Tracking anadromous fish over successive freshwater migrations reveals the influence of tagging effect, previous success and abiotic factors on upstream passage over barriers

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Abstract

Predicting and mitigating the impact of anthropogenic barriers on migratory fish requires an understanding of the individual and environmental factors that influence barrier passage. Here, the upstream spawning migrations of iteroparous twaite shad *Alosa fallax* were investigated over three successive spawning migrations in a highly fragmented river basin using passive acoustic telemetry (*n*=184). More fish approached and passed barriers in the lower river reaches than further upstream, with the median cumulative weir passage time (IQR) of 4.6 (1.8 - 9.2) days representing 18% of their time in river. Returning fish in their second year had significantly higher weir passage rates than in their tagging year, with passage rates also positively influenced by previous passage success. Higher water temperature and river level also had positive impacts on passage rates. Lower weir passage rates by newly tagged individuals suggests that reliance on within-year passage estimates in telemetry-based barrier impact assessments could result in conservative results, while higher passage rates of previously successful versus unsuccessful individuals suggests a conserved motivation and/or inherent ability to pass barriers.

Introduction

There are few rivers that now remain free-flowing along their entire length, particularly in developed regions (Jones *et al.*, 2019; Belletti *et al.*, 2020). Anthropogenic fragmentation of riverine ecosystems occurs primarily through river-regulation structures, such as dams and weirs, which are constructed for a variety of purposes, including power generation and navigation (Grill *et al.*, 2019). A major ecological impact of river fragmentation is its disruption to diadromous fish migrations (Hall, Jordaan & Frisk, 2011; Birnie-Gauvin *et al.*, 2017), which has contributed to their population declines in recent decades (Limburg & Waldman, 2009). These structures act as physical impediments that prevent or delay access of migrating adults to optimal spawning habitat (Lundqvist *et al.*, 2008; Castro-Santos, Shi & Haro, 2017; Newton *et al.*, 2018), and migration delays incurred at barriers can increase predation risk and have negative energetic consequences, especially when there are multiple passage attempts (Castro-Santos & Letcher, 2010; Nyqvist *et al.*, 2017). Moreover, where rivers contain multiple barriers, the effects of sequential barriers can be cumulative (Keefer *et al.*, 2013; Castro-Santos *et al.*, 2017; Davies *et al.*, 2021).

Barriers to migrating anadromous fish are often semi-permeable, with passage achieved by only a proportion of the upstream or downstream migrants and/or the migrating fish being delayed until conditions enable successful passage (Nyqvist *et al.*, 2017; Newton *et al.*, 2018). As migration and thus barrier passage are time-limited processes, analyses within telemetry studies often adopt a rates-based approach that enable assessments of the impacts of time-varying and time-constant covariates on passage rates (Castro-Santos & Haro, 2003). These studies have revealed that environmental factors, such as higher river discharge and water temperature, significantly affect barrier passage rates (Nyqvist *et al.*, 2017; Harbicht *et* *al.*, 2018). Individual factors, such as body size, shape and condition, can also affect the barrier passage rates of individuals (Keefer *et al.*, 2009; Nau *et al.*, 2017; Goerig *et al.*, 2020).

Iteroparous anadromous fishes that spawn multiple times in their natal river will potentially encounter the same barriers on multiple occasions, although the effect of these previous barrier encounters on passage is poorly understood (Nau *et al.*, 2017). Assessments of passage by the same individuals at the same barriers in different years should thus increase our understanding of how interactions of individual and environmental factors influence passage success (Pess et al., 2014). These assessments could also indicate whether potential biases are incurred in data that are reliant on only newly tagged fish, through comparing passage rates between their year of tagging and their subsequent return (Nau *et al.*, 2017). An example of iteroparous anadromous fish suitable for generating data on their successive migrations is the twaite shad *Alosa fallax*, which is distributed across the north-western Atlantic and Mediterranean (Aprahamian et al., 2003a). Recent declines and extirpations of their populations in European rivers have been attributed to pollution, overfishing and anthropogenic structures that act as barriers to their upstream spawning migration (de Groot, 1990; Aprahamian et al., 2003a; Antognazza et al., 2019). In their northern range, they are highly iteroparous, with previous spawners often representing over 50 % of all migrants (Aprahamian et al., 2003b). Although sensitive to handling and sedation, recent advances in surgical tagging protocols have enabled internal transmitter implantation (Bolland et al., 2019), enabling assessment of successive spawning migrations by the same individual (Davies et al., 2020).

Here, the freshwater spawning migration of twaite shad were assessed over multiple years to test how individual and environmental factors influenced anthropogenic barrier passage in the lower River Severn basin. The use of long-life acoustic tags enabled individuals to be tracked over several successive spawning migrations in different years. The primary objectives of the study were thus as follows: 1) estimate the impacts of anthropogenic barriers on twaite shad upstream migrations, including the proportion of upstream migrants passing each barrier and the migratory delay incurred by individuals during barrier passage; 2) determine the upstream extent of twaite shad spawning migrations within the basin relative to anthropogenic barriers and major tributaries, and the factors influencing the likelihood of approach of weirs; and 3) determine the individual and environmental factors influencing passage rates of anthropogenic barriers by twaite shad, including comparisons of passage rates of newly tagged versus returning individuals, and previously successful versus unsuccessful individuals.

Methods

Study duration and area

The study assessed the upstream spawning migrations of twaite shad in the River Severn basin in 2018, 2019 and 2020, which tend to commence in April and conclude in 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 basin 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 (T1, T2) and River Avon (A1, A2)) (Figure 1, Table 1). The normal tidal limit is at Maisemore (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 (S2). Between the spawning migrations of 2018 and 2019, two weirs on the River Teme (Figure 1) were modified to remediate fish passage. T1 was lowered, and a rock ramp installed to reduce the approach gradient at T2. With the exception of S2, which featured a notch fish pass, there were no fish-passage structures on study weirs in the rivers Severn or Avon during the study period (Table 1). Passage of weirs without fish passage structures could thus only be achieved through ascent of the weir face, and/or passage during elevated flow or high tide periods when the weirs were inundated. Environmental data (15-minute intervals) were obtained from Environment Agency gauging stations at Saxon's Lode (temperature, approximately 3 km upstream of S2), Ashleworth (river level, approximately 10 km downstream of S2), and T2 (discharge and temperature) (Figure 1).

Fish capture, tagging and release

At the commencement of their migration season in early-mid May 2018 and 2019, upstream-migrating adult twaite shad (referred to as 'shad' in methods and results) were captured by rod-and-line angling immediately downstream 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 fish were weighed (nearest 10g), measured (fork length, nearest mm) 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 migration history) using a projecting microscope (x48 magnification) (Baglinière *et al.*, 2001). Following the collection of their biometric data, the shad were surgically tagged with 69 kHz, V9 acoustic transmitters (www.innovasea.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 2), of which 173 were tagged with programmed long-life acoustic transmitters. At the end of June, these transmitters were programmed to switch from a randomized 60-second pulse interval (minimum interval between acoustic pulses 30 seconds, maximum interval 90 seconds) to a 600-second pulse interval until April the following year, when they were programmed to switch back to their randomized 60-second pulse interval. This was to increase the battery life of the transmitters to approximately three years, potentially enabling the tracking of three consecutive spawning migrations of tagged individuals. Non-programmed transmitters (11 shad) featured an identical initial pulse interval but did not switch to a 10-minute interval at the end of June, so tracking of these fish was possible in one season only.

At S1a, all tagged shad were captured downstream of the weir and released upstream of the weir (Figure 1) in order to quantify approach and passage at the next weir (S2) (Table 2). At S2, the majority of tagged shad caught downstream or in the upstream trap were released upstream of the weir to study the extent of their onward migration and the impact of the subsequent weirs in the rivers Severn, Teme and Avon. Some tagged shad were also released downstream of S2 in 2018, to increase the sample size of fish used to assess passage at this weir.

Acoustic array

Prior to the commencement of each spawning migration period, an array of acoustic receivers (VR2-W and VR2-Tx, www.innovasea.com) was installed throughout the study area (Table 1; Figure 1). The furthest downstream receiver in the array (51.8347, -2.2901; Figure 1) was located in the estuary, 8 km downstream of the tidal limit, at the approximate summer limit of saltwater intrusion into the river (Bassindale, 1943). Receivers were deployed upstream and downstream of each weir and in unobstructed reaches between weirs (Table 1; Figure 1).

Although no shad were tagged 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 riverbed. 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 approximately every two weeks. Most receivers were removed after a two-week period with no further movements were detected within the array since the previous download. The most downstream receiver remained in place to account for any individuals which emigrated after receiver removal, but this did not occur. 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 receiver deployment location. Step-by-step detection efficiency values for each receiver in the array was calculated for each study year using the R package *actel*. Detection efficiency for receivers in the array ranged from 52.5-100%; lower detection efficiencies were associated with receivers in narrow channels and/or high turbidity tidal areas (e.g. downstream Lower Parting annual efficiency: 52.5-93.1%; downstream S1b: 43-91.4%;); while detection efficiency in non-tidal areas was generally high (>99.7%).

Data analysis

Summary metrics

All statistical analyses were conducted using R statistical software (version 4.0.2, R Core Team, 2020). Initially, emigration and return rates were calculated for shad released in each tracking year, as well as for returning shad in each subsequent year. Shad were classed as having emigrated from the river if their final detection location was the most downstream receiver in the array (Figure 1) and they were classed as returning if they were detected moving upstream into the array in subsequent years.

To understand the relative impacts of weirs on upstream-migrating shad, the following key approach and passage summary metrics were calculated for each weir in the study area: *n* available, *n* approached, percent approach, *n* passed, percent passage and passage time (Table 3). These metrics were calculated separately for each of the study years, and for newly tagged versus returning individuals. To understand the overall impact of weir on the upstream migration of tagged individuals, the following summary metrics were calculated for each individual in each year: upstream extent, total passage time and delay proportion (Table 3). To further contextualise weir impacts on upstream movement, the upstream transit times of acoustic tagged individuals through a representative obstructed reach (downstream S2 to upstream S2) and unobstructed reach (upstream S1 to downstream S2) were calculated and compared using Kruskal-Wallis rank sum. Upstream transit times were calculated as the difference in time between the first detection on downstream and upstream receivers, and standardised by the river distance between upstream and downstream receivers in each reach (unobstructed reach; ~17 km; obstructed reach: ~1km).

Factors affecting approach of weirs

The individual factors affecting weir approach by newly tagged and returning shad were tested using binomial generalised linear mixed models (GLMMs) in the R package *lme4,* and generalised linear models (GLMs) in base R. Individuals that were available to approach S2 and/or S3/T1 were categorised as either approaching (1) or non-approaching (0). Two sets of models were constructed to test the effects of individual covariates on approach likelihood.

The first model set tested whether tagging status (newly tagged versus returner) affected the likelihood of weir approach, using GLMMs. These models included the approach classification (0/1) for fish that provided two years of approach data at a weir. Additional individual covariates were body length and spawning history (number of previous spawning events indicated by scale analysis). A fixed effect of weir was also included to test whether approach likelihood of individuals that were available to approach S2 differed from approach likelihood of those available to approach S3/T1. A random effect of individual fish i.d. was included in the models, to account for repeated measures from the same individuals across different years.

The second model set tested whether approach of S3 and/or T1 in the previous year affected the subsequent likelihood of approach of either weir for returning fish, using GLMs. These models included the approach classification (0/1) of returning individuals with known approach classifications in the previous year. Additional individual covariates were body length and spawning history. Approach of S2 was not included in this model, due to high approach rates by returning individuals at this weir.

Candidate model sets containing all possible combinations of covariates (body length, spawning history, river section, tagging status) without interactions, excluding pairs of covariates that were strongly tied (previous spawning and body size), 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 was 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).

Factors influencing passage rates of weirs

The factors influencing passage rates of newly tagged and returning shad were tested using time-to-event analysis (Castro-Santos & Haro, 2003; Goerig *et al.*, 2020). This analysis measured the relative effects of individual and time-varying covariates on passage rates at S2 (Figure 1), as this weir had the largest sample size of approach and passage over the three tracking years. Shad entered the ‘risk set’ (the set of individuals to pass) when they were detected on the receiver immediately downstream of S2 during an upstream approach (Figure 1). Individuals remained in the risk set until their retreat downstream (confirmed by detection on receiver approximately 1 km downstream of S2 (Figure 1)) or their passage over the weir. This approach ensured that fish were only considered to be candidates to passage (and subject to covariate conditions) while they were actually present. Mixed effects Cox models of passage rate, incorporating individual and environmental fixed effects and a random effect (fish i.d.), were constructed using the package *coxme* in R (R Core Team, 2020; Therneau, 2020). The random effect accounted for statistical dependence among repeated passage from the same fish in different years (Therneau, Grambsch, & Pankratz, 2003).

During data preparation, raw detection data for each shad were converted into 15-min observations of location, defined as the location of last detection, and observations of movements between receivers. Approach observations occurring at the receiver immediately downstream of S2, and passage observations (first detection upstream), were selected. These observations were then associated with individual metadata (body length, spawning history, previous success) and environmental data. Environmental covariates were downstream river level (m), water temperature (^{o}C) and diel period (as day/night, based on time of sunset and sunrise at weir S2, using the *maptools* package (Bivand & Lewin-Koh, 2019)). Individual body length (cm), spawning history (*n* previous spawning events, grouped into 0, 1, 2+) were also included as covariates. Shad that passed the weir were censored from the model dataset at the time of passage, and non-passing individuals following their final upstream approach.

Following data preparation, two model datasets were created to test specific factors relating to the tagging status and previous experience of individual tagged shad on passage rates at S2. Dataset 1 enabled testing of tagging status (newly tagged versus returning shad) on passage rates, and so contained approach and passage events for acoustic-tagged shad released downstream of S2 in 2018 and 2019 that also returned to the weir following year, i.e. 2019 and 2020. Dataset 2 enabled testing of the impact of previous success at passing weir S2 during the first year at liberty (2018 and 2019) on subsequent passage rates in the return year (2019 and 2020, respectively), so contained approach and passage events for returning acoustic-tagged shad with known passage (successful or unsuccessful) during their first year at liberty. Body length was excluded as a covariate from testing on Dataset 2 due to the unknown body length of returning individuals.

To analyse these two datasets, initial data exploration assessed collinearity between covariates (Zuur, Ieno & Elphick, 2010). Model selection was then conducted as per the GLMMs. The assumption of proportional hazards in the top-ranked Cox models was assessed by visual inspection of Schoenfeld residuals to confirm a zero slope for each covariate (Schoenfeld, 1982). Covariate effects from the top-ranked model were presented as hazard ratios (HR), which represent the effect on passage rates of increasing the value of continuous covariates by one unit (e.g. by 1 m for river level) or by changing the value of a categorical covariate. Survival curves for categorical predictive variables, and representative levels of continuous predictive variables, were plotted using the R package *survminer.*

Results

Summary of emigration and return

Of the 173 shad tagged with long-life acoustic transmitters in 2018 and 2019, 125 (72 %) emigrated from the river (Table 4). Of these emigrating fish, 71 (57 %) were subsequently detected returning to the River Severn for a second year, and of these 53 (75 %) emigrated for a second time. Emigration rates were similar between newly tagged fish and returning fish in each year, and return rates were the same (57%) for newly tagged fish that emigrated in 2018 and 2019 (Table 4). Of the 73 fish tagged in 2018, 7 (10 %) returned for a third year in 2020, all of which had also returned in 2019.

Weir approach, passage and passage time

The percentage of shad that approached and passed weirs in the River Severn basin varied spatially (between weirs), temporally (between years), and also between newly tagged and returning fish (Table 5). At S1a/b, the first weirs encountered by upstream-migrating shad, the combined percent approach and passage of returning individuals at these structures were very high (98-100 %) in 2019 and 2020 (Table 5). Of those that moved upstream of S1a/b, the percent approaching the next weir S2 was high in each tracking year, particularly for returning individuals (98-100%) relative to newly-tagged individuals (91-93%) (Table 5). Passage of S2 varied between tracking years and tagging status, being lowest for newly tagged individuals in 2019 (16 %) and highest for returning individuals in 2019 (81 %)

(Table 5). Passage rates of S3 were always low (Table 5). At T1, passage was 0 % in 2018 (*n* = 18), but following its modification in late 2018, passage rates increased to 50 % in 2019 (*n* =18), which included passage by both newly tagged and returning individuals, and 67 % in 2020 (*n* = 3) (Table 5). Of those shad that moved upstream of T1, few approached the next weir, T2, and no shad passed A2 in any year (Table 5). Of the shad that approached T1, most also approached S3 (newly tagged: 84%, returner 75%); a lower proportion of the shad that approached S3 also approached T1 (newly tagged: 60%, returners 26%.). No shad were detected approaching A1.

Passage times at S2 were the longest of the weirs where at least 10 passages occurred (i.e. S2, S1 and T1; Table 5); passage time also varied between years and tagging status, being longest for newly tagged fish in 2019 (median passage time (LQ-UQ) = 6.2 (2.8-33) days), and shortest for returning individuals in 2019 (1.8 (1.1-3.4) days) (Table 5). Median total passage times at weirs of 4.6 days (1.8 - 9.2) represented a delay proportion of 33 % of the total time to upstream extent (13 (6-20) days) for returning individuals tracked from the estuary into fresh water. Standardised upstream transit times through the unobstructed reach from upstream S1 to downstream of S2 (0.04 (0.02-0.09) days, *n* = 143) were significantly and substantially lower than passage times of S2 (2.9 (1.3 -6.1) days, *n* = 72) (Kruskal-Wallis χ^2 = 135, p<0.001) (Figure 2).

Of the movements recorded upstream of S1a/b (*n* individuals = 114; *n* upstream movements = 152), 94 % resulted in an approach of S2, with the others reached their upstream extent between 1 and 4 river km (rkm) downstream of S2 (Figure 3a). Of the upstream movements recorded upstream of S2 (*n* individuals = 127; *n* upstream movements = 164), 63 % approached S3 and/or T1, and upstream extents for non-approaching fish were concentrated around the lower River Teme and its confluence with the Severn (19 %, Figure 2b), with a further 19 % reaching an upstream extent within the 24 rkm section of the River Severn between S2 and the River Teme confluence (Figure 3b). Of the 11 migrations tracked upstream of T1 by 9 individuals, there were 3 approaches of T2, with the remaining 8 reaching upstream extents between 7 and 13 km downstream of T2 (Figure 3b). Overall, weirs formed the upstream extent for 64% of migrations tracked upstream from S1a/b, and 41% of migrations tracked upstream from S2.

Individual factors influencing approach of weirs

There were 16 GLMMs that tested the factors influencing approach of S2 and S3/T1 by all fish (Supplementary Table 1). The best-fitting model retained weir as a predictor of weir approach (ΔAIC from null model = 12.5), indicating that shad available to approach S3/T1 were less likely to approach these weirs than those available to approach S2 (Table 5, Figure 4a). Body length was also retained in the model but its effect was non-significant (P = 0.15; Table 6, Figure 4b), and a simpler model containing weir as the only predictor of approach also received good support (ΔAIC from best-fitting model: 0.18) There were seven GLMs that tested the likelihood of weir approach by returning fish at S3/T1 (Supplementary Table 1). The best fitting model (ΔAIC from null model = 1.3) retained the previous approach of S3/T1 as the sole predictor, with the model indicated a marginally significant positive effect of previous approach on approach likelihood (P= 0.06; Table 6, Figure 4c). There were no less complex models within 2 AIC of the best-fitting model.

Individual and environmental factors influencing passage rates of weir S2

Across the three study years, tagged shad approached weir S2 between mid-April and early June, with a peak in May (Figure 5). There were 32 mixed effects Cox models testing the individual and environmental factors influencing passage rates of weir S2 by newly tagged and returning fish (Dataset 1) (Supplementary Table 2). The best fitting model (ΔAIC from null model = 28.5; Akaike weight = 0.15) revealed that returning fish passed S2 at a significantly higher rate than newly tagged fish ($p < 0.01$; hazard ratio (HR) = 6.04 (2.11-17.27)), Table 7a, Figure 6). Shad passed S2 at a significantly greater rate during higher river level conditions and at higher water temperatures, although there was no significant difference between passage rates at early and mid-season temperatures (Table 7a, Figure 7). Diel period (higher passage during the day versus at night) and body length (positive effect of body size on passage rates) were also included in the best-fitting model, although these effects were non-significant (Table 7a).

A further 64 mixed effects Cox models tested factors influencing passage rates of weir S2 by returning fish (Dataset 2; Supplementary Table 3). The best fitting model (ΔAIC from null model = 21.0; total Akaike weight = 0.17) revealed that previous passage success significantly increased passage rates for returning fish relative to previously unsuccessful fish ($p = 0.04$; HR = 3.58 (1.15-11.6), Table 7b, Figure 6). Diel period, river level and water temperature were also included as predictors (Table 7b, Figure 7); hazard ratios for other covariates were of the same direction as in Dataset 1, although their magnitude varied (Table 7b). Previous spawning history and body length were not included as predictors in the top-ranked models of passage rates by newly tagged or returning shad, providing no support for an effect of these passage rates of acoustic tagged individuals. There were no less complex models within 2 AIC of the best-fitting models for Datasets 1 or 2.

Discussion

Weirs in the lower Severn basin impacted the upstream migration of threatened twaite shad, and passage rates and temporal delays to migration varied among weirs. Environmental conditions influenced passage rates, where episodes of elevated river levels and temperatures were important for facilitating passage. For returning tagged fish, there was evidence for a significant positive effect of previous success on passage rates, potentially suggesting a conserved ability and/or motivation to pass barriers between years. Returning fish also passed at higher rates than newly tagged fish, highlighting the importance of considering potential tagging effects when assessing barrier impacts using telemetry.

Impact of weirs on shad migration

The proportion of fish that passed each weir was variable, being generally high for the tidal weirs in the lower river basin but as low as 0% (in some study years) for weirs further upstream. These results suggest that once shad had moved into freshwater, a substantial percentage were prevented access to upstream spawning habitat. This has been heavily implicated in the decline of spawning populations of anadromous shads in the River Severn and elsewhere (e.g. Aprahamian et al., 2003; Limburg & Waldman, 2009; Buffery, 2018). The weirs also imposed considerable migration delays on the fish, with such migration delays known to have negative consequences on the reproductive success and survival of anadromous fish generally (Castro-Santos & Letcher, 2010), with delays also potentially subjecting migrants to elevated predation risk (Schmitt *et al.*, 2017; Alcott, Long & Castro-Santos, 2020). Weirs also formed the upstream limit of migration for the majority of acoustic-tagged shad (Figure 2), suggesting that weirs act to constrain the spawning distribution of shad in the Severn basin.

The results presented here emphasise the need for passage remediation work in the lower River Severn basin, supporting the work that has been continuing on the river in this respect (www.unlockingthesevern.co.uk). Facilitating shad passage at these structures can incorporate barrier removal with the retro-fitting of fish passes that take into account the specific knowledge base on passage requirements for alosines (Haro & Castro-Santos, 2012; Pess et al., 2014; Mulligan et al., 2019). Indeed, the preliminary results here indicated that modifying weir T1 did increase their passage rates, increasing from 0 % pre-modification to 50-67% post-modification, albeit these involved relatively low numbers of tagged individuals. Moreover, over 26000 upstream migrating Allis and Twaite shad were observed using a new fish pass on the River Mondego, Portugal, across five spawning migrations (Belo *et al.*, 2021). The results here provide a vital baseline for future monitoring of passage improvement work in the basin, as part of which telemetry should be an integral component, which is often lacking (Roscoe & Hinch, 2010; Noonan, Grant & Jackson, 2012).

Factors affecting approach of weirs

Although barriers formed the upstream limit of migration for the majority of the tagged shad, a subset of individuals within each impounded section did not approach weirs, particularly in the reaches of river upstream of S2 and T1. This potentially indicates the availability of apparently high-quality spawning habitat in the lower River Teme, which is characterised by shallow (0.75 – 2 m), fast-flowing riffle and run habitat (Antognazza et al., 2019). Twaite shad that reached their upstream extent further downstream may have spawned in considerably deeper (> 3 m) and slower-flowing habitat, which is consistent with studies suggesting the species spawns in the upper and middle reaches of estuaries (e.g. Magath & Thiel, 2013). There was also evidence that the likelihood of barrier approach was repeatable across years, with shad that approached S3 and/or T1 in the year of tagging more likely to approach the same weir(s) upon their return. This tentatively suggests these individuals had a conserved motivation to approach and pass barriers, and/or displayed some fidelity to their areas of previous spawning. This has relevance to river reconnection efforts as it suggests that not all upstream migrants may be motivated to exploit habitat upstream of a barrier following passage remediation (Pess et al., 2014).

Individual factors affecting weir passage rates

Returning twaite shad had significantly higher passage rates at weirs than newly tagged individuals, with this potentially being a negative consequence of their capture and/or tagging. A confounding factor here, is that the shad will have grown between tagging and subsequent return, but body size had a non-significant effect on passage rates. Likewise, analysis of spawning marks on scales enabled the effect of previous spawning experience to be tested, but there was no evidence that previous spawning experience affected passage rates. Thus, it is likely sublethal capture/tagging effects may have manifested as a reduced ability and/or motivation to pass weirs in the immediate post-tagging period. Tagging effects can be a pernicious feature of telemetry studies in alosines (Frank *et al.*, 2009; Eakin, 2017) with, for example, PIT-tagged alewife *Alosa pseudohaerengus* returnees having higher passage rates over weirs than newly tagged fish (Nau *et al.*, 2017; Gahagan & Bailey, 2020). Thus, in passage studies of iteroparous anadromous species, returning fish could be the most reliable indicators of weir passage rates, but not all tagged fish will return in subsequent years and thus higher costs may be incurred generating a reliable sample size (Raabe *et al.*, 2019).

Here, significantly higher passage rates were recorded in individual returning twaite shad that successfully passed a weir in the previous year when compared with previously unsuccessful fish. Inherent phenotypic traits (body size, body shape) (Goerig *et al.*, 2020) may enable certain individuals to be more successful at passing barriers, but there was little evidence for phenotypic traits being a predictor of passage success in this study. Another potential explanation relates to variation in migratory motivation linked to spatial fidelity or natal homing. A widely reported feature of shad spawning distributions in fragmented river basins is that spawning often occurs in areas immediately downstream of weirs (Acolas *et al.*, 2006; López *et al.*, 2007). This was also observed here and might lead to imprinting of juveniles to areas downstream of barriers, resulting in a reduced motivation to progress upstream upon their return. Further, there may also be learned spatial preferences in repeat-spawning adults, whereby they display preferences to using spawning areas that were used in previous years (Pess et al., 2014). Hatchery-reared American shad have demonstrated that imprinting is likely to occur at the tributary level (Hendricks *et al.*, 2002), although the mechanism of imprinting, and precision natal homing and spatial fidelity in alosines is generally poorly understood (Pess et al., 2014).

Environmental factors affecting weir passage rates

The successful passage of barriers, such as weirs, by fish can be influenced by swimming capacity and attempt rate, which in turn can be influenced by environmental variables, such as water temperature and discharge, as well as barrier characteristics, including head height and the presence of fish passage structures (Castro-Santos, 2004; Bunt, Castro-Santos & Haro, 2012). Here, increasing water temperature positively affected passage rates at weir S2. In upstream-migrants, changes in water temperature may invoke physiological and behavioural changes linked to maturation of reproductive organs, factors which then increase its motivation to ascend and pass a barrier (Lubejko *et al.*, 2017). Higher temperatures reduced the failure rates of alewife *Alosa pseudoharengus* attempting to use fishways (Franklin *et al.*, 2012) and increased the attempt rates but reduced swimming endurance of

American shad attempting to pass velocity barriers, indicating that the relationship between abiotic factors and barrier passage will be dynamic across the alosine spawning migration (Bayse, McCormick & Castro-Santos, 2019). Other studies have reported increased passage rates within the range of temperatures at which spawning occurs, and attributed this to increased motivation to move upstream and spawn (Raabe *et al.*, 2019).

Increasing river levels downstream of S2 significantly increased passage rates over this weir. Downstream river levels at S2 are affected by both tides and river discharge, and thus the relative effects of discharge and tide on passage are challenging to decouple. Nonetheless, the results suggest that prevailing hydraulic conditions at the weir are an important influence on passage by twaite shad. There are several mechanisms by which hydraulic conditions can influence passage of barriers. Water depth at the entrance to fish passes can increase passage rates in American shad (Mulligan *et al.*, 2019), a finding linked to reduced flow velocities at higher water depths. Passage of alosines may also be negatively affected by noise and entrained air and turbulence, all of which may be influenced by downstream river levels (Haro & Castro-Santos, 2012). There was also some evidence that the passage rates of S2 were greater during the day than at night. Shads tend to prefer daylight hours to migrate upstream (Haro & Castro-Santos, 2012; Raabe *et al.*, 2019), while twaite shad spawning is highly nocturnal (López *et al.*, 2011). The lower passage rate at night may thus reflect differences in motivation between day/night approaches, with weir approaches during the day being passage attempts and nocturnal approaches being upstream movements associated with spawning (Acolas et al., 2004; López et al., 2011). In anadromous shads, spawning activity immediately downstream of barriers has been attributed to ‘forced’ spawning of unsuccessful individuals, as well as the presence of relatively high quality habitat immediately downstream of weirs (Acolas et al., 2004; Acolas et al., 2006; López et al., 2011). Further work is required to understand potential spatial differences in nocturnal versus diurnal approaches to weirs by shad, which will improve current understandings of characteristics such as spatial fidelity and motivation.

Future research

The research presented here was a coarse-scale assessment of the factors affecting weir approach and passage. In future, a more precise spatial and temporal understanding of weir approach and rejection rates, incorporating rates-based analyses, in relation to temperature and river level could be obtained by performing finer-scale telemetry studies immediately downstream of certain weirs, e.g. radio telemetry or high-frequency acoustic telemetry. However, such technology would not be compatible with that employed to investigate the spatial ecology of the same fish during marine life-phases (Davies et al., 2020), although this could be mitigated by deploying marine receivers that function over a range of frequencies. Further work could also seek to provide a mechanistic understanding of reduced passage rates in newly tagged fish; experimental studies could elucidate and separate potential effects of capture, sedation and tagging on key predictors of passage ability such as motivation, orientation, swimming performance (Cooke *et al.*, 2011).

Summary

This study quantified the impact of weirs on upstream migrating twaite shad. While returning individuals to their spawning rivers are a rare feature of telemetry-based assessments of barrier passage, their use in this study, enabled by advancements in telemetry technology and tagging protocols, was crucial in their use as ‘controls’ for understanding potential tagging bias and for understanding the effect previous experience on passage ability. The results revealed that even with previous weir passage experience, migrating fish could still be delayed or not pass at all, with elevated river levels and water temperatures important for passage. Taken together, these results are important contributions to contemporary understandings of anadromous fish migration in fragmented river basins.

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Author contributions

Conceived and designed the field experiments: JDB, ADN, JRD, CC, RV, JRB, and PD. Conducted fieldwork: JDB, ADN, JRD, CC, JRB and PD. Conducted telemetry analysis: PD, with advice from TCS. Wrote the article: PD. Edited the article: JDB, TCS, JRB, ADN, JRD, CC, and RV.

Data availability

Data from this study will be made available upon reasonable request

Declaration of interest

The authors have no competing interests to declare.

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Tables

Table 1: Locations and characteristics of study weirs in the River Severn basin during the study period, which were used to assess the impacts of weirs and factors affecting approach and passage during the upstream migration of acoustic-tagged twaite shad. Weir heights represent drop in head at Q_{95} and during periods with no tidal influence.

Weir code	Name	River	Location, decimal degrees[1]	Distance from normal tidal limit, rkm	Height, m	Fish pass
S1a	Maisemore Weir	Severn (West Channel)	51.89318, -2.26574	0	1.8	NA
S1b	Llanthony Weir	Severn (East Channel)	51.86227 -2.26028	0	1.7	NA
S2	Upper Lode Weir	Severn	51.99346, -2.17407	16	1.6	Notch, larinier
S3	Diglis Weir	Severn	52.17926, -2.22597	42	2.5	NA
T1	Powick Weir	Teme	52.16975, -2.24712	44	2.8 (pre 2019) 1.4 (2019 onwards)	Larinier (pre 2019), NA (2019 onwards)
T2	Knightwick Weir	Teme	52.19908, -2.38940	60	1.2	NA
A1	Abbey Mill Weir	Avon	51.99133, -2.16325	16	1.8	NA
A2	Stanchards Pit Weir	Avon	51.99837, -2.15561	18	1.9	NA

Table 2: Summary metrics for acoustic tagged twaite shad *Alosa fallax* captured over two years in the River Severn

Year	**Capture location**	**Capture method**	**Release location**	***n***	**Length ± SD, mm**	**Weight ± SD, g**
2018	S1a	Angling	Upstream S1a	20	365.9 ± 24.9	653.8 ± 148.5
	S2	Angling	Downstream S2	10	375.4 ± 20.6	645 ± 106.6
	S2	Angling	Upstream S2	24	339.8 ± 31.6	479.2 ± 142.3
	S2	Trap	Downstream S2	8	357.6 ± 28.1	559.4 ± 182.7
	S2	Trap	Upstream S2	22	376.4 ± 16.9	736.4 ± 112.8
2019	S1a	Angling	Upstream S1a	50	350.9 ± 43.1	617.5 ± 255.2
	S2	Trap	Upstream S2	50	376.9 ± 37.9	776.5 ± 249.3
Total				184	362.8 ± 36.8	659.8 ± 227.7

Table 3: Definition of metrics used to quantify approach and passage of weirs in River Severn basin by acoustic-tagged twaite shad, and the impacts of weirs on individual migration

Metric	**Definition**	**Quantified for:**
n available	The number of fish detected moving upstream with an unobstructed upstream route to a weir	Each weir
n approached	The number of upstream-moving fish that were detected on the receiver immediately downstream of a weir	Each weir
Per cent approach, %	The proportion of *n* available fish that approached a weir	Each weir
n passed	The number of fish approaching a weir that were subsequently detected on an upstream receiver	Each weir
Per cent passage, %	The proportion of approaching fish that passed a weir	Each weir
Passage time, days	Time between the first detection on the downstream receiver at a weir and first detection on an upstream receiver	Each weir
Upstream extent, rkm	The furthest upstream location that a fish was detected within the catchment	Each individual
Total passage time, days	Sum total of passage times recorded at all weirs	Each individual
Delay proportion, %	Total passage time as a proportion of the time taken to reach the upstream extent of migration from immediately downstream of the first migration barrier	Each individual

Table 4: Summary of emigration and return rates by twaite shad tagged with 3-year acoustic transmitters in 2018 and 2019

Tagging year			**Year 2**		**Year 3**	
	n tagged	*n* emigrated (% of tagged)	*n* returned (% of emigrated)	*n* emigrated (% of returned)	*n* returned (% of emigrated)	*n* emigrated (% of returned)
2018	73	58 (79%)	33 (57%)	24 (72%)	7 (29%)	4 (57%)
2019	100	67 (67%)	38 (57%)	29 (76%)	NA	NA
Total	173	125 (72%)	71 (57%)	53 (75%)	NA	NA

Table 5: summary of weir passage metrics for acoustic tagged twaite shad migrating upstream in the River Severn basin in 2018, 2019 and 2020. Median passage time presented with lower and upper quartiles (LQ-UQ).

Weir	**Year**	**Fish status**	**n available**	**n approached (% of available)**	**n passed (% of approached)**	**Median passage time, days (LQ-UQ)**
S1a/S1b	2018	Newly tagged	NA	NA	NA	NA
	2019	Newly tagged	NA	NA	NA	NA
	2019	Returning	33	33 (100%)	33 (100%)	1.0 (0.4-3.9)
	2020	Returning	45	44 (98%)	44 (100%)	1.5 (1.0-2.8)
S2	2018	Newly tagged	33	30 (91%)	12 (40%)	5.9 (5.0-6.2)
	2019	Newly tagged	45	42 (93%)	7 (16%)	6.2 (2.3-33.0)
	2019	Returning	33	33 (100%)	27 (81%)	1.8 (1.1-3.4)
	2020	Returning	44	43 (98%)	28 (65%)	1.9 (1.3-4.7)
S3	2018	Newly tagged	57	29 (51%)	0 (0%)	NA
	2019	Newly tagged	56	30 (54%)	1 (3%)	21.0 (NA)
	2019	Returning	27	13 (48%)	2 (15%)	25.8 (24.6-27.1)
	2020	Returning	28	19 (67%)	0 (0%)	NA
T1	2018	Newly tagged	57	18 (32%)	0 (0%)	NA
	2019	Newly tagged	27	11 (41%)	6 (54%)	1.1 (1.1-3.8)
	2019	Returning	56	7 (13%)	3 (43%)	0.0 (0.0-0.5)
	2020	Returning	28	3 (11%)	2 (67%)	0.4 (0.3-0.5)
T2	2018	Newly tagged	0	0 (NA)	0 (NA)	NA
	2019	Newly tagged	6	1 (17%)	1 (100%)	NA[1]
	2019	Returning	3	1 (33%)	1 (100%)	NA[1]
	2020	Returning	2	1 (50%)	0 (0%)	NA
A2	2018	Newly tagged	57	21 (37%)	0 (0%)	NA
	2019	Newly tagged	27	6 (22%)	0 (0%)	NA
	2019	Returning	56	10 (18%)	0 (0%)	NA
	2020	Returning	28	12 (43%)	0 (0%)	NA

[1] Passage times unavailable due to missed detections on downstream receiver

Table 6: Covariate effects from best-fitting models of weir approach likelihood by twaite shad; a) two best fitting generalised linear mixed models including newly tagged and returning fish (Dataset 1). Covariates included are weir of approach (S3/T1 (null condition) versus S2) and body length at tagging; b) best fitting generalised linear model including only returning fish (Dataset 2) The single covariate included is previous approach i.e. whether a tagged fish approached a weir in its previous year or did not (null condition).

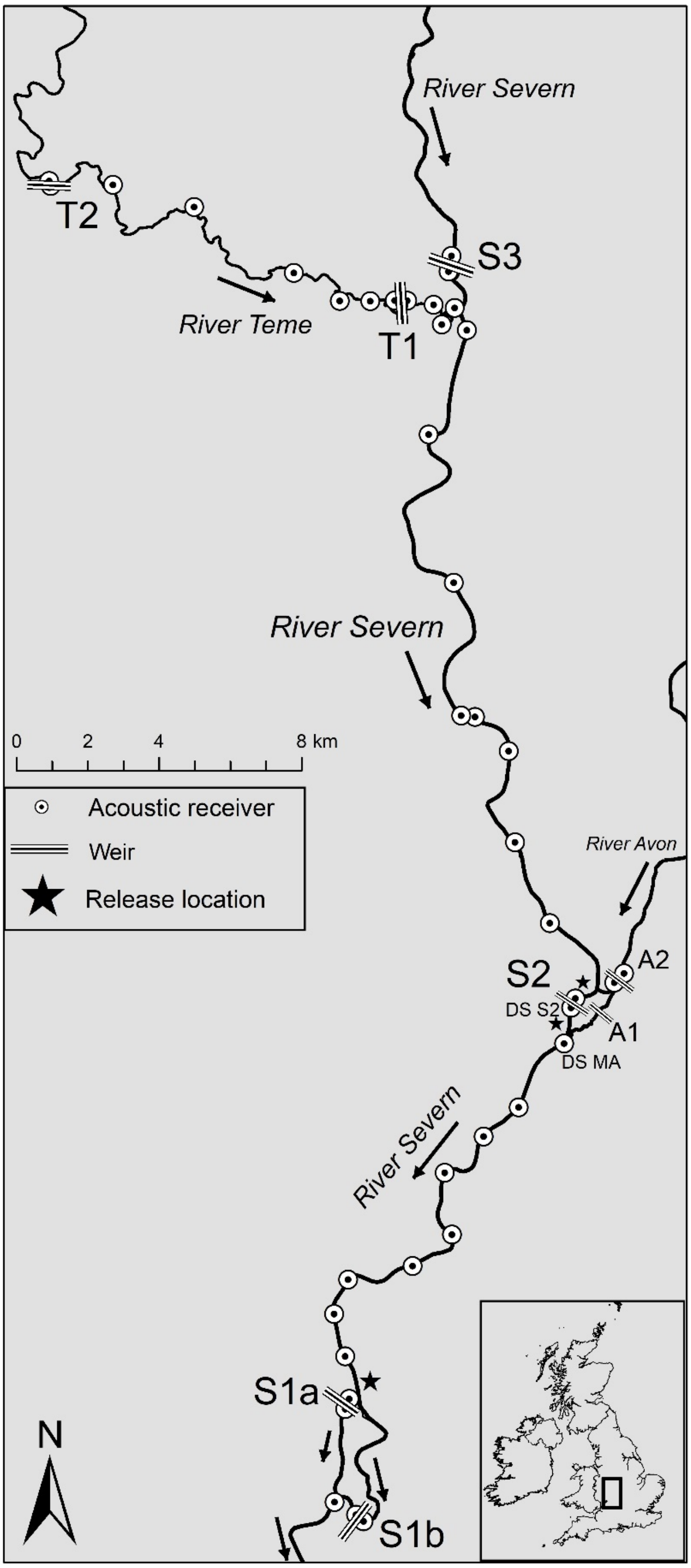
Parameter	**Estimate**	**SE**	**z**	**p**
a) All fish				
Best fitting				
(Intercept)	0.84	0.36	2.30	0.02
Weir: S3/T1	-	-	-	-
Weir: S2	2.34	0.80	2.95	<0.01
Body length	0.46	0.32	1.44	0.15
Second best fitting				
(Intercept)	0.91	0.37	2.46	0.01
Weir: S3/T1	-	-	-	-
Weir: S2	2.09	0.73	2.85	<0.01
b) Returners only				
(Intercept)	-0.41	0.65	-0.63	0.53
Previous: did not approach				
Previous: approached	1.50	0.80	1.88	0.06

Table 7: Results of best-fitting mixed-effects cox models describing effects of individual and environmental covariates on passage rate of weir S2 by twaite shad. (A) Model including newly tagged and returning fish released at weir S1a (Figure 1). Included covariates are tagging status (newly tagged (null condition) versus returning); river level, m, recorded at logger approx. 2km upstream of the weir; diel period (day (null condition) versus night), based on hours of sunset/sunrise at weir location; and water temperature (°C) collected by a logger immediately downstream of the weir, separated into three bins representing early (<11.5°C, null condition), mid 11.5-13.5°C and late run <13.5°C temperatures. (B) Model including only returning fish. Included covariates are previous success (successfully passed weir in the previous year or did not (null condition)); river level, m, recorded at logger approx. 2km upstream of the weir; diel period (day (null condition) versus night), based on hours of sunset/sunrise at weir location; and water temperature (°C) collected by a logger immediately downstream of the weir

Parameter	**Hazard ratio (95% confidence interval)**	**z**	**p**
(A) Newly tagged and returning fish			
Tagging status: newly tagged	-	-	-
Tagging status: returner	5.69 (1.95-16.55)	3.19	<0.01
River level, m	11.8 (4.21-33.03)	4.70	<0.01
Diel period: Day	-	-	-
Diel period: Night	0.26 (0.06-1.17)	-1.76	0.08
Water temperature: <11.5°C	-	-	-
Water temperature: 11.5-13.5°C	2.02 (0.58-7.06)	1.11	0.27
Water temperature: >13.5°C	3.95 (1.01-15.47)	1.97	0.05
(B) Returning fish only			
Previous success: Failed	-	-	-
Previous success: Passed	3.58 (1.15-11.16)	2.08	0.03
River level	20.4 (3.67-113.34)	3.47	<0.01
Diel period:Day	-	-	-
Diel period:Night	0.3 (0.05-1.74)	-1.24	0.22
Water temperature: <11.5°C	-	-	-
Water temperature: 11.5-13.5°C	2.78 (0.62-12.53)	2.33	0.18
Water temperature: >13.5°C	13.04 (2.58-65.78)	3.00	<0.01

0

Figure 1: The River Severn basin 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 weir codes are as in Table 1. The black arrows denote the direction of the flow.



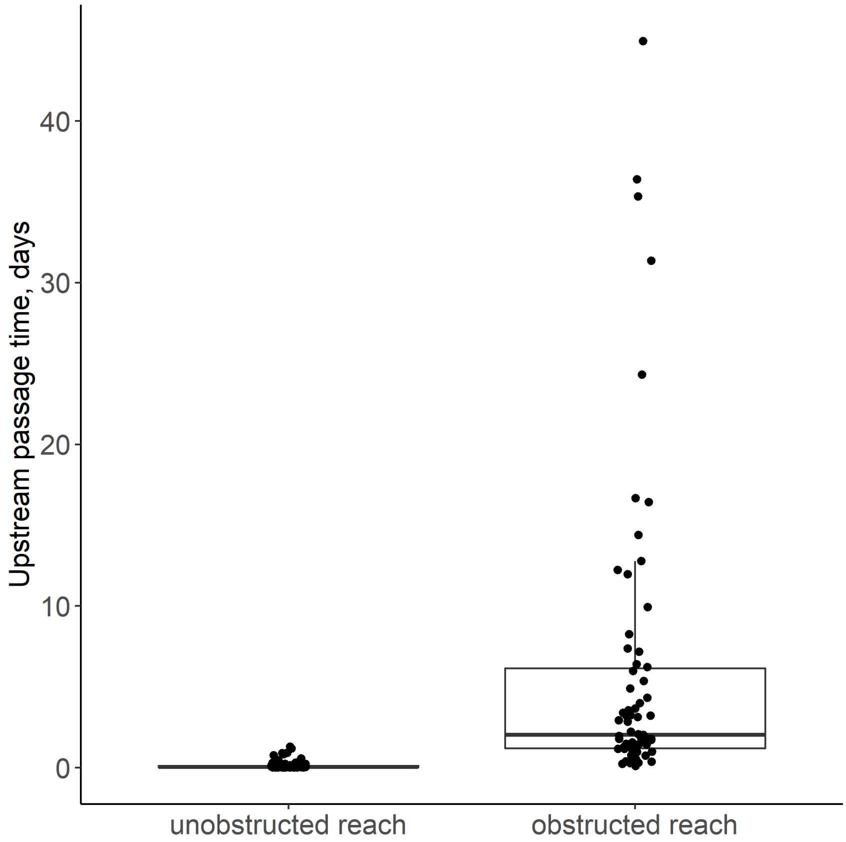


Figure 2: Upstream passage times of acoustic-tagged shad through unobstructed versus obstructed reaches of river. The obstructed reach was downstream S2 to upstream S2 (1 km) and the unobstructed reach was upstream S1 to downstream S2 (17 km) (see figure 1). Passage times were standardised to represent upstream passage times through one km of river reach.

Figure 3: Numbers of acoustic-tagged twaite shad detected and their upstream migratory extent in the River Severn basin tracked during spawning migrations in 2018-2020. The percentage of shad reaching each receiver, and the percentage of shad reaching their upstream extent of migration at each receiver, are represented by the size and colour intensity of the circles, respectively. Data are pooled for newly-tagged and returning fish. The weir codes are as in Table 1. **A**: Upstream extent of shad migrations recorded upstream of weir S1 (*n* migrations = 152). **B**: Upstream extent of shad recorded upstream of weir S2 (*n* migrations = 164).

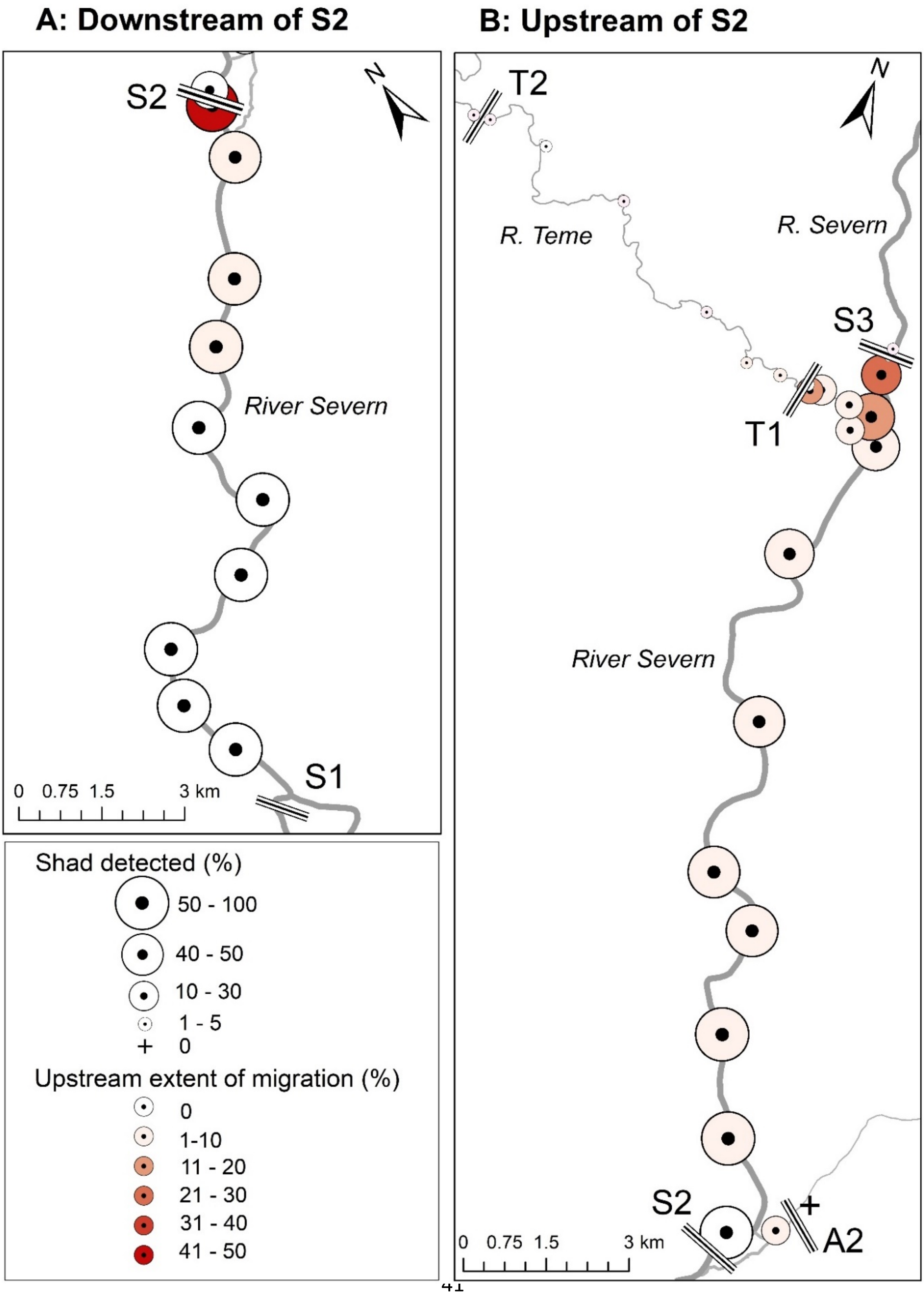


Figure 4: Summary of covariates from the best-fitting models of weir approach likelihood in twaite shad. A: Number of approaching/non-approaching individuals by weir for newly tagged and returning individuals. B: Body length of approaching/non-approaching individuals by weir for newly tagged and returning individuals. C: Number of approaching/non-approaching individuals at weirs S3/T1 by previous approach, for returning individuals.

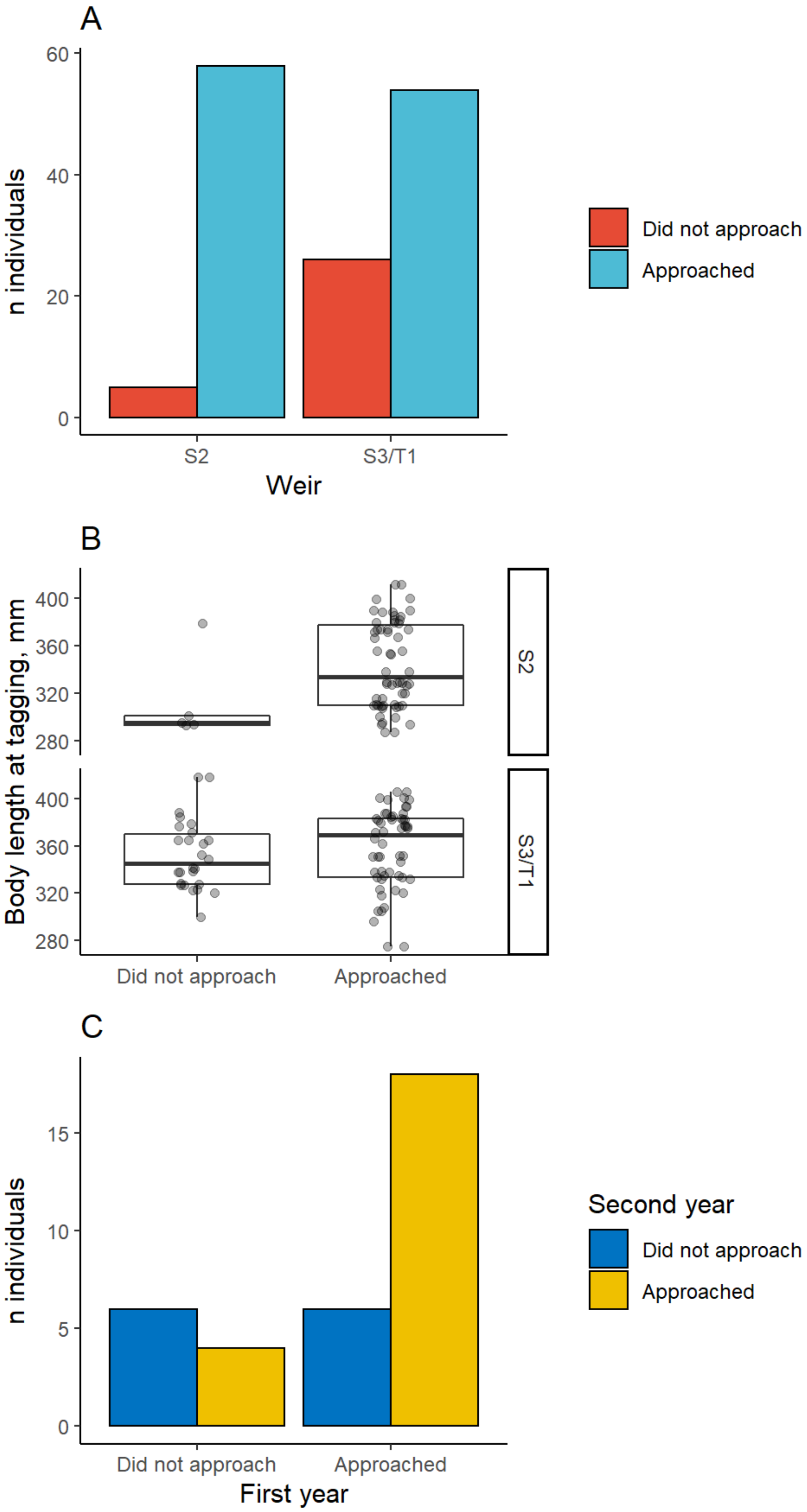


Figure 5: Distribution of first arrival times of newly tagged (red bars) and returning (grey bars) acoustic-tagged twaite shad at weir S2 during April and May across the three study years. Mean daily water temperatures are displayed as a red line.

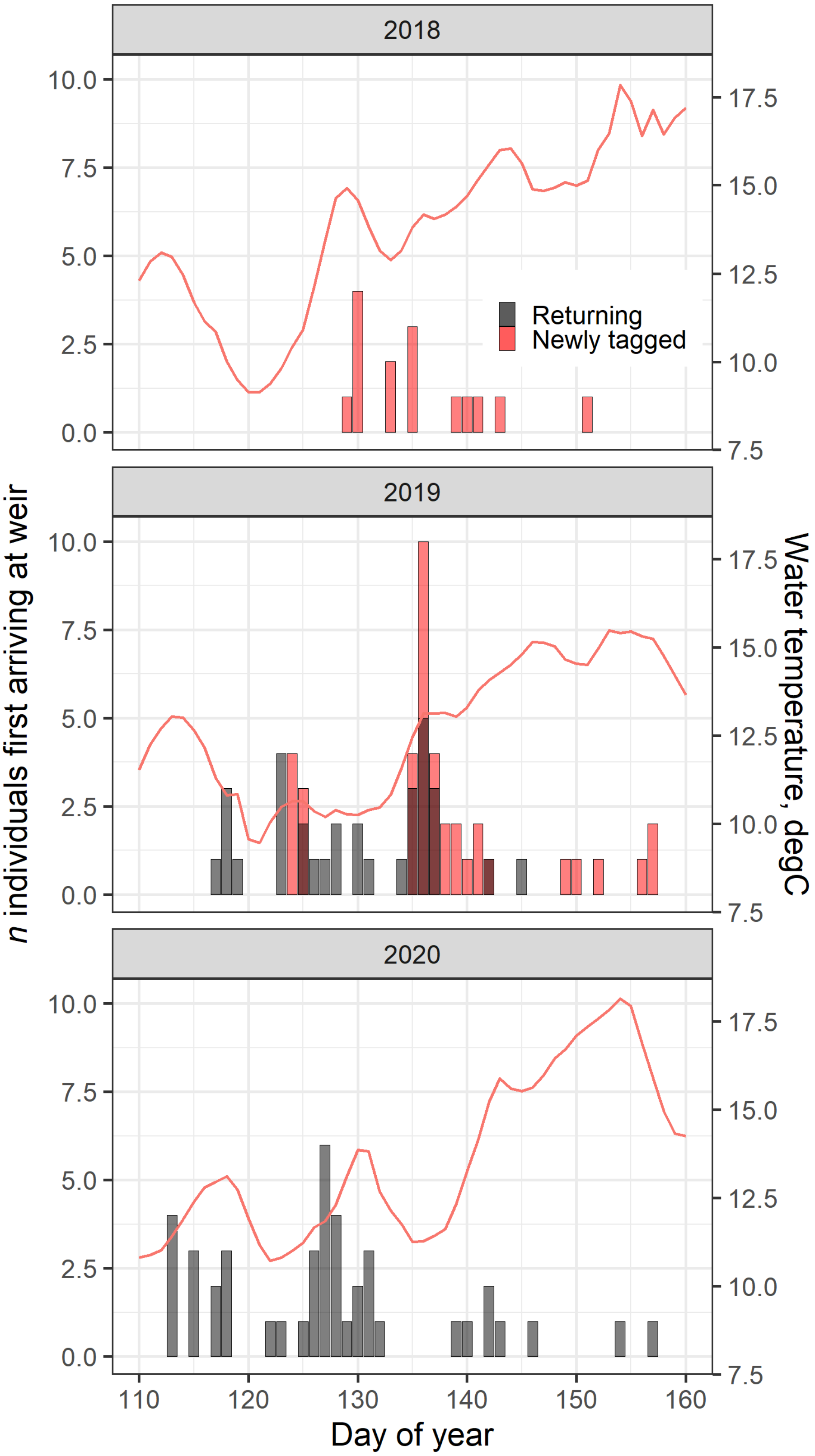


Figure 6: Kaplan-Meir depletion curves for passage of weir S2 by acoustic-tagged twaite shad. A: The effect of tagging status (newly-tagged versus returning) on passage rates. B: The effect of previous success on passage rates by returning individuals. Curves represent % of shad that are yet to pass the weir at each time point. Covariates effects presented are from individual covariates shown to have a significant effect on passage rates in the top ranked mixed-effects Cox model

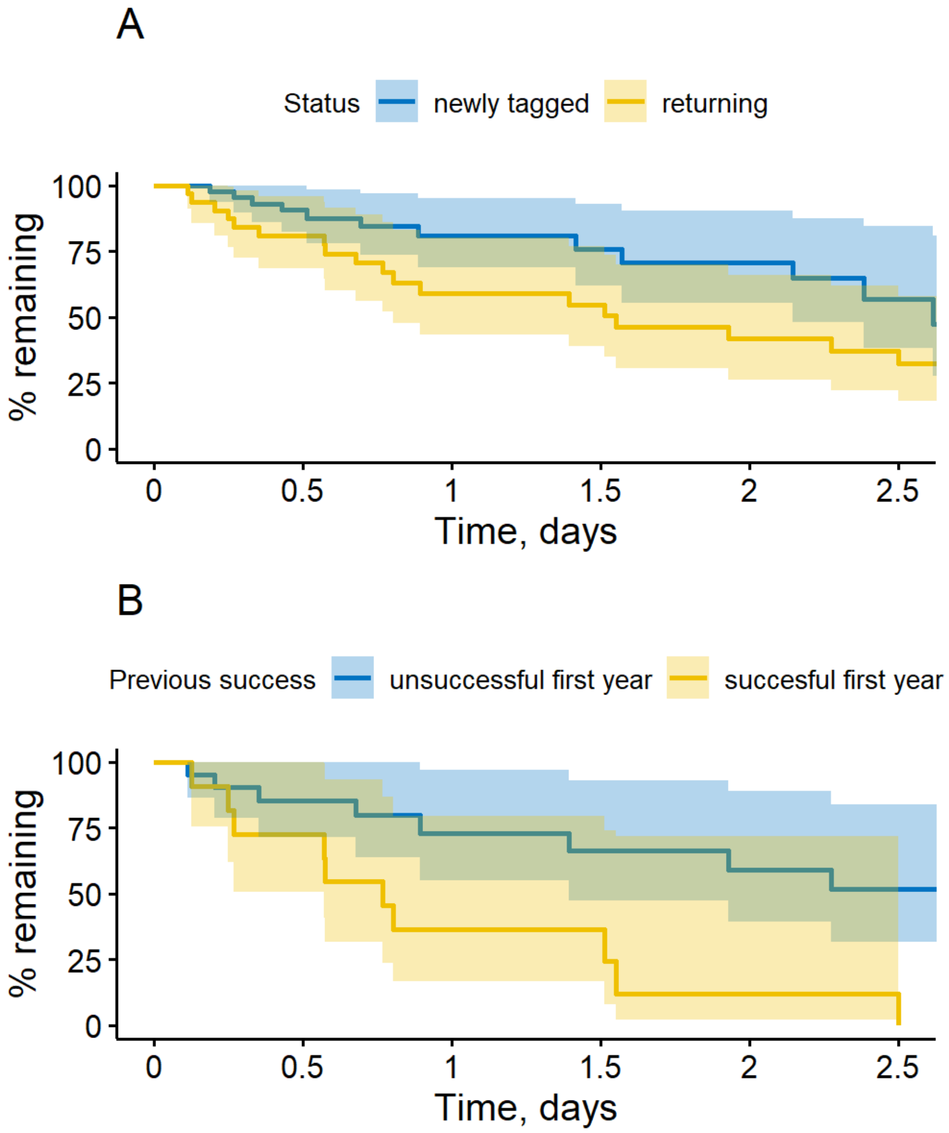


Figure 7: Kaplan-Meir depletion curves for passage of weir S2 by acoustic-tagged twaite shad. A: The effect of river level recorded on passage rates. B: The effect of temperature on passage rates. C: The effect of diel period on passage rates. For continuous covariates, survival distributions are displayed for representative data categories (Goerig et al. 2020). Curves represent % of shad that are yet to pass the weir at each time point. Covariates effects presented are environmental covariates shown to have a significant effect on passage rates in the top ranked mixed-effects Cox models.

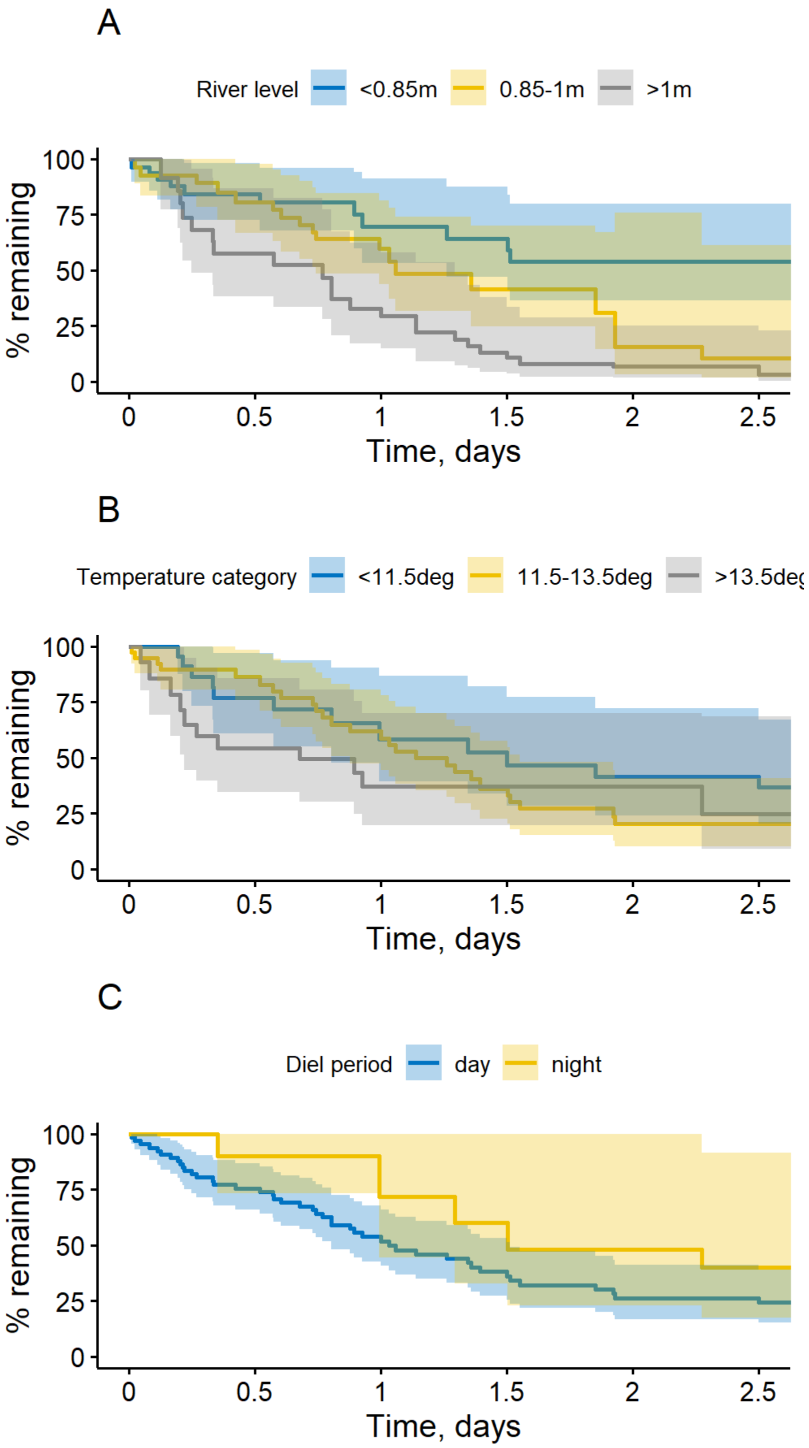


Table S1: Full set of fitted models to test the effect of individual covariates on the likelihood of weir approach by acoustic tagged twaite shad. a) generalised linear mixed models tested on Dataset 1 containing newly tagged and returning fish. b) generalised linear models tested on dataset 2 containing returning fish only

Model structure	**df**	**logLikelihood**	**AICc**	**delta**	**weight**
(a)					
length + weir	4	-66.01	140.32	0.00	0.26
weir	3	-67.16	140.49	0.18	0.24
length + previous spawning + weir	5	-65.44	141.32	1.00	0.16
length + tagging status	5	-65.96	142.35	2.03	0.09
previous spawning + weir	4	-67.13	142.55	2.23	0.08
tagging status + weir	4	-67.14	142.57	2.25	0.08
length + previous spawning + tagging status + weir	6	-65.41	143.43	3.11	0.05
previous spawning + tagging status	5	-67.03	144.50	4.18	0.03
null	2	-74.19	152.47	12.15	0.00
previous spawning	3	-73.80	153.77	13.45	0.00
length	3	-73.99	154.15	13.83	0.00
length + previous spawning	4	-72.99	154.28	13.96	0.00
tagging status	3	-74.15	154.47	14.15	0.00
previous spawning + tagging status	4	-73.31	154.91	14.60	0.00
length + previous spawning + tagging status	5	-72.57	155.59	15.27	0.00
length + tagging status	4	-73.98	156.25	15.94	0.00
(b)					
previous approach	2	-20.23	44.84	0.00	0.37
null	1	-22.07	46.27	1.43	0.18
previous approach + length	3	-19.96	46.72	1.88	0.14
previous approach + previous spawning	3	-20.21	47.23	2.39	0.11
previous spawning	2	-21.94	48.27	3.43	0.07
length	2	-22.05	48.48	3.64	0.06
length + previous spawning + previous approach	4	-19.89	49.16	4.32	0.04

Table S2: Full set of fitted mixed effects cox models to test the effect of individual covariates on the likelihood of weir approach by acoustic tagged twaite shad. Models tested on Dataset 1 containing newly tagged and returning fish

Model structure	df	logLikelihood	AICc	delta	weight
river level+diel period+tagging status+water temp	22	-83.61290907	212.2532986	0	0.266968684
river level+diel period+tagging status+previous spawning+water temp	21	-84.59140054	213.0651176	0.811818982	0.17790005
river level+diel period+tagging status	20	-85.81121241	213.1839146	0.930615966	0.167640764
river level+diel period+tagging status+previous spawning	20	-86.06475868	214.1504414	1.897142762	0.103395349
river level+tagging status	21	-85.88429207	214.8555319	2.602233292	0.072676255
river level+tagging status+water temp	23	-84.08405114	214.8695454	2.616246761	0.072168812
river level+tagging status+previous spawning+water temp	22	-85.49048615	215.7078453	3.454546688	0.047458613
river level+tagging status+previous spawning	21	-86.48190345	215.7813683	3.528069663	0.045745642
river level+diel period	22	-86.25133497	217.8538496	5.600550916	0.016229911
river level+diel period+previous spawning	22	-86.69122609	218.7555916	6.502292992	0.010339638
river level	22	-86.74678687	219.5535213	7.300222653	0.006938045
river level+previous spawning	22	-87.48664974	220.4380142	8.184715563	0.004458327
river level+diel period+water temp	24	-85.84435049	220.9273547	8.674056016	0.003490704
river level+diel period+previous spawning+water temp	24	-86.41763059	221.8355634	9.582264764	0.002216654
river level+water temp	24	-86.41534184	222.737542	10.48424336	0.001412004
river level+previous spawning+water temp	24	-87.17995094	223.6109595	11.35766086	0.00091238
diel period+tagging status	17	-98.61073795	232.7571766	20.50387799	9.42106E-06
diel period	14	-102.2128379	233.5693097	21.31601104	6.27693E-06
diel period+tagging status+previous spawning	18	-98.87230191	233.8301944	21.5768958	5.50931E-06
tagging status	20	-96.217941	234.270275	22.01697638	4.42114E-06
diel period+tagging status+water temp	19	-97.86590864	234.47871	22.22541138	3.98358E-06
diel period+previous spawning	15	-102.2221336	234.8673578	22.61405917	3.28004E-06
diel period+water temp	15	-101.7225749	235.0496655	22.79636683	2.99428E-06

tagging status+previous spawning	21	-96.55574465	235.2308173	22.9775187	2.73499E-06
diel period+tagging status+previous spawning+water temp	19	-98.23037557	235.505056	23.25175736	2.38454E-06
diel period+previous spawning+water temp	16	-101.8284124	236.3242035	24.07090488	1.58318E-06
tagging status+water temp	22	-95.71424525	236.3939584	24.14065975	1.52891E-06
	18	-99.72427544	236.6029794	24.34968074	1.37719E-06
tagging status+previous spawning+water temp	22	-96.1797351	237.3506492	25.09735053	9.47632E-07
previous spawning	18	-99.83478114	237.6549268	25.40162815	8.13892E-07
water temp	19	-99.46302332	238.3558187	26.10252008	5.73284E-07
previous spawning+water temp	19	-99.69224652	239.4134004	27.1601018	3.37846E-07

Table S3: Full set of fitted mixed effects cox models to test the effect of individual covariates on the likelihood of weir approach by acoustic tagged twaite shad. Models tested on Dataset 2 containing only returning fish

Model structure	**df**	**logLikelihood**	**AICc**	**delta**	**weight**
(a)					
previous success+river level+diel period+water temp	6	-39.238	91.29906	0	0.178354
previous success+river level+water temp	5	-40.085	91.7947	0.495641	0.139206
previous success+river level+diel period+body length_mm+water temp	7	-38.721	92.73467	1.435612	0.087005
river level+diel period+water temp	4	-41.9064	92.88729	1.588223	0.080613
previous success+river level+diel period+previous spawning+water temp	7	-39.1865	93.22619	1.927129	0.068048
previous success+river level+body length_mm+water temp	6	-39.9006	93.34491	2.045848	0.064126
previous success+river level+diel period+body length_mm+previous spawning+water temp	7	-39.6839	93.59703	2.297966	0.056531
previous success+river level+previous spawning+water temp	6	-40.0868	93.64399	2.344928	0.055219
river level+diel period+previous spawning+water temp	5	-42.0034	94.61727	3.318206	0.033943
river level+diel period+body length_mm+water temp	5	-41.752	94.65002	3.350954	0.033391
previous success+river level+body length_mm+previous spawning+water temp	6	-40.3589	94.66035	3.361286	0.033219
river level+water temp	3	-44.0928	95.34443	4.045366	0.023596
previous success+river level	2	-46.0579	96.13391	4.834849	0.0159
river level+diel period+body length_mm+previous spawning+water temp	6	-41.6803	96.22336	4.924298	0.015205
previous success+river level+diel period	3	-45.299	96.61729	5.318225	0.012487
river level+previous spawning+water temp	4	-44.2694	96.62147	5.322405	0.012461
river level+diel period	2	-46.5181	97.0555	5.756436	0.01003
river level+body length_mm+water temp	4	-44.1753	97.16804	5.868982	0.009481
previous success+river level+body length_mm	3	-45.6323	97.28294	5.98388	0.008952
previous success+river level+diel period+body length_mm	4	-44.7156	97.45103	6.151969	0.00823

previous success+river level+previous spawning	3	-45.7225	97.46345	6.16439	0.008179
previous success+river level+diel period+previous spawning	4	-44.8826	97.78527	6.486206	0.006963
river level	1	-48.0987	98.21612	6.917058	0.005614
river level+body length_mm+previous spawning+water temp	5	-44.2693	98.62252	7.323453	0.004582
river level+diel period+body length_mm	3	-46.4805	98.98032	7.681253	0.003831
river level+diel period+previous spawning	3	-46.5045	99.02816	7.729092	0.003741
previous success+river level+body length_mm+previous spawning	4	-45.5476	99.11474	7.81568	0.003582
previous success+river level+diel period+body length_mm+previous spawning	5	-44.6245	99.27048	7.971414	0.003314
river level+body length_mm	2	-48.0542	100.1266	8.827498	0.00216
river level+previous spawning	2	-48.0653	100.1486	8.849547	0.002136
river level+diel period+body length_mm+previous spawning	4	-46.4805	100.9813	9.682215	0.001409
previous success	1	-49.916	101.8504	10.55131	0.000912
previous success+body length_mm+water temp	15	-35.5362	102.0835	10.78444	0.000812
river level+body length_mm+previous spawning	3	-48.0505	102.1198	10.82069	0.000797
previous success+water temp	13	-37.8711	102.1911	10.89203	0.000769
previous success+previous spawning+water temp	15	-35.4089	102.4164	11.11731	0.000687
previous success+body length_mm+previous spawning+water temp	16	-34.4903	102.4496	11.15059	0.000676
previous success+diel period+body length_mm+water temp	16	-34.4497	102.9112	11.61215	0.000537
previous success+diel period+body length_mm+previous spawning+water temp	18	-33.4394	103.1685	11.86942	0.000472
previous success+diel period+previous spawning+water temp	17	-34.501	103.4147	12.1156	0.000417
previous success+diel period	2	-49.7191	103.4574	12.1583	0.000408
previous success+diel period+water temp	14	-37.1871	103.4879	12.18886	0.000402
previous success+previous spawning	2	-49.7716	103.5615	12.26247	0.000388
previous success+body length_mm	2	-49.7765	103.5711	12.27204	0.000386
previous success+diel period+previous spawning	3	-49.5568	105.1334	13.83429	0.000177

previous success+diel period+body length_mm	3	-49.5578	105.1351	13.83605	0.000177
previous success+body length_mm+previous spawning	3	-49.7434	105.5059	14.20686	0.000147
previous success+diel period+body length_mm+previous spawning	4	-49.523	107.0669	15.76782	6.72E-05
diel period	1	-52.6919	107.7337	16.43466	4.81E-05
water temp	18	-36.1652	108.6686	17.36955	3.02E-05
diel period+body length_mm	2	-52.6459	109.3111	18.01204	2.19E-05
diel period+previous spawning	2	-52.7192	109.4576	18.15859	2.03E-05
previous spawning+water temp	18	-36.644	109.7201	18.42099	1.78E-05
body length_mm+water temp	17	-36.8644	109.7697	18.47066	1.74E-05
body length_mm	2	-52.3039	109.8674	18.56838	1.66E-05
diel period+water temp	17	-37.0626	109.9152	18.61618	1.62E-05
previous spawning	2	-52.3281	110.3218	19.02273	1.32E-05
body length_mm+previous spawning+water temp	18	-36.6201	110.395	19.09596	1.27E-05
diel period+body length_mm+water temp	18	-37.2065	110.8036	19.50455	1.04E-05
diel period+previous spawning+water temp	18	-37.3698	110.9015	19.60239	9.88E-06
	5	-50.475	111.2076	19.90851	8.48E-06
diel period+body length_mm+previous spawning	3	-52.6455	111.311	20.01196	8.05E-06
diel period+body length_mm+previous spawning+water temp	18	-37.4189	111.7511	20.45204	6.46E-06
body length_mm+previous spawning	4	-51.8867	112.3027	21.0036	4.90E-06

Figure Supplementary 1

(A) Length and weight of acoustic tagged twaite shad *Alosa fallax; (*B) Relationship of body weight to previous spawning experience.