6 Movement, space use and spatial fidelity of threatened anadromous twaite shad *Alosa fallax* during their spawning migrations

6.1 Abstract

1) Knowledge of the movement ecology of anadromous fishes can aid conservation and management efforts, including identifying key spawning areas, and predicting how populations may respond to river reconnection. However, the movement ecology of repeat-spawning anadromous fish is poorly understood, particularly in non-salmonid groups such as shads (*Alosa* spp), for which there is a paucity of knowledge on the spatial characteristics of spawning migration, including freshwater residency, the drivers of space use, and spatial fidelity amongst repeat spawners.

2) Here, the movement distance, freshwater residency and space use core area size of threatened anadromous twaite shad *Alosa fallax* (*n* = 184) were quantified using multi-year acoustic telemetry during their spawning migrations in the River Severn catchment, western Britain. The effect of sex, body length, tagging status (newly tagged versus returning individuals), previous migratory experience and the extent of their genetic introgression with allis shad *Alosa fallax* on core area size were tested. There were 71 tagged fish that returned to spawn in the year after tagging, which enabled the hypothesis of spatial fidelity to areas occupied in the previous year, and factors affecting fidelity, to be tested.

3) Twaite shad were highly vagile during their spawning migrations (median movement rate = 7 km d^{-1} (LQ-UQ = 5-9 km d^{-1}, max = 19 km d^{-1})), and their movement patterns were characterised by multiple upstream and downstream journeys. Returning individuals, which were tracked from the onset of their movement into fresh water until emigration, recorded total freshwater movement distances of 247 km (188-304 km, 573 km), and total freshwater residency of 33 days (27-36 days, 56 days).

4) Female twaite occupied a significantly larger core area during their spawning migration than males. The effects of previous migratory experience, body length, tagging status, and extent of introgression with *A*. *alosa* did not significantly affect core area size. Returning individuals displayed fidelity to areas occupied in their previous spawning migration; mean similarity within individuals (mean ± SD = 55% ± 18) was significantly greater than between individuals (38% ± 21).

5) This work provides important new insights into the movement ecology of twaite shad during their spawning migration, demonstrating differences in space use between sexes, which potentially reflect differences in spawning strategy. The results suggest the ability of repeat spawners to locate previously occupied areas within river catchments, and highlight the utility of multi-year telemetry studies for eliciting information on the movement ecology of threatened anadromous fishes.

6.2 Introduction

The spawning migrations of anadromous fishes contribute to the functioning of freshwater and terrestrial ecosystems globally, and are both culturally and economically significant for humans (McClenachan, Lovell & Keaveney, 2015; Tonra et al., 2015; Lennox et al., 2019). Research on the movement ecology of anadromous fishes has tended to focus on species of the Salmonidae family, most likely due to their socioeconomic value (Chapman et al., 2012; Keefer & Caudill, 2014; Secor, 2015), yet salmonids represent only a small fraction of anadromous fish species (Lucas & Baras, 2001). The herring family (Clupeidae) features several anadromous species (e.g. shads, alewife) that support important fisheries in the northern hemisphere, are an important component in the diet of marine predators as ‘forage fish’ (Walters, Barnes & Post, 2009; McDermott et al., 2015; Hossain et al., 2019), and can drive substantial marine-freshwater nutrient fluxes (Walters, Barnes & Post, 2009; West et al., 2010). Severe declines in populations of anadromous clupeids have been recorded in contemporary times, linked to overfishing, poor water quality and riverine habitat fragmentation that prevents access to historical spawning grounds (de Groot, 1990; Limburg & Waldman, 2009; Hall, Jordaan & Frisk, 2012).

There is a general lack of understanding regarding the movement ecology of anadromous clupeids during their spawning migrations, partly linked to their sensitivity to handling and tagging relative to other anadromous groups, which has hampered catchment-scale telemetry studies (Olney et al., 2006; Frank et al., 2009; Breine et al., 2017). Information on the fidelity of anadromous clupeids to natal areas has primarily been derived indirectly, via assessing differences in genetic and physical characteristics of spawning adults in different rivers, which have indicated the presence of distinct sub-populations associated with river catchments and tributaries (Carscadden & Leggett, 1975b; Jolly et al., 2012). Spawning populations in different river catchments exhibit genetic isolation by distance, indicating that population differences in anadromous clupeids are most likely maintained by the homing of adults to natal river catchments (Hasselman, Bentzen & Bradford, 2010; Jolly et al., 2012). These observations are supported by mark-recapture studies indicating that adults return to natal tributaries (Melvin, Dadswell & Martin, 1986; Hendricks et al., 2002), as well as telemetry investigations suggesting that repeat-spawning adults return primarily to the catchment of previous spawning (Davies et al., 2020/Chapter 4). In general, homing and fidelity increase the likelihood that returning adult fish will find mates, and locate habitats that are favourable for spawning and juvenile survival (Hendry et al. 2004; Quinn 2005). However, how natal homing by first time spawners relates to spawning site fidelity by returning fish in subsequent years, remains poorly understood. For example, while there is evidence that migration timing can be ‘fine-tuned’ throughout the lifecycle of repeat spawning fish (Tibblin et al., 2016), evidence for spatial fine-tuning, or how repeat spawning anadromous fish may adjust their riverine space use in successive spawning migrations, is currently lacking. Assessing spatial fidelity by repeat spawning anadromous fish, as well as characterising movement patterns and space use, is important, as this knowledge can inform management strategies and help predict the outcome of efforts to increase riverine connectivity (Pess et al., 2014).

An anadromous 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 twaite shad populations (de

Groot, 1990; Aprahamian et al., 2003b) with concerns over these population declines reflected in international conservation designations, including their listing on Annexes II and V of the European Union Habitats Directive (Council of the European Communities, 1992). Twaite shad can be highly iteroparous, particularly in the north of their range, where previous-spawned fish often represent over 50 % of the spawning run (Aprahamian et al., 2003b). Twaite shad readily hybridise with sympatric allis shad *Alosa alosa*, a phenomenon that has been linked to anthropogenic fragmentation of rivers that has forced the two species to overlap in their spawning range (Jolly, Maitland & Genner, 2011; Taillebois et al., 2020). Between migratory subpopulations of animal species that display divergent migratory routes, hybrid individuals can display migration routes and destinations which are intermediate between the parental routes, as well as greater variability in their migration patterns (Alvarado, Fuller & Smith, 2014; Delmore & Irwin, 2014). However, the effect of hybridisation, and other individual factors on twaite shad space use are, however, largely unknown.

European shad species are considered to be sensitive to tagging and handling, although recent advances in surgical tagging protocols have allowed internal transmitter implantation, enabling the assessment of movement ecology through acoustic telemetry (Bolland et al., 2019b). Improvements in transmitter technology to prolong battery life have also now provided an opportunity to record individual movements across successive annual spawning migrations (Davies et al., 2020/Chapter 4), enabling assessment of the fidelity of returning tagged individuals to areas utilised in previous seasons. Consequently, using acoustic-tagged twaite shad tracked across up to three successive annual spawning migrations in the River Severn catchment, the objectives here were to: 1) quantify their movements, extent of freshwater residency and catchment-scale space during their spawning migrations; 2) test the individual and genetic factors affecting their space use in the river (core area size); and 3) assess the fidelity of returning individuals the areas of river occupied during their previous spawning migration(s).

6.3 Methods

6.3.1 Study duration and area

The study was conducted on the spawning migrations of *A. fallax* 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 Severn is the longest river in Great Britain, rising in mid-Wales and flowing for 354 km before discharging into the Bristol Channel, and has a drainage area of 11420 km^2 (Durand et al., 2014). The study area in the lower river catchment 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 6.1). The normal tidal limit is at Maisemore (hereafter S1a) and Llanthony Weirs (S1b) on the western and eastern branches of the river respectively (Figure 6.1), although large spring tides can penetrate the river up to Upper Lode Weir (hereafter S2).

6.3.2 Shad capture and tagging

At the commencement of their migration season in early-mid May 2018 and 2019, upstream-migrating adult shad were captured by rod-and-line angling in the weir pools of S1a and S2. In addition, shad were captured at S2 using a trap positioned at the upstream exit of the notch fish pass. Following their anaesthesia (Ethyl 3-aminobenzoate methanesulfonate; MS-222), all shad were weighed (to 10g), measured (fork length, nearest mm), sexed, and approximately three scales were removed for analysis of spawning history. These scales were analysed subsequently to determine their number of spawning-marks (and so their previous spawning history) on a projecting microscope (x48 magnification) (Baglinière et al., 2001). In addition, a tissue sample from a fin biopsy was taken from each individual for subsequent genetic analysis.

Following the collection of their biometric data, the shad were surgically tagged with 69 kHz, Vemco V9 acoustic transmitters (vemco.com), using the tagging protocol of Bolland *et al*. (2019), and following ethical review and according to UK

Home Office project licence PD6C17B56. A total of 184 shad were tagged over the two years (Table 6.1), of which 173 were tagged with programmed acoustic transmitters. At the end of June, to coincide with the conclusion of their spawning migration, the transmitters were programmed to switch from a randomized 1-minute pulse interval (minimum interval between acoustic pulses 30 seconds, maximum interval 90 seconds) to a 10-minute pulse interval until April the following year, when they were programmed to switch back to their randomized 1-minute pulse interval. This was to increase the battery life of the transmitters to approximately three years, so potentially enabling the tracking of three consecutive spawning migrations of tagged individuals.

Table 6.1: Summary of tagged twaite shad *Alosa fallax* captured over two years in the River Severn.

Year	Capture location	Capture method	Release location	*n*	Length ± SE, mm	Weight ± SE, g
2018	S1a	Angling	Upstream S1a	20	365.9 ± 5.6	653.8 ± 33.2
	S2	Angling	Downstream S2	10	375.4 ± 6.5	645.0 ± 33.7
	S2	Angling	Upstream S2	24	339.8 ± 6.5	479.2 ± 29.0
	S2	Trap	Downstream S2	8	357.6 ± 9.9	559.4 ± 64.6
	S2	Trap	Upstream S2	22	376.4 ± 3.6	736.4 ± 24.0
2019	S1a	Angling	Upstream S1a	50	350.9 ± 6.1	617.5 ± 36.1
	S2	Trap	Upstream S2	50	376.9 ± 5.4	776.5 ± 35.3
Total				184	362.8 ± 2.7	659.8 ± 16.8

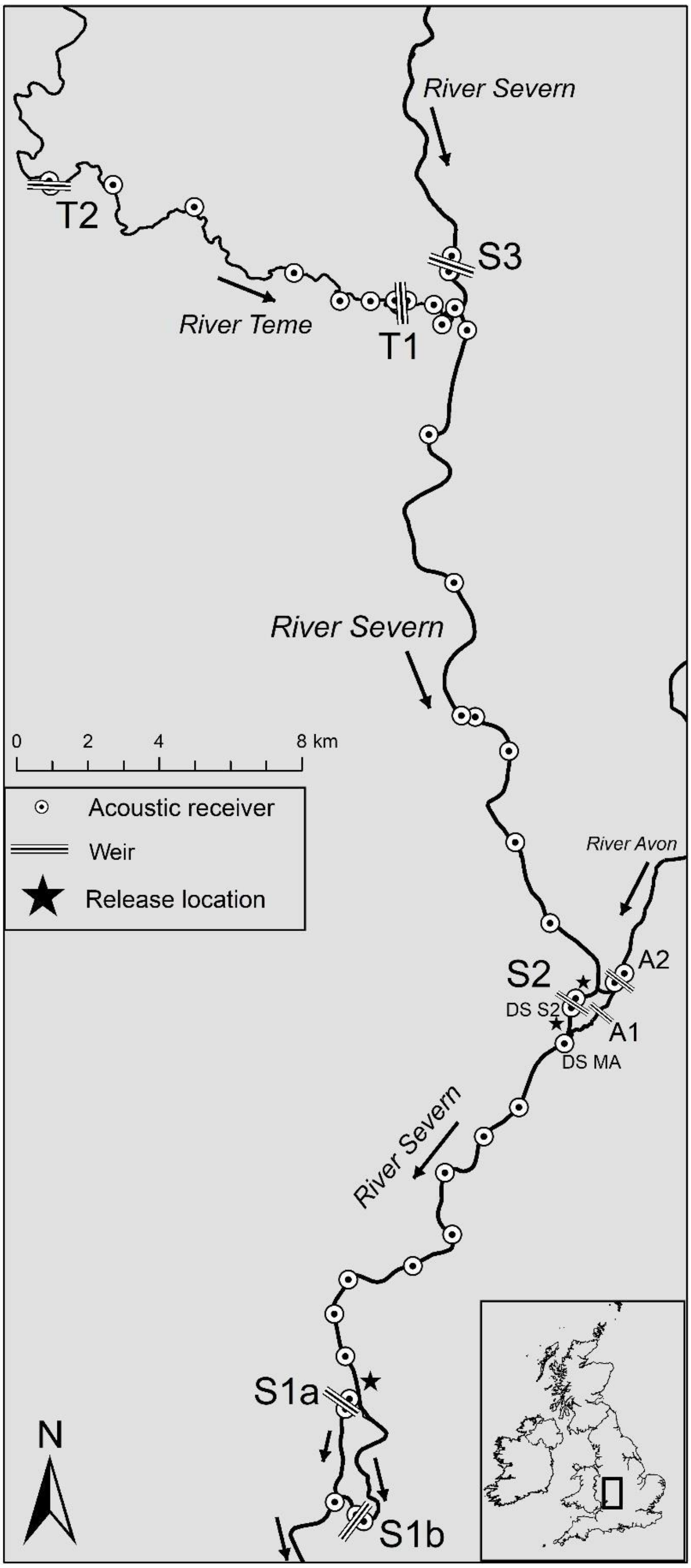
6.3.3 Estimation of sex and assignment of hybrid classes

Of the 184 captured individuals, 77 (42 %) were sexed by positive identification of gonads, eggs or milt during tagging. Since twaite shad display marked sexual size polymorphism, sex was estimated for unsexed individuals based on the length/weight ratio-at-age distributions of individuals with known sex. Individuals of a given age were conservatively assigned a sex if they fell outside the size range of individuals known to be of the other sex. After this process, 155 (84%) of individuals had a known or estimated sex classification while the remaining individuals fell within the overlapping size range for length/weight ratio at age for individuals of known sex, and so remained unsexed. Assignment of hybrid classes between twaite shad and allis shad *A. alosa* was conducted using the protocol of Taillebois et al., (2020) on the fin tissues of a subset of 95 individuals. Of these, 75 (79%) fish were identified as pure *A. fallax*, with 20 (21%) assessed as third generation backcrosses, indicating historical hybridisation with *A. alosa*.

6.3.4 Acoustic array

An array of Vemco acoustic receivers (VR2-W and VR2-Tx, www.innovasea.com) was installed throughout the study area (Figure 6.1), prior to the commencement of each 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, Avon and Mill Avon, with additional receivers deployed in unobstructed reaches between weirs (Figure 6.1). The furthest downstream receiver in the array (51.8347, -2.2901; Figure 6.1) 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 due to Covid-19 restrictions, the receiver array was installed to enable tracking of returning fish tagged in previous years. Receivers were anchored on steel fencing pins driven into the river bed. In the River Teme, which featured sections of fast-flowing riffle, receivers were deployed in slower-flowing pools to maximise detection distance. In each tracking year, data were downloaded from receivers every two weeks until no further movements were detected. Range tests revealed that 100% of test tag transmissions were detected a minimum of 100 m away from receivers in the River Severn, and a minimum of 50 m away from receivers in River Teme. In all cases, detection range was greater than river width at the receiver deployment location. Detection efficiency calculations (using three sequential receivers to determine the efficiency of the middle receiver) revealed that missed detections accounted for less than 0.1% of shad movements between receivers.

Figure 6.1: The River Severn catchment study area, including locations of release of acoustic-tagged twaite shad (black star), weirs (bars) and acoustic receivers (circles) in the rivers Severn, Teme and Avon, UK. The black arrows denote the direction of the flow.



6.3.5 Data processing

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

6.3.6 Quantifying survival and movement

To estimate the survival rates of newly-tagged and returning shad, acoustic-tagged shad were classed as surviving or non-surviving depending on whether they emigrated from the river. Shad 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 shad during their spawning migration in the River Severn catchment, summary metrics were calculated for each emigrating individual in each year. First, to estimate the duration of freshwater residency of shad during their spawning migration their time-at-large was calculated as the time between first and last detection. Then, to estimate the distance moved while in freshwater, total movement distance was calculated as the cumulative distance moved between receivers. Finally, daily movement rate was calculated as total movement distance standardised by time-at-large.

Movement metrics (time-at-large, total movement distance, daily movement rate) were summarised for newly tagged and returning individuals in each year as median, lower and upper quartiles (LQ-UQ). Individuals that were tracked for less than 10 days were excluded from calculations of these metrics, to avoid bias associated with post-spawning individuals, or ‘fallback’ individuals that emigrated soon after tagging. These individuals were also excluded from quantification of space use (Section 1.3.7) and assessing similarity in space use (Section 1.3.8), to avoid potential spatial biases associated with short tracking periods.

6.3.7 Quantifying space use

The space use of individuals during their spawning migration was quantified as a utilisation distribution (UD), that represents the relative probability distribution of a tagged shad within the river (Keating & Cherry, 2009). Detection histories were converted to utilisation distributions 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 R package *RSP* (Niella et al., 2020).

To visualise and understand the overall distribution of tagged individuals within the River Severn catchment, a mean UD was generated by calculating mean values of each cell in the UD across all individuals. Mean UDs were calculated separately for individuals tracked upstream of weir S2, and for those that did not pass weir S2. For individuals that passed weir S2 in a given year, detections that occurred prior to passage of this barrier were removed in order to reduce biases imposed by barrier passage behaviours on their overall space use distributions.

6.3.8 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 shad 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 models (LMMs) in the R package *lme4* (Bates et al., 2015). Individual covariates were body length, sex, spawning history (maiden fish versus previously spawned based on analysis of spawning marks on scales) and tagging status (newly tagged versus returning individuals). To account for repeated measures occurring from the same individuals, a random effect of individual i.d. 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). In addition, a univariate LMM containing hybrid class as the sole covariate was fitted on a reduced dataset, to compare to assess the effect of hybridisation on CSUA. In addition, to assess the effect of hybridisation on core area size, a univariate LMM containing hybrid class as the sole covariate was fitted on this smaller dataset.

6.3.9 Assessing individual similarity in space use

The degree of similarity in space use for returning individuals between their first and second year of tracking was examined by calculating the 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.

Inter-individual VI was calculated between the UD of each individual in year one with 10 randomly selected returning fish in year two. 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.

6.3.10 Modelling factors affecting fidelity in space use

Factors affecting variation in spatial fidelity (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) to assess the effect of hybridisation on fidelity.

6.4 Results

6.4.1 Summary of movement metrics

Of the 184 twaite shad tagged with acoustic transmitters, 133 (72%) emigrated from the River Severn after the end of their spawning migration. Of these, 71 (57% of fish that emigrated with long life acoustic transmitters) were detected returning to the catchment the following year and 53 (75 %) of these fish emigrated back to sea after spawning. Seven fish with long life transmitters returned for a third consecutive spawning migration in 2020 (representing 10% of the 73 fish tagged in 2018, and 29% of these that emigrated in 2019) (Table 6.2). Time-at-large for newly-tagged individuals (median (LQ-UQ) = 24 days (18-30)) was generally less than returning individuals in their second year (33 days (27-38)) (Table 6.2). The fish were generally highly vagile while in the river; newly tagged individuals moved 156 km (113-223) between first detection and emigration while returning individuals moved 247 km (188-304). However, distance moved per day by newly-tagged individuals (7 km day^{-1} (5-8), *n* = 184) and returning individuals in the second year (7 km day^{-1} (6-9)) were similar (Table 6.2). Shad tended to display multiple upstream and downstream movements prior to emigration, but the frequency, extent and magnitude of these movements varied markedly between individuals (Figure 6.2). This variation in movement was reflected in variation in their UD, whereby some individuals were resident within a relatively small area (Figure 6.2a,b), while others roamed more widely (Figure 6.2c,d).

Chapter 6

Table 6.2: Summary of movement metrics for acoustic-tagged twaite shad tracked during their spawning migration in the River Severn in 2018, 2019 and 2020

Year	Status	*n* individuals tracked	*n* emigrated (%)	Median time-at-large, days (LQ-UQ)	Median distance moved, km (LQ-UQ)	Median daily distance moved, km day^{-1} (LQ-UQ)	Median upstream extent, rkm (LQ-UQ)
2018	Newly tagged	84	66 (79%)	21 (17-27)	134 (97-163)	6 (5-8)	49 (24-52)
2019	Newly tagged	100	67 (67%)	27 (20-35)	195 (123-269)	7 (6-9)	49 (24-50)
	Returning year 2	33	24 (73%)	35 (28-39)	247 (185-292)	6 (6-8)	50 (48-52)
2020	Returning year 2	38	29 (76%)	30 (27-36)	245 (189-303)	8 (6-10)	31 (24-50)
	Returning year 3	7	4 (57%)	29 (24-34)	140 (117-264)	6 (5-9)	42 (33-54)
Overall	Newly tagged	184	133 (72%)	24 (18-30)	156 (113-223)	7 (5-8)	49 (24-51)
	Returning year 2	71	53 (75%)	33 (27-38)	247 (188-304)	7 (6-9)	49 (24-50)
	Returning year 3	7	4 (57%)	29 (24-34)	140 (117-264)	6 (5-9)	42 (33-54)

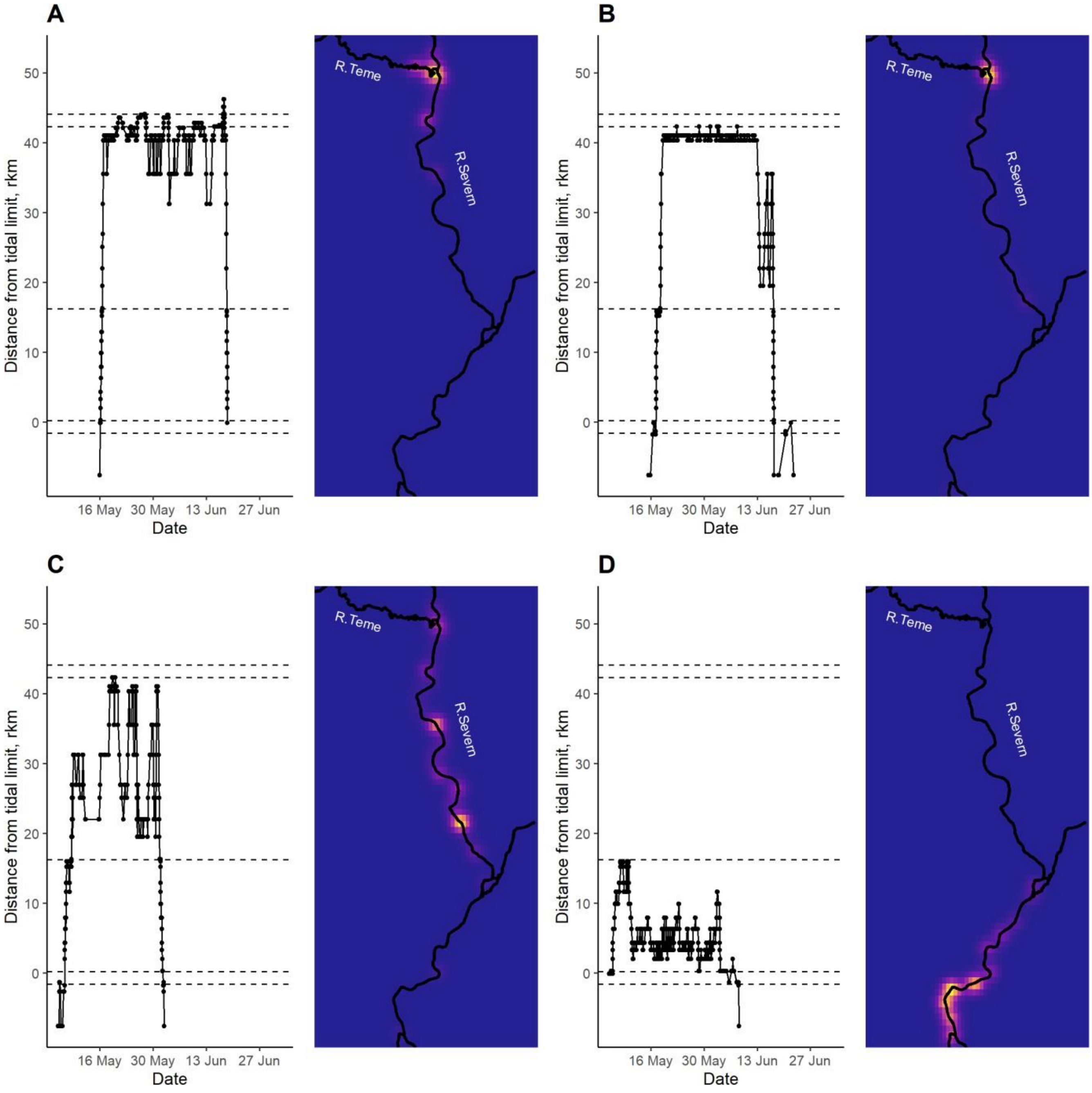


Figure 6.2: Illustration of diversity in movement and space use by acoustic-tagged twaite shad in the River Severn catchment using four individuals in 2019. Left panels show movement in the form of a track, with y-axis values representing river distance (rkm) of detections from the tidal limit by time (x-axis), and horizontal dashed lines represent location of main weirs withing the catchment. Right panels show utilisation distributions derived from dynamic Brownian bridge movement model. A: Individual predominately detected in lower River Teme and confluence with the River Severn; B: Individual with relatively constricted space use at the confluence of the River Teme and River Severn; C: Individual detected widely within the River Severn upstream of Weir S2; and D: Individual detected widely within the River Severn downstream of Weir S2.

6.4.2 Mean utilisation distribution and factors affecting KUD50 area

For acoustic-tagged individuals that did not pass S2, activity was concentrated in the upper half of the contiguous reach between S1 and S2, with the highest probability densities occurring at the confluence of the River Severn and River Avon (Figure 6.3). For acoustic-tagged shad 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 density occurring within the lower River Teme and the confluence of the River Teme and River Severn (Figure 6.3).

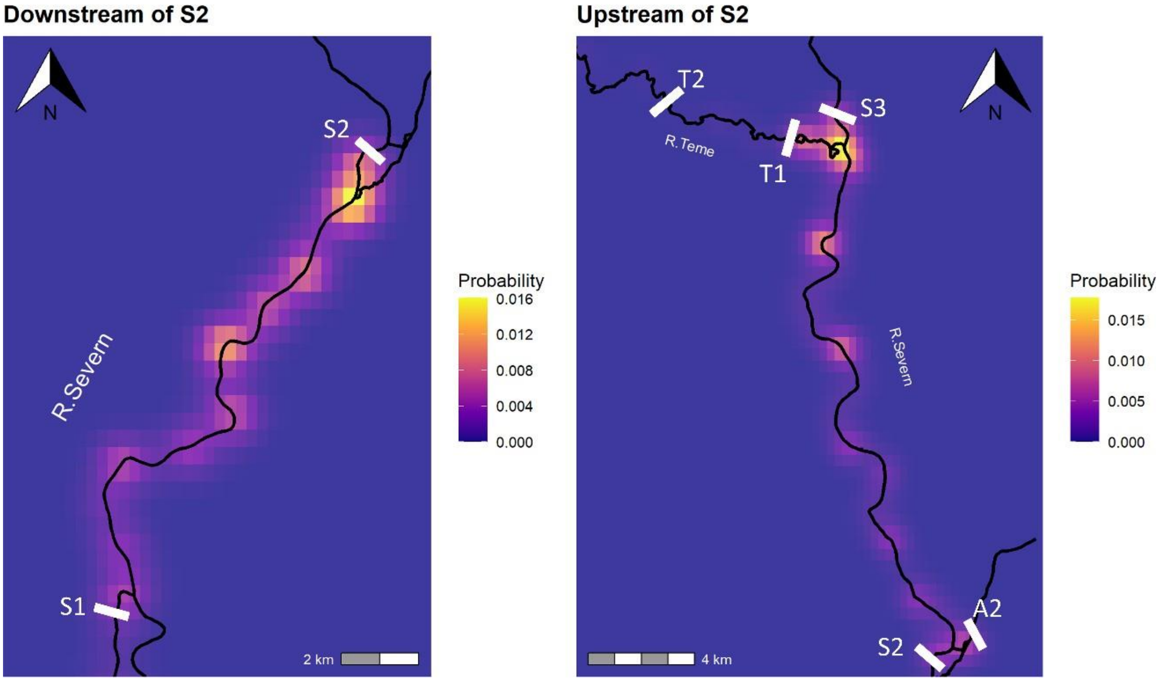


Figure 6.3: Mean utilisation distribution of acoustic-tagged twaite shad in the River Severn catchment. White bars indicate positions of major weirs. Left panel: utilisation distribution of individuals that did not pass weir S2 (*n* migration= 61, *n* individuals = 50). B: utilisation distribution of individuals tracked upstream of weir S2 (*n* migrations = 140*, n* individuals = 103). NB: tracks with a duration of less than 10 days were excluded to avoid bias associated with short tracking times.

For factors influencing KUD50 area, the best-fitting of 12 LMMs (Table A11) retained sex as the only significant predictor (ΔAIC from next best-fitting model 3.65, ΔAIC from null model = 8.35), indicating females had significantly larger CSUAs than males (Table 6.3, Figure 6.4). A univariate LMM indicated that there was little evidence that hybrid class was a predictor of KUD50 area (ΔAIC from null model = 0.5) (Table 6.3).

Table 6.3: (a) Covariate effects from best-fitting linear mixed effects model of 50% Kernel Utilisation distribution (KUD50) area for acoustic-tagged twaite shad (*n* observations = 168, *n* individuals = 125). (b) Covariate effects from univariate linear mixed effects model testing the effect of hybrid class on 50% Kernel Utilisation distribution (KUD50) area for acoustic-tagged twaite shad (*n* observations = 146, *n* individuals = 89).

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

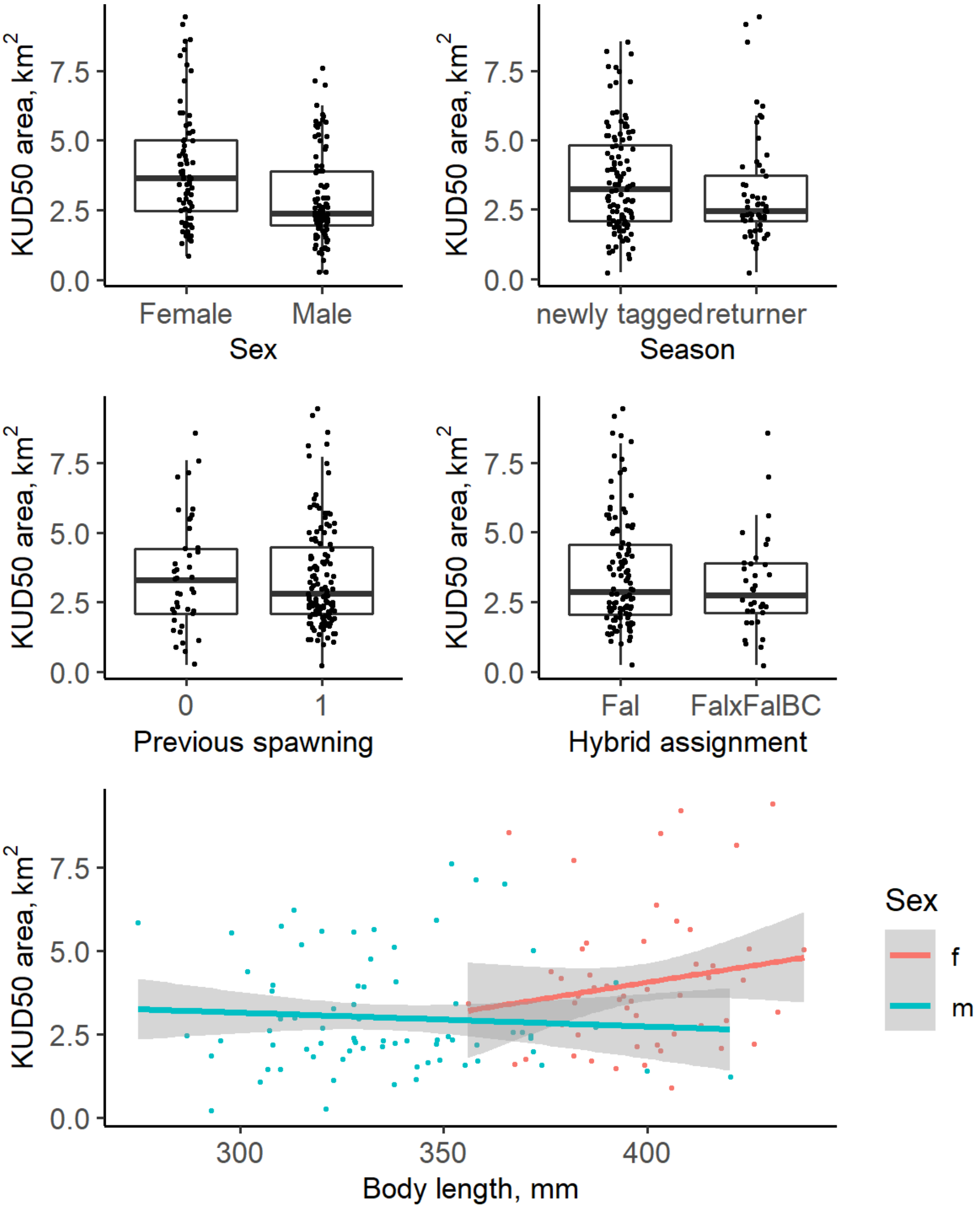


Figure 6.4: Factors tested for their effect on KUD50 area in acoustic-tagged twaite shad

6.4.3 Individual similarity in space use

For comparisons between shad tracked over 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 6.5), indicating that returning individuals having significant fidelity to river areas they occupied in previous years. The extent of intersection between utilisation distributions is illustrated for the seven individuals that provided three years of tracking data (Figure 6.6). Of the 14 GLMs fitted to tested factors influencing variation in VI, no model had better AIC support than the null model containing only the intercept (Table A12).

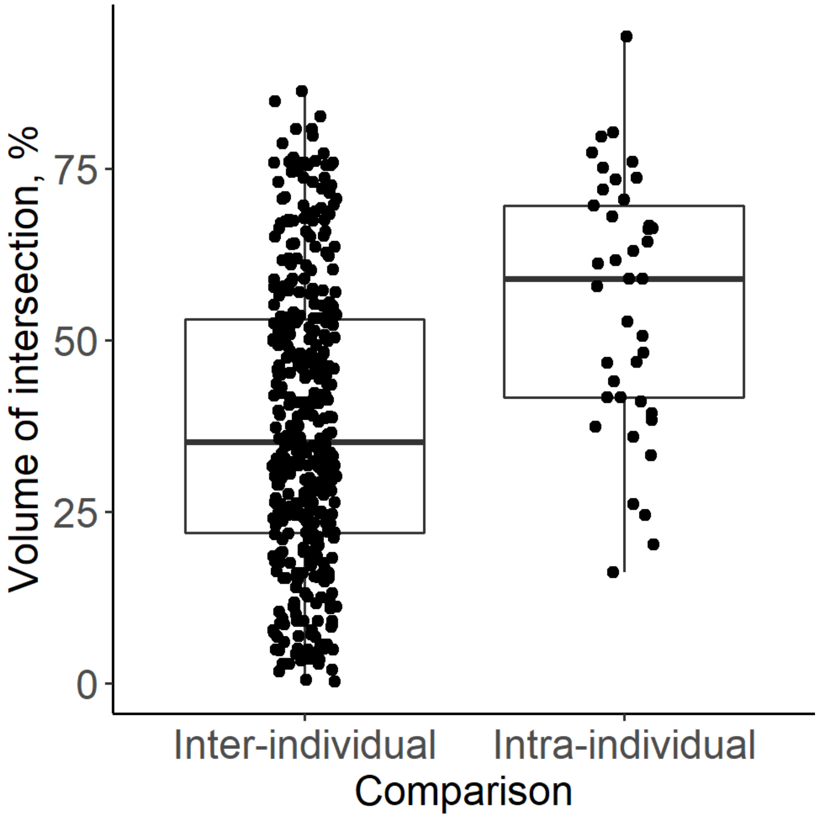


Figure 6.5: Boxplot showing inter- and intra-individual volume of intersection of utilisation distributions between first and second year of tracking by acoustic-tagged twaite shad.

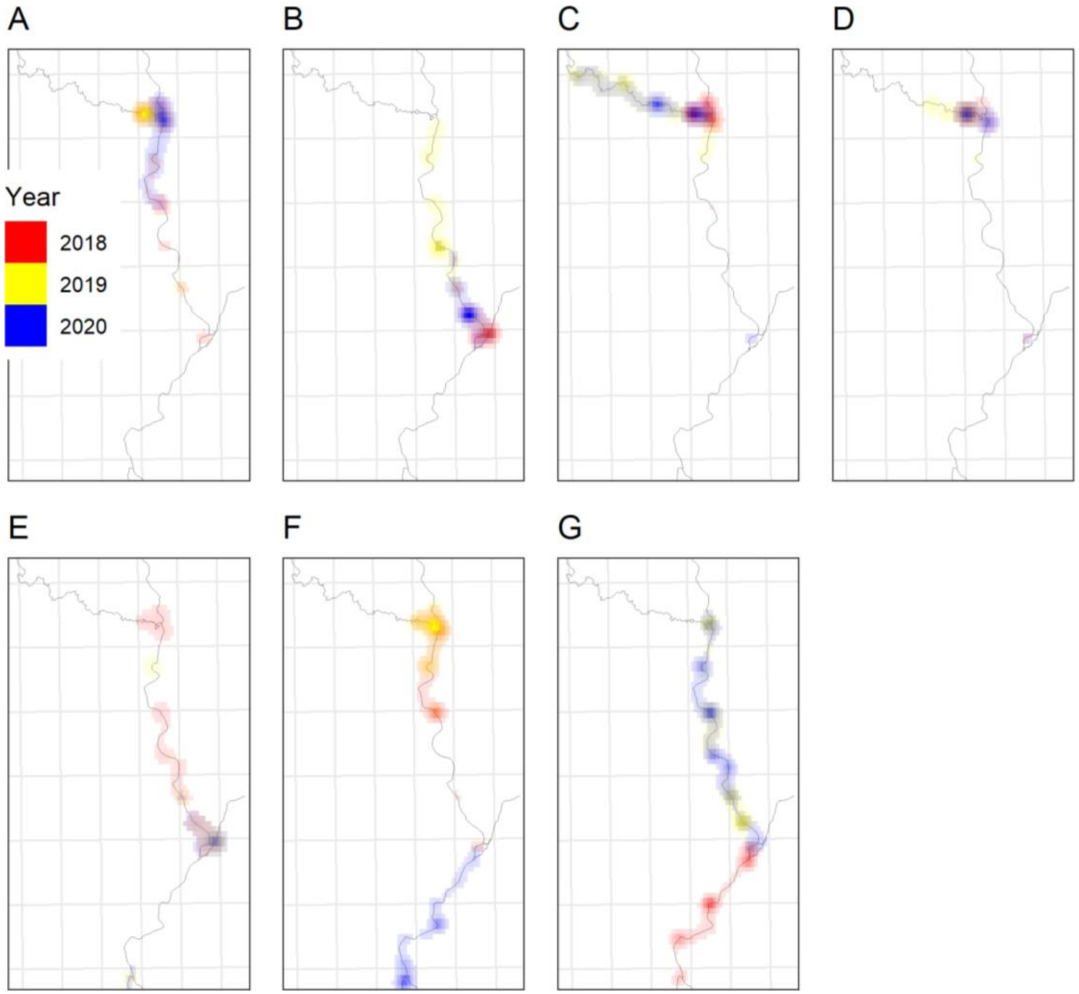


Figure 6.6: Utilisation distributions of seven acoustic-tagged twaite shad tracked over three consecutive spawning migrations in 2018 (red), 2019 (yellow), and 2020 (blue). Individuals A-E were tracked upstream of Weir S2 in all years, while F and G failed to pass Weir S2 in 2020 and 2018, respectively.

6.5 Discussion

Knowledge on the movement ecology of threatened anadromous fish during their spawning migration can inform conservation efforts, as well as help predict and mitigate the impact of habitat fragmentation. In this study of the movement, space use and spatial fidelity by repeat-spawning twaite shad, the tagged fish were highly vagile during their spawning migration, and displayed multiple upstream and downstream movements during their freshwater residency period. Evidence was provided for an effect of sex on space use, with females occupying significantly larger areas that males during their spawning migration. In addition, there was evidence for significant fidelity by returning individuals to areas occupied in previous years.

Telemetry studies in anadromous *Alosa spp.* have shown that members of this genus are often highly vagile during their spawning migration. In alewife *Alosa pseudoharengus*, long distance oscillations were observed between spawning grounds and downstream habitats (McCartin et al., 2019), while in allis shad, acoustic tagged individuals exhibited ‘exploratory’ behaviours that were attributed to the concurrent use of spawning and resting sites (Acolas et al., 2004; Acolas et al., 2006). In this study, the median distance moved by returning tagged individuals in their second year was 247 km, with newly tagged individuals moving 156 km. The lower total distances observed between newly-tagged and returning spawners likely reflect differences in their overall tracking time, since returning tagged spawners were observed from the onset of their movement into fresh water (median residency: 33 days), while the time in fresh water of newly tagged individuals (median residency: 24 days) prior to tagging could not be known. Overall, the time-standardised movement rates were similar (median: 7 km day^{-1}), suggesting that the tagging process did not substantially affect their movement behaviour. Overall, these estimates of movement distance are likely to be conservative, given that any oscillatory movements occurring outside the range of pairs of receivers were not recorded. Estimates of freshwater residency by returning tagged individuals in this study were then commensurate with a recent study in repeat-spawning American shad *Alosa sapidissima* which observed freshwater residency periods of 35 days in returning acoustic-tagged individuals

(Gahagan & Bailey, 2020), as well as newly tagged American shad in other studies where freshwater residency times of 7.8 - 33.0 days have been reported (Beasley and Hightower 2000; Aunins and Olney 2009; Aunins et al. 2013; Grote et al. 2014; Raabe and Hightower 2014). Understanding the potential environmental and individual factors affecting the temporal characteristics of shad migration, including freshwater residency and migration onset by returning shad, is a recommended objective of further studies.

The mean distribution of acoustic-tagged twaite shad in this study showed that certain locations were used relatively intensively during the spawning migration, potentially indicating spawning locations, as well as the impact of weirs on spatial distribution. For individuals that did not pass S2, the area where their space use was most intense was in the 1 km reach downstream of the weir. It is likely that this distribution represents both passage attempts and spawning behaviour. This finding is consistent with a study on acoustic-tagged allis shad (Acolas et al., 2004) that revealed tagged individuals spent the majority of their time in resting areas approximately 1.5 km downstream of a major migration barrier, as well as at the barrier itself. For individuals tracked upstream of S2, their mean distribution was similarly skewed towards the upper part of this reach, with the area around the lower River Teme and Severn confluence (1.5 km downstream of S3) being intensively occupied compared with areas downstream. This potentially reflects their use of the lower River Teme as a spawning site (Aprahamian, Lester & Aprahamian, 1998), as well as their attempts to pass S3. Nevertheless, the extent to which this intensity of space use reflects the locations of their spawning sites is unclear, especially as previous studies have suggested that acoustic tagged allis shad actually spent little time on spawning grounds, with most of their time spent in resting areas downstream (Acolas et al., 2004). In addition, visualisation of individual utilisation distributions revealed a high degree of individual variation in space use. Therefore, it is suggested that where spatial information is required on their actual spawning areas, then complementary approaches might be required, such as acoustic surveys of shad spawning activities (Langkau et al., 2016; Paumier et al., 2020) that can collate more specific data on where spawning occurs, as well as more high resolution acoustic telemetry to identify spawning-related movements.

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). Here, female twaite shad displayed a significantly larger core space use area than males during their spawning migration, indicating that their space use was more widely distributed through the river catchment. Histological studies in multiple shad species have suggested that female shad spawn in batches, with spawning events separated by a period of days, because females captured during their spawning migration often contain both post-ovulatory follicles and recently developed oocytes (Olney, Denny & Hoenig, 2001; Harris, McBride & Williams, 2007; Mouchlianitis, Minos & Ganias, 2020). In acoustic-tagged allis shad, batch-spawning by females was linked to observed movement differences between sexes (Acolas et al., 2004; Acolas et al., 2006), whereby males were more likely to be observed on spawning grounds on consecutive nights and engaged in more spawning acts in total, while females spent periods away from spawning grounds consistent with periods of egg maturation. The differences in space use reported here may thus just reflect differences in spawning behaviours between the sexes, with females moving away from spawning grounds to resting/holding areas during the egg maturation period, while males remain more closely associated with spawning grounds. This hypothesis is supported by a study in American shad, in which it was reported that males used upstream habitat at a higher proportion than females (Raabe & Hightower, 2014), potentially reflecting a tighter association to spawning grounds by males.

Philopatry is a widespread feature of animal migration, and natal philopatry is 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 philopatry, often termed ‘natal homing’, is thought to be heavily driven by olfactory imprinting, whereby juveniles form associations with the geochemical signature of water from their natal tributary during development (Dittman & Quinn, 1996; Keefer & Caudill, 2014). While understandings of this process has mainly been derived from salmonid fishes, natal homing to specific tributaries by *A. sapidissima* has been demonstrated, with marked hatchery-reared individuals returning to the same tributary that they emigrated from as juveniles (Hendricks et al., 2002). In this study, a spatial segregation of returning marked individuals across the river was also noted that suggested an olfactory-mediated location of natal tributaries. While fidelity to previous spawning rivers by adults has also been observed in repeat-spawning shad species (Melvin, Dadswell & Martin, 1986; Davies et al., 2020/Chapter 4), how natal homing and spawning fidelity interact has been unclear. Here, the results suggested that twaite shad displayed significant fidelity to previously occupied areas within the River Severn catchment, but the ‘precision’ of this fidelity is challenging to quantify using passive telemetry techniques, especially in the absence of knowledge of their actual spawning locations and also their natal origin. While inter-individual variability in fidelity was relatively high, there was little evidence here to suggest that previous spawning experience had an effect on the space use or degree of fidelity. Experience was not a well-supported factor in the modelling of core area size or VI - potentially suggesting that spawning area fidelity by adults could be a continuation of natal homing. This result is highly relevant to barrier remediation efforts, as it suggests that the initial success of fish passage remediation aimed at restoring connectivity for twaite shad may be limited if there is not already a spawning population upstream of the barrier. Correspondingly, recolonisation of upstream areas may be first achieved by a subset of exploratory ‘bold’ individuals, with natal homing and thus re-colonisation by their offspring in subsequent years (Pess et al., 2014).

Hybridization between different species or subpopulations with divergent migratory strategies can result in offspring that display intermediate movement patterns between the parent populations, or increased variability in movement patterns (Alvarado, Fuller & Smith, 2014; Delmore & Irwin, 2014). Where allis shad and twaite shad co-occur, allis shad generally roam further and occupy areas further upstream in the catchment, with river fragmentation posited as driving their hybridisation, as allis shad become forced to spawn in downstream areas also used by spawning twaite shad (Taillebois et al., 2020). Here, 21% of sampled twaite shad displayed introgression with allis shad (>3rd generation back cross), but there was no evidence that this introgression influenced their core area size. However, core area size is only one aspect of potential variation in movement and space use. Other aspects of variation, including migration timing, and the likelihood of exploiting upstream areas, could be assessed, potentially incorporating a greater sample size of tagged individuals with assigned hybrid classes, to more fully assess the consequences of hybridisation on movement.

In summary, this study reveals important new insights into the movement ecology of threatened twaite shad in a highly fragmented catchment, including their freshwater residency, movement distances and differences in space use between sexes which may reflect differences in the spawning strategy of males and females. Spatial fidelity demonstrated by returning spawners suggests an ability of adults to recognise and occupy previous spawning areas, which may be of relevance to future barrier passage remediation efforts.