factors affecting KUD50 area

For individuals that did not pass Weir S2, activity was concentrated in the upstream half of the contiguous reach between Weir S1 and S2, with the highest probability densities occurring at the confluence of the River Severn and River Avon (Figure 3). For fish tracked upstream of S2, mean UD was characterised by a peak of activity in the upstream half of the contiguous reach between Weir S2 and weirs S3/T1, with the highest probability densities occurring within the lower River Teme and the confluence of the River Teme and River Severn (Figure 3). Testing of factors influencing the 50% Kernel Utilisation distribution (KUD50) retained sex as the only significant predictor from 14 best-fitting LMMs (Supplementary Material: Table S1), indicating that females had significantly larger core space use areas than males (Table 3, Figure 4). A univariate LMM indicated that there was no evidence that hybridisation was a strong predictor of KUD50 (Table 3).

Riverine space use by individuals across successive spawning migrations

For the 71 fish tracked across two successive spawning migrations, intra-individual VI (mean ± SD = 55% ± 18) was significantly greater than inter-individual VI (38% ± 21) (one-way ANOVA, $F_{1,449} = 26.8$, $p < 0.01$) (Figure 5), indicating that returning individuals tended to return to areas of river they had used the previous year. There however, no significant predictors of variation in VI, with none of the 28 fitted GLMs tested having better AIC support than the null model (Table S2). A univariate GLM indicated that there was minimal evidence that hybridisation was a strong predictor of intra-individual VI (Table 4).

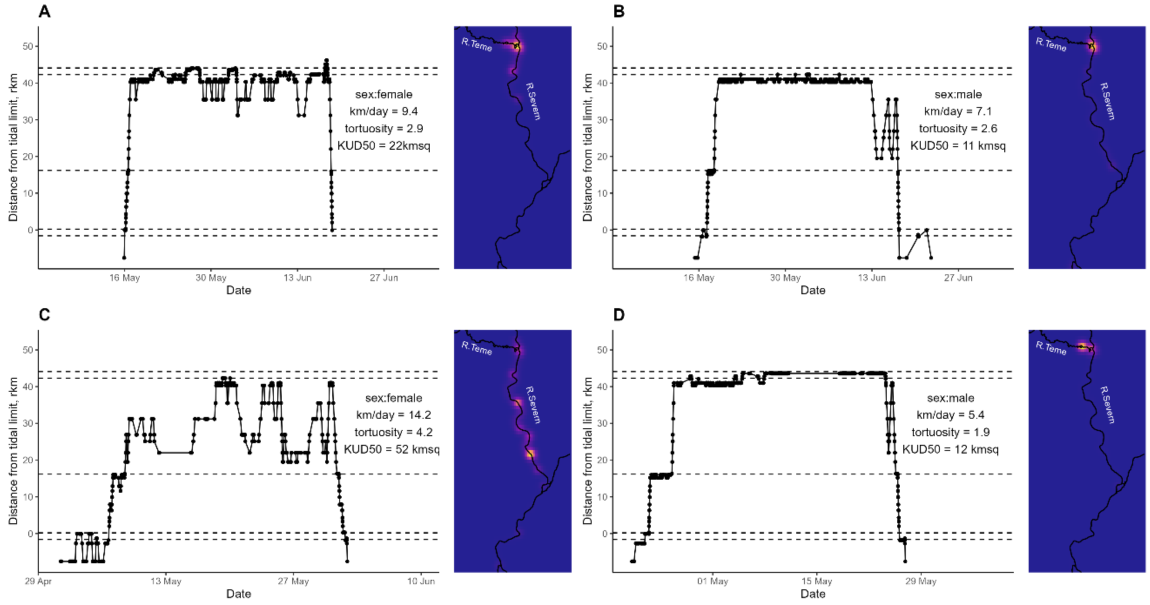

Figure 2: Movement and space-use of four returning acoustic-tagged twaite shad to the River Severn catchment. Left panels show movement in the form of a track, with y-axis values representing river distance (rkm) of detections from the tidal limit by time (x-axis). Horizontal dashed lines represent location of main weirs within the catchment. Right panels show utilisation distributions derived from dynamic Brownian bridge movement model. A: Female individual predominately detected in lower River Teme and confluence with the River Severn.; B: Male individual predominately detected at the confluence of the River Teme and River Severn; C: Female individual detected widely within the River Severn upstream of Weir S2; and D: Male individual detected predominately within the River Teme.

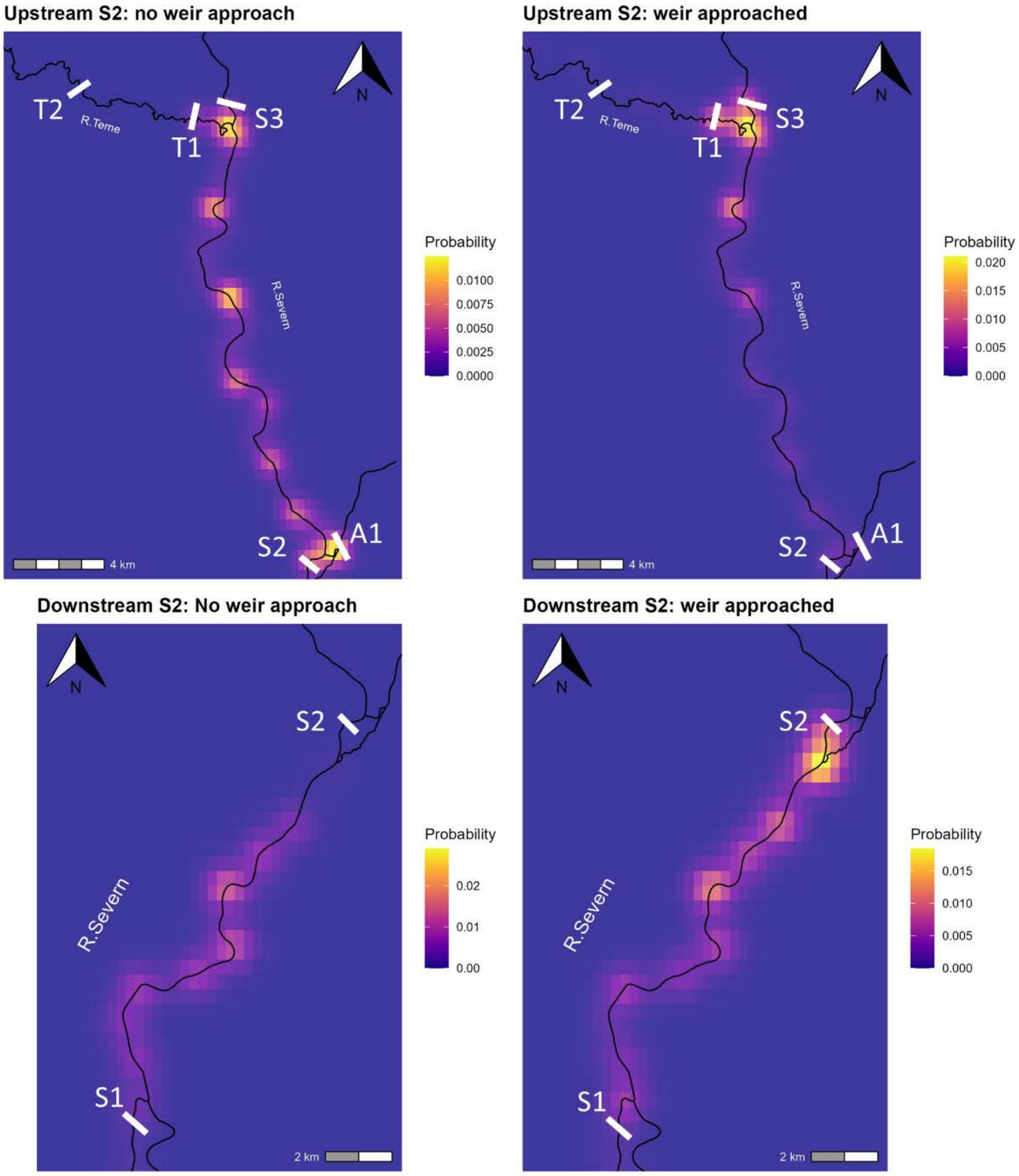

Figure 3: Riverine space use (mean utilisation distribution) of twaite shad in the River Severn catchment. White bars indicate the positions of major weirs. a) utilisation distributions of migrations upstream of Weir S2 but not approaching S3/T1, pooled across years (*n* migrations = 49); b) utilisation distribution of migrations upstream of Weir S2 approaching S3 and/or T1 pooled across years (*n* migrations = 91); c) utilisation distributions of migrations upstream of Weir S1 but not approaching S2, pooled across years (*n* migrations = 7) ; d) utilisation distributions of migrations upstream of Weir S1 and S2, pooled across years (*n* migrations =53).

Table 3: (a) Summary of covariate effects from best-fitting linear mixed-effects model of 50% Kernel Utilisation Distribution (KUD50) area for twaite shad (*n* individuals = 125, *n* observations = 168). (b) Summary of covariate effects from a univariate linear mixed-effects model testing the effect of hybrid class on 50% Kernel Utilisation Distribution (KUD50) area for twaite shad (*n* individuals = 89, *n* observations = 146).

Parameter	**Estimate**	**SE**	**T**	**P**
(a)				
Intercept	1.94	0.06	33.7	
Sex: female	-	-	-	-
Sex: male	-0.29	0.08	-3.8	<0.001
(b)				
Intercept	-1.81	0.05	35.2	
Class: purebred	-	-	-	-
Class: hybrid	-0.12	0.11	-1.1	0.26

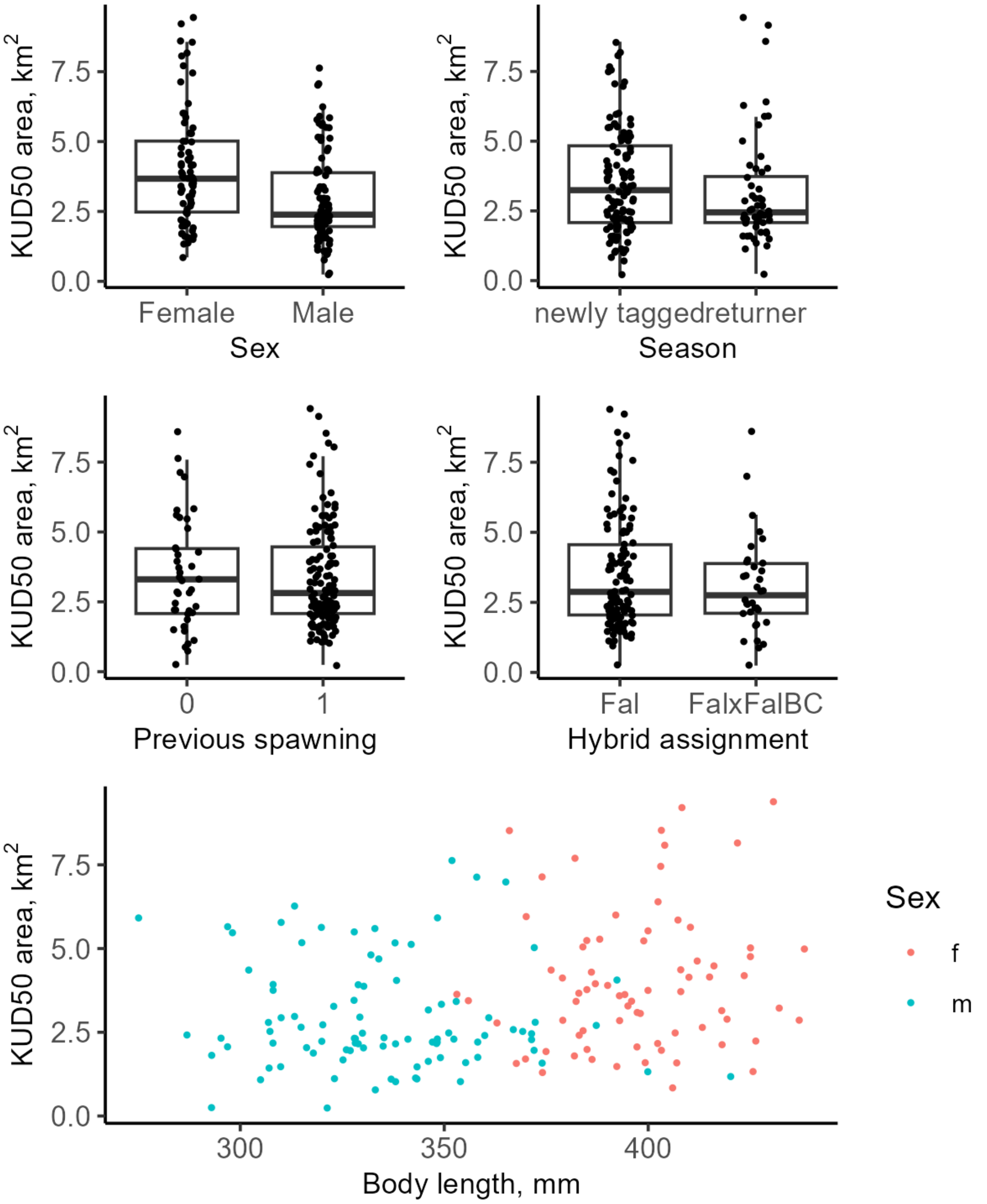

Figure 4: Factors tested for their effect on KUD50 area in twaite shad. Boxplot upper and lower boundaries represent upper and lower quartiles, and the central horizontal line represents the median. Filled circles represent individual data points.

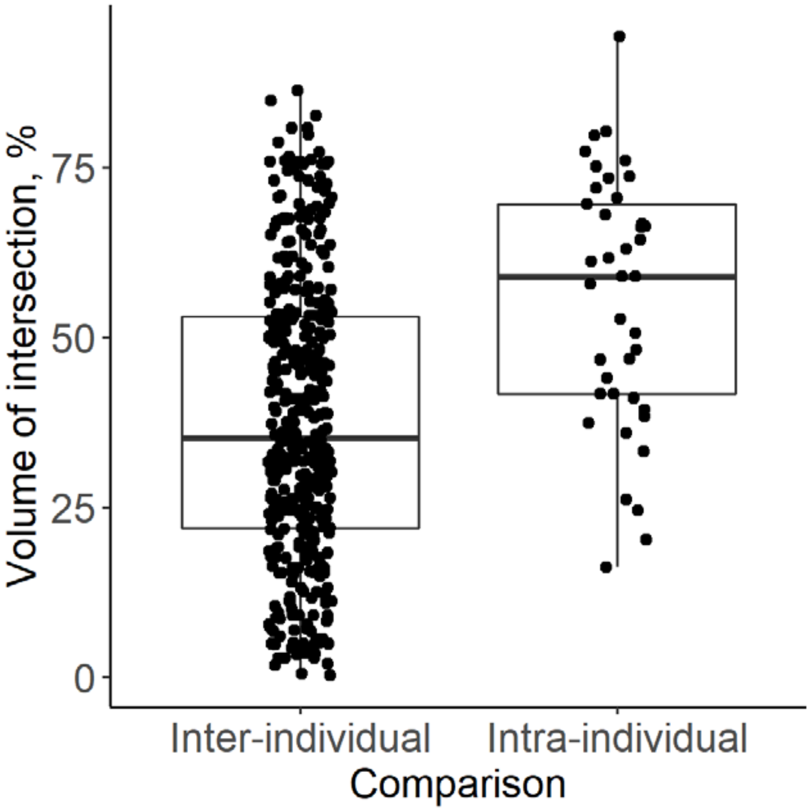

Figure 5: Boxplot showing inter- and intra-individual volume of intersection of utilisation distributions between first and second year of tracking by twaite shad. Boxplot boundaries represent upper and lower quartiles, central line represents the median. Filled circles represent individual data points.

Table 4: Summary of covariate effects from a univariate generalised linear model testing the effect of hybrid class on intra-individual volume of intersection of utilisation distributions for twaite shad tracked over multiple spawning seasons (*n* individuals = 40).

Parameter	**Estimate**	**SE**	**z**	**P**
Intercept	0.28	0.38	0.79	0.43
Class: purebred	-	-	-	-
Class: hybrid	-0.38	0.76	-0.51	0.61

Discussion

Twaite shad movements were highly tortuous during their riverine spawning migrations, undertaking multiple upstream and downstream movements, both in unobstructed reaches and during approach to man-made weirs. Females occupied larger core areas than males, but hybridisation was not a significant predictor of space use. There was evidence of philopatry, with returning fish occupying very similar locations in the river across successive spawning migrations.

Anadromous clupeids are often highly vagile during their spawning migrations. For example, long-distance ‘oscillations’ - back and forth movements between spawning grounds and downstream habitats - have been observed in alewife *Alosa pseudoharengus* (McCartin et al., 2019), and allis shad may exhibit ‘exploratory’ behaviours that have been attributed to the concurrent use of spawning and resting sites (Acolas et al., 2004; Acolas et al., 2006). Here, when comparing the distance moved by individuals relative to their upstream extent (i.e., tortuosity), it reflects how their freshwater migration is composed of multiple upstream and downstream movements. As the time-standardised movement rates between the consecutive migration periods were similar (median: 7 km day^{-1}), this suggests that the tagging process did not substantially affect their overall distance moved. The duration of freshwater residency by returning twaite shad (median: 33 days) was commensurate with a recent study on American shad *Alosa sapidissima* where periods of 35 days were observed in returning individuals (Gahagan & Bailey, 2020). Freshwater residency times of between 8 and 33 days have been reported in American shad tagged in the same year (Beasley and Hightower 2000; Aunins and Olney 2009; Aunins et al. 2013; Grote et al. 2014; Raabe and Hightower 2014). Consequently, the duration of spawning periods and vagility and duration of the spawning migration appear to be similar among other members of the *Alosa* genus.

The mean distribution of twaite shad in this study suggested that specific areas of river were used relatively intensively during the spawning migration, potentially indicating the impact of the weirs inhibiting upstream progression, as well as possible spawning locations. Specifically, the space use of individuals that did not pass weirs S2 and S3 was focused in the 1 to 2 km reaches downstream, and both are known spawning areas (Aprahamian, Lester & Aprahamian, 1998). The negative impact of anthropogenic barriers on the upstream migration of twaite shad in the River Severn has already been demonstrated (Davies et al., 2023). Nevertheless, this finding is also consistent with a study that revealed that allis shad spent the majority of their time either in resting areas approximately 1.5 km downstream of spawning grounds which were immediately downstream a major migration barrier (Acolas et al., 2004). (Aprahamian, Lester & Aprahamian, 1998). The possibility that shad were searching for alternative passage routes or spawning habitats after approaching weirs, as reported for sea lamprey *Petromyzon marinus* (Davies et al., 2022), also cannot be ruled out. Crucially, fish that did and did not approach S3/T1 both displayed areas of intensive space use in the areas immediately downstream of these barriers, thus it is difficult to disentangle the influence of anthropogenic barriers and biotic influences on space use during twaite shad freshwater spawning migrations. Future efforts to reconnect inaccessible upstream spawning areas through barrier removal and fish pass installation (www.unlockingthesevern.co.uk) may help further this understanding.

Sex has been widely linked to differences in the temporal and spatial characteristics of animal migration (Morbey & Ydenberg, 2001; Barnett et al., 2011; Bunnefeld et al., 2011). As a life history strategy, iteroparity should reduce the relative importance of individual spawning events by facilitating survival for future spawning events, with suggestions that the behaviours of females from iteroparous populations are more risk averse than males (Warner, 2005). Here, it was apparent that female twaite shad used significantly larger areas of the river than males during their spawning migrations, although it could not be ascertained whether this was related to reducing, for example, their risk of predation. Studies in multiple *Alosa* species have suggested that females are batch-spawners, with spawning events separated by a period of days (Olney, Denny & Hoenig, 2001; Harris, McBride & Williams, 2007; Mouchlianitis, Minos & Ganias, 2020). Moreover, batch-spawning by female allis shad has been linked to observed movement differences between sexes (Acolas et al., 2004; Acolas et al., 2006), with males more likely to be on spawning grounds on consecutive nights and engaging in more spawning acts, while females spent periods consistent with egg maturation away from spawning grounds. While it was beyond the scope of this paper to explore movement strategies of males and females underlying differences in space use, the male and female movement tracks presented in Figure 2, provide potential examples of how strategies may differ between sexes, whereby males spend more time in the upper reaches of rivers while females are more prone to long distance movements during their freshwater residency period. Consequently, the greater space use by females versus males here could just reflect movements by females from spawning to resting areas during the egg maturation period. This possibility is also supported by a study on American shad where males used upstream habitats more than females (Raabe & Hightower, 2014), potentially reflecting a stronger association with spawning grounds by males. Further studies should seek to understand the sex-based differences in movement strategy underlying space use patterns, and how these may interact with pressures such as anthropogenic barriers.

Philopatry is a widespread feature of animal migration, with natal philopatry being a strategy that increases the likelihood that migrants will encounter mates and suitable reproductive habitat (Greenwood, 1980; Dittman & Quinn, 1996). In anadromous fishes, the process of natal philopatry (or ‘homing’) is believed to be driven by olfactory imprinting, whereby juveniles form associations with the geochemical signature of water from their natal river (or tributary) during development (Dittman & Quinn, 1996; Keefer & Caudill, 2014). Although our understanding of this process has mainly been derived from salmonid fishes, natal homing to specific tributaries by American shad has been demonstrated, with marked hatchery-reared individuals returning to the same tributary that they emigrated from as juveniles (Hendricks et al., 2002). Spatial segregation of returning individuals across the river was also noted, suggesting that olfactory-mediated location of natal tributaries may occur. While fidelity to previous spawning rivers by adults has also been observed in iteroparous shad species (Melvin, Dadswell & Martin, 1986; Davies et al., 2020), how this homing interacts with spawning philopatry (i.e. the return of adults to specific spawning areas) has been unclear. Here, while we could not assess natal philopatry directly, the results revealed that twaite shad did return to similar areas of the river during consecutive spawning migrations, as evidenced by intra-individual VI being significantly greater than inter-individual VI. However, it is acknowledged that how the extent of this repeatability in riverine space use between migrations relates to spawning philopatry is unclear, as the method used (passive acoustic telemetry) was unable to provide information on the actual spawning locations of the fish. Complementary approaches, such as surveys of spawning activity (Langkau et al., 2016;

Paumier et al., 2020) and high-resolution telemetry, will therefore be needed if information on the actual spawning areas of twaite shad is required.

Hybridisation between different species or subpopulations with divergent migratory strategies can result in offspring that display intermediate or increased variability in movement patterns; this phenomenon has been best described in migratory birds (Alvarado, Fuller & Smith, 2014; Delmore & Irwin, 2014). Where allis shad and twaite shad co-occur, the former generally migrate further upstream, with river fragmentation posited as driving their hybridisation through the sharing of spawning areas in more downstream areas (Aprahamian et al., 2003b; Taillebois et al., 2020). Here, 21% of sampled twaite shad were introgressed with allis shad (third generation (or greater) backcrosses with a theoretical 12.5% of the genome from *A. alosa*), indicating infrequent historical hybridization with *A. alosa*, but there was no evidence that this influenced their core area size. Significant knowledge gaps remain on the status of *A. alosa* in the River Severn, including the extent to which this historical introgression with *A. fallax* derives from individual *A. alosa* straying from spawning populations in other rivers, or from a spawning population in the River Severn.

In summary, the twaite shad that were tracked during successive spawning migrations provided important insights into their spatial ecology in a highly regulated river catchment. The duration of their freshwater residency was similar to another *Alosa* species, differences in space use were greater in females than males, and spawning philopatry to areas within the river basin was apparent in returning individuals. These results should thus provide resource managers with considerable insights into this and similar anadromous and iteroparous species in regulated rivers that can be used to inform management measures, conservation strategies and further research.

Author contributions

Conceived and designed the field experiments: JDB, ADN, JRD, CC, RV, JRB, and PD. Conducted fieldwork: JDB, ADN, JRB, CC, JRD, and PD. Conducted genetic extraction and analysis: OL, SS, PD, DA. Conducted telemetry analysis: PD. Wrote the article: PD. Edited the article: JDB, DA, JRB, ADN, JRD, CC, OL, SS and RV.

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Supplementary material

Table S1: Full set of linear mixed effects models to test the effect of individual covariates on core area size in acoustic tagged twaite shad.

Model structure	df	Intercept	logLikelihood	AICc	delta	weight
Sex	4	1.94	-118.22	244.69	0.00	0.75
Sex+Tagging status	5	1.97	-118.98	248.33	3.65	0.12
Previous spawning + Sex	5	1.98	-119.61	249.58	4.90	0.06
Body length	4	1.78	-121.60	251.44	6.76	0.03
Null	3	1.78	-123.45	253.04	8.35	0.01
Body length+Tagging status	5	1.82	-121.49	253.34	8.65	0.01
Previous spawning +Sex+Tagging status	6	1.97	-120.42	253.36	8.67	0.01
Previous spawning + Body length	5	1.86	-122.37	255.10	10.42	0.00
Tagging status	4	1.81	-124.23	256.70	12.01	0.00
Previous spawning + Body length+Tagging status	6	1.86	-122.76	258.04	13.35	0.00
Previous spawning	4	1.79	-124.95	258.15	13.46	0.00
Previous spawning Tagging status	5	1.78	-125.51	261.40	16.71	0.00

Table S2:Full set of binomial generalised models to test the effect of individual covariates on spatial fidelity in acoustic tagged twaite shad.

Model structure	**df**	**logLikelihood**	**AICc**	**delta**	**weight**
(a)					
Null	1	0.18	-26.74	55.58	0.00
Previous spawning	2	-0.14	-25.76	55.84	0.26
Sex	2	0.02	-26.70	57.73	2.14
Previous spawning+Sex	3	-0.43	-25.55	57.78	2.20
Reach	2	0.06	-26.73	57.80	2.21
Body length	2	0.67	-26.86	58.06	2.48
Previous spawning+Reach	3	-0.17	-25.77	58.24	2.65
Body length+Previous spawning	3	1.67	-25.96	58.61	3.03
Body length+Sex	3	-1.46	-26.32	59.32	3.74
Reach+Sex	3	-0.22	-26.68	60.04	4.46
Previous spawning+Reach+Sex	4	-0.56	-25.58	60.34	4.76
Body length+Previous spawning+Sex	4	0.21	-25.66	60.49	4.91
Body length+Reach	3	0.78	-26.92	60.53	4.95
Body length+Previous spawning+Reach	4	1.72	-26.02	61.22	5.64
Body length+Reach+Sex	4	-1.50	-26.35	61.87	6.28
Body length+Previous spawning+Reach+Sex	5	0.13	-25.70	63.22	7.64