Movement ecology of two threatened anadromous species, twaite shad *Alosa fallax* and sea lamprey *Petromyzon marinus,* revealed by acoustic telemetry

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Abstract

Fragmentation of freshwater ecosystems due to man-made barriers (e.g. dams, weirs) poses a major threat to biodiversity, and has driven population declines and extirpations of once-abundant anadromous species. Understanding the movement ecology of anadromous species during all phases of their lifecycle is vital to understand, predict and mitigate the impacts of fragmentation. This is especially crucial for groups such as the Alosinae (shads) and Petromyzontiformes (lampreys), for which movements and space use during both freshwater spawning migrations and the marine life-phase is poorly understood, compared with anadromous species of the Salmonidae family. Here, the movement ecology of threatened twaite shad *Alosa fallax* ('shad') and sea lamprey *Petromyzon marinus* was investigated using acoustic telemetry during and between their spawning migrations in the heavily fragmented lower River Severn catchment in western Britain.

Fish passage studies often consider the impacts of single barriers, yet many rivers actually contain multiple barriers that potentially impose cumulative effects on migrants. Here, sea lamprey were acoustic-tagged at the beginning of their upstream migration in the River Severn catchment, to determine how multiple weirs in sequence impacted their upstream spawning migrations, and to quantify individual variation in movement behaviours associated with weirs. Sea lamprey were impeded and severely delayed by multiple weirs in a cumulative manner, which limited their spawning to atypical habitat. The results also demonstrated the crucial roles of tides and elevated discharge events in enabling weir passage. Exploratory downstream movements made by sea lamprey during delays at weirs represented a large proportion of the total distance moved during their spawning migration. Exploratory downstream movements enabled some individuals to locate alternative spawning tributaries, but these movements were subject to substantial individual variation. Individual variation in passage time at weirs reduced the predictability of arrival timing between downstream and upstream sites, highlighting the stochastic influence of weirs on upstream migration.

Iteroparous species that perform multiple spawning migrations throughout their lifecycle provide an opportunity to assess repeatability in barrier passage and space use during their spawning migration, as well as determine movements during their marine phase, using telemetry. However, few studies have applied multi-year telemetry to understand these aspects, particularly amongst alosine fishes. Here, shad were tagged with long-life acoustic transmitters during their spawning migration in the River Severn catchment, in order to 1) assess their movements and dispersal during their marine phase; 2) assess the impacts of man-made barriers on their upstream spawning migration and the environmental and individual factors affecting barrier passage and; 3) characterise and quantify their movement and space use during the spawning migration, test the individual factors affecting freshwater space-use, and assess spatial fidelity to previously occupied areas by individuals tracked over multiple spawning migrations.

During their marine phase, shad from the River Severn were detected at spatially distant receiver arrays in coastal waters, providing novel insights into their marine dispersal. Individuals were detected at the Taw-Torridge Estuary, 200 km to the south-west of the Severn’s tidal limit, and one individual was detected in the Munster Blackwater Estuary (Ireland) before returning to the Severn, a minimum movement distance of 950 km. During their upstream spawning migration, weirs consistently acted as impediments to shad, and represented the upstream extent of migration for most fish. At a major navigation weir, higher river levels and temperatures significantly increased passage rates. Previous passage success was a significant predictor of increased passage rates in returning individuals, and passage rates were significantly higher in returning fish than newly tagged fish. Shad were highly vagile during their spawning migrations, and their movement patterns were characterised by multiple upstream and downstream journeys prior to emigration. Their median total movement distance while in the river was 214 km and the median total freshwater residency time was 33 days. Females occupied larger core areas than males, and among returning shad, there was significant fidelity to areas occupied in previous years.

This research represents a substantial body of new knowledge relating to the movement ecology of two threatened anadromous fish species. The results highlight the impact of barriers in impeding the upstream distribution of these species within the catchment, as well as the importance of individual variation and spatial fidelity in shaping their movement patterns and distribution.

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Author's Declaration

I (PD) confirm that the research presented within this thesis is my own.

However, the assignment of shad hybrid classes conducted in Chapter 6 was carried out by Olivier Lepais (INRA), after the extraction of DNA from shad tissue samples by PD. In addition, the following research papers were published or prepared for publication in collaboration with J. Robert Britton (JRB), Jon Bolland (JDB), Andrew Nunn (AN), Jamie Dodd (JD), Charles Crundwell (CC), Chris Bainger (CB), Randolph Velterop (RV), Emma Sheehan (ES), Thomas Stamp (TS), Niall O (NM) and Ross O'Neill (RM). In all cases, all authors conceived the ideas, designed the methodology and/or collected the data, and PD analysed the data and led the writing of the manuscript:

Davies, P., Britton, J.R., Nunn, A.D., Dodd, J.R., Bainger, C., Velterop, R. & Bolland, J.D. Cumulative impacts of habitat fragmentation and the environmental factors affecting upstream migration in threatened sea lamprey *Petromyzon marinus.* Aquatic Conservation (Submitted March 2020, In minor revision, Chapter 2) https://doi.org/10.1002/aqc.3625

Davies, P., Britton, J.R., Nunn, AD, Dodd, J.R., Bainger, C., Velterop, R. & Bolland, J.D. Patterns, causes and consequences of individual movement variation in upstream-migrating sea lamprey *Petromyzon marinus* in a highly fragmented river. Freshwater Biology (Submitted December 2020, In review, Chapter 3) https://doi.org/10.1111/fwb.13869

Davies, P., Britton, R.J., Nunn, A.D., Dodd, J.R., Crundwell, C., Velterop, R., Ó'Maoiléidigh, N., O'Neill, R., Sheehan, E.V., Stamp, T. & Bolland, J.D. (2020). Novel insights into the marine phase and river fidelity of anadromous twaite shad *Alosa fallax* in the UK and Ireland. Aquatic Conservation: Marine and Freshwater Ecosystems, 30(7), 1291–1298. (Chapter 4) https://doi.org/10.1002/aqc.3343

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1 Introduction

1.1 Overview

The thesis is presented in an integrated format, whereby material is incorporated in a style suitable for submission and publication in a peer-reviewed journal. Thus, data chapters (Chapters 2 to 6) are each presented as a complete piece of research, either as a published paper (Chapter 4), a manuscript in review (Chapters 2 and 3), or a manuscript for submission (Chapters 5 and 6). An integrated thesis has been chosen as it provides flexibility around the format, number and type of papers included in the thesis. Finally, Chapter 7 discusses the implications of this research and concludes the thesis. Combined references from all chapters are provided at the end to avoid their replication, and to improve readability. This first chapter introduces the main themes of the thesis: anadromous fish migration, and how this is impacted by habitat fragmentation. The study method, species, area, aims and objectives, and thesis structure are then introduced.

1.2 The nature and importance of fish migration

Migration is a life history strategy that allows animals to exploit spatially discrete habitats at different times in their lifecycle, through movement (Dingle & Drake, 2007). Migration is widespread within the animal kingdom, and is undertaken by species within all major taxonomic branches (Dingle & Drake, 2007; Secor, 2015). Migratory movements can occur over distances ranging from a few hundred metres, to transoceanic movements spanning tens of thousands of kilometres (Chapman et al., 2012), and is performed for various functions, including feeding, reproduction, and for exploiting and adapting to ephemeral environmental conditions (Webster et al., 2002).

For humans, certain groups of migratory animals hold distinct cultural and economic significance, their appearance at predictable times and locations heralding a period of natural abundance (Schindler et al., 2003). Among these groups of animals are the anadromous fishes, which migrate from rivers to the sea as juveniles, before their return to rivers as adults for reproduction (Lucas & Baras, 2001). In river catchments where anadromous fishes are, or were once, abundant, their spawning migrations are embedded deeply within economies, norms and folklore of human populations that have relied on them for millennia (Campbell & Butler, 2010; Donkersloot et al., 2020). Today, commercial, subsistence and recreational fisheries for anadromous fish support millions of livelihoods globally. For example, the fishery for anadromous hilsa shad *Tenualosa ilisha* is the largest in Bangladesh, worth approximately USD 1.3 billion, and provides employment for 2.5 million people in one of the poorest nations on earth (Hossain et al., 2016); in the River Spey, it was estimated that rod-caught Atlantic salmon *Salmo salar* contribute £970 per fish to local household incomes (Butler et al., 2009). It has been demonstrated that anadromous fish enable people to retain a connection to ‘wildness’, and their conservation can instil a sense of agency, and ownership for people living within the watersheds that they frequent; thus they have considerable intrinsic value beyond their direct exploitation (McClenachan, Lovell & Keaveney, 2015).

Anadromous fishes can act as keystone species, importing marine-derived nutrients into fresh water through their carcasses, eggs, and excreta (Naiman et al., 2002; West et al., 2010; Tonra et al., 2015). This nutrient influx supports the function of both freshwater and terrestrial ecosystems, and increases their productivity (Bilby et al., 1998; Cederholm et al., 1999; Wipfli et al., 2003). As prey, they provide an important food source for marine and freshwater predators (Hall, Jordaan & Frisk, 2012; Nolan, Gutmann Roberts & Britton, 2019). Anadromous species that construct nests (redds) during spawning can physically alter the shape and composition of stream and lake beds, forming substantial ridges and depressions that can change water-flow patterns and promote channel migration (Holtgrieve & Schindler, 2011). Positive ecological interactions may exist between anadromous species, which can promote their coexistence through ecosystem ‘conditioning’; for example, the carcasses and excreta of anadromous species can increase invertebrate abundance, and thus stimulate the growth of juveniles of other species (Guyette, Loftin & Zydlewski, 2013).

Many anadromous species comprise multiple subpopulations, which are maintained by the homing of spawning adults to their natal river catchments, and fidelity to sites of previous spawning (Jolly et al., 2012; Hasselman, Ricard & Bentzen, 2013; Keefer & Caudill, 2014). Homing and fidelity increase the likelihood that returning adult fish will find mates, and locate habitats that are favourable for spawning and juvenile survival (Quinn, 2005). Return to natal sites thus provides fitness benefits, and contributes to the evolution of locally-adapted populations (Hendry et al., 2000; McDowall, 2001; Waples et al., 2004). In salmonids, the precision of homing varies between species, populations and individuals, ranging from very precise, such as to within metres of natal sites; (Quinn, Volk & Hendry, 1999; Stewart, Quinn & Bentzen, 2003; Quinn, Stewart & Boatright, 2006; Quinn et al., 2012) to relatively broad (within river reaches or catchments; Candy & Beacham, 2000; Hamann & Kennedy, 2012). However, not all anadromous fishes exhibit homing behaviours, such as the anadromous lampreys that instead use a ‘suitable river’ strategy (Waldman, Grunwald & Wirgin, 2008). Sea lampreys *Petromyyzon marinus* locate suitable spawning tributaries through the odour of larvae from previous years’ spawning, as well as pheromones released by spawning adults that have already arrived at spawning sites (Buchinger et al., 2015). Sub-adult anadromous lampreys feed parasitically on large marine vertebrates including fish, elasmobranchs and cetaceans (Silva et al., 2014); their location at sexual maturity may thus be highly dependent on the unpredictable movements of their host animal(s), and so their lack of homing complements their parasitic life history (Clemens et al., 2010).

A key aspect of variation both within and between anadromous fish species is the number of spawning migrations made during their lifetime. Some species, including most anadromous Pacific salmonids *Oncorhynchus spp.* and anadromous lampreys, are strictly semelparous, with only one spawning migration before death (Crespi & Teo, 2002). By contrast, individuals of iteroparous species can undertake multiple annual migrations between marine feeding areas and freshwater spawning sites (Eldøy et al., 2019; Jensen et al., 2020). The fitness advantage of iteroparity is that it enables individuals to maximise their lifetime fecundity through a ‘bet-hedging’ strategy that reduces the long-term risks of reproductive and/or recruitment failure in years when stochastic adverse environmental events occur (Hasselman, Ricard & Bentzen, 2013). The degree of iteroparity can vary within species; in shads (*Alosa* spp.), iteroparity is a feature of spawning populations in the northern part of their range, reflecting greater environmental instability during their spawning season at more northern latitudes, while populations at more southerly latitudes display reduced iteroparity or are fully semelparous (Carscadden & Leggett, 1975; Glebe & Leggett, 1981; Aprahamian et al., 2003a). Although iteroparous species have been shown to display repeatability in the timing of freshwater entry (Eldøy et al., 2019), how their natal homing and spatial fidelity to previous spawning sites may interact to influence their migratory behaviours remains poorly understood.

Despite the ecological, socio-economic and cultural importance of anadromous fishes, considerable knowledge gaps remain in our understanding of their movement ecology and behaviours, and the effectiveness of actions aimed at conserving them (Lennox et al., 2019). Notably, our understanding of salmonid ecology greatly outweighs that of other species (Pess et al., 2014), despite salmonids representing only a fraction of anadromous species (Lucas & Baras, 2001). Other anadromous groups, including Clupeids (e.g. shads, alewife, hilsa), and Petromyzontiformes (lampreys, a group of jawless vertebrates with several anadromous members) have received relatively little attention (Pess et al., 2014). Further, when compared to knowledge on the freshwater spawning migrations of these non-salmonid species, there is a paucity of knowledge on their movements and distribution in the marine environment – the marine phase – which in salmonids enables achievement of larger body sizes and higher fecundity, and can represent a substantial period of their lifecycle (Thorstad et al., 2016).

1.3 Habitat fragmentation and its impact on anadromous fishes

Habitat connectivity is a key component of functional ecosystems, enabling geo-physical, chemical and biological linkages across large spatial scales, and facilitating interactions between distant habitats (Beger et al., 2010). Further, connectivity allows organisms to move freely between habitats, enabling the flow of nutrients and genetic material between spatially discrete areas, and providing valuable ecosystem services (Kremen et al., 2007; Flitcroft, Arismendi & Santelmann, 2019). Functioning aquatic systems are shaped by connectivity along a continuum between terrestrial, freshwater, estuarine and marine environments, which can interact and shape each other (Beger et al., 2010). However, anthropogenic activities have greatly reduced the habitat connectivity of freshwater systems (Belletti et al., 2018; Grill et al., 2019), although examples of increasing connectivity exist - see Strecker & Brittain (2017). For millennia, humans have diverted, regulated and otherwise altered the flow of watercourses for many reasons, including power generation, irrigation and navigation (Malmqvist & Rundle, 2002; Nilsson et al., 2005). While useful to society, the negative environmental effects of such impoundments on freshwater ecosystems include altering seasonal variations in flow, transforming biological and physical characteristics of river channels and floodplains, fragmenting the continuity of rivers, and isolating populations and habitats (Baxter, 1977; Liermann et al., 2012; van Puijenbroek et al., 2019). Today, there are few rivers that remain unfragmented and free flowing, and the density of man-made riverine barriers is particularly high in developed regions (Jones et al., 2019; Belletti et al., 2020). Impact studies are often based on dams that are higher than 10 m (Vörösmarty et al., 2010), but existing databases in Europe suggest that these barriers only represent 3 % of the total and are outnumbered by thousands of low-head barriers (Belletti et al., 2018). Although the impact of low-head structures can be difficult to quantify, their impacts on fresh water biota can be severe (Benstead et al., 1999).

The migratory life history of diadromous fishes makes them particularly sensitive to reduced riverine connectivity (Lucas & Baras, 2001; Moser et al., 2020). For anadromous fishes, barriers such as dams, weirs and culverts represent a physical impediment to upstream and downstream migrations, preventing access to spawning grounds and disrupting seaward migrations of juveniles and post-spawning adults (Brown et al., 2013; Castro-Santos, Shi & Haro, 2017; Nyqvist et al., 2017; Newton et al., 2018). In addition, the altered flow regime imposed by barriers potentially causes alteration or loss of lotic habitat, the preferred spawning habitat of many anadromous species (Birnie-Gauvin, Aarestrup, et al., 2017). Migration delays imposed by barriers can potentially increase predation pressure (Ebel, 1979; Alcott, Long & Castro-Santos, 2020), and reduce reproductive fitness by causing resorption of gametes (Shikhshabekov, 1971). Population declines of anadromous fish due to impoundments have been severe (Hall, Jordaan & Frisk, 2012); in the north Atlantic, most populations for which data is available have declined by over 90% (Limburg & Waldman, 2009). Accurate estimates of the true decline in migratory fish populations are hampered by the absence of data on historical abundance, especially where declines occurred prior to the modern era (Pauly, 1998; McClenachan, Lovell & Keaveney, 2015). For example, in Northwest Europe, severe (>90%) declines in anadromous salmon populations occurred at least as early as the mediaeval period, largely driven by the rapid spread of watermills and other riverine infrastructure (Lenders et al., 2016).

Recognising the ecological problems posed by barriers in freshwater systems, managers have implemented various measures to restore connectivity between impounded sections. Fish passes (also referred to as fishways, fish ladders and bypass channels) are a widely implemented method of facilitating fish movement past dams and weirs. The design of fish passes varies greatly, from 'nature-like' passes which aim to create the complex hydraulic and hydromorphic conditions found in natural systems, to 'technical' fish passes including vertical slot, pool & weir, larinier and fish lock/elevator designs (Larinier & Marmulla, 2004; Franklin et al., 2012; Silva et al., 2018). However, the passage efficiency achieved by these structures is variable and often low for non-salmonid fishes. In a global review, Noonan, Grant and Jackson (2012) found fish pass efficiency was significantly higher for salmonids than other fish for both downstream (75% vs 40%) and upstream (61% vs 21%) passage. Brown et al. (2013) found that the passage of American shad (*Alosa sapidissima*) through fish pass structures specifically designed for this species was only around 3 %, while similar findings have been reported in technical fish passes at sites important for lamprey passage (Foulds & Lucas, 2013).

Calls are thus increasing for a more holistic approach to river reconnection that provides connectivity for a broader range of species (Tummers, Hudson & Lucas, 2016; Silva et al., 2018). Complete removal of barriers is now a more frequent component of river restoration, with projects of increasing size and ambition being undertaken, particularly as structures come to the end of their working lifespan (Ishiyama et al., 2018; Neeson et al., 2018). Targeted barrier removal allows migratory fish to reach upstream spawning grounds unimpeded, potentially enhancing reproductive success, but there may be negative ecosystem effects related to toxic sediment release and propagation of invasive species (Bednarek, 2001; Rubin et al., 2017; Milt et al., 2018). In general, effects of barrier removal are considered positive, and evidence of the ecological benefits of barrier removal is increasing (Xia et al., 2016; Watson et al., 2018). Some anadromous taxa have been shown to quickly recolonise previously inaccessible areas following barrier removal, with cascading ecosystem effects including the increased transfer of marine derived nutrients into freshwater food webs (Pess et al., 2014; McClenachan, Lovell & Keaveney, 2015; Tonra et al., 2015; Birnie-Gauvin, Larsen, et al., 2017).

Ecological information can guide the prioritisation of habitat reconnection actions, enabling maximum benefit for a given budget (Allen & Singh, 2016; Sethi et al., 2017). Best-practice river reconnection, including barrier removal and fish pass installation, requires intimate knowledge of the movement ecology of anadromous fish in fragmented ecosystems (Cooke et al., 2016), including the influence of individual traits and environmental conditions on barrier passage (Silva et al., 2018). In addition, conservation of anadromous species requires knowledge of their marine dispersal, to mitigate against threats during this aspect of their lifecycle (Klemetsen et al., 2003; Limburg & Waldman, 2009; Ogburn et al., 2017). While there is a range of methods that can enable these data to be generated, acoustic telemetry is a contemporary method that has developed considerably in recent years, and provides opportunities to measure the extent of animal movements across both freshwater and marine environments.

1.4 Acoustic telemetry

To fully understand the movement ecology of migratory animals requires the monitoring of their movements through time, but directly observing the movement behaviour of species that migrate over large spatial scales is challenging, particularly in large, open aquatic systems (Nielsen et al., 2009). Within the last 60 years, developments in the electronic tagging of animals (biotelemetry) have enabled researchers to monitor animal movements remotely, which has greatly advanced our understanding of animal migration (Ropert-Coudert & Wilson, 2005). In aquatic systems, a range of telemetry techniques now exists, which the researcher must select based on their specific study species, research questions and study systems (Cooke et al., 2012). In fresh waters, radio telemetry is suitable for tracking animals in turbulent, fast flowing shallow waters, while passive integrated transponder (PIT) telemetry offers small, relatively cheap long-lasting tags for high-throughput tagging, enabling the detection of tagged animals upon recapture or during their passage over fixed antennae placed within narrow channels such a fish passes (Cooke et al., 2013). Acoustic telemetry is an increasingly popular method used to track fine-scale and broad-scale movements of animals that transit between riverine, estuarine and marine systems where conditions are conducive to the passage of sound (Cooke et al., 2013; Donaldson et al., 2014; Hussey et al., 2015).

The primary tools of acoustic telemetry are transmitters (‘tags’) and receivers (Figure 1.1). Tags, internally implanted or externally attached to the study organism, emit unique ultrasonic signals that can be detected by submerged receivers. Tagged animals can be tracked actively using a mobile receiver, or passively, using one or more fixed receivers arranged strategically in an array. As the method has developed, improvements in battery technology have increased the deployment time of tags and receivers, enabling multi-year passive tracking of individual animals (Crossin et al., 2017) and the miniaturisation of tags has enabled the tagging of a broader range of species including flatfishes (Neves et al., 2018), anguillids (Bolland et al., 2019a), cephalopod molluscs (Hofmeister & Voss, 2017) and crustaceans (Holsman, McDonald & Armstrong, 2006), as well as juveniles of many fish species (Hussey et al., 2015). Technological developments have included combining tags with temperature, pressure and heart-rate sensors, which enable transmission of the depth and physiological state of the study organism as part of the coded acoustic signal (Donaldson et al., 2014), as well as sensors that enable identification of predation events (Klinard et al., 2019).

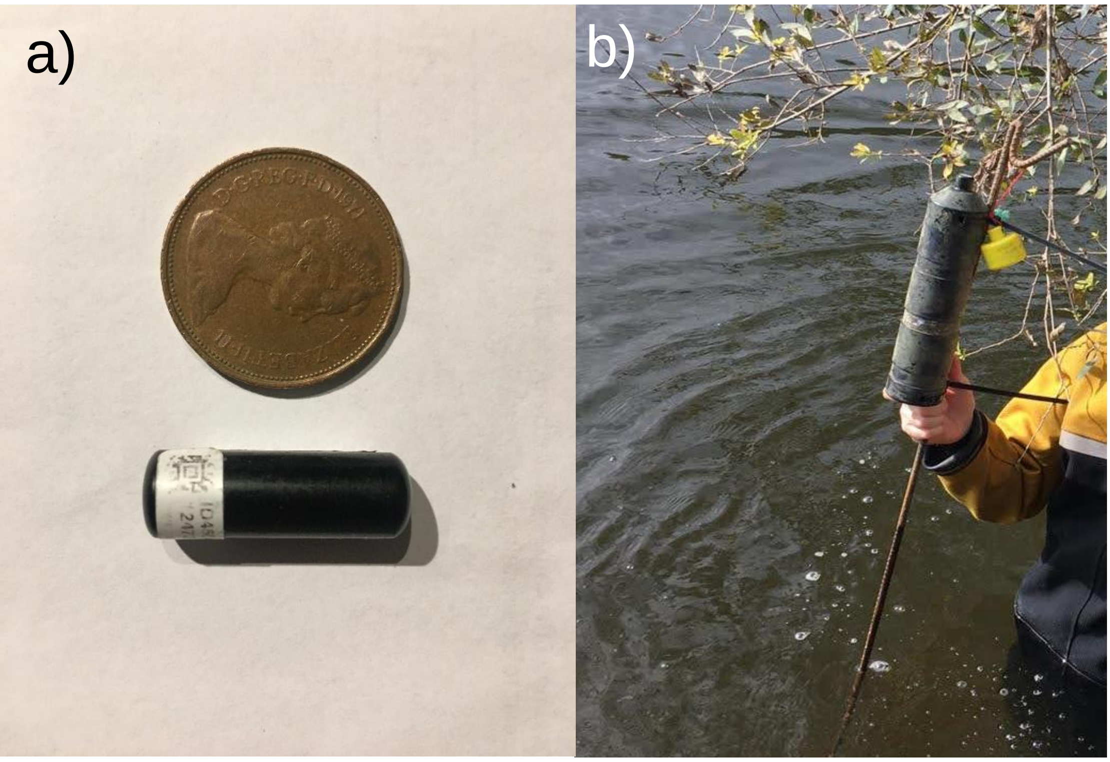

Figure 1.1: a) VEMCO v9 acoustic transmitter; b) VEMCO VR2-W acoustic receiver secured to steel fencing pin, with temperature logger (yellow)

Acoustic telemetry has found many applications, including in fisheries stock assessments, managing habitats, monitoring invasive species and assessing trophic interactions (Donaldson et al., 2014; Crossin et al., 2017). The method is well suited for use in dendritic systems such as river and canal networks, where discrete sections of river can be delineated by receiver ‘gates’ (Bruneel et al., 2020). Gated receiver arrays enable the timing and drivers of movements between river sections of interest, such as the passage of man-made barriers, to be assessed with precision (Piper et al., 2013; Dodd et al., 2018; Enders et al., 2019). New applications of acoustic telemetry continue to be developed, increasingly facilitated by bespoke open-source software; for example, arrays of receivers with overlapping detection ranges can be deployed to enable fine-scale positioning of tagged animals through triangulation, based on the time-of-arrival (TOA) of coded signals (Hawkins et al., 1974; Baktoft et al., 2017). This process has enabled ‘reality-mining’ studies in aquatic animals where accurate positional fixes on tagged individuals can be achieved with high temporal (< 1s) and spatial (< 1m) precision (Baktoft et al., 2015; Aspillaga et al., 2021).

While extremely versatile and widespread, some negative effects of acoustic telemetry on the study organism have been reported, which must be considered in tracking studies; these can include reduced survival or unrepresentative behaviour of the organism as a result of tagging (‘tagging effects’) (Olney et al., 2006; Cooke et al., 2011; Eakin, 2017), or an effect of the coded signal itself, such as increased predation of tagged individuals through ‘dinner bell’ effects (Wargo Rub & Sandford, 2020). Achieving true ‘controls’ in acoustic telemetry studies in the wild is challenging, because it would require the continuous direct observation of untagged individuals (Cooke et al., 2011); however, comparing the movements and performance of newly tagged individuals with previously tagged individuals that are assumed to be free of short term tagging effects, may enable the short-term effects of tagging and handling on movement to be assessed (Gahagan & Bailey, 2020). Such studies are rare, but are essential to fully understand potential biases imposed on tagged animals by telemetry (Cooke et al., 2011).

Acoustic telemetry can be assisted when different groups of researchers have arrays of receivers deployed in different regions and habitats, as this increases the spatial area in which tagged animals can be detected (Taylor et al., 2017). Indeed, researchers often encounter ‘unknown’ detections on their receivers, arising from animals tagged as part of other studies; reciprocal sharing of detection data helps to identify these tagged animals, thereby advancing knowledge on species undertaking long-distance movements (Taylor et al., 2017). Increasingly, data sharing is facilitated by integrating individual acoustic arrays into large-scale telemetry networks that involve multiple organisations at continental scales (Cowley et al., 2017; Brodie et al., 2018; Krueger et al., 2018; Iverson et al., 2019). Such networks have revealed novel insights on the dispersal and migration of wide ranging species (e.g. the long distance migrations of Atlantic tarpon *Megalops atlanticus* (Griffin et al., 2018)), and facilitated retrospective, multi-species studies that reveal broad ecological insights (e.g. spatial segregation amongst co-occurring reef sharks (Heupel, Lédée & Simpfendorfer, 2018)).

As telemetry studies increase in size and scope, large datasets are generated which require advanced processing and statistical analysis techniques

(Whoriskey et al., 2019). Recently, attempts have been made to standardise the calculation of movement metrics and guide researchers through statistical analyses (Udyawer et al., 2018). Common approaches include generalised modelling, survival (time-to-event) analysis, mark-recapture models and network analysis, although ultimately, data interpretation is study- and species-specific (Whoriskey et al. 2019). As a result of the considerable advances in the technology of acoustic telemetry outlined earlier, and the increasing availability of these data analysis tools and modelling techniques, this thesis applies these tools to its focal species, the twaite shad *Alosa fallax* and sea lamprey *Petromyzon marinus*.

1.5 Focal species

1.5.1 Twaite shad

The twaite shad (Figure 1.2) is an anadromous fish belonging to the herring (Clupeidae) family of bony fishes, with a distribution across the coastal northeastern Atlantic to southern Norway, and the Mediterranean (Aprahamian et al., 2003a). Adult twaite shad enter rivers to spawn in spring, and peak spawning periods ranging from February in the southern part of their range to May/June in the north (Aprahamian et al., 2003a). Spawning occurs pelagically, generally over gravel substrates, and is highly nocturnal (López et al., 2011). Across the northern part of their range, twaite shad are iteroparous, with individuals that have spawned in previous years often representing a large proportion of the spawning run, while populations are more frequently semelparous in the south (Aprahamian et al., 2003a). After emerging from the egg, juveniles inhabit brackish estuarine waters for approximately two years (Aprahamian et al., 2003a), before occupying coastal and offshore waters at depths generally less than 100 m (Trancart et al., 2014).

Considerable declines and local extinctions of anadromous twaite shad in Europe have been attributed to man-made impoundments, declining water quality and overexploitation (de Groot, 1990; Aprahamian et al., 2003a; Rougier et al., 2012). In relative terms, the spatial impact of artificial structures on shad migrations can be more severe than for salmonids, due to their smaller body sizes and weaker swimming ability, which generally prevents them from navigating high flows (Larinier & Travade, 2002). While the species is currently listed as 'Least Concern' by the International Union for the Conservation of Nature and Natural Resources (IUCN) (https://www.iucnredlist.org/species/904/174776207), concerns over twaite shad population declines in Europe are reflected in regional conservation legislation, with the species listed in Annexes II and V of the European Union Habitats Directive and Appendix III of the Bern Convention (Aprahamian, Aprahamian & Knights, 2010). Twaite shad readily hybridize with the closely related allis shad *Alosa fallax,* a phenomenon that has been attributed to artificial structures which cause the two species to overlap in their spawning range (Coscia et al., 2010; Taillebois et al., 2020).

Although declines in shad populations have been attributed to habitat fragmentation, there is little actually known about their movements during their spawning migration within fragmented river catchments. Due to their high rate of iteroparity in the northern part of their range, shad potentially represent an excellent model organism for studying spatial fidelity of adults to previous spawning areas, where telemetry methods provide the opportunity for capturing data on their movement ecology (Section 1.4). Twaite shad have traditionally been considered a species sensitive to sedation and handling (Breine et al., 2017), a trait typical of many alosines (Frank et al., 2009; Eakin, 2017), which has previously precluded assessments of their movements using telemetry. However, there has been some recent success using acoustic telemetry in the species, initially using external tagging to track shad in estuarine and coastal waters (Breine et al., 2017). Further advances in the surgical tagging protocol has now enabled internal tag implantation under general anaesthesia (Bolland, Nunn, et al., 2019). This latter approach has opened the possibility of recording shad movements over multiple spawning seasons, potentially enabling assessments of fidelity to spawning rivers and sites, repeatability in behaviours (e.g. relating to barrier passage), and investigations into their marine movements and distribution.

In Great Britain, twaite shad spawning populations are now restricted to four river catchments (the rivers Tywi, Usk, Wye and Severn) although relict populations might occur elsewhere (Aprahamian et al., 2003a; Maitland & Lyle, 2005). The species is a primary designating feature of five Special Areas of Conservation (SACs) in the Tywi, Usk and Wye, the Severn estuary and Carmarthen Bay (https://sac.jncc.gov.uk/species/S1103/). Their core spawning areas in Britain are thus rivers draining into the Bristol Channel. Historically the River Severn is believed to have hosted substantial spawning populations of considerable cultural and economic value (Buffery, 2018), but these populations underwent severe declines following the construction of multiple navigation weirs in the 19th Century. Correspondingly, the River Severn is used as the focal river for investigating the effect of barriers on the spawning migrations of twaite shad (Section 1.6).

1.5.2 Sea lamprey

The sea lamprey (Figure 1.2) is the largest member of the Petromyzontidae, a group of jawless vertebrates found in oceans and rivers in most temperate regions (Potter et al., 2015; Guo, Andreou & Britton, 2017). Sea lamprey are native to the North Atlantic; adults migrate into rivers in Europe and North America to spawn in spring (Potter et al., 2015; Guo, Andreou & Britton, 2017). The species is semelparous, ceasing feeding after entering freshwater, and relies on stored energy reserves to migrate upstream and spawn (Araújo et al., 2013; Moser et al., 2015). Spawning occurs in shallow riffle areas, where individuals, usually in male/female pairs (Figure 1.2), excavate a depression in gravel/cobble substrates to deposit eggs. After hatching, larval lampreys (ammocoetes) burrow into the substrate and filter feed (Dawson et al., 2015). This larval stage lasts five years on average, before they undergo a metamorphosis and migrate into salt water as sub-adults, to parasitise marine vertebrates including sharks, cetaceans (Figure 1.2) and fish (Maitland, 2003; Nichols & Hamilton, 2004). Silva et al., (2014) identified 54 known host species of sea lamprey, from a wide range of taxonomic groups with varying life histories, indicating low host selectivity. When sexually mature, adult sea lamprey detach from their hosts and migrate into freshwaters, with males generally arriving earlier on spawning grounds than females (Clemens et al., 2010; Moser et al., 2015; Guo, Andreou & Britton, 2017). Adults identify suitable spawning tributaries through the odours of larvae (ammocoetes) and pheromones released by upstream spawning adults, while alarm cues, which signal areas of high mortality to predation, may deter their entry into tributaries (Buchinger et al., 2015).

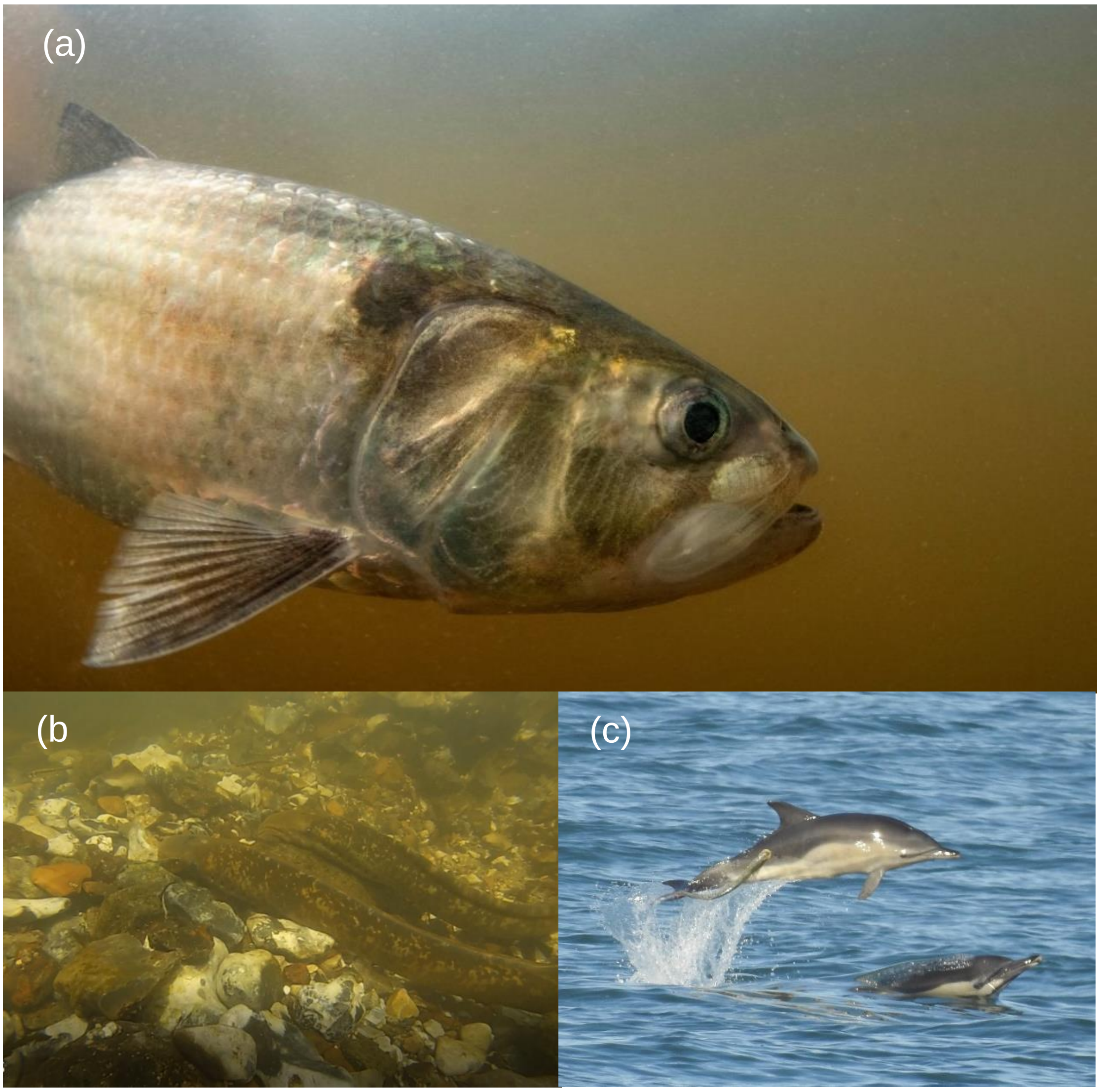

Figure 1.2: (a) Twaite shad *Alosa fallax;* (b) Two sea lamprey *Petromyzon marinus* constructing a nest; (c) sea lamprey attached to a marine host (common dolphin *Delphinus delphis*). Photographs courtesy of (a) Jack Perks, (b) Dr Adrian Pinder and (c) Mike Langman.

Sea lamprey have experienced population declines across their native range due to the construction of barriers, water pollution and overexploitation (Mateus et al., 2012). Sea lamprey are not rapid swimmers and technical fish passes designed primarily for salmonids have been shown to be poor at facilitating sea lamprey passage (Laine, Kamula & Hooli, 1998; Foulds & Lucas, 2013). Although fish pass designs are now incorporating a broader range of taxa (Silva et al., 2018), it is recognised that mitigation of migration barriers for sea lamprey using fish passes requires more knowledge on their specific requirements (Lucas et al., 2020). Like the twaite shad, sea lamprey are currently listed as ‘Least Concern’ by the IUCN (https://www.iucnredlist.org/species/16781/18229984), but concerns over population declines in Europe are reflected in regional conservation legislation, with the species listed in Annex II of the European Union Habitats Directive and Appendix III of the Bern Convention. Concurrently, sea lamprey have become highly invasive in the North American great lakes, where the development of control efforts has provided much of our knowledge on the migratory behaviour of sea lamprey (Hansen et al., 2016). The inability of sea lamprey to pass low-head barriers is exploited in control efforts in the Great Lakes through the construction of weirs with co-located traps (McLean & McLaughlin, 2018). In Great Britain, sea lamprey have become absent from many rivers where man-made barriers prevent their access to suitable spawning habitat (Maitland, 2003), but the species is currently a primary designating feature of nine riverine and estuarine SACs in Great Britain, and a qualifying feature of 14 other SACs (https://sac.jncc.gov.uk/species/S1095/). Several major river catchments support sea lamprey spawning populations despite heavy fragmentation; one of these, the River Severn, is used here to test the impact of barriers on sea lamprey movements and behaviours during their spawning migrations (Section 1.6).

1.6 The study system: The River Severn catchment

Rising in the gritstone plateau of central Wales, the River Severn flows northeast to Shrewsbury before turning southward and terminating in the Bristol Channel. The Severn is the longest river in the British Isles and seventh in terms of annual discharge (Durand et al., 2014), and is a heavily impounded system in its lower reaches (Buffery, 2018) (Figure 1.3). Navigation weirs were first constructed during the industrial revolution in the 19th century to allow barge transport of goods to the rapidly growing cities of Gloucester and Worcester. There are now six navigation weirs and locks on the main channel of the Severn, between Maisemore near Gloucester and Stourport in Worcestershire, with additional barriers further upstream as well as on the main tributaries of the Severn including the Warwickshire Avon and River Teme (Table 1.1; Figure 1.3). Despite these impoundments, the catchment is subject to a number of national and international conservation designations. The estuary is classified as a Special Protection Area

(SPA) for birds under the EU Birds Directive (E.U., 2009) and is a Special Area of Conservation (SAC) under the EC Habitats Directive (E.U., 1992). The River Teme, a major tributary, is designated a Site of Special Scientific Interest (SSSI).

In the River Severn catchment, the impacts of man-made barriers on the migration of aquatic species are currently being addressed as part of ‘Unlocking the Severn’ (unlockingthesevern.co.uk). This project, one of the largest of its kind in Europe, is aiming to improve ecological connectivity in the River Severn catchment by restoring access for twaite shad to historical spawning grounds that became inaccessible when navigation weirs were built during the 19th century. To achieve this aim, fish passes are being constructed at four of the weirs described in this thesis (S3, S4, S5, S6, Figure 1.3; Table 1.1; Appendix i). Three of these weirs (S3, S5, S6) will feature modern deep vertical slot fish passes, and the fourth (S4) will a feature bypass channel and rock-ramp. While the fish passes being constructed as part of Unlocking the Severn vary in specification, they have been designed to accommodate the needs of non-salmonid species, such as twaite shad, in accordance with fish passage designs used elsewhere in Europe (Larinier & Travade, 2002; Pereira et al., 2017). In addition, Powick Weir and Knightwick Weir (T1 and T2) on the River Teme underwent lowering between 2019 and 2020.

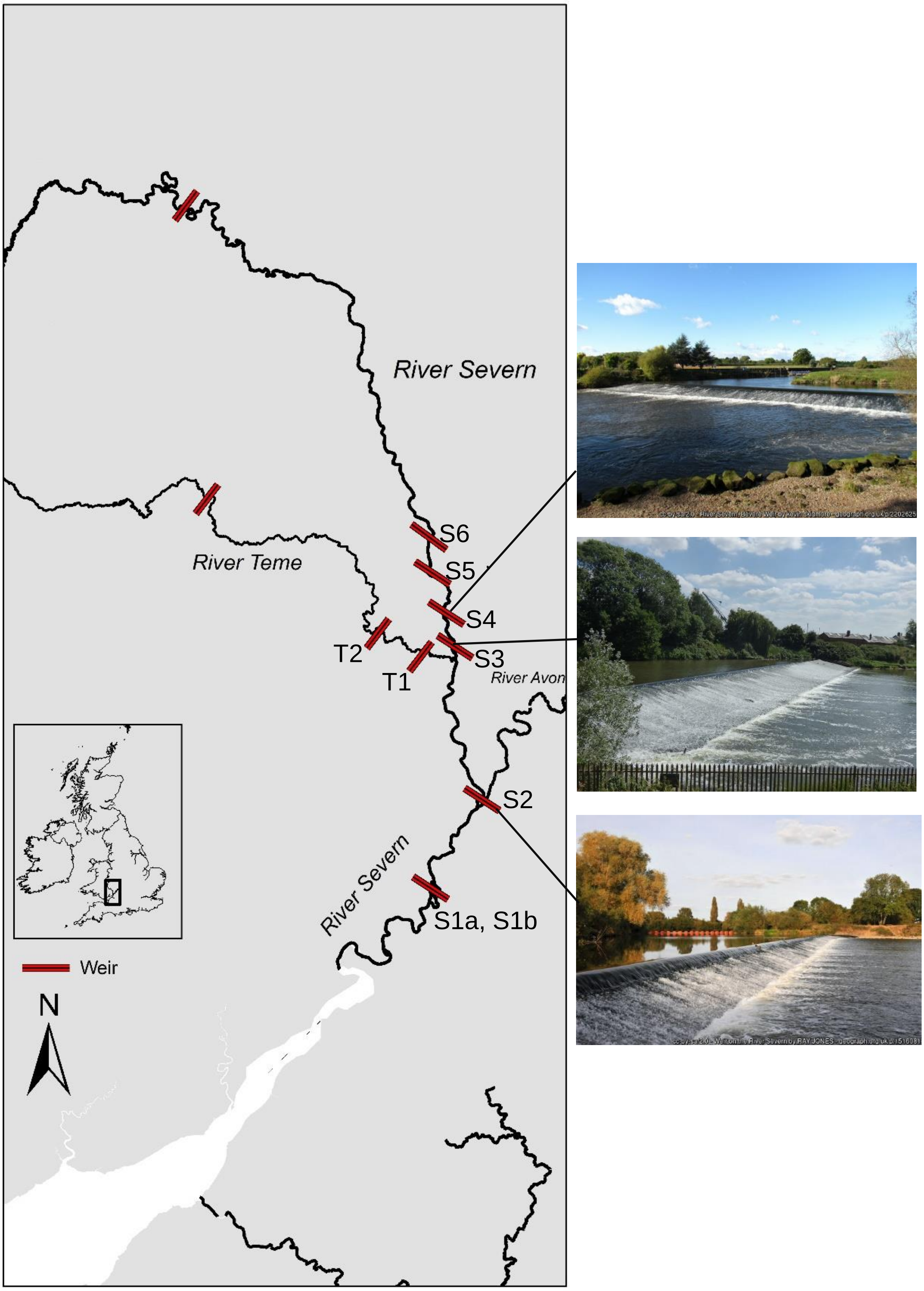

Figure 1.3: River Severn catchment, indicating approximate location of major navigation and flow regulation weirs on the rivers Severn and Teme. Weir codes as in Table 1.1. Representative images of three weirs at Tewkesbury (lower), Worcester (middle) and Bevere (upper). Images of all weirs are provided in Appendix .

Table 1.1: Navigation and flow regulation weirs within the study area in the lower River Severn catchment. See Figure 1.3 for relative positions of weirs within the catchment.

Weir code	**Name**	**River**	**Location, decimal degrees[1]**	**Construction**	**Height, m**	**Distance from tidal limit, rkm**	**Fish pass type**	**Original function**	**Modifications as part of 'Unlocking the Severn'**
S1a	Maisemore	Severn	51.893N, 2.265W	Blockstone	1.8	0	NA	Navigation	NA
S1b	Llanthony	Severn	51.862N, 2.260W	Blockstone	1.7	0	NA	Navigation	NA
S2	Upper Lode	Severn	51.993N, 2.174W	Blockstone	1.6	16	Larinier, notch	Navigation	NA
S3	Diglis	Severn	52.179N, 2.225W	Blockstone	2.2	42	NA	Navigation	Deep vertical slot fish pass, completed 2020
S4	Bevere	Severn	52.232N, 2.240W	Blockstone	1.5	49	NA	Navigation	Bypass channel and rock ramp, completed 2020
S5	Holt	Severn	52.268N, 2.265W	Blockstone	1.6	54	NA	Navigation	Deep vertical slot fish pass, works in progress
S6	Lincomb	Severn	52.322N, 2.265W	Blockstone	2.2	61	NA	Navigation	Deep vertical slot fish pass, works in progress
T1	Powick	Teme	52.169N, 2.247W	Blockstone	2.8	44	Larinier *	Flow regulation	Partial removal, completed 2019
T2	Knightwick	Teme	52.199N, 2.389W	Concrete	1.2	60	NA	Flow regulation	Partial removal, completed 2019

1.7 Research aims and objectives

The aim of this research is to reveal the movement ecology of threatened, data-poor anadromous species that spawn in fragmented river systems. By applying acoustic telemetry methods to the spawning populations of twaite shad and sea lamprey of the lower River Severn catchment in western Britain, the research objectives (O) are to:

O1) Quantify the cumulative impacts of weirs on the upstream migration of sea lamprey and twaite shad, and the individual and environmental factors affecting barrier passage;

O2) Quantify individual variation in sea lamprey movements associated with navigation weirs and assess the consequences of individual variation on migration success;

O3) Assess dispersal within marine environments by over-wintering twaite shad and evaluate their inter-annual fidelity to spawning rivers;

O4) Quantify the movements and space use of twaite shad during their spawning migration, and assess individual factors affecting space use and spatial fidelity to spawning areas within the River Severn catchment.

These research objectives are met in the data chapters as follows:

Chapter 2: Cumulative impacts of multiple weirs and environmental factors affecting upstream migration in sea lamprey *Petromyzon marinus* (O1)

Chapter 3: Patterns, causes and consequences of individual movement variation in upstream-migrating sea lamprey *Petromyzon marinus* in a highly fragmented river (O2)

Chapter 4: Novel insights into the marine dispersal and river fidelity of anadromous twaite shad *Alosa fallax* in the UK and Ireland (O3)

Chapter 5: Tracking repeat-spawning anadromous fish over multiple migrations reveals individual repeatability, tagging effects and environmental factors influence barrier passage (O1)

Chapter 6: Movement, space use and spatial fidelity of threatened anadromous twaite shad *Alosa fallax* during their spawning migrations (O4)

2 Cumulative impacts of habitat fragmentation and the environmental factors affecting upstream migration in threatened sea lamprey *Petromyzon marinus*

2.1 Abstract

1. Riverine ecosystems are often fragmented due to man-made structures, such as weirs. By impeding access to upstream spawning sites, the effects of these structures on anadromous species can be severe, ultimately leading to population declines.

2. This study focused on the freshwater spawning migration of sea lamprey *Petromyzon marinus*, a species threatened by habitat fragmentation across its native range. To quantify the cumulative impacts of multiple weirs on upstream-migrating adults, and explore the environmental factors affecting migratory movements, passive acoustic telemetry was applied to 56 individuals during their spawning migration in the heavily fragmented River Severn catchment, UK.

3. While 89% of tagged sea lamprey passed the first weir upstream of the release site on the main river, only 4% passed the fifth. For 85% of migrants, the upstream extent of migration was immediately downstream of a weir. Individuals that passed weirs upstream of the release site (n = 50) took 21.6 ± 2.8 days to reach their most upstream location, experiencing cumulative passage times at weirs of 15.7 ± 2.8 days; these delays constituted a median of 84% of total upstream movement times.

4. Multistate models revealed that weir passage rates by sea lamprey in tidal and non-tidal areas increased significantly when downstream river level and discharge were elevated. Upstream-to-downstream changes in direction were frequent downstream of weirs, but rare in unobstructed river sections.

5. The results provided evidence for a cumulative effect of multiple weirs on sea lamprey movements, substantially delaying upstream migrants and limiting their spawning to atypical habitat; they also demonstrated the crucial roles of tides and elevated discharge events in enabling weir passage. While the Severn estuary features conservation designations for sea lamprey, this study reveals that barriers are inhibiting upstream migration, an issue which should be addressed to assist their conservation.

2.2 Introduction

Dams and weirs are major man-made disturbances on rivers that interrupt longitudinal connectivity, inhibit fish migrations across ecosystem boundaries (marine-freshwater), modify gene-flow and impact population sustainability (Dudgeon et al., 2006). The effects of these structures on populations of anadromous fishes can be particularly severe as they impede or inhibit access to spawning sites in the upper reaches of rivers (Lucas & Baras, 2001; Rolls et al., 2014). Population declines in anadromous species attributable to man-made structures have had considerable adverse ecological, economic and cultural impacts (Limburg & Waldman, 2009; van Puijenbroek et al., 2019).

Anadromous species threatened by disrupted river connectivity include the sea lamprey (*Petromyzon marinus* L.), which have protected status in Europe but are highly invasive in the Great Lakes of North America (Hansen et al., 2016; Hume et al., 2021). Sub-adults of this jawless vertebrate, native to the northern Atlantic and Mediterranean (Guo, Andreou & Britton, 2017), feed parasitically on large marine vertebrates, before migrating into fresh water to spawn in shallow, fast-flowing river habitats (Maitland, 2003; Rooney et al., 2015). Concerns over sea lamprey population declines - attributed primarily to overharvesting, pollution, habitat loss and man-made barriers to migration (Guo, Andreou & Britton, 2017; Silva et al., 2019; Moser et al., 2020) - are reflected in international conservation legislation. The species is listed in the European Habitats Directive, both on Annex II, which requires European Union member states to designate high-quality sites that contain listed species as Special Areas of Conservation (SACs), and Annex V, which ensures any exploitation of listed species is sustainable

(Council of the European Communities, 1992). In addition, the sea lamprey is listed on Appendix III of the Bern Convention, a treaty which aims to ensure protection for vulnerable migratory species and their habitats across Europe.

Traditional monitoring of anadromous sea lamprey populations has focused on quantifying densities of their larvae (ammocoetes), a key indicator of spawning success, and shown that the spatial distribution of ammocoetes is limited by weirs (Andrade et al., 2007; Nunn et al., 2008; Nunn et al., 2017). Visual spawning surveys (nest counts) have also documented areas of high spawning activity immediately downstream of structures that were assumed to inhibit migration (Pinder et al., 2016). Modern telemetry techniques (e.g. radio, passive integrated transponder (PIT) and acoustic) are increasingly being used to quantify the riverine movements of migrating adult sea lamprey. Much of the knowledge on sea lamprey migration ecology is from studies completed in the North American Great Lakes, where the species is invasive and threatens economically important populations of freshwater fish through parasitism (Hansen et al., 2016). Consequently, telemetry studies have informed sea lamprey control efforts by identifying spawning areas (Holbrook et al., 2016) and characterising migration strategies (Meckley, Wagner & Gurarie, 2014; McLean & McLaughlin, 2018). In their native range, telemetry studies have identified diel behavioural patterns, upstream movement rates, resting sites and potential spawning grounds, and demonstrated the influence of environmental conditions on upstream passage (Almeida, Silva & Quintella, 2000; Andrade et al., 2007; Rooney et al., 2015). Several authors have quantified the negative spatial impacts that man-made structures can have on sea lamprey spawning migrations, including delaying upstream migration and preventing access to optimum spawning grounds (Almeida, Quintella & Dias, 2002; Castro-Santos, Shi & Haro, 2017; Silva et al., 2019).

In Great Britain, over 99% of catchments contain man-made barriers, and one barrier is estimated to exist for every 1.5 km of watercourse length (Jones et al., 2019). Understanding the movements of sea lamprey through highly fragmented river catchments typical of such areas is important, as the cumulative effects of multiple barriers can be considerable (Castro-Santos, Shi & Haro, 2017; van

Puijenbroek et al., 2019). The aim of this study was thus to quantify the spatial and temporal impacts of a series of man-made structures on sea lamprey migratory movements in the heavily fragmented River Severn catchment in western England. Sea lamprey are known to use this river system for spawning (Bird et al., 1994), with historical evidence suggesting that the construction of navigation weirs in the 19th Century resulted in rapid reductions in spawning populations of anadromous fishes upstream of the weirs, including of sea lamprey (Buffery, 2018). Today, the Severn Estuary has been designated as an SAC for which sea lamprey are a primary reason for designation (sac.jncc.gov.uk/site/UK0013030). Sea lamprey are also a feature of the Severn Estuary Site of Special Scientific Interest (SSSI) under the Wildlife and Countryside Act (designatedsites.naturalengland.org.uk), and further upstream in the catchment, the River Teme SSSI is noted as featuring sea lamprey spawning habitat (APEM, 2014). Here, through the application of passive acoustic telemetry, the objectives were to: (1) determine the passage and passage time, as well as cumulative spatial and temporal effects, of ten weirs for upstream-migrating sea lamprey in the River Severn catchment; (2) identify the individual and environmental drivers of migratory movements in obstructed and unobstructed river sections.

2.3 Methods

The River 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 lower river catchment is characterised by confluences with two major tributaries, the River Teme and River Avon, and by 10 major weirs (six on the main river channel, plus two on each of the lower reaches of the River Teme and River Avon) that result in high fragmentation (Figure 2.1, Table 2.1). The normal tidal limit is at Maisemore (hereafter S1a) and Llanthony Weirs (S1b) on the western and eastern branches of the river, respectively (Figure 2.1). Spring tides penetrate the river up to Upper Lode Weir (hereafter S2). With the exception of S2 and Powick Weir on the River Teme (T1), which had notch and Larinier fish passes, respectively, there were no fish-passage structures on the weirs at the time of study.

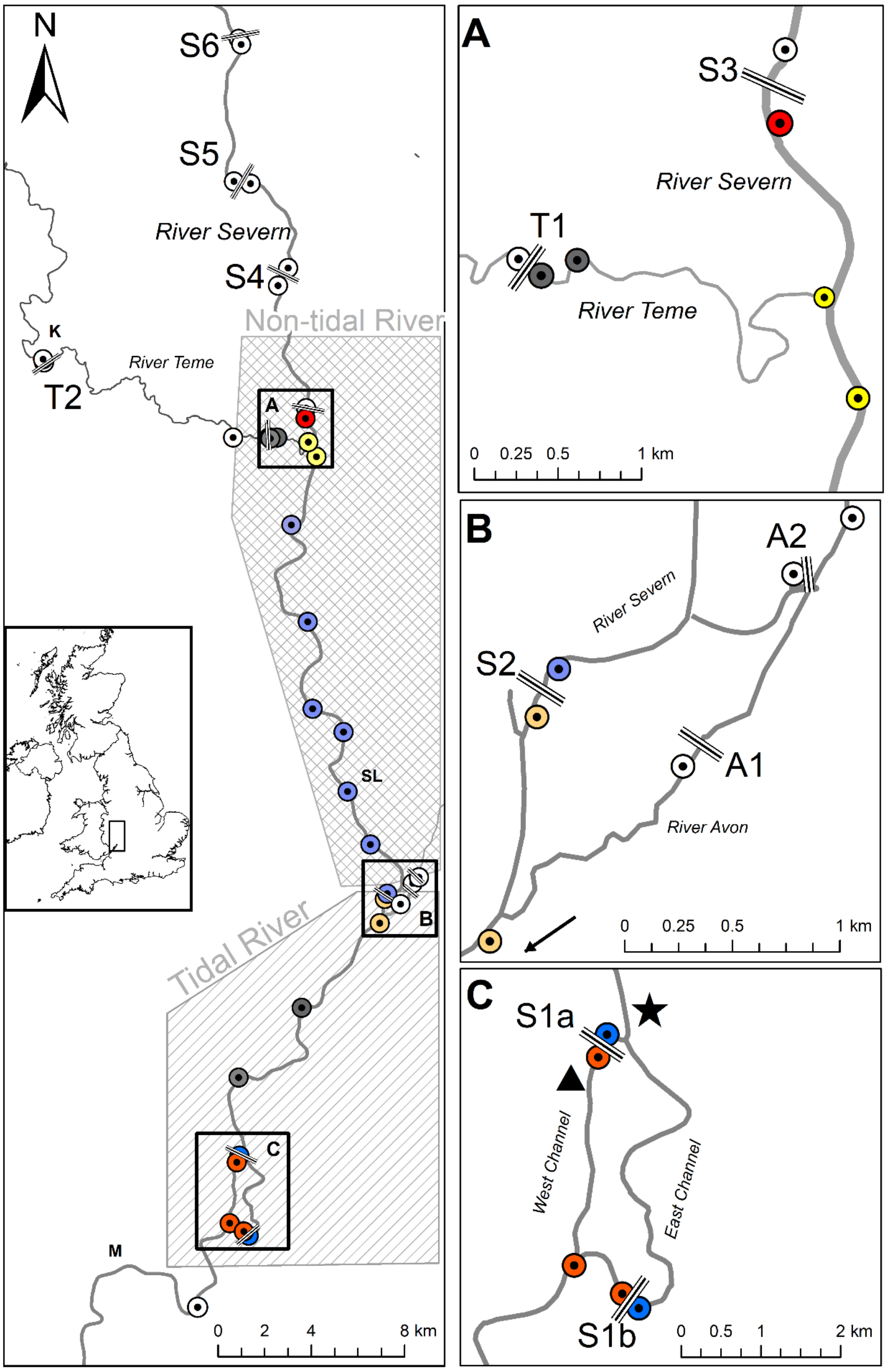

Figure 2.1: The River Severn catchment study area, including locations of capture (black triangle) and release (black star) of acoustic-tagged sea lamprey, weirs (bars) and acoustic receivers (circles) in the rivers Severn, Teme and Avon, UK. The weir codes are as in Table 2.1. Colour groupings of the receivers represent the river sections used in the modelling of sea lamprey movements; white receivers were not included. The dashed area (Tidal River) was used to model sea lamprey movements between the furthest downstream receiver and S2, and comprised four sections: Downstream S1a/S1b (three receivers, red), Upstream S1a/S1b (two receivers, blue), Middle Reach (two receivers, grey), Downstream S2 (two receivers, orange). The hatched area (Non-tidal River) was used to model movements in the river sections bounded by S2, S3 and T1 and comprised four sections; Upstream S2 (seven receivers, blue), Severn/Teme Confluence (two receivers, yellow), Downstream S3 (one receiver, red), Downstream T1 (two receivers, grey). The black arrow denotes the direction of the flow. M (Minsterworth), SL (Saxon's Lode) and K (Knightsford Bridge) denote the positions of gauging stations from which discharge and river level data were derived.

2.3.1 Sea lamprey sampling, tagging and tracking

The study was performed between May and July 2018 to coincide with the peak sea lamprey migration period in western Britain (Maitland, 2003). Migrating sea lamprey (‘lamprey’ in methods and results) were captured approximately 200 m downstream of S1a (Figure 2.1) using un-baited two-funnel eel pots (Lucas et al., 2009), and held in water-filled containers (100 L) prior to general anaesthesia (MS-222), weighing and measuring (nearest g, cm), and surgical implantation with a V9 acoustic transmitter (29 x 9 mm, 4.7-g weight in air, 69 kHz; www.innovasea.com). The transmitters featured a randomized 1-minute pulse interval (minimum interval between acoustic pulses 30 seconds, maximum interval 90 seconds). In all cases, tag weight in air was less than 2% of lamprey mass. In total, 60 adult lamprey were tagged and released over a three week period (Table 2.2). All lamprey were released immediately upstream of S1a, in order to assess the impacts of the multiple weirs upstream of this structure (which was not initially considered a major impediment to migration due to its tidal nature). All surgical procedures were completed under UK Home Office project licence PPL 60/4400. A summary of the lamprey biometric data and movement metrics is provided in the Appendix (Table A1). Four individuals did not move upstream after release so were removed from the dataset; thus analyses in this study focused on the movements of the 56 remaining individuals.

Table 2.1: Locations of study weirs in the River Severn catchment, which were used to assess the cumulative impacts of multiple weirs on the 2018 upstream migration of acoustic-tagged sea lamprey *Petromyzon marinus.* See Table 1.1 for more information on specific barriers on the Rivers Severn and Teme.

Weir code	Name	River	Location, decimal degrees[1]	Distance from normal tidal limit, rkm	Original function
S1a	Maisemore Weir	Severn (West Channel)	51.89318, -2.26574	0	Navigation
S1b	Llanthony Weir	Severn (East Channel)	51.86227 -2.26028	0	Navigation
S2	Upper Lode Weir	Severn	51.99346, -2.17407	16	Navigation
S3	Diglis Weir	Severn	52.17926, -2.22597	42	Navigation
S4	Bevere Weir	Severn	52.23256, -2.24027	49	Navigation
S5	Holt Weir	Severn	52.26812, -2.26576	54	Navigation
S6	Lincomb Weir	Severn	52.32290, -2.26596	61	Navigation
T1	Powick Weir	Teme	52.16975, -2.24712	44	Flow regulation
T2	Knightwick Weir	Teme	52.19908, -2.38940	60	Flow regulation
A1	Abbey Mill Weir	Avon	51.99133, -2.16325	16	Flow regulation
A2	Stanchards Pit Weir	Avon	51.99837, -2.15561	18	Flow regulation

[1] Coordinates provided use the World Geodetic System (WGS) 1984 geographic coordinate system

Lamprey were tracked using an array of 36 acoustic receivers (VR2-W, www.vemco.com) (Figure 1) deployed upstream and downstream of each navigation weir on the main channel and the flow-regulation weirs on the Rivers Teme, Avon and Mill Avon, with additional receivers deployed in unobstructed reaches between weirs. Receivers were anchored on steel fencing pins driven into the river bed. In the River Teme, which featured sections of fast-flowing riffle, receivers were deployed in slower-flowing pools to maximise detection performance. Data were downloaded from receivers every two weeks until no further movements were detected. Range tests revealed that 100% of test tag transmissions were detected a minimum of 100 m away from receivers in the River Severn, and a minimum of 50m away from receivers in River Teme. In all cases, detection range was greater than river width at receiver deployment location. Detection efficiency calculations (using three sequential receivers to determine the efficiency of the middle receiver) revealed that missed detections accounted for less than 0.1% of lamprey movements between receivers.

Table 2.2: Lengths and weights of sea lamprey *Petromyzon marinus* tagged in the lower River Severn in 2018

Date	***n***	**Mean ± SE length, mm (range)**	**Mean ± SE weight, g (range)**
3 May 2018	14	866 ± 35 (760-960)	1268 ± 144 (875-1700)
10 May 2018	26	835 ± 19 (710-920)	1186 ± 95 (800-1650)
15 May 2018	18	817 ± 25 (740-910)	1130 ± 105 (775-1650)
21 May 2018	2	840 ± 254 (820-860)	1337 ± 158 (1325-1350)

2.3.2 Environmental data

Environmental data were obtained by request from the Environment Agency’s gauging stations at Saxon’s Lode (‘SL’; discharge, River Severn) and Knightsford Bridge (‘K’; discharge, River Teme) (Figure 2.1). River levels for the tidal reaches downstream of S1a and S1b were determined by adjusting the levels at Minsterworth gauging station (position M on Figure 2.1) forward by 30 minutes (visually calibrated), to account for the observed delay between high tide at Minsterworth and S1a/S1b. All environmental data were collected at 15-minute intervals. In addition, water level and temperature data were collected by a logger immediately downstream of S2. To assess the representativeness of hydraulic conditions encountered by tagged lamprey during the study period, daily mean discharge values occurring during the study period (May-June 2018) measured at Saxon’s Lode gauging station were converted to exceedance percentiles and compared to the equivalent time period during the 10 previous years (2008-2017), using data obtained from the National River Flow Archive (https://nrfa.ceh.ac.uk/). This revealed discharge during May-June 2018 was not significantly different to the previous 10-year period (Wilcoxon Rank Sum, W = 87630, p = 0.96) (Figure 2.2).

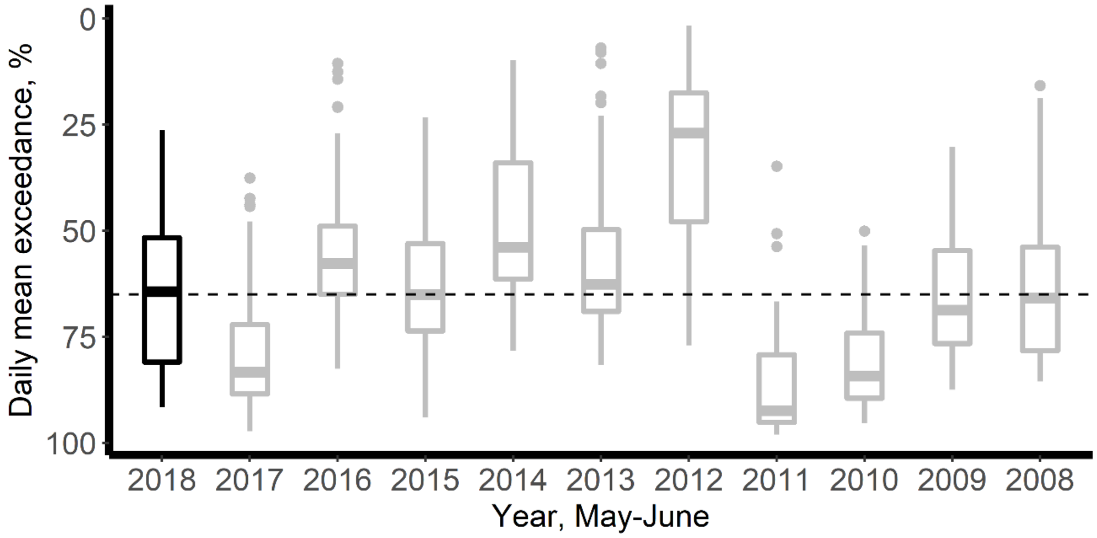

Figure 2.2: Boxplot of mean daily river discharge (exceedance, %) measured at Saxon's Lode gauging station on the River Severn during the study period (May-June 2018) and during the same period for the previous 10 years (2008 to 2017). The horizontal dashed line represents the median daily discharge during May-June, 2008-2017.

2.3.3 Per cent passage and passage time at weirs

For each weir in the study (Table 2.1), the number of lamprey that approached was calculated as a proportion of *n* available to approach, with available individuals defined as those that ascended the previous weir downstream. Then, per cent passage was calculated as the proportion of individuals detected on the downstream receiver (*n* approached) that were subsequently detected on the upstream receiver (*n* passed). To quantify migration delay for individuals that passed each weir, passage time was calculated as the time between the first detection on the downstream receiver and first detection on the upstream receiver; for comparison, passage times between successive receivers in unobstructed reaches upstream of the release site were also calculated.

2.3.4 Upstream extent, cumulative passage time and delay proportion

To understand the cumulative impact of successive weirs on movements, the proportion of the original cohort of 56 acoustic-tagged lamprey that passed each weir was calculated. To understand the upstream spatial distribution of migrants in the study area (and so the overall impact of the structures on the upstream migration of all tagged individuals), the furthest upstream extent for each individual lamprey was estimated as its location of furthest upstream detection on the receiver array. To quantify the cumulative time spent by lamprey between first approach and passage of weirs, total passage time was calculated for each individual as the sum total of passage times recorded at all weirs. To quantify the temporal impact of weir passage on total migration times, delay proportion (%) was calculated for each individual as the total passage time of weirs, as a proportion of the time between first upstream movement from the release site and upstream extent of migration. Delays incurred at S1a/S1b by lamprey that moved downstream of the release site immediately post-release (interpreted as fall back related to capture and tagging) were not included in total passage time calculations, but delays incurred by individuals that returned downstream of these structures after an initial upstream movement were included.

2.3.5 Continuous-time multistate Markov models

Continuous-time multistate Markov models (CTMMs) treat animal movements as a series of transitions between discrete states in continuous time (Miller & Andersen, 2008), and enable testing of the effects of time-dependent variables on the instantaneous rates of movements between different states (referred to as ‘transition rates’) (Nakayama, Ojanguren & Fuiman, 2011; Bravener & McLaughlin, 2013). Here, CTMMs were used to analyse the effects of time-dependent environmental variables (river discharge, river level, water temperature, day/night) and individual variables (body length, capture date) on upstream transition rates through sections of river that were either obstructed or unobstructed by weirs. Explanations of the terms used in the description and results of the CTMM process are provided in Table 2.3.

Table 2.3: Definitions of terms used in the continuous-time multistate Markov models of sea lamprey *Petromyzon marinus* movements in the River Severn catchment, measured in 2018

Term	Definition
Section	Contiguous length of river either unobstructed (no weir at upstream boundary) or obstructed (weir at upstream boundary)
Area	Tidal or non-tidal portions of the river
Transition rate	Modelled daily rate of movement from one section to another, i.e transitions/day, which can take any non-negative value. Baseline transition rates were modelled with covariates set to their mean value within the dataset
Downstream reversal	Upstream to downstream change in direction (not including final downstream movements)
Hazard ratio	Estimates of the effect on transition rates of increasing the value of a covariate by one unit, e.g. increasing river discharge by 1 m^3s^{-1}

In the model design, acoustic receivers were grouped into defined sections of river and into two section categories: obstructed and unobstructed. Obstructed sections encompassed between one and three receivers, and upstream exit by a lamprey from the section required passage of a weir. Unobstructed sections encompassed between two and seven receivers, and contained no weirs at their upper boundary. These groupings were used to compare upstream transition rates and the probability of downstream movements in obstructed versus unobstructed sections. In addition, they allowed the effects of environmental variables on upstream transition rates to be tested. To minimise the number of sections and thus avoid issues with non-convergence during modelling, the tidal (downstream of S2) and non-tidal river (upstream of S2) were modelled separately (Figure 2.1). S2 was used as the tidal limit as it is the upstream extent of most spring tides. The tidal river and non-tidal river both comprised of four sections, with receivers in each section grouped by colour in Figure 2.1. In the tidal river, the three receivers downstream of S1a (West Channel) and S1b (East Channel) were pooled (*Downstream S1a/S1b*) to reduce complexity and because the weirs are similar in terms of altitude, head-height and hydraulic conditions (Figure 2.1).

Correspondingly, lamprey left the tidal river at the time of their upstream passage of S2, and left the modelled area of the non-tidal river at the time of passage at either S3 or T1. Individuals were conservatively censored from the dataset after their final upstream movement, after which it was uncertain whether they remained motivated to migrate upstream, and their status could not be determined. Lamprey that moved downstream immediately after release, which was interpreted as capture-related fall back, were included in the model dataset at the point of their first upstream movement. Areas upstream of S3 and T1, were not included in the models, as the number of lamprey entering these areas was considered too low and the range of environmental conditions experienced was too narrow.

During data preparation, raw detection data for each lamprey were converted into hourly observations of location (section) and observations of transitions between sections, i.e. observations occurring at the exact time of the first detection on a receiver in the destination section. Observations were classified as occurring during the day or night using the *maptools* package (Bivand & Lewin-Koh, 2019), according to sunrise and sunset at the release site. Observations were then associated with individual metadata (body length, capture date) and hourly mean environmental data in the two datasets representing movements in the tidal and non-tidal river.

CTMM models were parameterised in the *msm* R package (Jackson, 2011). Upstream transition rates out of each section were modelled separately according to whether a lamprey had entered the section from a downstream or upstream direction. This was to avoid violating the Markov assumption that transitions depend only on the identity of the current section, since downstream-moving lamprey may have been more likely to leave in a downstream direction than upstream-moving lamprey. Model fitting was then conducted according to an information-theoretic approach (Burnham & Anderson, 2002); the model selection procedure is further described in Appendix 1. Following derivation of the best-fitting model in the tidal and non-tidal river areas, the daily transition rates of upstream-migrating lamprey were calculated for each transition between the river sections. Transition rates were considered significantly different if their 95% confidence intervals were non-overlapping (Nakayama, Ojanguren & Fuiman, 2011). For each section, the probability of upstream to downstream direction changes by upstream-migrating lamprey ('downstream reversals') were also derived. The effects of environmental covariates on upstream transition rates from each section were calculated and expressed as hazard ratios. A covariate effect was considered significant if the 95% confidence interval of its hazard ratio did not overlap with 1 (Nakayama, Ojanguren & Fuiman, 2011). All data analyses were completed in the R statistical software (version 3.5.1, R Core Team 2018).

2.4 Results

2.4.1 Approach, per cent passage and passage time at weirs

At the nine weirs upstream of the release site (Figure 2.1), the numbers of approaching lamprey and the per cent passage was highly variable (Table 2.4). The lowest per cent passage where at least 10 individuals approached was 12 % at S5 (*n* approached = 17, *n* passed = 2) and 40 % at T1 (*n* approached = 10, *n* passed = 4), and the highest was 100% at S4 (*n* approached and passed = 17). Approach rates at weirs in the River Avon were low; one individual approached A1 (2% of available), two approached A2 (4% of available), and no lamprey passed these structures. The greatest passage times occurred at S2 (median passage time (LQ-UQ) = 10.4 days (0.4 - 18.6), *n* approached = 56, *n* passed = 50) and at S3 (5.3 days (4.1 - 13.0), *n* approached = 40, *n* passed = 17) (Table 2.4). Passage times at these weirs were substantially greater than unobstructed passage times between receivers in the River Severn, where median passage times by upstream-migrating individuals were exclusively less than 0.2 days (Figure 2.3).

Table 2.4: Approach, per cent passage, passage time and cumulative impact of sea lamprey *Petromyzon marinus* at weirs in the River Severn catchment during their 2018 spawning period

Weir	*n* available[1]	*n* approached[2] (% of *n* available)	*n* passed (per cent passage)	Median passage time, days (25% quartile – 75% quartile)	% of tagged cohort passing
S1a	18	15 (83%)	15 (100%)	1.6 (0.1-2.8)	N/A[4]
S1b	18	3 (17%)	3 (100%)	N/A[5]	N/A[4]
S2	56	56 (100%)	50 (89%)	10.4 (0.4-18.6)	89%
S3	50	41 (82%)[3]	17 (41%)	5.3 (4.1-13.0)	30%
S4	17	17 (100%)	17 (100%)	0.2 (0.1-0.3)	30%
S5	17	17(100%)	2 (12%)	6.1 (4.9-7.2)	4%
S6	2	0 (0%)	N/A	N/A	0%
T1	50	10 (20%)[3]	4 (40%)	0.1 (0.0-0.1)	7%
T2	4	4 (100%)	4 (100%)	N/A[5]	7%
A1	56	1 (2%)	0 (0%)	N/A	0%
A2	50	2 (4%)	0 (0%)	N/A	0%

[1] Individuals moving upstream through the unobstructed reach of river downstream of the weir

[2] Individuals detected immediately downstream of the weir

[3] Includes three individuals (S3, *n* = 1; T1, *n* = 2) missed by the downstream receiver but detected upstream

[4] Tagged sea lamprey were released upstream of S1a and S1b

[5] Passage times unavailable due to missed detections on the downstream acoustic receivers

There were 13 lamprey detected in the River Teme, of which four moved into this tributary during their first upstream movement from S2. The remaining nine moved upstream in the Severn past the Teme confluence, and approached S3, before returning downstream and entering the River Teme. Eighteen lamprey moved downstream of the release site at S1a before returning upstream and passing either weir S1a (*n* approached and passed = 15, 100 %) or S1b (*n* approached and passed = 3, 100 %).

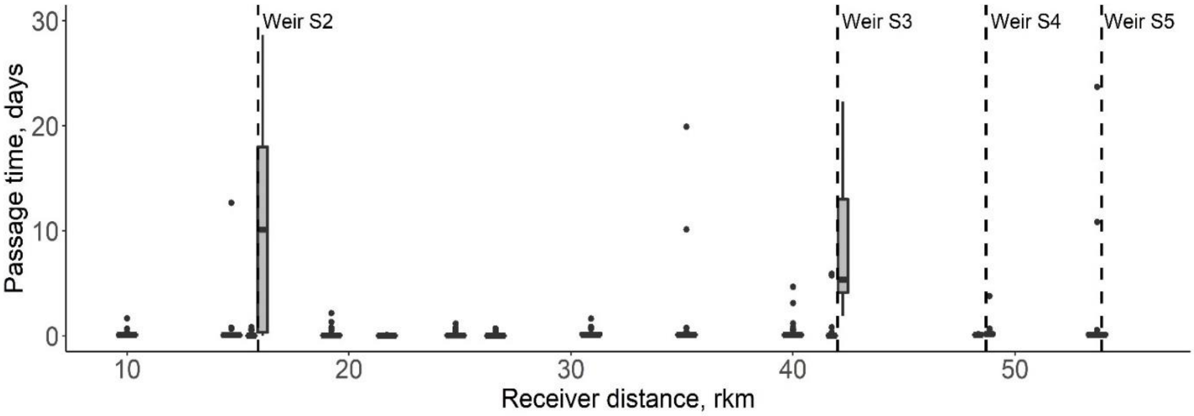

Figure 2.3: Net upstream passage time of sea lamprey recorded between receivers in the River Severn during their 2018 spawning migration. Passage time was calculated as the difference in time between the last detection on the downstream receiver and first detection on the upstream receiver. Passage times are displayed at the location (rkm) of the upstream receiver in each pair. Vertical dashed lines represent the location of weirs lying between receivers.

2.4.2 Upstream extent, cumulative passage time and final location

The mean (± 95% CI) distance moved upstream by lamprey relative to the release site was 50.0 ± 3.4 rkm (Figure 2.4). Four lamprey passed T2 into an area outside of the receiver array, so the upstream extent of their movements could not be determined. Of the remaining 52 lamprey, 44 (85 %) reached the upstream extent of their migration immediately downstream of a weir; S3 = 17 (33 % of remaining individuals), S5 = 15 (29 %), S2 = six (12 %) and T1 = six (12 %) (Figure 2.4). Six (12 %) lamprey that passed S2 did not approach S3 or T1, with the most upstream detection occurring at the confluence of the Teme and Severn (2 rkm downstream of S3) (*n* = 2), Severn Stoke (11 rkm downstream of S3) (*n* = 2) or immediately upstream of S2 (*n* = 2) (Figure 2.4). The two lamprey that passed S5 did not approach S6. Individuals that passed weirs upstream of the release site took 21.6 ± 2.8 days to reach their upstream extent after their first upstream movement (*n* = 50), and experienced cumulative passage times at weirs of 15.7 ± 2.8 days. Cumulative passage time at weirs constituted a median of 84 % of the time taken to reach the upstream extent of migration (mean proportion: 68 ± 9 %). For 13 lamprey (23%), their upstream extent of migration was also their final detection location, while 43 (67%) made downstream movements after reaching their most upstream location. Of these, 31 were last detected on a receiver within the array, and 12 were last detected on the most downstream receiver and their approximate final location could not be determined.

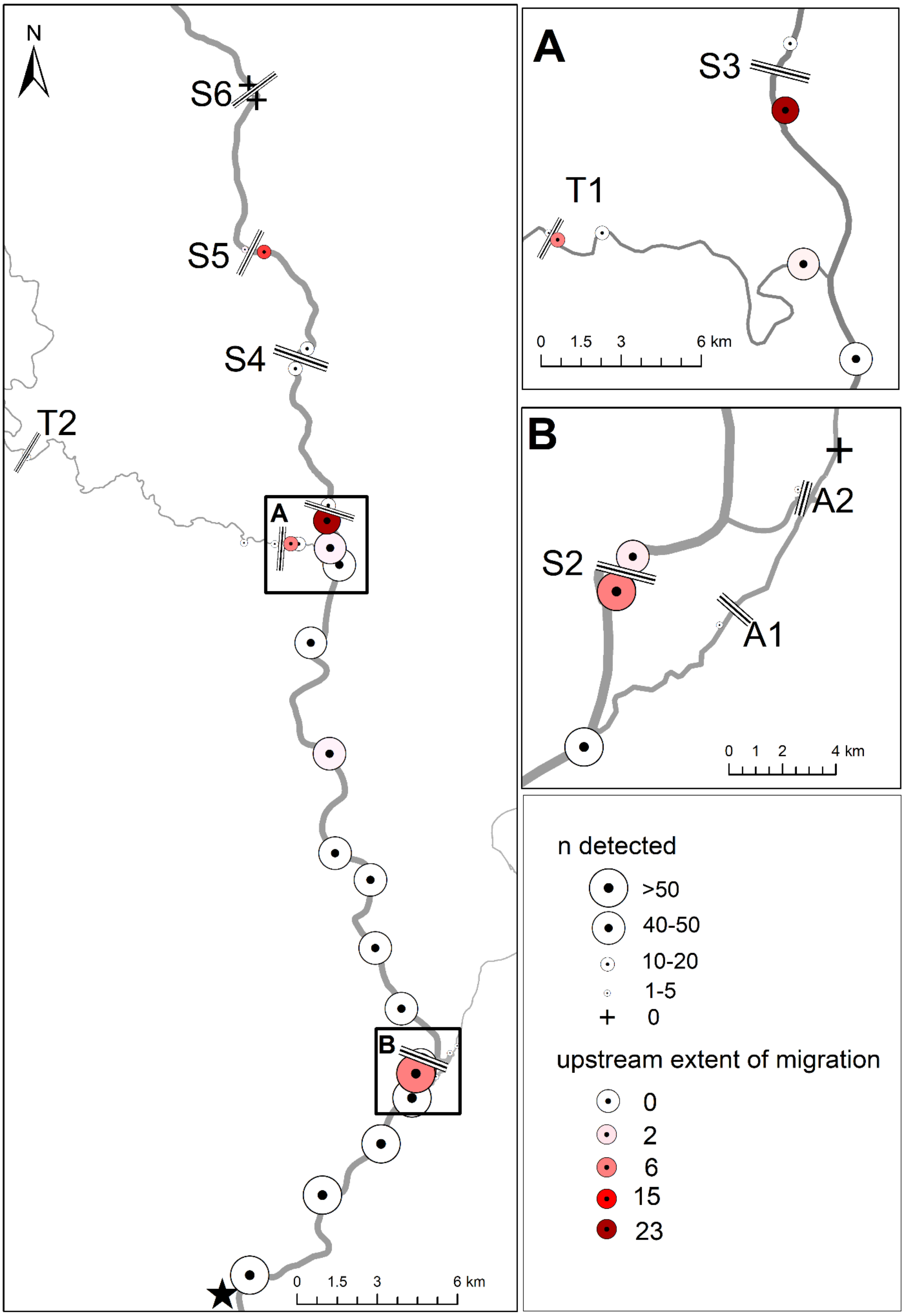

Figure 2.4: The upstream extent of 56 acoustic-tagged sea lamprey in the River Severn catchment during the 2018 spawning migration. The number of sea lamprey reaching each receiver, and the number of upstream extents of migration by individual sea lamprey at each receiver, are represented by the size and colour intensity of the circles, respectively. The weir codes are as in Table 2.1.

2.4.3 Continuous-time multistate Markov modelling of lamprey movements

The best fitting CTMM describing the movements of lamprey between river sections in the tidal and non-tidal river are presented in Tables 2.5 and 2.6, respectively. The full ranked suite of tested models is provided in Appendix Table A2

In the tidal river, the rate of upstream passage by lamprey at weirs S1a/S1b was positively affected by river level associated with spring tide periods, and the rate of upstream passage at S2 was positively affected by river discharge during an elevated discharge event (Table 2.5; Figure 2.5). The effect of discharge was non-significant for upstream movements through unobstructed sections, and upstream transition rates were significantly higher at night than during the day for all sections (Table 2.5). The probability of downstream reversal during upstream migration was significantly greater in *Downstream S2*, where approximately half of upstream movements resulted in a downstream reversal (probability, 95% CI = 0.51, 0.40-0.62), than in the two unobstructed sections, where downstream reversals were relatively unlikely (*Middle reach*: 0.02, 0.00-0.15; *Upstream S1a/S1b*: 0.01, 0.00-0.10) (Table 2.5).

Table 2.5: Best-fitting continuous-time multistate Markov model for the Tidal River Severn describing the upstream movements of 56 sea lamprey between four sections of the River Severn in 2018 and including passage at S1a/S1b and S2 (Figure 2.1). Baseline transition rates with covariates set to their mean values. Coefficients with a hazard ratio not overlapping 1 (**bold**) were considered significant for each transition.

Transition	**Length, km**	**Obstructed**	**N transitions**	**Baseline transition rate (transitions day^{-1})**	**Coefficient hazard ratios (95% CI)**			**Probability of downstream reversal**
					Discharge, m^{3}s^{-1}	**River Level, m**	**Light:night**	
Downstream S1a/1B → Upstream S1a/S1b	3.0	Yes	30	0.11 (0.06-0.19)	NA	**4.1 (2.6-6.6)**	**4.5 (2.0-10)**	NA
Upstream S1a/S1b → Middle Reach	4.0	No	74	0.75 (0.56-1.06)	1.1 (1.0-1.2)	NA	**5.1 (3.1-8.5)**	0.01 (0.00-0.10)
Middle Reach → Downstream S2	11	No	76	1.54 (1.10-2.10)	1.0 (0.9-1.1)	NA	**4.2 (2.5-7.2)**	0.02 (0.00-0.15)
Downstream S2→ Upstream S2	1.3	Yes	50	0.05 (0.03-0.08)	**1.5 (1.4-1.6)**	NA	**6.1 (3.3-11)**	0.51 (0.40-0.62)

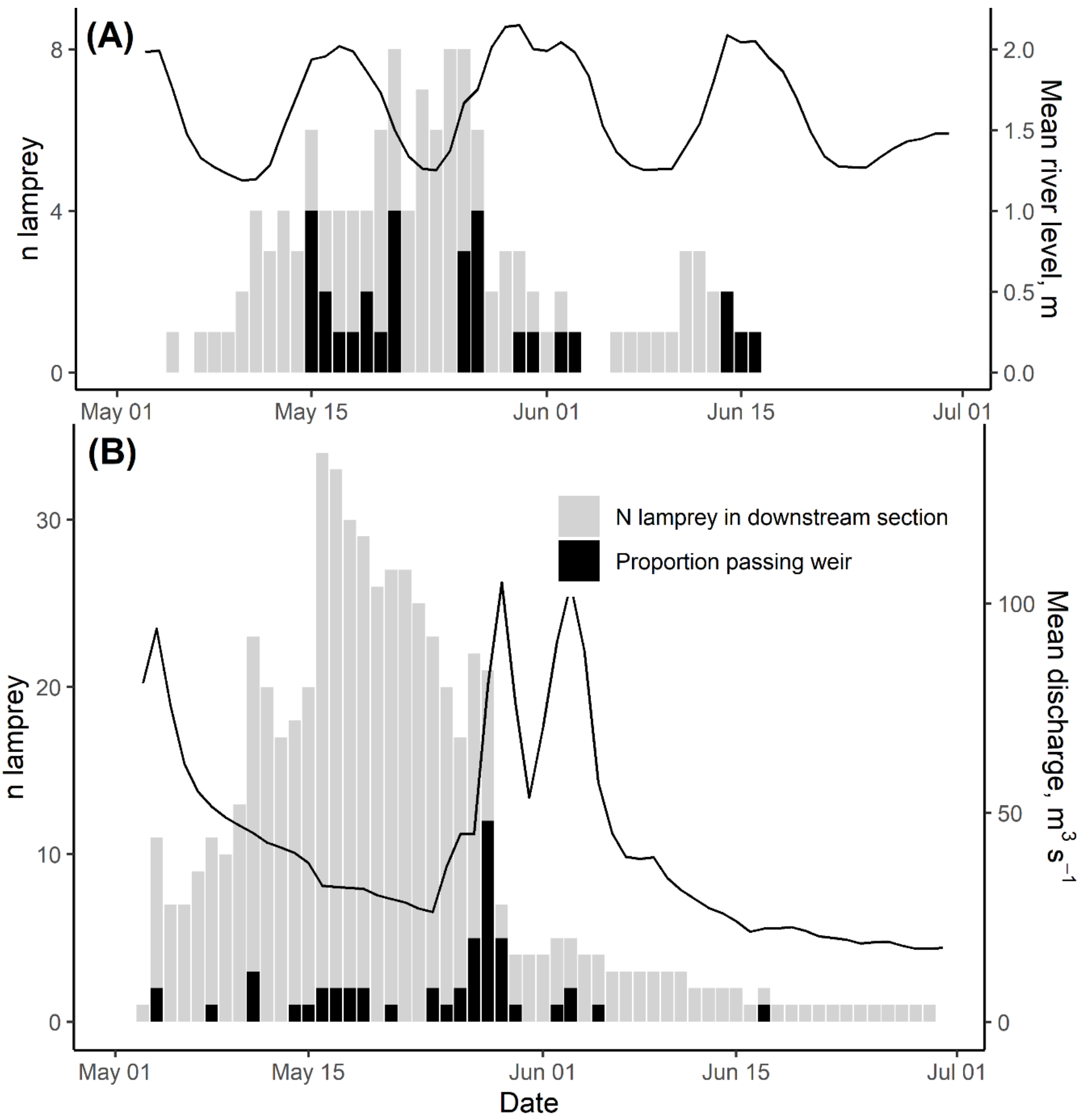

Figure 2.5: (A) Daily presence of acoustic-tagged sea lamprey (grey bars) in the 'Downstream S1a/S1b' section of the River Severn, and the proportion passing the weirs (black bars) into the 'Upstream S1a/S1b' section during May-June 2018. (B) Daily presence of acoustic-tagged sea lamprey (grey bars) in the 'Downstream S2' river section, and the proportion passing the weir (black bars) into the 'Upstream S2' section. Daily mean river level (Minsterworth gauging station) and river discharge (Saxon's Lode gauging station) are presented as black lines.

In the non-tidal river, increasing river discharge had a significant positive effect on the passage rates of S3 and T1 (Table 2.6), with weir presence/passage data revealing that lamprey passed these structures exclusively during elevated discharge events when mean daily discharge exceeded 60 m^3s^{-1} / Q_{45} in the River Severn and 30 m^3s^{-1} / Q_{17} in the River Teme (Figure 2.6). Discharge also had a positive effect on most unobstructed transition rates (Table 2.6). For all sections, upstream transition rates were greater at night, although uncertainty around the hazard ratios was high and non-significant for passage at S3 and T1. The best-fitting model in the non-tidal river included an interaction term between river discharge and day/night. This interaction was significant for upstream transitions from *Upstream S2* to *Severn/Teme Confluence*, with a hazard ratio less than 1 indicating that the positive effect of night on transition rates between these sections decreased as discharge increased. The section-specific probability of downstream reversal was significantly greater in *Downstream S3* (probability, 95% CI = 0.66, 0.47-0.74) and *Downstream T1* (0.55, 0.25-0.83) than in *Severn/Teme Confluence* (0.02, 0.00-0.12) (Table 2.6).

Table 2.6: Best-fitting continuous-time multistate Markov model describing the upstream movements of 50 sea lamprey between four sections of the rivers Severn and Teme during their 2018 spawning migration, and including passage at S3 and T1. Baseline transition rates with covariates set to their mean values. Coefficients with a hazard ratio not overlapping 1 (**bold**) were considered significant for each transition

Transition	**Length, km**	**Obstructed**	**N Transitions**	**Baseline transition rate (transitions day^{-1})**	**Coefficient hazard ratios (95% CI)**				**Probability of downstream reversal**
					Discharge Severn m^3s^{-1}	**Discharge Teme, m^3s^{-1}**	**Light (night)**	**Discharge: light(night)**	
Upstream S2 → Severn Teme Confluence	24	No	46	0.34 (0.19-0.37)	**1.2 (1.1-1.4)**	NA	**13 (2.8-61)**	**0.7 (0.6-0.9)**	NA
Severn/Teme Confluence →Downstream S3	1.8	No	45	1.04 (0.46-1.48)	**1.4 (1.3-1.5)**	NA	**20 (4.0-96)**	**0.8 (0.7-1.0)**	0.02 (0.00-0.12)
Downstream S3 →Upstream S3	1	Yes	17	0.01 (0.00-0.02)	**1.7 (1.4-2.1)**	NA	13 (0.03-585)	1.0 (0.7-1.6)	0.62 (0.47-0.74)
Severn/Teme Confluence → Donwstream T1	3.3	No	12	0.11 (0.04-0.20)	NA	2.3 (0.9-5.5)	34 (0.2-460)	1.2 (0.7-2.1**)**	0.02 (0.00-0.12)
Downstream T1 →Upstream T1	1	Yes	4	0.08 (0.00-0.30)	NA	**1.2 (1.0-1.4)**	188 (0.1-300)	0.4 (0.2-1.2)	0.55 (0.25-0.83)

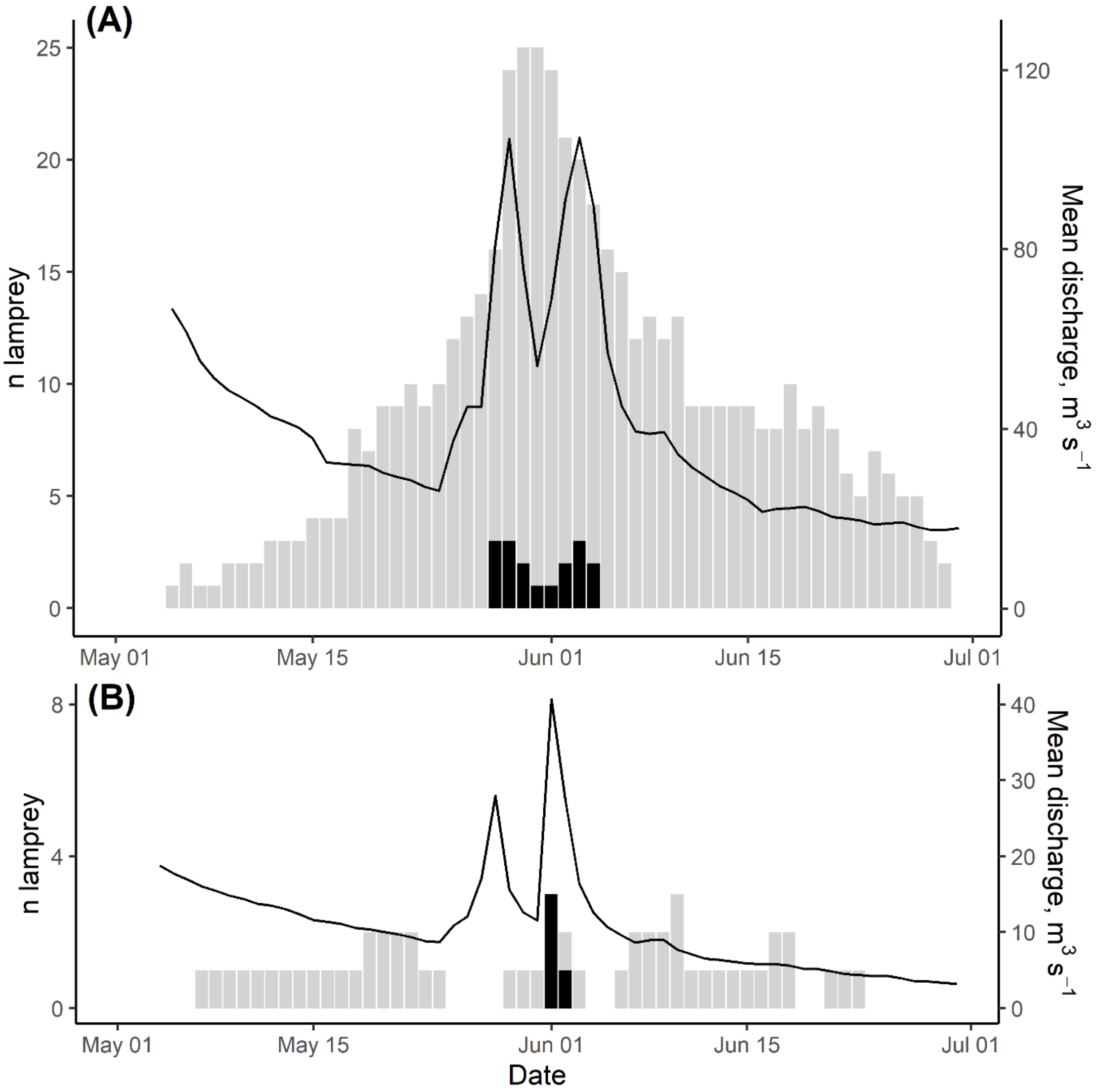

Figure 2.6: (A) Daily presence of acoustic-tagged sea lamprey (grey bars) in the ‘Downstream S3’ section of the River Severn and the proportion passing the weir (black bars) into the ‘Upstream S3’ section during May-June 2018. (B) Daily presence of acoustic-tagged sea lamprey (grey bars) in the ‘Downstream T1’ river section, and the proportion passing the weir (black bars) into the ‘Upstream T1’ section. Daily mean river discharge (Saxon’s Lode gauging station, River Severn, and Knightsford Bridge gauging station, River Teme) is presented as black lines.

2.5 Discussion

Knowledge of animal movements in fragmented ecosystems is essential to understand, predict and mitigate the impacts of fragmentation. Here, passive acoustic telemetry provided strong evidence that weirs consistently acted as impediments to the upstream migration of adult sea lamprey in the River Severn catchment. The impacts of these impediments on sea lamprey migration were both spatial (inhibiting access to favourable spawning areas upstream, inducing downstream exploratory movements) and temporal (delaying passage and restricting the opportunity for upstream migration to episodic environmental events).

2.5.1 Cumulative impacts of man-made structures on upstream-migrating sea lamprey

Low-head weirs and other structures (< 2 m head loss), which are estimated to represent around 99.5% of man-made impediments globally (Lehner et al., 2011), can impact the ability of anadromous aquatic species to complete their spawning migrations through physical impediment and habitat loss (Gibson, Haedrich & Wernerheim, 2005; Lucas et al., 2009; Birnie-Gauvin, Aarestrup, et al., 2017). The consequences of riverine habitat fragmentation on anadromous populations can been severe (Limburg & Waldman, 2009; Hall, Jordaan & Frisk, 2011). For sea lamprey, the negative impacts of man-made structures on their migration have now been observed in telemetry studies across their native range (Andrade et al., 2007; Castro-Santos, Shi & Haro, 2017; Silva et al., 2019), with historical evidence suggesting that access to available spawning habitat is drastically reduced (Mateus et al., 2012). Here, the impacts of multiple man-made structures on upstream sea lamprey migration appeared to be cumulative; while no weir on the Severn or Teme was a complete barrier to upstream migration, the majority of structures inhibited a proportion of the upstream-migrating cohort, to the extent that no individuals migrated as far as the most upstream navigation weir on the River Severn. This cumulative effect of low-head weirs on lamprey migration has been apparent elsewhere, where low per cent passage across multiple weirs resulted in only a small fraction of upstream migrants passing all weirs (Keefer et al., 2009; Castro-Santos, Shi & Haro, 2017). The temporal effects of weirs on individuals were also cumulative, with median total passage times of 16.2 days, constituting 84 % of the time taken to reach the most upstream location. In other migratory species, temporal delay to migration has been linked to multiple impacts on fitness, including loss of condition and increased risk of predation (Nyqvist et al., 2017; Newton et al., 2018); here, temporal and spatial effects were likely to be interlinked, with sexual maturation and energetic consequences of delay reducing the ability of individuals to pass weirs.

2.5.2 Downstream movements during upstream migration

Overall counts or percentages of animals that pass man-made structures are important metrics for describing the impacts of barriers on migration, but further temporal and behavioural/energetic impacts should be considered to provide a comprehensive impact assessment (Castro-Santos, Shi & Haro, 2017; Silva et al., 2018; Birnie-Gauvin et al., 2019). In addition to temporal delays experienced by sea lamprey at weirs, this study highlighted that downstream reversals occurred with substantially higher probabilities in obstructed sections versus unobstructed sections during upstream migration. These downstream movements, a rarely considered consequence of barriers, might represent a behavioural mechanism to locate alternative passage routes and spawning grounds when upstream access is impeded; however, when this exploration is unsuccessful, the energetic costs incurred may be a further impact of habitat fragmentation on their migration. The energetic impacts of such movements in sea lamprey remain poorly understood, but may be particularly significant given that the species is semelparous, ceasing feeding after entering freshwater, and relying on stored energy reserves to migrate upstream and spawn (Araújo et al., 2013). While the section-specific probabilities of downstream movements presented here are a simplistic descriptor and did not account for temporal variation, the biotic and abiotic factors affecting downstream movements, and impacts of exploratory movements on individual migration success, are recommended as requiring further exploration.

2.5.3 Impact of weirs on probable spawning areas of sea lamprey

Here, of the 52 individuals that did not leave the array, 44 (85%) achieved a maximum upstream extent that was immediately downstream of a man-made structure. Sea lamprey are known to aggregate and spawn downstream of weirs (Smith & Marsden, 2009; Pinder et al., 2016), but the reaches downstream of weirs in the River Severn did not feature the ‘typical’ sea lamprey spawning characterised by shallow riffle areas of gravel and cobble (Maitland, 2003; Andrade et al., 2007; Rooney et al., 2015). It was thus assumed that a high proportion of sea lamprey in this study spawned in ‘atypical’ habitat, which has potential implications for subsequent recruitment. For the 14 % of individuals that achieved an upstream extent that was not immediately downstream of a weir, their fate was unknown, including whether they located spawning habitat within the impounded reaches of the lower River Severn or were predated during their upstream migration (Boulêtreau et al., 2020). Although some studies have visually quantified lamprey spawning habitat in relation to the location of tagged individuals (Andrade et al., 2007; Lucas et al., 2009), it was not possible in the lower River Severn due to its relatively high turbidity and depth. A study in the Connecticut River, where high-quality sea lamprey spawning habitat exists in the reaches of river between man-made structures, found that between 36 and 75 % of lamprey that passed weirs did not then approach the next weir (Castro-Santos, Shi & Haro, 2017), although non-approaching individuals were subject to substantial delays which reduced their ability to approach the next structure. Here, relatively few individuals (14%) reached an upstream extent in the unobstructed areas between weirs, potentially suggesting a relative lack of suitable spawning habitat in these areas. Notably, the final detection location for the majority of sea lamprey was downstream of their most upstream location, which was potentially indicative of an abandonment of the upstream migratory effort and an attempt to locate the most suitable spawning habitat further downstream. While it was beyond the scope of this study to attempt to identify exact spawning locations, it was also notable that some of these terminal downstream movements were extensive, including a proportion of individuals that returned to the estuary downstream of the receiver array. However, such long-distance movements are difficult to interpret, and have been interpreted elsewhere as post-spawning movements (Holbrook et al., 2016), or even the movements of dead or dying individuals being carried downstream (Havn et al., 2017).

2.5.4 Influence of environmental conditions on weir passage

Several studies have observed inconsistent ammocoete length distributions in areas upstream of weirs; weak annual length classes are often coincident with low discharge during the corresponding spawning periods, implying that upstream passage by adult sea lamprey at man-made structures may only be possible during favourable environmental conditions (Andrade et al. 2007; Nunn et al. 2008, 2017). Here, rates of upstream passage at weirs S2, S3 and T1 increased during episodic periods of elevated river discharge. Indeed, upstream passage at the latter two of these structures occurred exclusively during two periods of elevated discharge following heavy rain at the end of May and in early June. The results indicate that the prevailing flow conditions during the migration season may strongly impact the ultimate distance upstream achieved. For example, at S3, the passage of 17 individuals occurred exclusively above a flow exceedance of Q_{45}; historical discharge data for the previous ten years (Figure 2), thus indicates certain years (2017, 2011, 2010) would have provided few opportunities for passage of S3 during the typical sea lamprey migration, and other years (2012, 2014) where upstream migration may have been aided by higher than normal discharge. The results also suggest that passage times during high discharge periods may be short; indeed, at S4, approach and passage occurred exclusively during the same high flow event that enabled passage at S3, and resulted in 100% passage over a median of 0.2 days. The results highlight that under certain flow conditions, barriers become ‘passable’, potentially due to the weir being inundated and thus reducing flow velocities experienced by sea lamprey attempting to ascend the weir face. In highly tidal areas downstream of the release site, CTMM indicated that river level significantly increased upstream passage rates at the tidally affected S1a/S1b. Spring tides overwhelming these two weirs appeared to be an enabling factor for sea lamprey passage, and probably contributed to the relatively high per cent passage and upstream transition rates of sea lamprey at these structures compared with less tidally influenced weirs further upstream.

2.5.5 Movements in unobstructed reaches

In the non-tidal river, upstream passage rates in unobstructed sections increased significantly with increasing river discharge, suggesting that elevated flow events may act as a stimulus to upstream migration. Previous studies have shown that sea lamprey may halt migration away from weirs, with episodic flow pulses stimulating further upstream movements (Almeida, Quintella & Dias, 2002), and this effect is widely reported in other migratory species (Lucas & Baras, 2001; Thorstad et al., 2008). Here, sea lamprey movements were generally highly nocturnal, but during elevated flow periods there was evidence that this nocturnality decreased in the unobstructed sections upstream of S2, but not for weir passages. Consistent with these findings, other studies have found that nocturnality in Pacific lamprey *Entosphenus tridentatus* may be context dependent, and can be affected by reach type, with nocturnality strongest around weirs, and weakest in unfragmented reaches (Keefer, Caudill, et al., 2013).

Sea lamprey are unusual among anadromous species in that they do not exhibit homing behaviour to natal rivers, but rather select rivers based on innate physiochemical cues (Bergstedt & Seelye, 1995; Waldman, Grunwald & Wirgin, 2008), with tributary selection positively influenced by the presence of pheromones released by ammocoetes, as well as nesting males (Buchinger et al., 2015). In the present study, sea lamprey displayed a preference for certain migration paths when presented with tributary choices; only one entered the Mill Avon (i.e. A1) and two entered the Warwickshire Avon (i.e. A2), with all three ultimately returning to continue up the River Severn. For upstream-migrating sea lamprey at the Severn/Teme confluence, transition rates were significantly higher towards S3 on the River Severn, than T1 in the Teme, suggesting that the Severn was the preferred upstream migration route. Indeed, of the 13 sea lamprey that were detected in the River Teme, nine were first detected at the receiver downstream of S3 (1.3 km upstream of the confluence with the River Teme), and were subsequently detected in the River Teme after a downstream movement away from S3.

2.5.6 *Implications for conservation and management of sea lamprey*

The River Severn once supported extensive fisheries for sea lamprey that declined following construction of the navigation weirs in the 19th century (Buffery, 2018). Today, the sea lamprey is a designated feature of the Severn Estuary SAC under the European Union Habitats Directive, and a feature of the Severn Estuary SSSI under the Wildlife and Countryside Act (Joint Nature Conservation Committee 2015). The condition of the sea lamprey population in the Severn Estuary SAC is currently assessed as ‘unfavourable’, and the unimpeded passage of adults within spawning tributaries in the catchment is recognised as being required, in order to achieve favourable status (Natural Resources Wales, 2018; Natural England & the Countryside Council for Wales, 2009). While the persistence of sea lamprey within the fragmented Severn catchment is ultimately reliant on the ability of adults to spawn and larvae to then survive in sub-optimal habitats (Almeida and Quintella, 2002; Dawson et al., 2005), this study highlights the issue of migration blockages that inhibit the access of adults to optimal spawning areas in the upper catchment. Generally, physical barriers that limit access to historical river habitat, combined with poor water quality are thought to be responsible for the low numbers of sea lamprey within the UK rivers, with improvements required to maintain the species at favourable conservation status (Joint Nature Conservation Committee, 2019). Consequently, the results emphasise the need for barrier removal, or the retro-fitting of fish passes on structures in the Severn catchment that inhibit passage but that cannot be removed. Previous studies have demonstrated that such actions, when well-implemented, have the potential to allow rapid colonisation of upstream areas (Moser et al., 2020). Fish passage improvement works in the Severn should incorporate the needs of sea lamprey, as well as other species, in their design if target passage rates are to be achieved (Silva et al., 2018), and the species-specific knowledge base (e.g. Hume et al., 2020) should be integrated within fish pass designs.

More widely, the results presented here are relevant for the restoration and conservation of sea lamprey populations across their native range, and illustrate how knowledge of riverine connectivity for sea lamprey can present managers with alternative remediation strategies to consider. For example, based on the cumulative impact of multiple weirs in this study, it could be argued that passage remediation efforts should focus initially on improving passage at the furthest downstream structures before working on structures further upstream. An alternative strategy would be to improve passage in the tributaries that provide the greatest area of available upstream spawning habitat, provided that mainstem barriers further downstream allow a proportion of adults to access such tributaries. As Moser et al. (2020) summarise, multiple studies indicate that when an opportunity to exploit reopened habitat is presented, rapid colonisation can occur by pioneering individuals, establishing new core areas of larval production that promotes further attraction of adults in future years. This point is especially relevant given the finding here that sea lamprey can move downstream to locate alternative spawning tributaries when their primary route is inhibited; the majority of sea lamprey that moved into the River Teme tributary only did so having first moved upstream in the Severn. Therefore, barrier remediation at T1 would open an important spawning tributary for sea lamprey that were unable to pass S3. In other rivers that have channels that are more braided or have more tributaries than the Severn, greater consideration might be needed on deciding which channels and tributaries are the most appropriate for these remediation efforts; these decisions should be underpinned by an intimate knowledge of barrier permeability (Moser et al., 2020), which as demonstrated here has the potential to vary substantially depending on environmental conditions within and between years.

2.5.7 Further research

While the results indicated that weirs limit the upstream distribution of sea lamprey spawning in the catchment to impounded sections, the impacts of habitat fragmentation on ultimate spawning success remains unknown and requires further investigation. In particular, the importance of areas immediately downstream of weirs as spawning habitat needs more consideration, and quantifying habitat availability, spawning activity and reproductive success in these areas should be prioritised in fragmented river catchments (Pinder et al., 2016). Further investigations, potentially coupling telemetry in adults with assessments of ammocoete distribution, are required to study the effects of inter-annual variation and trends in environmental conditions during the migration season on catchment-wide distributions of sea lamprey, especially in the context of changing climatic patterns. Finally, given the emphasis here on fish passes having high potential for increasing passage connectivity, further work is needed to find optimal designs that maximise sea lamprey passage rates. While challenging, this work will be essential to ensure that sea lamprey populations are to remain sustainable in fragmented lowland rivers.

3 Patterns, causes and consequences of individual movement variation in upstream-migrating sea lamprey *Petromyzon marinus* in a highly fragmented river

See https://doi.org/10.1111/fwb.13869 for the published article

See https://eprints.bournemouth.ac.uk/36323/ for an accepted version of the article in a university repository

4 Novel insights into the marine phase dispersal and river fidelity of anadromous twaite shad

4.1 Abstract

1. Most research on anadromous fishes has been invested in their freshwater life-phases, resulting in a relatively sparse understanding of their spatial ecology during marine life-phases. However, understanding the marine dispersal of anadromous fishes is essential to identify threats, and implement conservation measures that fully encompass their lifecycle.

2. The twaite shad *Alosa fallax* is an anadromous fish increasingly imperilled across its range due to pollution, harvesting and impediments to freshwater migration, but little is known about its distribution and movements during its marine life-phase. Here, the application of acoustic telemetry provided novel insights into the coastal dispersal of twaite shad in the UK and Ireland during 2018/19, and the freshwater entry of individuals during the 2019 spawning season.

3. Of 73 twaite shad acoustic-tagged during their upstream migration in the River Severn in May 2018, 58 emigrated from the river. Twelve were subsequently detected 200 km to the south-west at the Taw-Torridge Estuary between July 2018 and April 2019, where estuarine movements up to 5.8 km inland occurred in summer, winter and spring. One was subsequently detected in the Munster Blackwater Estuary (Ireland) and then in the River Severn, indicating a minimum movement distance of 950 km. Thirty-four (59%) of the emigrating individuals from 2018 re-entered fresh water in the Rivers Severn (n = 33) and Wye (n = 2) in April and May 2019.

4. These results suggest year-round use of estuarine and nearshore habitats by at least a subset of the twaite shad population during their marine phase, and provide evidence of potential range overlap between populations that spawn in different areas in the UK and Ireland, which may be facilitated by substantial dispersal. The results also highlight the potential of telemetry for estimating

freshwater and marine mortality, and the benefits of sharing detection data across networks.

4.2 Introduction

Populations of anadromous fishes are increasingly threatened by anthropogenic disruptions to their lifecycles, occurring in freshwater and marine environments (Limburg and Waldman, 2009). In many anadromous species, the research focus has tended to be on their freshwater life-phase, but marine processes and anthropogenic threats may be a principle driver of population declines in some species and populations (Chaput, 2012). In order to implement conservation measures that fully encompass their lifecycle, a more complete understanding of the marine life-phases of anadromous fish is required (Drenner et al., 2012). Key knowledge gaps relate to their spatial ecology while at sea, including habitat use, dispersal and mortality rates, as well as population-specific distribution and connectivity (McLean et al., 1999). Addressing these knowledge gaps may help to mitigate marine-specific threats including harvesting and accidental bycatch, and to understand the impacts of human-induced climate change (Dunton et al., 2015)

An anadromous fish that is becoming increasingly imperilled across its range is the twaite shad (*Alosa fallax*), which has a distribution across the north-eastern Atlantic and Mediterranean. Their riverine migration period lasts for approximately three months, with peak river entry periods varying from February in the south of its range to May/June in the north (Aprahamian et al., 2003a). Individuals that have spawned in previous years often represent over 50 % of the spawning run (Aprahamian et al., 2003b). After spawning, surviving adults return to the marine environment, and initial seaward migration by the young-of-the-year occurs in summer and autumn (Aprahamian, 1988). Severe declines and extirpations of twaite shad populations in European rivers have been attributed to pollution, overfishing in fresh water, and man-made structures which inhibit their upstream spawning migration (de Groot, 1990; Aprahamian et al., 2003a; Antognazza et al., 2019). Concerns over twaite shad population declines are reflected in conservation legislation, with the species listed in Annexes II and V of the Habitats Directive and Appendix III of the Bern Convention (Aprahamian et al., 2010). Spawning populations of twaite shad in the UK, where twaite shad are subject to additional protection under the Wildlife and Countryside Act, are now limited to four rivers: the Severn, Wye, Usk and Tywi. Four rivers in Ireland also support spawning populations: the Munster Blackwater, and the Barrow/ Nore/ Suir river system (King and Roche, 2008).

Despite spending the majority of their life at sea, little is known about the movements, feeding areas, distribution and population overlap of twaite shad in the marine environment (Aprahamian et al., 2003b) with previous knowledge obtained indirectly. For example, in the UK and Ireland, spawning populations of twaite shad display genetic isolation by distance (Jolly et al., 2012), suggesting fidelity to natal rivers by returning spawners. Likewise, analyses of landings data have suggested coastal distributions of twaite shad in relatively shallow areas (<50 m depth) that centre around known spawning rivers (Taverny and Elie, 2001; Nachón et al., 2016), while modelling of marine catch distribution in the Bay of Biscay and English Channel has suggested a winter migration from coastal to oceanic areas (Trancart et al., 2014). The impacts of both targeted fisheries and accidental bycatch on twaite shad populations remains poorly understood, and this knowledge gap is compounded by their scarcity, negligible commercial value and legislative protection in some areas that, in combination, result in a general lack of reporting in fisheries and bycatch statistics (Hillman, 2003).

Acoustic telemetry is a rapidly developing method that is useful for tracking the movements of aquatic species (Hussey et al., 2015). When different groups of researchers share data from networks of acoustic receivers (which detect and record tagged animals in the vicinity) deployed in multiple regions and habitats, the spatial area over which wide-ranging species can be recorded is increased (Taylor et al., 2017). The perceived sensitivity of twaite shad to handling and sedation has limited progress in understanding their movements through telemetry (Breine et al., 2017). However, recent refinements have enabled internal transmitter implantation under general anaesthesia in twaite shad, providing a potential opportunity to record individual movements over multiple spawning seasons and during their marine life-phase (Bolland et al., 2019b).

Correspondingly, the aim of this study was to document the marine detections and subsequent freshwater entry of acoustic-tagged adult twaite shad that emigrated from the River Severn (western England). Using shared detection data from inshore and estuarine receiver arrays in south-west England and south-east Ireland, the objectives were to: (1) identify the location and timing of coastal and estuarine detections of tagged twaite shad that emigrated from the River Severn following spawning; (2) quantify the extent of twaite shad movements into estuaries outside the spawning period; (3) assess the fidelity of repeat-spawning individuals to the River Severn and (4) provide initial estimates of freshwater, marine and annual mortality for tagged individuals.

4.3 Methods

In May 2018, 73 upstream-migrating adult twaite shad were surgically tagged with 69 kHz, Vemco V9 programmed acoustic transmitters (vemco.com), using the tagging protocol of Bolland et al. (2019), and following ethical review and according to UK Home Office project licence PD6C17B56. Twaite shad were captured at two locations (Maisemore Weir, 51.8928, -2.2668, n = 20, Upper Lode Weir, 51.9935, -2.1739 n = 53) using two techniques (angling n = 44, trapping n = 29). Tagging occurred on seven different days between the 9 and 24 May 2018, with between 1 and 14 fish tagged each day. The mean length ± 95% CI (range) of tagged individuals was 359 ± 7 mm (275 - 411 mm), and mean weight was 612 ± 40 g (250 - 950 g) (Appendix 3: Table A7). Analysis of spawning-marks on scales on a projecting microscope (x48 magnification) suggested that 43 (58%) of the tagged fish had spawned at least once previously (Table A7).

Acoustic-tagged individuals were tracked in the River Severn using an array of 38 Vemco VR2-W acoustic receivers between early May and mid-June, 2018, as part of a wider program of work focusing on the spawning migration of twaite shad (cf. Antognazza et al., 2019; Severn Rivers Trust, 2020). Acoustic-tagged twaite shad were classed as having emigrated from the river following their final detection location on the most downstream receiver in the array (51.8347, -2.2901; Figure 4.1). This receiver was located in the estuary, 8 km downstream of the tidal limit. Fish that failed to emigrate were assumed to have died within the river (e.g. due to predation or failure to recover from spawning activities). At the end of June 2018, the acoustic transmitters switched from a randomized 1-minute pulse interval (minimum interval between acoustic pulses 30 seconds, maximum interval 90 seconds) to a 10-minute pulse interval until April 2019, when they were programmed to switch back to their randomized 1-minute pulse interval. The rationale of this programming was to prolong the battery life of the transmitters to approximately three years (to enable tracking of three spawning migrations), whilst maintaining the possibility of tagged fish being detected on other receiver arrays during the marine phase of their lifecycle. The shorter delay interval allowed more detailed tracking of individuals entering the river during their known breeding season between April and end-June (Aprahamian, 1988).

To ensure that any subsequent detections of acoustic-tagged twaite shad during the marine phase of their migration were reported, transmitter IDs of emigrating individuals were distributed to researchers at institutions known to be operating acoustic telemetry arrays in western Great Britain and eastern Ireland to track the movements of bass (*Dicentrarchus labrax*), Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) in multiple coastal and estuarine locations (Table 4.1; Figure 4.1). The areas covered by receiver arrays in south-west England were the Taw-Torridge Estuary (n = 31 receivers; TT, Figure 4.1), the Kingsbridge-Salcombe Estuary (n = 15; KS) and River Dart Estuaries (n = 26; RD) (University of Plymouth, 2020). In south-east Ireland, receivers were present in the estuarine reaches of the River Bandon (RB, n = 4), Munster Blackwater (MB, n = 4), River Barrow (RBA, n = 4), River Slaney (RS, n = 4), Bannow Bay (BB, n = 4), Cullenstown (CU, n = 2) and Rogerstown Inlet (RI, n = 3) (Marine Institute, 2020). All receivers in these arrays listened at 69 kHz and were thus capable of detecting tagged twaite shad from the Severn. The receivers 1 km outside the estuary mouth at TT (hatched area; Figure 4.1) were removed between September and November 2018. All other receivers remained active and in place between June 2018 and July 2019.

Table 4.1: Acoustic receiver arrays present in estuarine and coastal waters of south-western UK and southern Ireland between May 2018 and July 2019

Country	Estuarine array	Map code	*N* receivers	Deployment period
UK	Taw-Torridge Estuary	TT	31	July-August 2018 until after study period. Note: receivers in hatched box in Figure 4.1 removed between September-November 2018
	Kingsbridge Salcombe Estuary	KS	15	July-August 2018 until after study period
	River Dart Estuary	RD	26	Throughout study period
Ireland	River Bandon	RB	4	Throughout study period
	Munster Blackwater	MB	4	Throughout study period
	River Barrow	RBA	4	Throughout study period
	Bannow Bay	BB	4	Throughout study period
	Cullenstown Inlet	CU	2	Throughout study period
	River Slaney	RS	4	Throughout study period
	Rogerstown Inlet	RI	3	Throughout study period

To identify the rivers entered by returning acoustic-tagged twaite shad in 2019 and thus estimate their rate of return to the River Severn during the spawning period, single receivers were installed in early April 2019 at the tidal limit in the rivers Wye, Usk and Tywi (Figure 4.2). These receivers were placed downstream of known twaite shad spawning areas in these rivers (Aprahamian et al., 1998). In the River Severn, a receiver was placed at the tidal limit (Figure 4.2). This was in addition to an array of 48 receivers upstream, as part of a freshwater investigation (data not reported here). The receivers remained in place until late July 2019, well beyond the conclusion of the known twaite shad spawning season in the region (Aprahamian et al., 2003a).

Freshwater mortality of upstream migrating acoustic-tagged twaite shad was calculated based on the proportion that did not emigrate from the River Severn. Marine mortality of emigrating individuals was calculated as the proportion of tagged individuals that did not return to fresh water in 2019. Annual mortality of all upstream-migrating twaite shad tagged in 2018 was then calculated by combining freshwater and marine mortality. For the purpose of estimates, emigrating individuals in 2018 that were not detected in fresh water in the rivers Severn, Wye, Usk or Tywi during the spawning period in 2019 were assumed to have died during their marine phase.

4.4 Results

Of the 73 twaite shad acoustically tagged during their upstream spawning migration in the River Severn in May 2018, 58 were detected emigrating from the river; thus, the rate of freshwater mortality was 0.21. The median emigration date was 6 June (range 9 May to 23 June). Of the 58 emigrating fish, 12 were subsequently detected in north Devon, in the Taw-Torridge Estuary array (Figure 4.1), representing a minimum movement distance of approximately 200 km from the tidal limit in the River Severn (Figure 4.1). Detections outside of the Taw-Torridge estuary mouth occurred between July and November 2018, but with no individual detected on more than 5 individual days (Table 4.2). Also, 3 of the 12 twaite shad were detected on receivers within the macrotidal Taw-Torridge Estuary (Figure 4.1), with detections in August 2018, December 2018, and March/April 2019 (Table 4.2). All detections within the estuary occurred within two hours either side of high tide (Bideford Tide Times, www.tidetimes.org).

An individual twaite shad (ID 26250; Table 4.2) was detected entering the Munster Blackwater Estuary in southern Ireland in December 2018 (Figure 4.1), four months after its last detection in north Devon, with this representing a linear distance of 270 km. Its detection in this estuary coincided with the start of a flooding tide (Youghal Tide Times, www.tidetimes.org), and was subsequently detected returning to the River Severn in late April 2019. Thus, this twaite shad had a minimum movement distance of 950 km between the freshwater-phase of its spawning migration in 2018 and 2019.

Table 4.2: Summary of acoustic-tagged twaite shad from the River Severn detected in the Taw-Torridge Estuary array. ‘n days detected’ refers to the number of distinct days a tagged twaite shad was detected on the array. ‘n journeys into estuary’ refers to the number of distinct journeys each individual made from outside the estuary mouth to within the estuary mouth. ‘Distance into estuary’ represents the maximum distance of detection for each individual on estuarine receivers relative to the estuary mouth (cf. Figure 4.1). *The individual that was subsequently detected in the Munster Blackwater Estuary and the River Severn.

Fish ID	*n* detections	Detection period	*n* days detected	*n* journeys into estuary	Distance into estuary (km)
26317	2	December 2018	1	1	5.8
26330	32	July-August 2018	4	1	5.4
26331	35	March-April 2019	5	2	5.4
26245	1	September 2018	1	n/a	n/a
26248	41	July-August 2018	2	n/a	n/a
26250*	6	August 2018	2	n/a	n/a
26251	2	October 2018	1	n/a	n/a
26258	15	September 2018	3	n/a	n/a
26278	27	August 2018	2	n/a	n/a
26284	12	September 2018	2	n/a	n/a
26301	2	November 2018	1	n/a	n/a
26309	31	September-November 2018	5	n/a	n/a

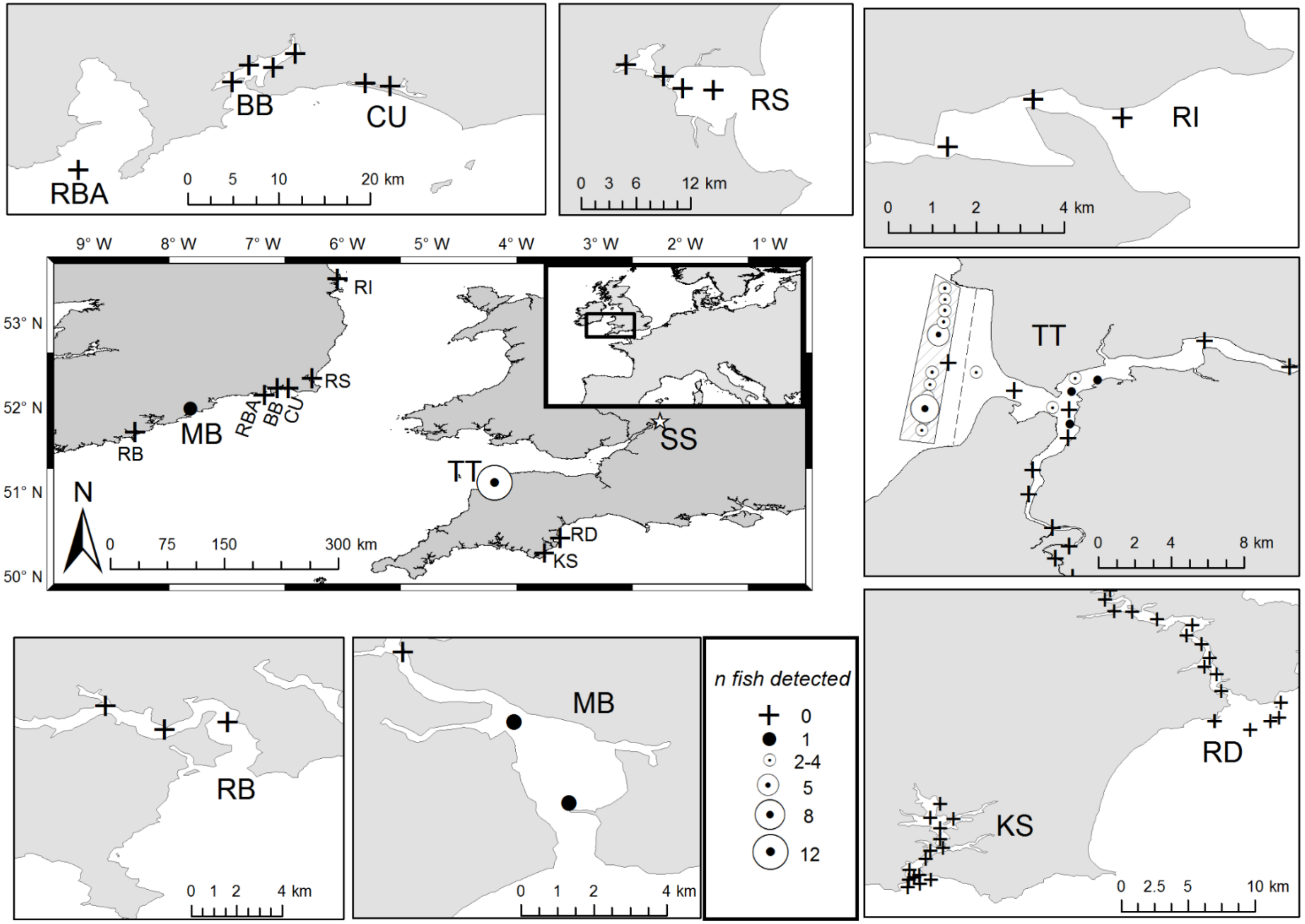

Figure 4.1: Map of the study area used to interpret the marine movements of twaite shad in the western UK and Ireland. SS = final detection location of emigrating post-spawning acoustic tagged fish in the River Severn array in May/June 2018. Circles denote known estuarine arrays and specific receivers where shad were detected, and + denote known estuarine arrays and specific receivers where shad were not detected between July 2018 - April 2019. Riverine receivers (n = 3, no detections) in the River Barrow (RBA) not shown.

Of the 58 emigrating tagged twaite shad in 2018, 34 (59 %) were re-detected on receivers in fresh water in April and May 2019 (Figure 4.2); thus, the rate of marine mortality for the 58 emigrating individuals was 0.41. These returning twaite shad comprised 10 individuals that had been detected on coastal receiver arrays during their marine phase, and 24 not detected since emigrating from the River Severn in 2018. Of the 34 returners, one was detected only in the River Wye (Figure 4.2), one was detected entering the River Wye before subsequently migrating into the River Severn one week later, and 32 were detected only in the River Severn. Combining freshwater and marine mortality, the annual mortality rate for the 73 tagged individuals was 0.53.

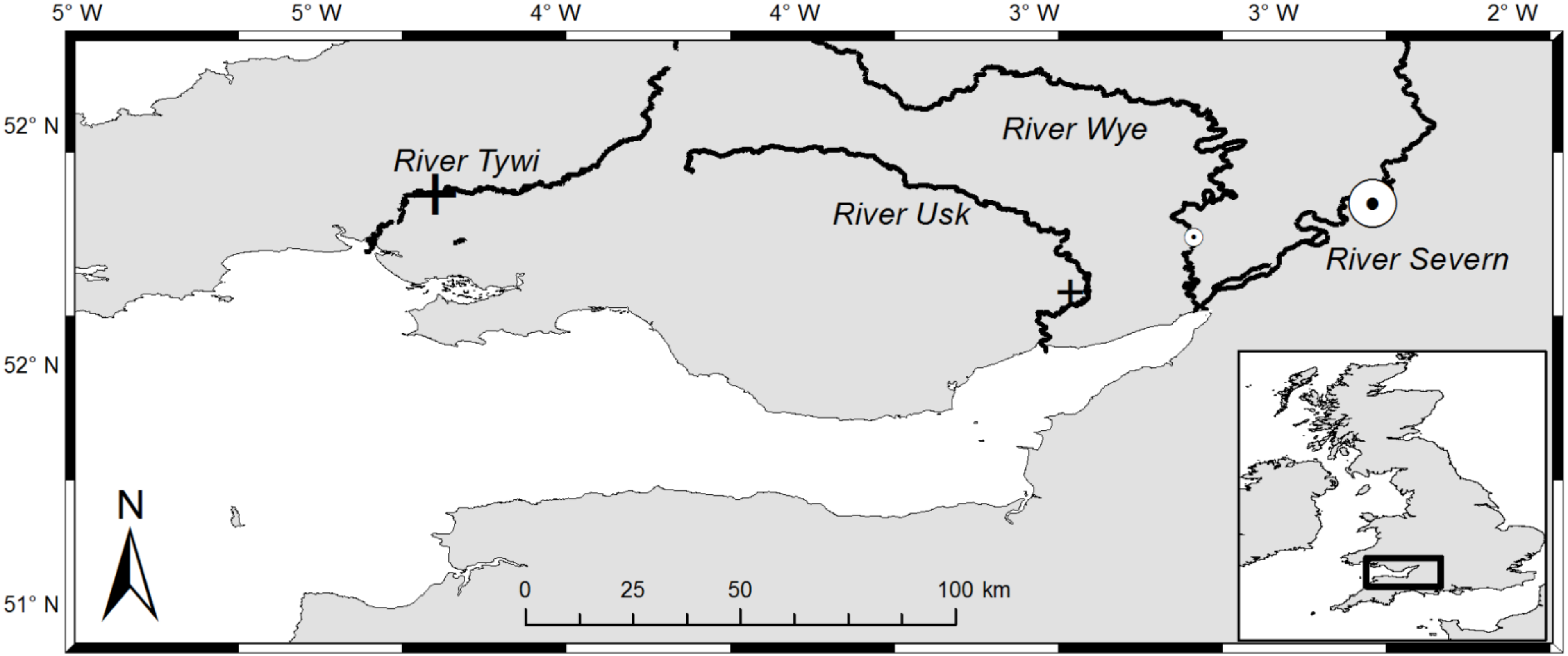

Figure 4.2: Location of freshwater detection of 34 acoustic-tagged twaite shad in April/May 2019 that emigrated from the River Severn post-spawning in 2018. Circles denote the location of receivers at the tidal limit where twaite shad were detected in the River Severn (n = 33) and River Wye (n = 2). + denotes the location of receivers in known twaite shad spawning rivers where shad were not detected during the same period. Note: one fish was detected in both the River Wye and River Severn.

4.5 Discussion

The detection of 12 twaite shad in coastal environments in the UK and Ireland between July 2018 and April 2019, following their tagging in the River Severn in May 2018, revealed novel insights into the spatial ecology of this threatened species. These initial findings represent the first definitive record of twaite shad dispersal during the marine phase of their lifecycle in the UK and Ireland. In addition, the return of 33 out of 34 individuals to the River Severn in spring 2019 provided new information on the fidelity of twaite shad to the river of their previous spawning, as well as broad estimates of marine mortality.

Evidence regarding the marine distribution of twaite shad elsewhere in Europe has primarily been derived from landings data from coastal and pelagic fisheries which have pointed towards coastal distributions that are centred in shallow marine areas around known spawning rivers (e.g. Taverny and Elie, 2001; La Mesa et al., 2015; Nachón et al., 2016). Whilst others have proposed an offshore migration of twaite shad in northern areas of their range in winter (Trancart et al., 2014), here, the detection of some twaite shad within two estuaries during December suggests that coastal habitats may be used by at least some individuals from the River Severn year-round. At the Taw-Torridge Estuary, during the five-month period when receivers outside the estuary mouth were in place, individual twaite shad were detected on a maximum of five different days, suggesting a transient use of the immediate coastal area. Recent evidence from otolith microchemistry has suggested a substantial dispersal capacity of twaite shad, with marine-captured individuals shown to originate from rivers up to 600 km away (Nachón et al., 2020). Here, direct evidence is provided to support this, with an estimated minimum 950 km round trip migration made by a returning individual twaite shad to the River Severn. This finding is also consistent with minimum dispersal distances proposed for other Alosa fishes (e.g. Dadswell et al., 1987; Martin et al., 2015). Further telemetry studies may be useful for answering questions on shad marine distribution, potentially if complemented by otolith microchemistry (Nachón et al., 2020) or genetic studies to determine their natal origin (Martin et al., 2015).

Here, the detection of a twaite shad in an Irish estuary known to support spawning populations of shad suggests that at least some of the UK and Irish populations share or overlap their ranges. This finding supports recent work indicating that capture location may not be a reliable indicator of origin (Nachón et al., 2020), as well as marine capture data of tagged individuals in other Alosa species suggesting that different spawning populations mix at sea (Melvin et al., 1986; Dadswell et al., 1987). Four rivers in south-east Ireland, including the Munster Blackwater, are designated as Special Areas of Conservation (SACs) under the European Union Habitats Directive because they support spawning populations of twaite shad (King and Roche, 2008). Detection of a tagged individual from the Severn here in December suggests these estuaries could provide important habitats for non-spawning individuals belonging to populations from other rivers and thus their protections could be extended to cover non-spawning twaite shad that spend periods of their winter in these areas.

Of the 34 tagged individuals detected in known UK shad spawning rivers in spring 2019, 33 of 34 (97 %) returned to the River Severn. This figure is comparable to a mark-recapture study in American shad *Alosa sapidissima*, where fidelity to a previous spawning river was estimated at 97 % (Melvin et al., 1986). Note, however, that in the current study, the possibility of tagged individuals entering rivers without receivers cannot be ruled out. Twaite shad populations in the UK and Ireland display genetic isolation-by-distance, with spawning populations in the neighbouring rivers Severn and Wye showing a lack of genetic differences, while the Tywi, Usk and Irish populations are genetically distinct from the Severn population (Jolly et al., 2012). This genetic structuring between populations is potentially supported by this study, because no straying of acoustic-tagged individuals into the rivers Usk, Tywi, Munster Blackwater or Barrow/Nore/Suir was detected during the spawning period, while two were detected in the River Wye (although spawning cannot be confirmed). These observations are in line with those for allis shad *Alosa alosa*, where straying behaviour is more common between neighbouring rivers (Martin et al., 2015). One of the individuals detected in the Wye entered the Severn a week later; is unclear whether this individual spawned in the Wye or entered as part of an exploratory movement, but its subsequent return to the Severn further supports fidelity to this previous spawning river.

The return of 34 twaite shad to fresh water during the spawning season in 2019 represents the first successful tracking of individuals in this species over multiple spawning seasons. This is a highly encouraging step towards understanding the spatial ecology of repeat spawning migrations, as well as factors affecting annual mortality. Their return provided an initial mortality rate estimate of 0.53 for the original 73 tagged individuals, which is comparable to Aprahamian (1988) (0.53 ± 0.18) and Aprahamian and Lester (2001) (0.47), and slightly lower than Aprahamian et al. (2010) (0.67 ± 0.14), which were estimated from the relative proportion of age classes represented among captured individuals. The marine mortality rate of emigrating individuals between the 2018 and 2019 spawning period was 0.41, and these figures are broadly comparable with similar studies in repeat spawning sea trout (Aarestrup et al., 2015) although rates of return may be highly population-specific (Thorstad et al., 2016). These initial results suggest that further telemetry studies in twaite shad may allow the partitioning of annual mortality into marine and freshwater components, allowing annual variation in mortality rates to be assessed, and individual and environmental factors affecting mortality to be determined (Berg and Jonsson, 1990). Further years of data from returning twaite shad are required to determine whether skipped spawning by adults, as well as the potential effects of tagging and handling on survival, may affect the accuracy of mortality rate estimates (McGarvey, 2009).

The estuary of the River Severn drains into the Bristol Channel, bordered by the coastlines of south Wales and the south-west England peninsula. During the study period the Taw-Torridge estuary array was the only active acoustic array in this area, covering less than 1% of approximately 600 km of coastline. Considering this sparse spatial coverage, it is perhaps unsurprising that of the 34 tagged twaite shad that re-entered the Severn to spawn in 2019, 24 had not been detected on coastal arrays during the 2018/19 during the marine phase of their migration. It was not possible to assess any aspects of their movements between emigrating from the river in 2018 and returning in 2019; including whether they remained coastally distributed within the Severn estuary/Bristol Channel, used other river estuaries, or indeed were entirely oceanic during their marine phase. Likewise, individuals detected in the Taw Torridge were recorded on a maximum of five different days, representing only a small fraction of their time in the marine environment. Dedicated acoustic telemetry studies on the marine phase of twaite shad in this region would benefit from a greater spatial coverage of acoustic receivers, especially if used in conjunction with reduced tag pulse interval to increase the probability of detection on coastal arrays. These actions should provide greater resolution on the marine movements of twaite shad, which could then be used to inform conservation strategies that aim to protect the species throughout its lifecycle.

The results presented highlight the general paucity of knowledge regarding the movements of twaite shad during the marine phase, and the potential benefits of addressing this knowledge gap for shad conservation. For example, the supposed overlap in non-spawning range and potentially extensive migration of twaite shad suggests a need for cooperative management in the marine environment between the UK and Ireland. This includes more thorough recording of accidental commercial bycatch and recreational capture, beyond the current level of anecdotal data (Hillman, 2003), and bycatch statistics which often do not distinguish between twaite and allis shad (Centre for Environment, Fisheries and Aquaculture Science, unpublished data). Further, the apparent fidelity shown by twaite shad to previous spawning rivers highlights the potential local benefits of population-specific management actions aimed at increasing survival of these returning adults, such as strictly minimising estuarine and early marine mortality, and river restoration to increase freshwater survival (Waldman et al., 2016). Finally, the results here would not have been gained without the sharing of telemetry data between three organizations across two European countries. Abecasis et al. (2018) noted that while the rate of publication of acoustic telemetry papers in Europe increased sevenfold between 2007 and 2017, only one study (Huisman et al., 2016) featured an acoustic array that spanned more than one country. This study highlights the potential benefits of implementing a coordinated acoustic tracking network in Europe (and beyond) (Reubens et al., 2019) for providing vital information on the movements of this and other poorly understood migratory species.

5 Tracking repeat-spawning anadromous fish over multiple migrations reveals individual repeatability, tagging effects and environmental factors influence barrier passage

This chapter has been redacted because it contains information about research in progress where there is an intention to publish later. See https://eprints.bournemouth.ac.uk/36872/

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

This chapter has been redacted because it contains information about research in progress where there is an intention to publish later. See https://eprints.bournemouth.ac.uk/36874/

7 General Discussion

In this final chapter, the results from the individual data chapters are briefly synthesised (Section 7.1). Then, the implications of the results for future management and research objectives are explored, with a particular focus on how the results may help justify, inform and assess ongoing and future fish passage remediation efforts in the River Severn catchment (Section 7.2). Research questions that may extend the work presented here are then explored, broadly separated into two categories; in Section 7.3, applied research questions are suggested to help further understand the impacts of fragmentation, reconnection, and the use of biotelemetry in fish migration research, and in Section 7.4, theoretical questions relating to the ecology of migration in data-poor anadromous species are proposed.

7.1 Synthesis

The increasing disconnection of freshwater ecosystems is recognised as a major disruption to the lifecycles of migratory fish species, that has resulted in severe and widespread population declines and extirpations (Limburg & Waldman, 2009; Hall, Jordaan & Frisk, 2011). Exploring the movement ecology of animals within disconnected fresh waters presents challenges, but is vital for informing river restoration and reconnection efforts (Pess et al., 2014; Foley et al., 2017; Sethi et al., 2017). As telemetry technology and methods have developed, the ability to understand their migration ecology over time and space has greatly improved (Hussey et al., 2015; Crossin et al., 2017). The aim of this research was to explore the movement ecology of threatened anadromous species and investigate the impacts of anthropogenic barriers on upstream migration in a fragmented lowland river catchment.

Overall, twaite shad and sea lamprey provided strong study species for assessing the movement behaviour of threatened migratory species, given their anadromous life history, historical significance and contemporary conservation designations (Aprahamian et al., 2003a; Maitland, 2003). The River Severn catchment, as a large, longitudinally fragmented riverine system, featuring a broad range of lotic habitats and multiple anthropogenic barriers, provided a strong focal system for investigating fish migration within disconnected lowland rivers. In addition, the semelparous and iteroparous lifecycles of sea lamprey and twaite shad respectively has provided some contrasting perspectives on their spawning migrations.

For both sea lamprey (Chapter 2) and twaite shad (Chapter 5), navigation and flow regulation weirs in the River Severn catchment acted to delay and prevent upstream migration towards historical spawning grounds, and formed the upstream extent of migration for the majority of individuals. These results add to the evidence body detailing the disruptive impacts of anthropogenic structures in freshwater ecosystems (Dudgeon et al., 2006; Vörösmarty et al., 2010; Hall, Jordaan & Frisk, 2011; Birnie-Gauvin, Aarestrup, et al., 2017), which for both species studied here have restricted the extent of their spawning migrations to lower areas of river catchments, and caused population declines and extirpations across their range (Aprahamian et al., 2003a; Mateus et al., 2012). The results provide an important baseline for further assessment in the context of ongoing passage remediation in the catchment (Section 7.2). For both twaite shad and sea lamprey, environmental factors, including increased river level, were important for reducing delays at navigation weirs (Keefer et al., 2009; Castro-Santos, Shi & Haro, 2017). While the gated acoustic telemetry array used here enabled a broad understanding of delay, further inference on the nature and causes of delay in both species may require higher resolution tracking techniques (Section 7.3).

In Chapter 3, individual variation in the movement responses and ability to pass weirs by sea lamprey was explored, highlighting how different strategies may exist to overcome migratory obstacles and locate alternative passage routes (Kirk & Caudill, 2017; McLean & McLaughlin, 2018; Shaw, 2020). While some individuals performed multiple exploratory downstream movements during delays at weirs, others remained highly resident in the area downstream of weirs. There were no clear causal factors driving this movement variation, nor were there clear consequences of variation on subsequent upstream movement speed or upstream distance achieved. Nonetheless, the results highlighted the potential for fitness tradeoffs for upstream migrants between the energetic costs of exploratory movements and the advantages of successfully locating alternative routes (Ziv & Davidowitz, 2019), which deserve further attention. In twaite shad, individual variation in migration was explored in the context of space use (Chapter 6), with females shown to occupy significantly larger core areas than males during their spawning migration, potentially reflecting differences in spawning strategy (Acolas et al., 2004). Further inference on the nature and drivers of individual variation in migratory strategies in sea lamprey and twaite shad may require the use of complementary methods to assess fine-scale movements (Section 7.3) and spawning distribution and intensity (Section 7.4)

In this thesis, inferences on the movement ecology of twaite shad were greatly enhanced by tracking individuals using long-life tags over multiple spawning seasons. This allowed repeatability in barrier passage (Chapter 5) and spatial fidelity (Chapters 4, 6) to be assessed, and revealed insights into their marine movements (Chapter 4). In Chapter 4, substantial marine dispersal of twaite shad was recorded, and this chapter also served to highlight the paucity of knowledge on twaite shad marine dispersal, an issue which may be further addressed using novel tag technologies (Section 7.4). Of the 34 individuals that were detected re-entering fresh water a year after tagging in Chapter 4, 97% were detected in the River Severn, indicating fidelity to their catchments of previous spawning and complementing previous mark recapture studies in American shad which found a similar rate of catchment-scale fidelity (Melvin, Dadswell & Martin, 1986). Furthermore, in Chapter 6, spatial fidelity was shown to occur within the River Severn catchment; individuals showed significant fidelity to areas previously occupied within the catchment, but the degree of fidelity was not significantly affected by the degree of spawning experience. This potentially indicates that fidelity to previous spawning areas by twaite shad is a continuation of natal homing (Hendricks et al., 2002), but more information on natal origin and spawning locations is required to assess the precision of their fidelity (Section 1.4). Returning individuals also enabled an assessment of repeatability in barrier passage and approach (Chapter 5), with previously successful individuals shown to pass a major barrier at significantly higher rates, and individuals that approached weirs in the previous year were more likely to approach upon return. The findings of catchment-scale fidelity and repeatability in barrier passage and approach are highly relevant in the context of ongoing barrier passage mitigation efforts in the River Severn catchment (see Section 7.2).

The presence of valuable data from returning twaite shad in this thesis was a direct result of refinements to tagging protocols (Bolland et al., 2019b), that enabled intracoelomic tagging with acoustic transmitters under general anaesthesia. Although alosines are considered highly sensitive to handling, recent studies indicate that surgical tagging is increasingly being considered in alosines, in light of the potential benefits it provides (American shad: Gahagan & Bailey, 2020; Alewife: Tsitrin et al., 2020). However, these studies, and most other telemetry studies in alosines regardless of tagging method, have noted that capture and tagging is associated with lethal and/or sublethal effects for at least a subset of tagged individuals (e.g. Olney et al., 2006a; Frank et al., 2009; Eakin, 2017). Emigration rates of newly tagged and returning individuals were similar in this thesis (Chapters 5, 6), suggesting that the lethal effects of tagging were minimal. However, in Chapter 5, passage rates of returning individuals over a major navigation weir were significantly greater than for newly-tagged individuals, potentially indicating a sublethal tagging effect that should be considered when using newly tagged individuals to assess barrier impacts. Further research on twaite shad in the River Severn, enabled by new fish passage infrastructure, may be able to address the mechanistic basis of this observed tagging effect (see Section 7.3), as well as addressing factors affecting mortality rates in the species more generally (Section 7.4).

7.2 Management implications for ‘Unlocking the Severn’

In response to the ecological problems posed by barriers in freshwater systems, managers have implemented various measures to restore connectivity. Fish passes are now widely implemented to facilitate fish movement past dams and weirs (Silva et al., 2018), and complete barrier removal is an increasingly implemented strategy (Bednarek, 2001; Lasne et al., 2015; Ishiyama et al., 2018). Relative to the history of man-made barriers in fresh water, however, the history of fish passage engineering is short, and the success of some projects has been limited, particularly when passage solutions do not effectively consider the physical requirements of target species (Noonan, Grant & Jackson, 2012; Brown et al., 2013; Foulds & Lucas, 2013). However, where successful, river reconnection can profoundly improve the functioning of riverine ecosystems, and reconnect people with lost aspects of their culture (McClenachan, Lovell & Keaveney, 2015). In the River Severn catchment, the impacts of man-made barriers on the migration of aquatic species described in this thesis are currently being addressed as part of ‘Unlocking the Severn’ (unlockingthesevern.co.uk). This project, one of the largest of its kind in Europe, is aiming to improve ecological connectivity in the River Severn catchment by restoring access for twaite shad to historical spawning grounds that became inaccessible when navigation weirs were built during the 19th century. To achieve this aim, fish passes are being constructed at four of the weirs described in this thesis (S3, S4, S5, S6, Chapter 2). Three of these weirs will feature modern deep vertical slot fish passes, and the fourth will a feature bypass channel and rock-ramp (Figure 7.1). While the fish passes being constructed as part of Unlocking the Severn vary in specification (Figure 7.1), they have been designed to accommodate the needs of non-salmonid species, such as twaite shad, in accordance with fish passage designs used elsewhere in Europe (Larinier & Travade, 2002; Pereira et al., 2017). In addition, Powick Weir and Knightwick Weir (T1 and T2) on the River Teme were lowered between 2019 and 2020, as described in Chapter 5.

Figure 7.1: Ongoing fish passage remediation efforts in the River Severn catchment. a) Downstream-facing view of ongoing construction of deep vertical slot fish pass at Weir S3 (Diglis, Worcester); b) aerial view of recently -completed bypass channel and rock ramp fish pass at Weir S4 (Bevere, Worcester). Photographs courtesy of a) Charles Crundwell and b) Skynique DGI.

Knowledge of the movement ecology of migratory fish in fragmented river systems is highly valuable, as it can aid in the justification, planning and assessment of river reconnection efforts (Sethi et al., 2017). The results provided in this thesis are thus of direct relevance and value to the ongoing ‘Unlocking the Severn’ project in several key ways, which are presented in this section.

7.2.1 Justification for remediation

Although the influence of the weirs on population declines of twaite shad and sea lamprey in the Severn catchment has long been strongly suspected (Buffery, 2018), contemporary empirical evidence for this has been lacking. The results of this thesis provide a potential mechanistic explanation for population declines relating to disruptions to the movement ecology of the two species.

In Chapters 2 and 5, the impacts of weirs on the upstream migration of sea lamprey and twaite shad were assessed. While 89% of tagged sea lamprey passed the first weir upstream of the release site on the main river, only 4% passed the fifth, and for 85% of migrants, the upstream extent of migration was immediately downstream of a weir (Chapter 2). This suggested that the impact of multiple weirs was cumulative, with delays at weirs constituting a median of 84% of total upstream movement times. Upstream passage by sea lamprey at major navigation and flow regulation weirs was restricted to periods of increased river discharge, indicating that successful sea lamprey migration in a given year within the catchment was highly dependent on environmental conditions. These results corresponded with telemetry studies elsewhere that described the poor passage of lamprey species at man-made barriers (Lucas et al., 2009; Foulds & Lucas, 2013) and the cumulative impacts of man-made barriers on upstream-migrating tagged cohorts (Keefer et al., 2009; Castro-Santos, Shi & Haro, 2017).

For twaite shad (Chapter 5), the proportion of fish that approached and passed barriers varied between years and weirs, but weir passage rates were generally lower than recommended passage targets for migratory fish (Lucas & Baras, 2001), and at the major non-tidal navigation weirs, passage rates were very low across all years (< 5 %). Median cumulative passage times at weirs represented 18 % of the total time in fresh water recorded by tagged individuals, indicating that weirs were imposing some considerable delays to upstream migrants in the context of their overall spawning migrations.

In entirety, these results highlight the manner in which these weirs on the River Severn constrain the spawning migrations of threatened anadromous fish, primarily limiting their spawning distributions to the lower river. As such, it can be argued that these insights provide strong justifications for remediation efforts that are underway within ‘Unlocking the Severn’, as well as suggesting potential targets for further passage improvements (Section 7.3).

7.2.2 Informing expectations

It may be expected that migratory species will readily exploit reconnected habitats following fish pass installation, but recolonisation rates by anadromous fish are highly dependent on life history characteristics (Pess et al., 2014). Multiple studies have indicated that sea lamprey can rapidly recolonise upstream areas after river reconnection (summarised in Pess et al., 2014). Here, sea lamprey displayed high approach rates of the weirs that are being remediated within ‘Unlocking the Severn’, and also exploited episodic passage opportunities at five (of six) of these weirs. This suggests that improving passage of these structures may immediately increase the numbers of sea lamprey reaching upstream spawning sites.

There were, however, several key outcomes that suggest that the full impact of ‘Unlocking the Severn’ on the extent of migration by twaite shad within the River Severn catchment may not be immediately realised. For example, in Chapter 5, the approach of weirs designated for remediation was relatively low (S3, T1), with evidence that approach was repeatable among returning individuals. It could be thus be interpreted that only a subset of individuals may be motivated to take advantage of newly opened fish passes and progress upstream. In addition to the repeatability of weir approaches, passage rates of Weir S2 by returning individuals were positively affected by passage success in previous years. This result is highly pertinent in the context of predicting recolonisation of upstream habitats. For example, at the newly opened fish pass at weir S3 (where shad passage was low in all study years), it is considered likely that approaching fish will: i) have no prior experience of passing the weir, and ii) have originated from eggs deposited downstream of the weir and thus imprinted to downstream areas. A caveat to this is that recolonisation studies in alosines in America have shown that recolonisation of upstream areas can be rapid (Pess et al., 2014). However, these findings tend to be based on observations of increased migratory fish populations upstream of the barrier following remediation, as opposed to continuous quantitative assessment of approach and passage rates that begin in the years prior to reconnection (Pess et al., 2014). Further monitoring of passage rates at newly opened fish passes, conducted over a time series spanning the reproductive lifespan of twaite shad, may enable inferences about motivation and prior experience to be made (Section 7.3).

7.2.3 Baseline for assessment

The full impacts of river reconnection on migratory species require assessment, with this appraisal process important for gaining insight to assist future efforts, as well as potentially modifying existing structures to increase their efficacy (Birnie-Gauvin et al., 2019). However, the essential assessment phase of river reconnection actions is often considered only as an ‘afterthought’ (Brown et al., 2013; Silva et al., 2018). Where fish passes are installed but are ineffective, they are an example of a conservation action that is ‘worse than useless’, as they provide an illusion of improved connectivity, when in reality, there is none or very little (Brown et al., 2013). By contrast, where evidence of effectiveness is provided, this can provide justification and garner support for future projects (McClenachan, Lovell & Keaveney, 2015). In this thesis, vital baseline information on the current impacts of barriers on twaite shad and lamprey were provided, which will enable comprehensive assessments of the outcomes of 'Unlocking the Severn' when compared with the extent of migration of future tagged migrants within the catchment (Foley et al., 2017). Beyond simple metrics, such as per cent passage (Chapters 2 and 5), which can be directly compared with future per cent passage for a general assessment of changes in passage rates as a result of remediation, the results provided in this thesis should be of direct use for detailed comparative assessments of the pre- versus post-remediation periods. For example, in Chapter 2, a threshold discharge value (60 m^3s^{-1}/Q_{45}) was estimated below which passage of weir S3 (Diglis Weir) by sea lamprey was severely restricted. By comparing the discharge values recorded at the point of passage by tagged individuals after the completion of the fish pass, a more thorough understanding of passage improvements can be reached that can also account for environmental stochasticity.

7.3 Informing anadromous fish migration science in fragmented river catchments

In this section, future applied research questions are proposed that relate to the migration of anadromous fishes in the River Severn catchment, and build upon the results presented in this thesis.

7.3.1 Fine scale positioning

Acoustic telemetry was a highly appropriate method for addressing catchment-scale movements and impacts of sea lamprey and twaite shad in this thesis, but certain limitations of the method meant that questions relating to the fine scale behaviour of fish at barriers were not addressed. In particular, the hydrological conditions close to weirs (high noise, entrained air) are unsuitable for acoustic telemetry using 69kHz transmitters (Shroyer & Logsdon, 2009) due to the severely reduced detection range of receivers in such conditions. However, it is in the areas immediately downstream of weirs that positional information on fish can be of particularly high value. For example, in Chapter 3 of this thesis, long-term downstream residency periods at weirs were described for sea lamprey, but the behaviour of individuals during these delay periods was unknown, including whether they made repeated efforts to locate passage routes, or whether their long delay periods represented an adaptive ‘quiescent’ response to delayed passage (Chanseau, Croze & Larinier, 1999). Similarly, it remains unknown to what extent the delays and failed passage rates reported for twaite shad (Chapter 5) reflected a behavioural response to high turbulence areas (a feature of passage of alosines (Haro & Castro-Santos, 2012) or failed passage attempts. Such fine scale movement information is also valuable for the assessment of fish pass performance when it provides a measure of attraction efficiency in relation to the proportion of available fish downstream (Dodd et al., 2018). Future research efforts could thus attempt to address these knowledge gaps by employing different telemetry techniques, including a combination of acoustic and passive integrated transponder (PIT) telemetry which can be useful for assessing the attraction efficiency of existing fish passes (Bunt, Castro-Santos & Haro, 2012; Steffensen et al., 2013), and/or fine scale positioning telemetry employing high frequency transmitter-receiver systems that perform effectively in high noise environments (Jung et al., 2015).

7.3.2 Understanding tagging bias

The sensitivity of alosine fishes to handling, sedation and tagging has resulted in potentially unrepresentative movement behaviours, as well as high rates of post-tagging mortality and ‘fallback’ that have made the results of telemetry investigations difficult to interpret (Olney et al., 2006; Frank et al., 2009; Grote, Bailey & Zydlewski, 2014). In this thesis, freshwater and marine mortality rates of acoustic-tagged twaite shad were high in the context of alosine telemetry studies (Gahagan & Bailey, 2020), but there was evidence of tagging bias in the performance of newly-tagged versus returning fish at a major navigation weir (Chapter 5). While the cause(s) of these tagging effects remain unknown, they may be related to the effects of capture, handling, sedation and/or tagging on sampled fish (Cooke et al., 2011; Thiem et al., 2011; Tsitrin et al., 2020). The construction of fish passes with PIT-antennae as part of ‘Unlocking the Severn’ may enable questions regarding the mechanistic bases for these tagging biases to be addressed. Relative to acoustic-telemetry, PIT telemetry is a low-cost method, with potential sample sizes limited more by the ability to capture fish rather than the cost of purchasing tags. This provides the ability to tag relatively large numbers of individuals, coupled with experimental designs which can enable inferences to be made on the impact of various tagging, handling and sedation treatments on upstream movement and weir passage (Bolland, Nunn, et al., 2019; Tsitrin et al., 2020). For example, the fish pass attraction and passage rates of downstream PIT-tagged cohorts that have been experimentally exposed to different treatments may be compared. Experimental treatments may include different capture methods (e.g. angling versus trapping), handling treatments (e.g. duration of handling, extent of air exposure), sedatives, surgery techniques (e.g. incision closure types) and tag burdens (e.g. acoustic tag and PIT, versus PIT only) (Wargo Rub & Sandford, 2020)). By experimentally comparing these different treatments in terms of passage performance, especially when further coupled with data from returning individuals, a clearer picture of what drives potential tagging biases may emerge, and thus be minimised in future work.

7.3.3 Estuarine energy and tidal barriers

Understanding fish movements in dynamic estuarine environments is inherently challenging, but the estuarine phase of anadromous fish is a very poorly understood life-phase. In particular, knowledge of the timing and characteristics of entry into and exit from freshwater (Silva, Macaya-Solis & Lucas, 2017), and how the estuarine zone is used during the early migration phase (McCartin et al., 2019), can provide important insights to aid anadromous fish conservation. In allis shad, estuarine zones have been shown to act as hypoxic barriers during low flow events, the impacts of which may be exacerbated due to environmental change (Tétard et al., 2016). The Severn estuary features the second-largest tidal range globally (Bassindale, 1943), which makes aspects of a telemetry study focused on fish movements highly challenging. However, the high emigration and return rates of acoustic-tagged shad described in this thesis make such research possible through the deployment of a receiver array within the Severn estuary, enabling the movements of twaite shad through this area to be monitored. While challenging, such information would be of particularly value in light of ongoing interest in the River Severn estuary as a site for tidal power generation (Aprahamian, Aprahamian & Knights, 2010; Baker et al., 2020).

Many rivers, including the River Severn catchment, feature head-of-tide barriers that form the normal tidal limit of the river and represent the transition between tidal waters and riverine habitats with unidirectional flow. Depending on their characteristics, head-of-tide barriers have the potential to cause severe delays to the riverine entry of anadromous populations, which have been implicated in the complete extirpation of anadromous species from some rivers, especially when head-of-tide barriers are impassable and no suitable spawning habitat exists downstream (Maitland, 2003; Alcott et al., 2021). The tidal weirs described in this thesis (S1a, S1b, S2, Chapter 2) represent the first man-made barriers to migration encountered by migratory fish entering the River Severn catchment. For twaite shad and sea lamprey, average delays at S1a and S1b weirs were low relative to other barriers over the study period of this thesis (Chapter 2, Chapter 5) and passage remediation is not planned at these structures. However, a more thorough assessment of their impacts over a range of environmental conditions is required. This should incorporate generating understandings of the factors that drive fish to initiate their upstream migration, given that the downstream position of these weirs means their overall impact may be severe, especially if the timing of peak migration occurs during neap tide periods (Aprahamian et al., 2003a). Further, evidence was provided here for substantial temporal delays to upstream migration caused by S2 (Upper Lode Weir), the significance of which may be heightened in light of the relatively short freshwater residency period estimated for twaite shad (Chapter 6); further, there was evidence that adequate sea lamprey passage of this structure is strongly reliant on episodic high flow events (Chapter 2). Taken together, these results suggest that fish passage remediation should be considered at S2. Given the extensive remediation work currently being completed at weirs further upstream, improved passage at S2 has the potential to substantially increase the abundance of migrants that could then benefit from these upstream reconnections (Nunn & Cowx, 2012).

7.4 Towards a more complete understanding of the ecology and lifecycle of data-poor anadromous fish species

In this section, future research questions are proposed which relate to the ecology of threatened anadromous species, building upon the results presented in this thesis.

7.4.1 Combining telemetry and acoustic surveys to understand reproductive ecology

In Chapter 6, potential spawning areas exploited by twaite shad within the River Severn were identified through the movement and distribution of acoustic-tagged individuals. In addition, differences in space use between males and females were described, with females occupying a large core area, although it was beyond the scope of the study to identify specific movement behaviours related to spawning. Much of our knowledge regarding the drivers of spawning activity in shads derive from acoustic surveys of nocturnal spawning activity, taking advantage of their spawning behaviour, which creates loud splashing which can be actively surveyed or passively monitored to create a relative measure of spawning intensity (Langkau et al., 2016; Paumier et al., 2020). Throughout the shad spawning season, spawning intensity on any given day can vary markedly depending on environmental conditions, including water temperature and river discharge, which is believed to reflect a tactic employed by shad to maximise juvenile recruitment and survival (Lambert et al., 2018). However, it is not known how this variation in spawning intensity manifests in relation to the movement behaviours of individuals. Thus, a useful future avenue of research could see the coupling of acoustic surveys with telemetry in order to relate variation in spawning intensity to variation in movement behaviours.

7.4.2 Assessing the factors affecting marine and freshwater mortality

The high degree of iteroparity and relatively high rate of annual survival in twaite shad was reflected in the high emigration and return rates, the estimation of which was made possible by advancements in the surgical implantation of acoustic tags (Bolland, Nunn, et al., 2019) (Chapters 4, 5, 6). The high proportion of repeat spawners within the population may indicate that adult survival is an important influence on population viability, and thus understanding the factors affecting the mortality of adults is an important objective. In Chapter 4, the opportunity of using acoustic-tagged individuals to partition marine-phase and freshwater-phase mortality was highlighted. In addition to this, further research opportunities now exist to assess the factors affecting fresh water and marine mortality in twaite shad, using multiple years of survival data for acoustic tagged individuals. Potential factors affecting mortality include environmental (temperature, river discharge), and individual (condition, age) factors, predation, as well as other factors which have emerged as important modulators of survival in anadromous fishes, including microbiota (Llewellyn et al., 2014), nutritional condition (Bordeleau et al., 2019) and parasite loads (Gjelland et al., 2014; Bass et al., 2019). By using tagged shad in these assessments, the opportunity further exists to examine mortality in relation to individual variation in migratory behaviour and timing (Tibblin et al., 2016; Jensen et al., 2020). For example, whether increased freshwater residency times, indicating a greater commitment of somatic resources to reproduction, is reflected in increased mortality, and how environmental factors interact with this.

7.4.3 New opportunities and technologies to assess marine-phase dispersal

In Chapter 4, new insights into the marine dispersal of twaite shad were provided, which included extensive over-wintering migration distances (an individual detected in south-eastern Ireland which returned to the River Severn), year-round entry into estuarine areas, as well as fidelity to their river of previous spawning. While these results represented substantial new insights, they also served to highlight the lack of knowledge regarding twaite shad marine dispersal. Improving receiver coverage, with their potential integration into formal receiver networks, may improve detection rates of acoustic-tagged shad in coastal areas. However, monitoring their movements into offshore areas during winter (Trancart et al., 2014) may be more difficult using acoustic telemetry due to the challenges of mooring and retrieving acoustic receivers in deep water (Goossens et al., 2020).

A further option to explore marine dispersal in twaite shad is the use of data-storage tags (DSTs). These tags continuously record temperature and pressure, enabling approximate locations and tracks of individuals to be derived using known sea surface temperatures and depths (Thorstad et al., 2014). DSTs have been successfully used to record long distance marine migrations in a range of anadromous and coastal fishes, including Atlantic salmon *Salmo salar* (Guðjónsson et al., 2015; Einarsson et al., 2018), sea trout *Salmo trutta* (Kristensen et al., 2018) and European bass *Dicentrarchus labrax* (de Pontual et al., 2019). A major challenge of DSTs is that they require recovery, which is usually achieved through marine or freshwater capture of tagged individuals, or coastal recovery of floating tags from individuals that have died (Thorstad et al., 2014). In the case of twaite shad in the River Severn, the likelihood of recovery of DST-tagged individuals is improved by the fish passes, which may facilitate a means of capture through trapping, potentially aided by combining DSTs with acoustic or PIT tagging to provide a means of locating DST-tagged returning individuals within the catchment.

7.5 Summary

In summary, this thesis has provided important insights into the movement ecology of anadromous species that undertake their spawning migration within a highly fragmented lowland river catchment. Important results included the cumulative temporal and spatial impacts that man-made barriers impose on upstream migration, and the environmental factors affecting barrier passage. Further, the research provided rare observations on the marine dispersal of twaite shad, highlighting the general lack of knowledge regarding the marine life-phase movements of this species and the importance of collaborative research networks. Finally advancements to our understanding of the individual factors affecting barrier passage, exploratory behaviour and space use were provided;

these advancements are of direct relevance for assessing and prioritising monitoring programmes and management interventions. Future possibilities for research, explored above, can build on and expand these findings to address the ecological implications of river reconnection, and the drivers of individual variation in movement behaviour.

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9 Appendices

9.1 Appendix i: Introduction

9.1.1 Images of weirs within the study area on the Rivers Severn and Teme

Maisemore weir, S1

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Upper Lode Weir, S2. Photo taken by the author.

Diglis Weir, S3. Photo credit: Elliot Brown. License CC BY-NC-ND 2.0. https://www.flickr.com/photos/39415781@N06/43027967595

Bevere Weir, S4

Holt Weir, S5. Photo credit: Richard Wise. License CC BY-NC-ND 2.0. https://www.flickr.com/photos/rickardowise/16378478076/in/photostream/

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Lincomb Weir, S6

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Powick Weir, River Teme. Photo taken by the author.

Knightwick Weir, River Teme. Photo taken by the author,

9.2

9.3 Appendix 1: Cumulative impacts of habitat fragmentation and the environmental factors affecting upstream migration in threatened sea lamprey *Petromyzon marinus*

9.3.1 CTMM development of candidate models

Initially, the potentially confounding individual variables of body length and capture date were investigated for their effects on upstream movements, before being combined with environmental covariates (Bravener & McLaughlin, 2013). The first step was to parameterise univariate models containing only body length or capture date and compare these to the 'null model' that contained no covariates using Akaike's Information Criterion values (AIC). In both the tidal river and non-tidal river, univariate models containing body length performed better than the null model, but inspection of transition rates between sections revealed no significant effect of body size; in addition, there was also no significant correlation between body length and upstream distance travelled (Pearson, t = 1.2 df = 58, p = 0.25). Therefore, body length was not included in subsequent models to reduce complexity. For the tidal river, the univariate model containing capture date performed significantly better than the null model. However, data exploration revealed that for the tidal river, capture date and river flow were co-correlated, with the batch of 18 individuals released on 15 May (Table 2.2) experiencing significantly lower average discharge than the earlier batches while in the lower river (Kruskal Wallis, df = 2, p > 0.01). A univariate model containing capture date as the sole explanatory variable was compared to a univariate model containing only river discharge, with the latter a better fit according to AIC; as such, capture date was not included in subsequent models.

For the tidal and non-tidal river areas, candidate models containing combinations of environmental variables were constructed according to hypotheses about the effect of environmental variables on upstream movement. Due to the highly co-correlated nature of the hydraulic variables of discharge and river level measured at different locations, alternative models containing only one of these variables were parametrised and compared. CTMMs allow inclusion of transition-specific covariates that act on only selected transitions (Lewandoski, Bishop & McKinzie, 2018), and so for both the tidal and non-tidal river, candidate model sets containing one hydraulic variable were compared to ‘local conditions’ models, where hydraulic conditions most relevant to each transition were included in models and constrained to act only on certain transitions. For example, a local conditions model set in the tidal river contained the river level at Minsterworth acting on transitions between *Downstream S1a/S1b* and *Upstream S1a/S1b*, and river discharge at Saxon’s Lode acting on all other transitions (Figure. 2.1). The best-fitting model set in each area was selected according to AIC – in each area the best-fitting model was greater than 5 AIC ahead of the next best models, and thus competing models were not considered. All candidate models are described in Appendix 1: Table A2.

Table A1: Metadata and movement information for the 60 acoustic-tagged sea lamprey

Capture date	Length, mm	ID	*N* detections	Total distance moved, km	Time until final movement, days	Most Upstream Location	Most upstream distance, km
03/05/2018	895	26264	7123	64	26.3	Downstream of S5	61.6
03/05/2018	775	26265	1631	53	28.4	Downstream of S2	23.6
03/05/2018	905	26266	10124	71	32.1	Downstream of S5	61.6
03/05/2018	810	26267	2197	100	37.1	Downstream of S3	49.7
03/05/2018	850	26268	4226	54	23.2	Downstream of S5	61.6
03/05/2018	840	26269	9566	98	47.0	Downstream of S3	49.7
03/05/2018	760	26270	2235	157	32.4	Downstream of S5	61.6
03/05/2018	830	26271	13813	81	49.2	Downstream of S3	49.7
03/05/2018	930	26272	5997	247	58.0	Downstream of S3	49.7
03/05/2018	860	26273	3582	109	60.9	Downstream of S3	49.7
03/05/2018	960	26274	6919	193	55.2	Downstream of S5	61.6
03/05/2018	900	26275	12254	120	35.4	Upstream of S2	23.6
03/05/2018	950	26276	24594	181	55.2	Downstream of S3	49.7
03/05/2018	860	26277	7700	43	18.3	Downstream of T1	51.6
10/05/2018	810	26222	1179	168	47.4	Downstream of T1	51.6
10/05/2018	850	26223	6156	121	48.1	Downstream of S3	49.7
10/05/2018	710	26224	2626	97	11.3	Downstream of S3	49.7
10/05/2018	875	26225	423	93	24.6	Downstream of S5	61.6
10/05/2018	890	26226	7931	78	40.1	Downstream of S3	49.7
10/05/2018	780	26227	8709	122	31.0	Downstream of T1	51.6
10/05/2018	880	26228	1134	110	54.5	Downstream of S5	61.6
10/05/2018	860	26229	240	63	22.8	Upstream of T2	67.9
10/05/2018	820	26230	1165	49	54.8	Downstream of S2	23.6
10/05/2018	780	26231	1284	51	24.0	Teme Confluence	48.6
10/05/2018	840	26232	354	54	29.4	Downstream of S5	61.6
10/05/2018	830	26233	299	99	51.1	Downstream of S3	49.7
10/05/2018	730	26234	3585	114	52.7	Downstream of S3	49.7
10/05/2018	860	26235	2997	68	34.9	Downstream of S2	23.6
10/05/2018	765	26236	543	31	5.3	Severn Stoke	38.8
10/05/2018	860	26237	1375	125	31.6	Downstream of S5	61.6
10/05/2018	840	26238	312	42	1.5	Downstream of S3	49.7
10/05/2018	830	26239	3632	29	32.1	Release site	7.9
10/05/2018	890	26240	2525	107	11.3	Downstream of S2	23.6
10/05/2018	830	26241	2395	123	30.4	Downstream of T1	51.6
10/05/2018	880	26242	2222	68	42.1	Upstream of S5	62.3
10/05/2018	870	26243	21	11	0.4	Release site	7.9
10/05/2018	840	26244	9678	42	4.0	Downstream of S2	23.6
10/05/2018	840	26327	4292	100	29.3	Downstream of S3	49.7
10/05/2018	830	26328	10326	60	31.3	Downstream of T1	51.6
10/05/2018	920	26329	175	60	23.1	Upstream of T2	67.9
15/05/2018	800	47600	5372	173	16.2	Upstream of T2	67.9
15/05/2018	825	47601	2857	211	34.6	Downstream of T1	51.6
15/05/2018	780	47602	308	54	37.0	Downstream of S5	61.6
15/05/2018	890	47603	1653	62	19.2	Downstream of S5	61.6
15/05/2018	815	47609	103	8	0.2	Release site	7.9
15/05/2018	750	47610	6773	107	24.4	Teme Confluence	48.6
15/05/2018	835	47611	737	82	46.9	Downstream of S3	49.7
15/05/2018	805	47612	4036	154	44.3	Downstream of S5	61.6
15/05/2018	910	47613	2961	67	34.1	Upstream of S5	62.3
15/05/2018	900	47614	459	73	25.4	Upstream of T2	67.9

15/05/2018	850	47615	2938	161	38.0	Downstream of S5	61.6
15/05/2018	780	47616	291	54	19.7	Downstream of S5	61.6
15/05/2018	790	47617	771	70	28.1	Severn Stoke	38.8
15/05/2018	740	47620	12285	82	50.2	Downstream of S3	49.7
15/05/2018	780	47621	1530	72	49.1	Downstream of S5	61.6
15/05/2018	875	47622	2136	55	26.2	Downstream of S3	49.7
15/05/2018	825	47647	13711	25	21.2	Upstream of S2	23.6
15/05/2018	760	47698	180	11	0.1	Release site	7.9
21/05/2018	860	47618	33574	23	25.4	Downstream of S2	23.6
21/05/2018	820	47619	1690	91	39.1	Downstream of T1	51.6

Table A2: Candidate covariate sets tested in continuous-time multistate Markov models of sea lamprey movements in tidal and non-tidal areas of the River Severn catchment, UK. Candidate models are ranked according to Akaike's Information Criterion (AIC). SL = Saxon's Lode gauging station, MW = Minsterworth level gauging station, KN = Knightsford Bridge flow gauging station, S2 = Upper Lode level gauge.

Model covariates	**Hypothesis**	**AIC**	**d.f.**
Tidal river			
~ flow (SL) + level (MW) + light	Local model; movements best predicted by local hydraulic conditions and light	866	33
~ level (MW) + light	Movements best predicted by river level and light	871	33
~ level (S2) + level (MW) + light	Local model; movements best predicted by local river level and light	872	33
~ light	Movements best predicted by light	948	22
~ level (MW)	Movements best predicted by river level at Minsterworth	1063	22
~ level (S2)	Movements best predicted by river level at Upper Lode Weir, S2	1089	22
~ flow (SL)	Movements best predicted by river flow	1090	22
~ temperature (S2)	Movements best predicted by water temperature	1140	22
~ body length	Movements best predicted by body length	1156	22
Null model		1163	11
Non-tidal river			
~ flow (SL) + flow(KN) + light + flow*light	Local model; movements best predicted by local hydraulic conditions and light + interaction between light and local hydraulic conditions	702	56
~flow (SL) + light + flow(SL) *light	Movements best predicted by river flow (Severn) and light + interaction between light and river flow (Severn)	714	56
~ flow (SL) + light	Movements best predicted river flow (Seven) and light	719	42
~ flow (SL) + flow(KN) + light	Local model; movements best predicted by local hydraulic conditions and light	735	42
~ flow (SL)	Movements best predicted by river flow (Severn)	812	28
~ temperature (S2)	Movements best predicted by water temperature	821	28
~ light	Movements best predicted by light	834	28
~ flow (KN)	Movements best predicted by river flow (Teme)	904	28
~ body length	Movements best predicted by body length	907	28
~ Null		922	14

9.4 Appendix 2: Patterns, causes and consequences of individual movement variation in upstream-migrating sea lamprey *Petromyzon marinus* in a highly fragmented river

Table A3: Lengths and weights of sea lamprey tagged in the lower River Severn in 2018

Date	*n*	Mean ± SE length, mm (range)	Mean ± SE weight, g (range)
3 May 2018	14	866 ± 35 (760-960)	1268 ± 144 (875-1700)
10 May 2018	26	835 ± 19 (710-920)	1186 ± 95 (800-1650)
15 May 2018	18	817 ± 25 (740-910)	1130 ± 105 (775-1650)
21 May 2018	2	840 ± 254 (820-860)	1337 ± 158 (1325-1350)

Table A4: summary of five best-fitting generalised linear models of sea lamprey passage time at Weir S2 (delayed vs non-delayed)

Model structure	df	Log Likelihood	AICc	ΔAICc	Weight
Intercept only	1	-31.34	64.8	0	0.23
Water temperature	2	-30.9	66.1	1.4	0.12
Discharge	2	-30.9	66.1	1.4	0.11
Movement speed	2	-31.1	66.4	1.7	0.10
Body length	2	-31.3	66.9	2.2	0.08

Table A5: summary of best-fitting generalised linear models of sea lamprey upstream extent of migration, post-passage of Weir S2

Model structure	df	Log Likelihood	AICc	ΔAICc	Weight
Intercept only	2	-183	369.7	0	0.24
Body length	3	-182	369.8	0.078147	0.24
Movement distance during delay	3	-182	370.2	0.48053	0.19
Body length + movement distance during delay	4	-181	370.5	0.836653	0.16
Delay length	3	-183	371.8	2.059241	0.09
Body length + delay length	4	-182	372.0	2.268743	0.08

Table A6: Summary of best-fitting generalised linear models of sea lamprey upstream movement speed post-passage of weir S2

Model structure	df	Log Likelihood	AICc	ΔAICc	Weight
Intercept only	2	-65.60	135.48	0.00	0.38
Body length	3	-65.07	136.71	1.23	0.20
Delay length	3	-65.37	137.31	1.83	0.15
Movement distance during delay	3	-65.53	137.63	2.14	0.13
Body length + delay length	4	-64.80	138.57	3.09	0.08
Body length + movement distance during delay	4	-65.04	139.05	3.57	0.06

9.5 Appendix 3: Novel insights into the marine phase and river fidelity of anadromous twaite shad *Alosa fallax* in the UK and Ireland

Table A7: Capture and biometric data of the 73 acoustic-tagged twaite shad tagged in the River Severn in May 2018.

Fish ID	**Tagging date**	**Tagging location**	**Emigration date**	**Capture method**	**L (mm)**	**W (g)**	**Sex**	***N* previous**	**Detected**	**Returned**
26248	########	51.892776, -2.266282	09/05/2018	Angling	353	600	nd	*1*	Yes	Yes
26301	########	51.993539, -2.173897	25/05/2018	Angling	341	525	nd	*1*	Yes	Yes
26317	########	51.993539, -2.173897	29/05/2018	Angling	305	375	nd	*0*	Yes	Yes
26250	########	51.892776, -2.266282	06/06/2018	Angling	374	650	nd	*1*	Yes	Yes
26258	########	51.892776, -2.266282	06/06/2018	Angling	327	525	nd	*2*	Yes	Yes
26284	########	51.993539, -2.173897	07/06/2018	Trap	351	425	nd	*1*	Yes	Yes
26331	########	51.993539, -2.173897	11/06/2018	Trap	346	525	nd	*1*	Yes	Yes
26330	########	51.993539, -2.173897	13/06/2018	Trap	385	625	nd	*1*	Yes	Yes
26278	########	51.993539, -2.173897	13/06/2018	Trap	352	400	nd	*2*	Yes	Yes
26309	########	51.993539, -2.173897	14/06/2018	Angling	338	425	nd	*2*	Yes	Yes
26251	########	51.892776, -2.266282	27/05/2018	Angling	393	850	nd	*0*	Yes	No
26245	########	51.892776, -2.266282	08/06/2018	Angling	374	750	nd	*0*	Yes	No
26325	########	51.993539, -2.173897	24/05/2018	Trap	379	625	nd	*1*	No	Yes
26324	########	51.993539, -2.173897	08/06/2018	Trap	393	825	nd	*0*	No	Yes
26318	########	51.993539, -2.173897	08/06/2018	Angling	365	600	nd	*0*	No	Yes
26314	########	51.993539, -2.173897	24/05/2018	Trap	383	800	f	*1*	No	Yes
26311	########	51.993539, -2.173897	20/06/2018	Angling	335	475	m	*0*	No	Yes
26310	########	51.993539, -2.173897	06/06/2018	Angling	296	300	nd	*0*	No	Yes
26308	########	51.993539, -2.173897	09/06/2018	Angling	275	250	nd	*0*	No	Yes
26307	########	51.993539, -2.173897	04/06/2018	Angling	323	350	m	*0*	No	Yes
26299	########	51.993539, -2.173897	06/06/2018	Angling	328	425	m	*0*	No	Yes
26263	########	51.892776, -2.266282	27/05/2018	Angling	320	400	nd	*0*	No	Yes
26257	########	51.892776, -2.266282	21/05/2018	Angling	388	775	nd	*0*	No	Yes
26256	########	51.892776, -2.266282	24/05/2018	Angling	382	750	nd	*1*	No	Yes
26255	########	51.892776, -2.266282	30/05/2018	Angling	379	825	nd	*0*	No	Yes
26254	########	51.892776, -2.266282	13/06/2018	Angling	390	750	nd	*1*	No	Yes
26247	########	51.892776, -2.266282	12/06/2018	Angling	374	600	nd	*1*	No	Yes
26246	########	51.892776, -2.266282	04/06/2018	Angling	338	525	nd	*1*	No	Yes
26294	########	51.993539, -2.173897	05/06/2018	Angling	383	750	nd	*0*	No	Yes

26297	########	51.993539, -2.173897	25/05/2018	Angling	365	550	nd	*1*	No	Yes
26298	########	51.993539, -2.173897	11/06/2018	Angling	375	625	nd	*1*	No	Yes
26303	########	51.993539, -2.173897	02/06/2018	Angling	351	475	nd	*1*	No	Yes
26305	########	51.993539, -2.173897	28/05/2018	Angling	358	400	nd	*1*	No	Yes
26285	########	51.993539, -2.173897	03/06/2018	Trap	406	950	nd	*0*	No	Yes
26286	########	51.993539, -2.173897	09/06/2018	Trap	366	700	nd	*2*	No	Yes
26291	########	51.993539, -2.173897	29/05/2018	Trap	323	425	nd	*1*	No	Yes
26333	########	51.993539, -2.173897	11/06/2018	Trap	385	825	nd	*1*	No	No
26332	########	51.993539, -2.173897	23/06/2018	Trap	373	725	nd	*1*	No	No
26326	########	51.993539, -2.173897	22/06/2018	Trap	370	775	nd	*1*	No	No
26320	########	51.993539, -2.173897	20/06/2018	Trap	357	675	nd	*1*	No	No
26302	########	51.993539, -2.173897	08/06/2018	Angling	365	700	nd	*2*	No	No
26300	########	51.993539, -2.173897	03/06/2018	Angling	343	500	nd	*1*	No	No
26262	########	51.892776, -2.266282	04/06/2018	Angling	348	450	nd	*2*	No	No
26261	########	51.892776, -2.266282	14/06/2018	Angling	388	825	nd	*1*	No	No
26260	########	51.892776, -2.266282	06/06/2018	Angling	408	850	nd	*0*	No	No
26259	########	51.892776, -2.266282	05/06/2018	Angling	363	725	nd	*0*	No	No
26253	########	51.892776, -2.266282	05/06/2018	Angling	326	400	nd	*2*	No	No
26252	########	51.892776, -2.266282	18/06/2018	Angling	346	500	nd	*1*	No	No
26249	########	51.892776, -2.266282	23/05/2018	Angling	368	625	nd	*1*	No	No
26319	########	51.993539, -2.173897	06/06/2018	Angling	347	525	nd	*2*	No	No
26292	########	51.993539, -2.173897	02/06/2018	Angling	297	300	nd	*1*	No	No
26304	########	51.993539, -2.173897	23/06/2018	Angling	338	450	nd	*0*	No	No
26280	########	51.993539, -2.173897	30/05/2018	Trap	315	400	m	*1*	No	No
26282	########	51.993539, -2.173897	08/06/2018	Trap	370	800	f	*1*	No	No
26283	########	51.993539, -2.173897	06/06/2018	Trap	400	925	nd	*1*	No	No
26289	########	51.993539, -2.173897	10/06/2018	Trap	383	700	nd	*1*	No	No
26290	########	51.993539, -2.173897	28/05/2018	Trap	356	625	nd	*3*	No	No
26321	########	51.993539, -2.173897	26/05/2018	Trap	351	700	nd	*0*	No	No
26313	########	51.993539, -2.173897	NA	Trap	363	600	f	*1*	NA	NA
26315	########	51.993539, -2.173897	NA	Trap	411	950	nd	*2*	NA	NA
26322	########	51.993539, -2.173897	NA	Trap	374	775	nd	*1*	NA	NA
26323	########	51.993539, -2.173897	NA	Trap	383	775	nd	*1*	NA	NA
26306	########	51.993539, -2.173897	NA	Angling	337	450	nd	*1*	NA	NA
26316	########	51.993539, -2.173897	NA	Angling	281	250	nd	*0*	NA	NA
26293	########	51.993539, -2.173897	NA	Angling	398	725	nd	*1*	NA	NA

26295	########	51.993539, -2.173897	NA	Angling	382	675	nd	*1*	NA	NA
26296	########	51.993539, -2.173897	NA	Angling	361	575	nd	*1*	NA	NA
26312	########	51.993539, -2.173897	NA	Angling	342	450	nd	*1*	NA	NA
26279	########	51.993539, -2.173897	NA	Trap	397	850	f	*1*	NA	NA
26281	########	51.993539, -2.173897	NA	Trap	375	725	nd	*1*	NA	NA
26287	########	51.993539, -2.173897	NA	Trap	365	725	nd	*1*	NA	NA
26288	########	51.993539, -2.173897	NA	Trap	377	650	f	*1*	NA	NA
26334	########	51.892776, -2.266282	NA	Trap	379	700	f	*1*	NA	NA

9.6 Appendix 4: Tracking repeat-spawning anadromous fish over multiple migrations reveals individual repeatability, tagging effects and environmental factors influence barrier passage

Table A8: 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
river reach	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 A9: Full set of fitted mixed effects cox models to test the effect of individual covariates passage rates of weir S2 by acoustic tagged twaite shad. Models tested on Dataset 1 containing newly tagged and returning fish

Model structure	**df**	**logLikelihood**	**AICc**	**delta**	**weight**
(a)					
river level+diel period+body length_mm+tagging status+water temp	20	-83.65	209.01	0.00	0.36
river level+diel period+tagging status+water temp	21	-82.67	209.34	0.33	0.30
river level+body length_mm+tagging status+water temp	20	-84.69	211.28	2.27	0.11
river level+tagging status+water temp	22	-83.24	211.92	2.91	0.08
river level+diel period+tagging status	20	-85.81	213.18	4.17	0.04
river level+diel period+body length_mm+tagging status	20	-86.39	213.37	4.36	0.04
river level+tagging status	21	-85.88	214.86	5.85	0.02
river level+body length_mm+tagging status	19	-87.44	214.91	5.90	0.02
river level+diel period+body length_mm	22	-85.85	217.26	8.25	0.01
river level+diel period	22	-86.25	217.85	8.84	0.00
river level+diel period+body length_mm+water temp	23	-84.92	217.87	8.86	0.00
river level+body length_mm	22	-86.77	218.68	9.67	0.00
river level+diel period+water temp	24	-85.35	218.79	9.78	0.00
river level+body length_mm+water temp	23	-85.92	219.49	10.48	0.00
river level	22	-86.75	219.55	10.54	0.00
river level+water temp	24	-86.01	220.68	11.67	0.00
diel period+tagging status	17	-98.61	232.76	23.75	0.00
diel period+tagging status+water temp	19	-96.99	232.97	23.96	0.00
diel period+body length_mm+tagging status	17	-99.39	233.35	24.34	0.00
diel period+body length_mm+tagging status+water temp	18	-97.71	233.44	24.43	0.00
diel period	14	-102.21	233.57	24.56	0.00
diel period+body length_mm	14	-102.43	234.00	24.99	0.00
tagging status	20	-96.22	234.27	25.26	0.00
tagging status+water temp	22	-95.01	234.45	25.44	0.00
body length_mm+tagging status	20	-97.30	234.98	25.97	0.00
body length_mm+tagging status+water temp	21	-96.07	234.99	25.98	0.00
diel period+water temp	15	-102.19	235.30	26.29	0.00
diel period+body length_mm+water temp	15	-102.36	235.68	26.67	0.00
NULL	18	-99.72	236.60	27.59	0.00
body length_mm	18	-100.20	236.77	27.76	0.00
water temp	19	-99.73	238.33	29.32	0.00
body length_mm+water temp	19	-100.19	238.45	29.44	0.00

Table A10: Full set of fitted mixed effects cox models to test the effect of individual covariates on passage rates of weirs S2 by acoustic tagged twaite shad. Models tested on Dataset 2 containing only returning fish.

Model structure	**df**	**logLikelihood**	**AICc**	**delta**	**weight**
previous success+river level+diel period+water temp	5	-40.24	91.26	0.00	0.23
previous success+river level+water temp	5	-40.57	91.79	0.52	0.18
river level+diel period+water temp	3	-42.53	92.17	0.91	0.15
previous success+river level+diel period+body length_mm+water temp	6	-39.76	92.80	1.54	0.11
previous success+river level+body length_mm+water temp	6	-40.30	93.40	2.14	0.08
river level+water temp	2	-44.14	93.65	2.39	0.07
river level+diel period+body length_mm+water temp	4	-42.34	93.88	2.61	0.06
river level+body length_mm+water temp	3	-44.18	95.58	4.32	0.03
previous success+river level	2	-46.06	96.13	4.87	0.02
previous success+river level+diel period	3	-45.30	96.62	5.36	0.02
river level+diel period	2	-46.52	97.06	5.79	0.01
previous success+river level+body length_mm	3	-45.63	97.28	6.02	0.01
previous success+river level+diel period+body length_mm	4	-44.72	97.45	6.19	0.01
river level	1	-48.10	98.22	6.95	0.01
river level+diel period+body length_mm	3	-46.48	98.98	7.72	0.00
river level+body length_mm	2	-48.05	100.13	8.86	0.00
previous success+body length_mm+water temp	16	-33.75	100.95	9.69	0.00
previous success	1	-49.92	101.85	10.59	0.00
previous success+diel period+body length_mm+water temp	17	-33.19	102.19	10.93	0.00
previous success+water temp	12	-38.22	102.44	11.18	0.00
previous success+diel period	2	-49.72	103.46	12.20	0.00
water temp	20	-31.22	103.50	12.24	0.00
previous success+body length_mm	2	-49.78	103.57	12.31	0.00
previous success+diel period+water temp	13	-38.12	104.07	12.81	0.00
previous success+diel period+body length_mm	3	-49.56	105.14	13.87	0.00
body length_mm+water temp	19	-33.00	105.95	14.69	0.00
diel period	1	-52.69	107.73	16.47	0.00
diel period+water temp	18	-35.78	108.93	17.67	0.00
diel period+body length_mm	2	-52.65	109.31	18.05	0.00
body length_mm	2	-52.30	109.87	18.61	0.00
diel period+body length_mm+water temp	18	-36.10	109.89	18.63	0.00
null	5	-50.47	111.21	19.95	0.00

9.7 Appendix 5: Movement, space use and spatial fidelity of threatened anadromous twaite shad *Alosa fallax* during their spawning migrations

Table A11: Full set of linear mixed effects models to test the effect of individual covariates on core area size in acoustic tagged twaite shad.

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

Table A12:Full set of binomial generalised models to test the effect of individual covariates on spatial fidelity in acoustic tagged twaite shad.

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