River barriers as a driver of elevated mortality rates in an iteroparous anadromous fish

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Abstract

Anadromous fishes are vulnerable to anthropogenic stressors, especially river fragmentation, with the conservation of iteroparous populations requiring an understanding of survival during their freshwater migrations. Here, spatial, temporal and biological drivers of mortality were determined during the spawning migrations of iteroparous anadromous twaite shad *Alosa fallax* in the highly fragmented River Severn basin, western Britain. Acoustic telemetry tracked 393 individuals over seven successive spawning migrations. Shad mortality rates in areas immediately downstream of migration barriers were more than double compared to unimpeded river sections, but the extent of excess mortality varied between individual barriers. In-river mortality differed between years for returning shad, but there were no significant temporal patterns of mortality within migrations. Newly tagged shad and returning individuals had similar survival rates, and increasing size was the only significant biological predictor of mortality, with sex and spawning history not significant. These results suggest that where migration barriers increase mortality rates, the population-stabilizing and resilience benefits of iteroparity may be reduced, so river fragmentation mitigations should focus on both improving passage and reducing hazard exposure.

Keywords: twaite shad, *Alosa fallax*, fish passage, predation, survival, life-history

Introduction

Freshwater ecosystems support a rich diversity of species but also face disproportionately high rates of population collapse and extinction (Reid et al. 2019; Tickner et al. 2020). Declines are particularly pronounced in species and populations reliant on long-distance movement and migration as part of their life strategies, such as diadromous fishes (Deinet et al. 2024). These species are particularly vulnerable to the impacts arising from river fragmentation due to constructed anthropogenic barriers (e.g. dams and weirs, hereafter “barriers”) that inhibit their upstream and downstream movements (Katano et al. 2006; Waldman and Quinn 2022). While mitigation measures can improve passage by modifying the barrier or constructing artificial fishways (also “fish pass”, “fish ladder”) (Katopodis and Williams 2012; Błońska et al. 2025), barriers often continue to impose energetic and fitness costs on fish through delays and passage attempts (Rubenstein et al. 2023; Silva et al. 2018; Thiem et al. 2016). Proximity to river barriers and fishways can also increase vulnerability to other drivers of mortality such as injury and predation facilitated by migration bottlenecks (Agostinho et al. 2012; Bell and Kynard 1985; Garcia de Leaniz 2008).

Diadromous fishes can express iteroparity, where the reproductive effort is spread over multiple reproductive cycles at the risk of death before reaching full lifetime fecundity, or semelparity, where individuals only reproduce once, investing all reproductive output in a single spawning season before the end of life (Hughes 2017). Where both strategies co-occur within a species or population of fish (Birnie-Gauvin et al. 2023), the degree of expression is often selected for by extrinsic factors. Semelparity may result from high adult mortality and is often concurrent with high juvenile survival, whereas iteroparity is characterized by high year-to-year adult survival but variable recruitment success (Christiansen et al. 2008; Crespi and Teo 2002; Murphy 1968). In iteroparous anadromous populations, mature adults may die while in freshwater for spawning, during either their upstream or downstream migration (Kraabøl et al. 2009; Yeldham et al. 2024). Influences on the survival of iteroparous anadromous fishes in freshwater can thus adversely affect both the current and future spawning stock, reducing the population stabilizing benefits provided by iteroparous individuals (Murphy 1968; Narum et al. 2008) and their conserved ability to navigate past barriers (Davies et al. 2023). Further, selection towards first-time spawners can adversely influence genetic population structure and viability (Birnie-Gauvin et al. 2023).

The management and conservation of iteroparous anadromous fish populations thus requires an understanding of the drivers of in-river mortality of spawning adults, especially how this mortality is affected by anthropogenic impacts, including barrier-driven fragmentation (Kraabøl et al. 2009). Studies on the impacts of riverine barriers on iteroparity in anadromous fishes have tended to focus on salmonids, particularly on delays and passage mortality of emigrating post-spawned individuals ("kelts") at hydropower dams (e.g. Baktoft et al. 2020; Simmons et al. 2024; Wertheimer and Evans 2005). However, Castro-Santos and Letcher (2010) applied a bioenergetics-based modelling approach to associate longer upstream migration distances of American shad *Alosa sapidissima* with their ability to pass dams resulting in higher subsequent reproductive success, but at the cost of reduced iteroparity due to energetic depletion and with mortality exacerbated by barrier delays. Their approach did not, however, consider drivers of mortality other than energy expenditure (Castro-Santos and Letcher 2010), such as hazards linked to the barrier itself or the proximity to it. While hydropower dams, similar to those investigated by Castro-Santos and Letcher (2010), may contribute to fish mortality through entrainment and impingement (Algera et al. 2020), they make up only 10% of river barriers in Europe. By contrast, 31% of river barriers in Europe are over-crest flow weirs (Belletti et al. 2020; Jones et al. 2021), and the mechanisms which affect fish mortality at weirs differ from those at hydropower dams. Consequently, substantial knowledge gaps remain on how river barriers with over-crest flows (weirs) affect the mortality of iteroparous anadromous fishes across the entire riverine spawning migration and across several migrations.

The iteroparous anadromous twaite shad *Alosa fallax* of the Clupeidae family is distributed in the North-West Atlantic Ocean between Morocco and Iceland, plus the Mediterranean Sea (Sabatié et al. 2009). The extent of iteroparity expressed by populations increases with latitude, where in northern populations, repeat spawning individuals generally comprise most of the spawning population (Aprahamian et al. 2003). This is likely due to higher inter-annual variability in abiotic conditions at more northern latitudes impacting annual recruitment success, which results in a bet-hedging iteroparous strategy being more successful than semelparity (Hasselman et al. 2013; Legget and Carscadden 1978). River fragmentation has reduced the freshwater habitat available to twaite shad (van Puijenbroek et al. 2019), and the species has been assessed against the categories and criteria of the International Union for Conservation of Nature (IUCN) Red List as Vulnerable in Britain and Wales and Endangered in England (Nunn et al. 2023). Even where river barriers are semi-permeable to shad – either due to environmental conditions (e.g. elevated river level) or mitigation measures (e.g. fishways) – artificial selection pressures will be exerted as only a proportion of the population pass, and substantial passage delays may be incurred in successful individuals (Belo et al. 2021; Davies et al. 2023). The effects of such barriers on shad mortality rates have, however, not been assessed. Consequently, the aim here was to identify patterns of mortality during the freshwater spawning migration of iteroparous anadromous twaite shad in the highly fragmented River Severn catchment in western Britain using data from 393 acoustic-tagged individuals collected over seven successive spawning migrations. Objectives were to determine spatial, temporal and biological drivers of mortality that, when considered in future management and conservation efforts, may help to improve the viability of iteroparous anadromous fish populations.

Materials and Methods

Study area and period

Twaite shad spawning migration data were collected for seven successive spawning seasons between 2018 and 2024 using acoustic telemetry in the lower River Severn basin, western Britain, and its two major tributaries River Teme and River Avon (Figure 1). The spawning migration period of twaite shad in the basin typically spanned from late April to early July. The rivers Severn and Avon are slow-flowing lowland rivers maintained for navigation by weirs with Q50 flows of 68.5 and 10.1 m^3/s, respectively, whereas the River Teme is of pool-riffle type with a steeper gradient and a Q50 flow of 10.0 m^3/s. While parts of data collection spanned reaches further upstream on the Severn and Teme, the focus here was on a core study area consisting of the lower 52 km of the Severn mainstem between the city of Worcester and the estuary, as well as the lower 7 and 3 km of the Teme and Avon tributaries respectively (Figure 1). This area was fragmented by seven barriers that obstructed fish movements, three of which have been modified to improve fish passage (Błońska et al. 2025; Yeldham et al. 2025a). The first barriers encountered by fish migrating upstream from the Severn estuary were Maisemore (S1a) and Llanthony (S1b) weirs that are located on two branches of a split-channel (Figure 1), and that usually pose the limit of tidal influence but are flooded out during high spring tides, and have not been modified for fish passage

(Yeldham et al. 2025b). The next upstream barriers on the Severn mainstem are Upper Lode Weir (S2), which has a Denil-type baffle fishway designed for Atlantic salmon *Salmo salar*, as well as a notch in the weir face to ease fish passage (both installed prior to this study), and Diglis Weir (S3), which has a vertical slot fishway which opened prior to the shad spawning migration in 2021. The River Avon (A1a) and its Mill Avon distributary (A1b) are regulated by two weirs without mitigation measures for non-anguilliform fishes, blocking access to this river for shad 0.8 km and 1.3 km from the confluence with the Severn, respectively. The most downstream barrier on the River Teme is Powick Weir (T1), 3.1 km from its confluence with the Severn, which underwent remediation by lowering and rock ramp infilling in 2018/19.

Shad capture, tagging and release

Shad were captured at Maisemore (S1a) and/or Upper Lode (S2) weirs in all study years (2018 to 2024), except in 2020 when Covid-19 pandemic restrictions prohibited fieldwork. Capture was facilitated by either a manually operated trap located just upstream of the notch in Upper Lode Weir (S2) (*n* = 281) or by angling in weir pools (*n* = 112) (Table 1). Immediately after capture, shad were anesthetized (ethyl 3-aminobenzoate methanesulfonate; MS-222; 0.4 g/L), weighed (nearest 5 g), measured (fork length, nearest mm), and approximately 3 to 5 scales taken from between the dorsal fin and the lateral line (Baglinière et al. 2001). Each shad was then tagged intraperitoneally with a 69 kHz acoustic transmitter using a surgical ventro-lateral incision (~ 20 mm) anterior to the muscle bed of the pelvic fin that was closed with a single suture, following the protocol of Bolland et al. (2019). Of the 393 acoustic transmitters, 382 were 9.0 mm in diameter, either 27.5 or 31.0 mm in length, and weighed 4.5 or 4.9 g respectively (V9-2x, V9TP-2x, Innovasea, NS, Canada). The remaining 11 acoustic transmitters were 8.0 x 20.5 mm and weighed 2.0 g (V8-4x, Innovasea). All shad were also tagged with a 23 x 3.85 mm, 0.6 g PIT tag (HDX, Stream-Innov, France) using the same incision and 11 shad in 2024 further received a 12.7 x 5.7 mm, 0.7 g 180 kHz transmitter for an unrelated pilot study (V5-2x, Innovasea). Tag burden never surpassed 2% body weight in air (Jepsen et al. 2015) and surgery lasted approximately 60-80 seconds. Sex was recorded only when gametes became visible during surgery. There was no selection among captured fish for tagging except for the rejection of < 1% of individuals that displayed fresh injuries from predation attempts.

Following the conclusion of surgery, shad were recovered in the river while being held facing upstream until the return of body equilibrium and normal swimming behavior. All tagged fish were released upstream of the barrier they were captured at, except for 18 fish released downstream of Upper Lode Weir (S2) in 2018 for the purposes of a separate study (Table 1) (Davies et al. 2023). All procedures were conducted with ethics approval under UK Home Office project licenses PPL 60/4400, PD6C17B56, and PP9326830 under the Animals (Scientific Procedures) Act (1986). The majority (*n* = 332) of the acoustic transmitters were programmed to enable three spawning migrations (tagging year and two returns) to be tracked (Table 1). Exceptions were 11 shad in 2018 and 50 shad in 2023 where battery life enabled one and two spawning migrations to be tracked, respectively (Table 1).

Acoustic telemetry array

Receivers were cable-tied to steel fencing pins driven into the riverbed or fixed to permanent structures in the river. Receivers were strategically located in relation to shad migration and for hydrological conditions to enable successful transmitter detection (Davies et al. 2023); detection efficiencies were checked in the *actel* R package (Flávio and Baktoft 2021) for each receiver and year (median = 99%, 10th percentile = 90%, 5th percentile = 78%). For each shad spawning season, an array of 31 to 37 acoustic receivers (VR2-W and VR2-Tx, 69 kHz, Innovasea) were deployed throughout the core study area. Receivers were continuously and consistently deployed downstream and upstream of each weir between years, except for 2019, when the receiver deployed upstream of Upper Lode Weir (S2) was only in place until 30/05/2019, as it was then lost in a major flood. Receivers were also deployed at regular intervals throughout the unimpeded river sections between weirs, albeit with variations in the exact number between years due to resourcing and receiver availability.

The most downstream receiver was placed in the Severn estuary, approximately 6 km downstream from the most downstream weir (S1b) and the tidal limit (Yeldham et al. 2023) (Figure 1). The most upstream core study area receiver on the River Severn was located immediately upstream of Diglis Weir (S3) in 2018 and 2019 (before the weir was mitigated for fish passage), and an additional receiver 1.5 km upstream of it constituted the most upstream receiver in all other years. The receiver upstream of the two weirs (A1a, A1b) on the double-channeled confluence of the River Avon with the River Severn confirmed their impassability, blocking off this tributary for shad (Figure 1). The most upstream core study area receiver on the River Teme was on an unimpeded river section 4.2 km upstream of T1. Receivers were deployed upstream of the core study area in the rivers Severn and Teme in some years, however they varied in their number, distribution, and consistency and only generated < 1% of total shad detections.

Data processing

During analyses, a tagged shad was considered to have emigrated back to the marine environment when its final detection was on the most downstream receiver in the estuary (Davies et al. 2023) (Figure 1). A tagged shad that was detected in the river, but whose final detection was at a receiver upstream of this estuary receiver, was considered dead, except for *n* = 2 individuals that returned to the river the next year despite being missed by the estuary receiver during emigration. A dead fish was classed as dead at the time of arrival at the last receiver station it was detected on, i.e. at the time of its last recorded movement. Shad detected in the River Severn in a subsequent year were classed as a “returning” fish, whereas shad in their tagging year were classed as “newly tagged”.

To assign the time spent in river to the respective areas of residence, each shad was associated with a receiver station until movement was confirmed by detection at another station, with this positioning completed in the *actel* R package. Tag detections recorded after 1st August were discarded as all tags detected after this time were stationary; there is no evidence of live adult shad remaining in the river after this point in the year (Yeldham et al. 2024). Following criteria similar to those of Raabe and Hightower (2014), we included tagging-year data only from shad that made an upstream movement past their release location, thereby ensuring that data collection was based on individuals tagged during their upstream migration. Distances between receivers and to the estuary were calculated as the lengths of river centerline between the points on the line closest to the deployed receivers. GIS shapefiles for the centerlines were taken from Environment Agency (2024) and completed manually with satellite image overlay where necessary. All data processing was conducted in R (R Core Team 2025). Where error is provided around mean values it represents standard error unless stated otherwise. All model residuals were examined using the *DHARMa* R package (Hartig 2024).

Temporal and biological patterns of mortality

Testing for patterns of mortality related to temporal and biological factors was completed using survival analysis in the *survival* and *survminer* R packages (Kassambara et al. 2016, Therneau 2015). Time-to-event was defined as the interval (days) between tagging or return and either death (event) or emigration (censoring) for the respective groups of newly tagged and returning shad. In cases where individuals temporarily dropped out from the study area to the estuary within a migration season, they were censored from the risk set until their return to fresh water. Survival analyses were performed throughout the entire receiver array deployed in each year, including those upstream of the core study area in some years (Figure 1), to determine the time of death with the best possible accuracy.

Temporal variations in mortality: between- and within-year differences

To assess whether mortality rates differed between years and if mortality rates were uniform throughout a spawning migration, newly tagged and returning shad were analyzed separately, as newly tagged fish had already spent time in fresh water when tagged. Data for a year and group (newly tagged, returning) were included when the sample included at least 10 fish. The analysis included data from 357 newly tagged shad over 6 years with 118 mortalities and 147 return migrations from 118 individuals over 5 years with 58 mortalities. Survival was compared between years using Cox proportional hazard models for both newly tagged and returning shad. Where significant differences in survival between years were detected, post-hoc Tukey's pairwise comparison was conducted to identify differing pairs of years. Kaplan-Meier survival estimates were then generated for each year and group (newly tagged, returning). The mortality m_t for every time step t (day post tagging, return) was calculated as $m_t = \frac{D_t}{R_t}$, where D_t was the number of shad that died during the time step and R_t was the number of shad in the risk set at the beginning of that time step. Time steps with risk sets of $R_t < 4$ fish were excluded to minimize overdispersion at the tail end of the data. Generalized linear mixed-effects models (GLMMs, glmmTMB R package (Brooks et al. 2017)) then examined the relationship between daily mortality m_t and time (days post tagging, return) for each group. The models included the year as a random effect to account for variability in sampling between years and assumed the daily mortality rates to follow Tweedie distributions:

$$m_t \sim t + (1|year)$$

For returning fish, mortality was modeled as a linear function of time. For newly tagged fish, although the mean mortality was also modeled linearly, the variance of mortality increased over time, requiring the dispersion parameter to vary with time. This was implemented in the GLMM using a dispersion formula.

Biological variations in mortality: effects of spawning history, size, sex, and tagging

Among newly tagged shad, survival was compared between virgin (*n* = 115) and previous (*n* = 227) spawners, based on the absence or presence of spawning marks on scale samples (Baglinière et al. 2001, Yeldham et al. 2025a). A Cox proportional hazards model assessed survival in relation to spawning history (virgin, previous spawner) and body length, with year included as a stratification factor. Similarly, survival was tested against sex and length for 107 female and 119 male shad while stratifying for five tagging years. Spawning history and sex were tested in separate models to maximize sample size in the former; a combined model would have excluded 121 fish that could not be sexed.

To assess potential differences in survival between newly tagged and returning shad, a further Cox proportional hazard model was built. Here, shad migrations were only included from the time a fish was first located upstream of Upper Lode Weir (S2) to allow for comparability between the two groups of fish. Specifically, newly tagged fish were included if they were released upstream of S2, newly tagged fish released downstream of S2 and upstream of S1a as well as returning fish were included from the time they passed S2. The analysis included data from 309 newly tagged shad and 102 return migrations by 87 individual shad, with 5 out of 7 years used in the model including data for both groups. Survival was compared between groups (newly tagged, returning) in a Cox proportional hazards model while controlling for year by a stratification term.

Spatial patterns of mortality

Shad mortality in the proximity of weirs and in unimpeded river sections

To investigate the effect of proximity to weirs on shad mortality, receiver stations in the core study area were categorized into three types based on their location; “DS Weir” or “US Weir” if they were the first receiver downstream or upstream of a weir, respectively, and all others were “unimpeded”. For each year y and receiver station s, the sum of time associated with the receiver station $T_{y,s}$ was calculated for each group (newly tagged, returning shad). $M_{y,s}$ was the number of shad classified as dead at a receiver station in a year. $T_{y,s}$ and $M_{y,s}$ associated with receivers upstream of the core study area and the four receivers located at the edge of the core study area array were not calculated, as these could potentially have been attributed with time and mortalities that occurred far away from the actual receiver station. GLMMs with negative binomial distributions were used to assess the influence of time spent at a receiver station (hours, scaled) and its type (DS Weir, US Weir, unimpeded) on observed mortalities (*n* = 169). The models assumed a quadratic variance-mean relationship. Year was included as a random effect to account for variability in tagging and receiver array layout between years. Incident rate ratios (IRRs) and 95% confidence intervals were calculated from effect sizes and SEs. The model structure was:

$$M_{y,s} \sim T_{y,s,\,scaled} + Type + (1|year)$$

To identify receiver stations that contribute to shad mortalities disproportionately, an index of excess mortality $\Delta M_{y,s}$ was calculated as:

$$\Delta M_{y,s} = \ (M_{obs,y,s} - \ M_{exp,y,s}) \times \frac{1}{n_y} \times 100.$$

Here, $M_{obs,y,s}$ were the observed mortalities at a receiver station in a year and $M_{exp,y,s}$ were the expected mortalities based on the total number of observed mortalities in that year multiplied by the fraction of time spent at the station by the respective group (all newly tagged, all returning shad), assuming equal rates of mortality across all stations. $\Delta M_{y,s}$ is expressed as a percentage of the sample n_y in a year. For each group, the mean and standard deviation (SD) of $\Delta M_{y,s}$ were calculated across years where the number of total observed mortalities for the sample was greater than 4.

The direction (upstream, downstream) of the last movement before being classified as dead was inspected for different receiver station types (DS Weir, US Weir, unimpeded) to, in part, rule out systematic downstream drift post death (Havn et al. 2017).

Effects of catchment penetration and river characteristic on mortality

To assess the effect of catchment penetration on mortality, the observed mortalities of newly tagged and returning shad were tested against distance to the estuary for receiver stations along the unimpeded river sections. GLMMs (negative binomial distribution with quadratic variance–mean relationship) were used that included time spent at a station (scaled) and distance to the estuary (scaled) as fixed effects as well as year as a random effect:

$$M_{y,s} \sim T_{y,s,scaled} + estuary\ distance_{scaled} + (1|year)$$

Given the different characteristics of the main River Severn (slow-flowing lowland river) and the River Teme (pool-riffle dominated tributary), the mortalities were also compared between the two rivers for unimpeded receiver stations while controlling for time spent (scaled) (GLMM, negative binomial distribution):

$$M_{y,s} \sim T_{y,s,scaled} + river$$

Biological influences on the spatial distribution of mortality

To explore biological influences on the spatial distribution of mortality, shad length, sex, and spawning history were compared between fish that died at the different receiver station types (DS Weir, US Weir, unimpeded). A linear mixed-effects model (LMM) assessed the lengths of dead newly tagged shad in dependence on the receiver station types (n = 112). Year was included as a random effect to account for potential interannual differences in sampling, river conditions, and receiver array layout. Lengths of fish that died at receiver station types were then compared to each other using pairwise comparisons in the *emmeans* R package (Lenth et al. 2021). Fisher's exact tests (FET) with Monte Carlo simulation were used to investigate whether sex distributions of all sexed shad that died in tagging and return years (*n* = 120) and spawning history of fish that died in their tagging year (*n* = 108) differed between receiver station types.

Results

Temporal and biological patterns of mortality

Among 357 newly tagged shad included in the analysis, 118 (33%) died in the river and 239 (67%) emigrated back to the estuary. Of the 147 shad returning in subsequent years, 58 (39%) died in the river and 89 (61%) emigrated. Time to emigration was 23.0 ± 12.1 days (mean ± SD) for newly tagged and 31.8 ± 10.6 days for returning shad. Between-year differences in the survival of newly tagged shad were not significant (Cox proportional hazards model: Likelihood ratio test: χ^2 (5) = 7.38, $p = 0.20$; Figure 2). For returning fish, survival differed significantly between years (Likelihood ratio test: χ^2 (4) = 38.03, $p < 0.001$), with significantly lower survival in 2023 versus 2019 (HR = 3.70, 95% CI: 1.60–8.59, $p = 0.017$), 2020 (HR = 3.02, 95% CI: 1.42–6.42, $p = 0.029$), and 2021 (HR = 12.28, 95% CI: 2.63–57.36, $p = 0.011$), and significantly lower survival in 2024 versus 2019 (HR = 6.58, 95% CI: 2.87–15.11, $p < 0.001$), 2020 (HR = 5.37, 95% CI: 2.55–11.31, $p < 0.001$), and 2021 (HR = 21.82, 95% CI: 4.70–101.31, $p < 0.001$) (Figure 2). Daily mortality rates in the river did not show significant temporal trends for either newly tagged (GLMM; intercept = –4.29, $\beta \pm \mathrm{SE} = 0.01 \pm 0.01$, $p = 0.365$) or returning shad (GLMM; intercept = –4.46, $\beta \pm \mathrm{SE} = 0.01 \pm 0.01$, $p = 0.467$) (Figure 2). However, for newly tagged shad, model diagnostics indicated that the variance in mortality increased with time (dispersion slope = 0.06 ± 0.01, $p < 0.001$).

The Cox proportional hazards model for survival relating to spawning history and body length was significant (Likelihood ratio test: χ^2 (2) = 15.96, $p < 0.001$), where mortality significantly increased with increasing length (HR = 1.01, 95% CI: 1.00–1.01, $p = 0.002$), but not if a fish was a virgin spawner (HR = 0.70, 95% CI: 0.45–1.11, $p = 0.130$). Although the model assessing influences of sex on survival after controlling for length was significant (Likelihood ratio test: χ^2 (2) = 11.86, $p = 0.003$), shad length was significantly and positively associated with mortality (HR = 1.01, 95% CI: 1.00–1.02, $p = 0.001$), but sex was not (male versus female; HR = 1.46, 95% CI: 0.77–2.78, $p = 0.251$). Survival did not differ significantly between returning versus newly tagged shad (Likelihood ratio test: χ^2 (1) = 0.32, $p = 0.60$; HR = 1.15, 95% CI = 0.72–1.81, $p = 0.566$).

Spatial patterns of mortality

A total of 169 shad were considered to have died in the core study area, 62 of which near river barriers (51 downstream and 11 upstream of weirs) and 107 on unimpeded river sections (Table 2). The prevalence of mortalities in relation to the time spent by each group (newly tagged, returning shad) varied between station types with DS Weir stations displaying disproportionately high fractions of total mortality (Table 2). Of the 169 mortalities, 76 (45%) last moved downstream and 93 (55%) last moved upstream. The last movement before death was in a downstream direction for 100% of shad that died upstream of weirs ($n = 11$) compared to 92% in upstream direction of shad that died downstream of weirs (47 of $n = 51$). Of the 107 shad that died in unimpeded river sections, the last movements were in an upstream direction for 46 individuals (43%) and in a downstream direction for 61 individuals (57%).

The time spent and number of mortalities at a receiver station were positively associated in newly tagged shad (IRR = 1.97, 95% CI: 1.65–2.34, p < 0.001; Table 3), with significantly higher mortality at DS Weir stations (IRR = 2.20, 95% CI: 1.32–3.67, p = 0.003) but not at US Weir stations (IRR = 0.93, 95% CI: 0.46–1.91, p = 0.847) when compared to unimpeded stations (Table 3). Similarly, the number of returning shad that died also increased significantly with time spent at a station (IRR = 1.41, 95% CI: 1.12–1.77, p = 0.003), and mortality at DS Weir stations was significantly higher than at unimpeded stations (IRR = 2.09, 95% CI: 1.17–3.73, p = 0.013), but this was not the case for US Weir stations (IRR = 0.17, 95% CI: 0.02–1.30, p = 0.088) (Table 3).

For excess mortality $\Delta M_{y,s}$, the receiver stations DS Upper Lode (S2) and DS Diglis (S3) weirs ranked first and second for both newly tagged and returning shad (Figure 3). The receiver stations downstream of the tidal weirs on the River Severn (S1a, b) and the remediated Powick Weir on the River Teme (T1) had near zero excess mortality for both newly tagged and returning shad (Figure 3). US Upper Lode Weir (S2) was the only US Weir station with evidence of excess mortality and only for newly tagged shad, with all other stations upstream of weirs showing near zero excess mortality (Figure 3).

Catchment penetration was not a significant predictor of mortality in unimpeded river sections for both newly tagged (GLMM: z = -0.505, p = 0.614) and returning shad (GLMM: z = -0.531, p = 0.595). Similarly, the number of observed mortalities at receiver stations in the River Teme (pool-riffle type) did not vary from those on the River Severn (slow-flowing) after accounting for time spent (newly tagged: GLMM: z = -1.172, p = 0.241; returning: GLMM: z = 0.013, p = 0.990). The length of newly tagged fish that died did not differ significantly between the receiver station types

(LMM; Estimate ± SE: DS Weir 368 ± 7 mm, unimpeded 375 ± 8 mm, US Weir 349 ± 14 mm) (pairwise comparisons: all $p > 0.05$). There were also no differences between individuals that died at the respective receiver station types for sex (FET: $p = 0.169$) and for spawning history (FET: $p = 0.10$)

Discussion

The spatial patterns of mortality in iteroparous anadromous twaite shad during their freshwater spawning migration revealed that increased rates of mortality occurred downstream of river barriers compared to unimpeded river stretches, with the extent of excess mortality varying between barriers. Mortality rates were not, however, elevated upstream of barriers. Mortality rates differed between years for returning shad that could be tracked throughout their entire migration, but not for those newly tagged. Newly tagged shad did not experience reduced survival when compared to returning shad. Among biological predictors of mortality, length had a significant positive effect, but not sex or spawning history, and none of these predictors significantly influenced the spatial distribution of shad mortalities. Here we discuss how proximity to barriers may thus be exposing shad to site-specific hazards that should be considered during restoration measures aimed at improving passage and population viability.

In populations of iteroparous anadromous fishes, adult mortality does not only reduce the number of individuals that contribute to reproduction each year, but may also reduce the fraction of disproportionally important repeat spawning individuals among the population, suggesting that the benefits of iteroparity might be diminished (Birnie-Gauvin et al. 2023, Hixon et al. 2014, Moore et al. 2014). In river systems with barriers, previous migration experience – such as the conserved ability to pass obstacles and reach suitable spawning habitat – might further increase the importance of repeat spawning individuals (Davies et al. 2023). Where adult mortality is elevated by anthropogenic river barriers, populations of iteroparous anadromous fishes may thus be adversely affected through the frequent exposure of repeat spawning individuals to the additional hazards, resulting in their proportion among the spawning population decreasing. Despite the inflation of mortality by river barriers presented here, 66% of captured shad were repeat spawners. This estimate falls within the wide range of region- and river-specific iteroparity estimates (0 – 97.6%) reported across the range of twaite shad by Aprahamian et al. (2003), indicating high plasticity along the itero–semelparity continuum among populations. While it was not possible here to assess whether there has been a barrier-driven shift towards semelparity in this population, additive adult mortality caused by weirs could be a factor that results in more individuals expressing semelparous life-histories in highly fragmented rivers. Notwithstanding, factors that select for the expression of iteroparity in these populations, such as environmentally driven differences in larval and juvenile annual survival rates (Aprahamian et al. 2003, Legget and Cascadden 1978), will persist. If there is a consequent decline in the proportion of fish spawning across multiple years, then the population resilience to environmental changes could thus decline.

Here, mortality rates of twaite shad on average were significantly higher downstream but not upstream of barriers when compared to unimpeded sections of river for the time spent there. Furthermore, the degree of excess mortality downstream of barriers varied between barriers. None or negligible excess mortality was found downstream of the two tidal weirs (S1a and S1b) and for Powick Weir (T1) on the River Teme that had been remediated by lowering and a rock ramp for all but the first year of this study. By contrast, the receiver stations downstream of weirs S2 and S3 ranked first and second in excess mortality for both newly tagged and returning shad, despite S2 having fish passage mitigation measures throughout and S3 for the last four of seven study years. While data are insufficient to compare effects on mortality pre- and post-mitigation at S3, these findings suggest that the installed fishways did not prevent the occurrence of excess mortality. This may be associated with the low post-mitigation passage rate at S3 (7.5% compared to 3.2% before; Yeldham et al. 2025a) and the hazards associated with these barriers might be inherent to the environment they create by their presence regardless of mitigation schemes. Consideration of barrier-inherent effects and the benefits of full remediation (i.e. weir removal) compared to a focus on improved passage alone could improve management efforts aiming to benefit populations of diadromous fishes. Notwithstanding, 63% of mortality occurred along unimpeded river stretches and thus is likely tied to the freshwater environment and spawning migration itself. We found evidence that in-river mortality rates varied between years, but only for returning fish. While the seven-year dataset used for this study does not allow for conclusions on between-year influences, it is likely that there are effects of fluctuating environmental variables (Bayse et al. 2021, Raabe and Hightower 2014). Spatial factors, other than barrier influences, such as characteristics of the rivers Severn and Teme as well as distance from the estuary, did not significantly affect shad mortality rates.

Previous studies (based on some of the same data as presented here) have shown that the barriers on the River Severn impose delays of multiple days on the fraction of shad that pass them in either direction (e. g. Davies et al. 2023; Yeldham et al. 2024). Here, all mortalities upstream of barriers occurred in individuals that last displayed downstream movements, and conversely, the majority of mortalities downstream of barriers followed upstream movements (92%), i.e., mortalities predominantly occurred during barrier approach or delay rather than after passage. Delays between first approach and passage may further extend the period that individuals are exposed to the hazards at barriers and the freshwater environment, as well as experiencing other negative effects induced by the delays, e.g. at tidal weirs S1a and S1b, despite no apparent excess mortality (Yeldham et al. 2025b).

While our methods (i.e. acoustic transmitters without digestion sensors) do not allow for direct determination of cause of death, predation is likely to be responsible for at least a proportion of the observed mortalities and may play a role in the excess mortality downstream of some of the study weirs. Barrier-induced delays and multiple passage attempts can exacerbate predation risk as a result of crowding, exposure, disorientation, and exhaustion, coupled with the energetic and physiological costs of migration (e.g. Boulêtreau et al. 2018; Garcia de Leaniz 2008; Larinier 2001; Schilt 2007). Weir pools are also preferred foraging areas for cormorants *Phalacrocorax* spp. (Garcia de Leaniz 2008) that were repeatedly observed foraging below Upper Lode Weir (S2) during sampling. Elsewhere, cormorants were found to almost exclusively feed on adult twaite shad during the month of May in the Elbe estuary, Germany (Magath et al. 2016), as well as consuming 30% of the 2005 alewife *Alosa preudoharengus* spawning population of Bride Lake, USA, thereby accounting for 48% of overall alewife mortality in that year (Dalton et al. 2009). Shad have also been identified as contributing to the diet of Northern pike *Esox lucius* in the study rivers (Nolan et al. 2019), with Upper Lode (S2) Weir pool renowned for its pike angling (Britton and Nolan 2021). In a study by Schmitt et al. (2017), particularly high alosine predation by fish predators was identified in the tailwater of a dam, highlighting that barriers may facilitate the predation of *Alosa* spp. by other fish. Predation of twaite shad has also been observed by grey heron *Ardea cinerea* and Eurasian otter *Lutra lutra* during fishway passage attempts at weirs S2 and S3 respectively (OJP, unpubl. video recordings).

Alosa spp. are known to use areas immediately downstream of river barriers for spawning (e.g. Acolas et al. 2006; Beasley and Hightower 2000; López et al. 2007; Walburg and Nichols 1967), and thus energetic and physiological costs of reproduction could also be a driver of the observed mortalities. Furthermore, twaite shad spawning aggregations and behavior could also increase vulnerability to predation (Boulêtreau et al. 2021, Magnhagen 1991). In a scenario where migration barriers spatially concentrate fish spawning efforts, they must be considered a passive anthropogenic driver of mortalities for their facilitation of predation. Finally, the potential for the presence of tagging effects in newly tagged shad must be considered. However, a Cox proportional hazards model found no evidence of reduced survival of newly tagged shad compared to returning shad. Elsewhere, Seitz et al. (2010) found no significant difference in mortality between acoustic-tagged Pacific herring *Clupea palasii* (4%) and a control group (0%) during a 135-day comparison, suggesting that intraperitoneal tagging of clupeids does not result in significantly elevated mortality.

The time and location of death in this study were inferred from the disappearance or stationarity of intraperitoneally implanted acoustic transmitters. This inference was reliant on the assumption that cessation of relocations was the result of death of the tagged fish and, vice versa, that death of a fish resulted in cessation of tag relocations. The cessation of relocations could also be caused by tag malfunction or expulsion, but both were considered as highly unlikely. All tags were confirmed as transmitting before implantation (often many days after activation) and expected battery lifetimes exceeded the end of the freshwater migration cycles tracked. While there are no experiments on tag retention in twaite shad, tag retention in clupeids is generally high. Castro-Santos and Vono (2013) and Tsitrin et al. (2020) reported 100% retention for intraperitoneally implanted PIT (23.0 x 3.8 mm) and dummy acoustic (12.7 x 5.8 mm) tags in adult alewives after 38 and 3 days, respectively. By contrast, Seitz et al. (2010) revealed a 6% tag expulsion rate for V9 dummy tags and 2% for V7 dummy tags in Pacific herring over a 135-day monitoring period, with all expulsions (*n* = 6) occurring between 39 and 53 days post-surgery. However, the mean V9 tag burden in relation to body weight in Seitz et al. (2010) was 1.7% compared to only 0.9% in our study, and we therefore consider significant rates of tag expulsion unlikely. It was also considered unlikely that acoustic transmitters were shed with gametes during spawning, given the large tag diameter (9 mm) relative to twaite shad intraovarian egg size in the River Severn (0.44 – 1.61 mm; Aprahamian 1982). We consider a significant degree of misassignment of death for emigrated fish unlikely, given only 1.3% of fish that returned had been missed by the most downstream receiver station during emigration in the previous year.

Our analyses rely on the premise that the movements of the tags of dead fish cease at the place and time of death, despite the potential for dead fish drifting or being moved by predators and scavengers. Elsewhere, the carcasses of dead fish have been moved downstream by river flows to varying degrees, lasting for up to multiple days and kilometers (Giraldo et al. 2017; Havn et al. 2017; Strobel et al. 2009). An inspection of the last movement before a fish was classified as dead revealed that more individuals had moved upstream (55%) than downstream (44%). Among the subset of fish that died below barriers, 92% of individuals did so following upstream movements, indicating that this result was not inflated by drifting. Tags of predated fish may be retained in predators and scavengers for extended periods of time and can lead to misassigned movements in telemetry studies (Klinard and Matley 2020; Shorgan et al. 2024; Waters et al. 2024). Indeed, upstream movements of scavenged tags have been observed by Havn et al. (2017), though the study relied on radio tags that are also detected when outside of the river, as opposed to the acoustic transmitters used in our study. While we cannot rule out misassigning some relocations of eaten shad as active movements, the disproportionate number of dead shad tags in weir pools would require systematic tag movement by predators from further downstream, which is considered unlikely.

In summary, mortality rates of anadromous twaite shad during their spawning migration were more than double in areas immediately downstream of man-made barriers in the River Severn catchment compared to unimpeded reaches. Between-year variation in mortality was significant only for returning shad, and mortality rates did not follow temporal trends within individual migration periods. Shad length was positively associated with mortality, but there were no significant influences of sex and previous spawning history. Catchment penetration, river characteristics, and whether a shad was newly tagged versus returning from previous years did not influence mortality rates. Gaps in knowledge remain on the exact mechanisms through which anthropogenic barriers drive mortalities, e.g. the roles of predation and energetic expenditure and how these drive discrepancies between barriers, and further study is required. Notwithstanding, anthropogenic barriers that exacerbate mortality may be particularly impactful for iteroparous fishes, where population stability depends on adult survival and repeat spawning. Management strategies for anadromous iteroparous fish should therefore consider mortality linked to river barriers as a factor that disproportionately affects multi-year spawners through repeated exposure, and that should be considered when weighing different options for the mitigation or remediation of migration barriers.

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Competing Interests

The authors declare no competing interests. The views expressed in this publication are those of the authors and do not necessarily represent those of their affiliated institutions.

Data and Code Availability

The data and code underlying the analyses are available at DOI:10.5061/dryad.stqjq2cgf.

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Figure Captions

Figure 1: The River Severn basin study area, including the locations of weirs (bars), and acoustic receivers (circles) in the rivers Severn, Teme, and Avon, Western Britain. The core study area is depicted by solid river lines.

Figure 2: Kaplan-Meier survival curves for newly tagged (left) and returning (right) twaite shad during freshwater migration. Hash marks on the curves represent censoring events (emigration).

Figure 3: Top: Orientation diagram of receiver station positions in relation to the study rivers and weirs. Distances not to scale. Bottom: Index of excess mortality $\Delta M_{y,s}$ as difference of observed mortalities to expected mortalities as percentage of the yearly sample at each receiver station under the assumption of equal hazard throughout the study area, for newly tagged (upper plot) and returning twaite shad (lower plot). Grey points represent $\Delta M_{y,s}$ at a station in a year where > 4 mortalities were observed for the sample in total. Colored points and error bars indicate mean and SD between years. Receiver stations without estimates are the outermost stations of the core study

area (highest on Teme and Severn, lowest on Severn), stations where no detections were logged (DS A1b), or both (highest on Avon).

Table 1: Numbers of acoustically tagged twaite shad, locations and modes of capture and release, and transmitter type & programming by capture year. Capture and release locations refer to Maisemore (S1a) and Upper Lode (S2) weirs on the River Severn, with post-tagging release locations upstream (US) and downstream (DS) of the respective weirs.

Year	n	Capture Location	Capture Method	Release Location	Expected Transmitter lifetime (seasons)	Transmitter type	Transmission interval (s)
2018	9	S2	Rod	DS S2	1	V8-4x	60 (30 – 90)
	2	S2	Trap	DS S2	1	V8-4x	60 (30 – 90)
	24	S2	Rod	US S2	3	V9-2x	60 (30 – 90)
	1	S2	Rod	DS S2	3	V9-2x	60 (30 – 90)
	6	S2	Trap	DS S2	3	V9-2x	60 (30 – 90)
	22	S2	Trap	US S2	3	V9-2x	60 (30 – 90)
	20	S1a	Rod	US S1a	3	V9-2x	60 (30 – 90)
2019	50	S2	Trap	US S2	3	V9-2x	60 (30 – 90)
	50	S1a	Rod	US S1a	3	V9-2x	60 (30 – 90)
2021	2	S2	Rod	US S2	3	V9-2x	60 (30 – 90)
	45	S2	Trap	US S2	3	V9-2x	60 (30 – 90)
2022	100	S2	Trap	US S2	3	V9-2x	60 (30 – 90)
2023	50	S2	Trap	US S2	2	V9TP-2x	60 (30 – 90)
2024	6	S2	Rod	US S2	3	V9TP-2x	120 (80 – 160)
	6	S2	Trap	US S2	3	V9TP-2x	120 (80 – 160)

Table 2: Number of mortalities among the groups of newly tagged and returning twaite shad, and mortality distribution between station types. Time spent refers to the respective groups consisting of both emigrated and dead individuals.

Mortalities	DS Weir	US Weir	Unimpeded
Newly Tagged n = 112	27% (n = 30) 10% of time spent	9% (n = 10) 10% of time spent	64% (n = 72) 80% of time spent
Returning n = 57	37 % (n = 21) 21% of time spent	2 % (n = 1) 6% of time spent	61 % (n = 35) 73% of time spent

Table 3: Model results and incident rate ratios (IRRs) for the number of mortalities among newly tagged and returning twaite shad in dependence on time spent (scaled) and receiver station type with reference to receivers on unimpeded river sections.

Group	Fixed predictor	Estimate ± SE	z-value	*p*-value	IRR (95% CI)
Newly tagged	(Intercept)	-0.976 ± 0.207	-4.710	< 0.001	0.38 (0.25 – 0.57)
	Hours (scaled)	0.678 ± 0.089	7.617	< 0.001	1.97 (1.65 – 2.34)
	Type: DS Weir	0.787 ± 0.262	3.010	0.003	2.20 (1.32 – 3.67)
	Type: US Weir	-0.070 ± 0.365	-0.193	0.847	0.93 (0.46 – 1.91)
Returning	(Intercept)	-1.432 ± 0.320	-4.482	< 0.001	0.24 (0.13 – 0.45)
	Hours (scaled)	0.345 ± 0.116	2.966	0.003	1.41 (1.12 – 1.77)
	Type: DS Weir	0.736 ± 0.296	2.483	0.013	2.09 (1.17 – 3.73)

	Type: US Weir	-1.750 ± 1.026	-1.706	0.088	0.17 (0.02 – 1.30)

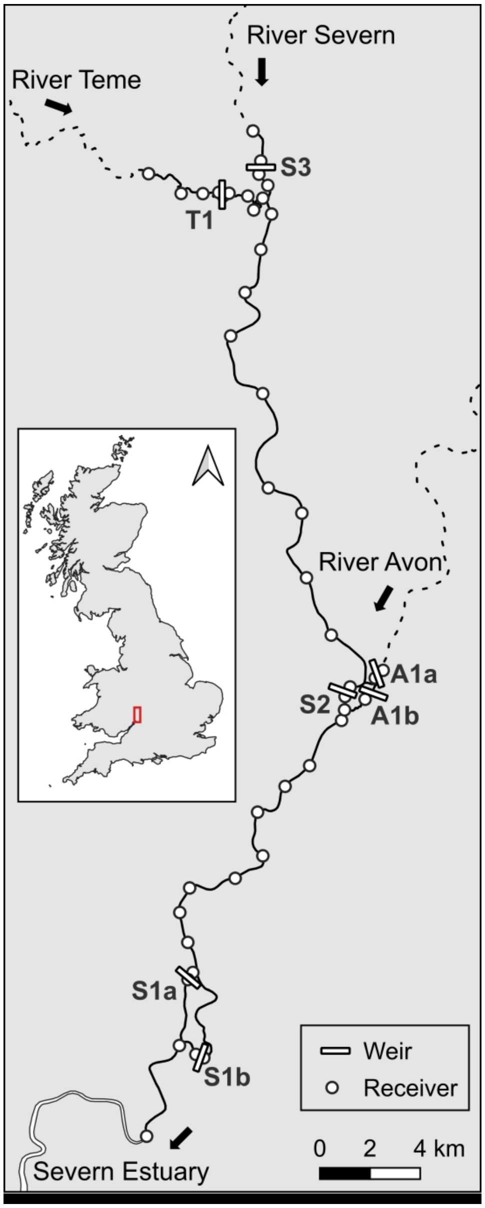

Figure 1

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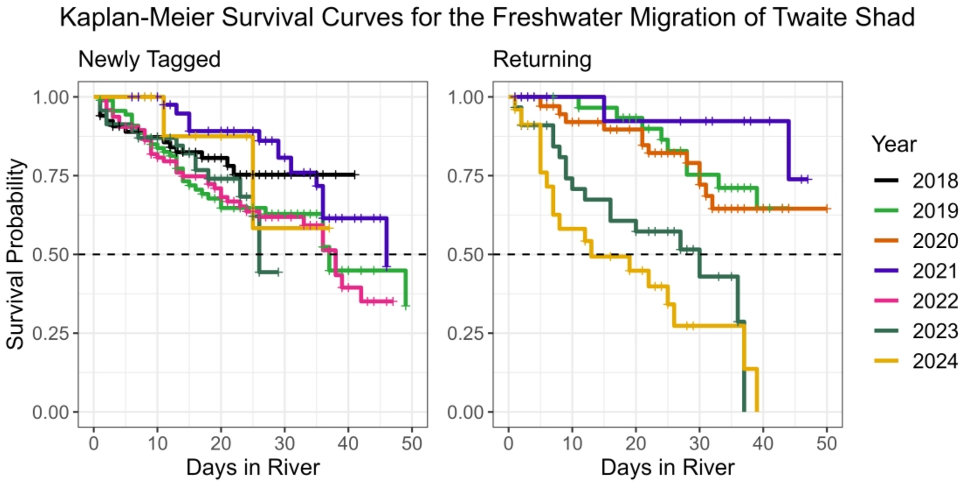

Figure 2

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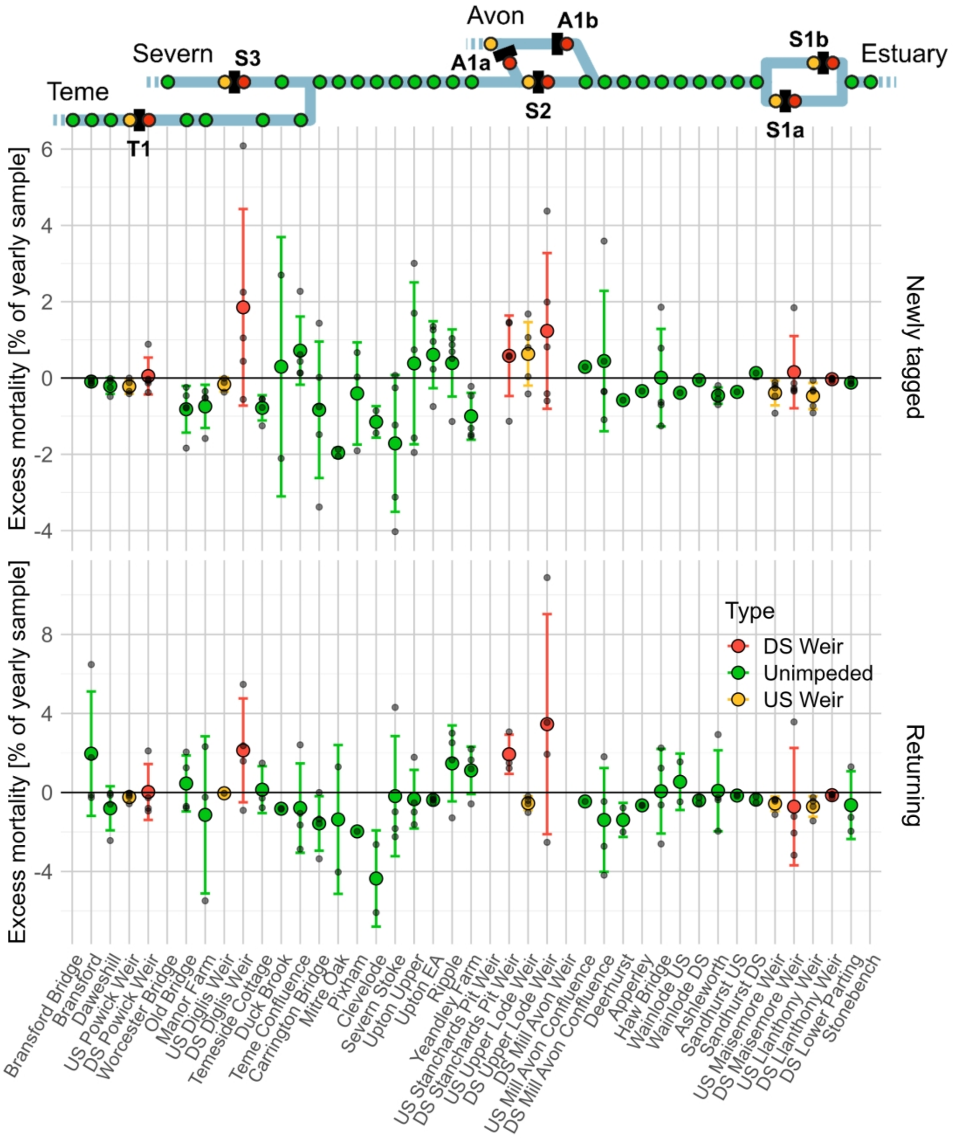

Figure 3

521x628mm (130 x 130 DPI)