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Tracking the invasive and euryhaline pikeperch *Sander lucioperca* in the lower River Thames using acoustic telemetry indicates no movements into areas of relatively high salinity

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Abstract

Native to Central and Eastern Europe, the euryhaline pikeperch *Sander lucioperca* can acclimatize to elevated salinity levels (e.g., up to 30‰), but it remains unknown whether their invasive populations use this ability to inhabit and/or disperse through brackish waters, such as estuaries and inshore areas. To test whether invasive pikeperch show a propensity to move into areas of relatively high salinity, their spatial use and movement patterns (e.g., home range, distances moved, and movement rates) were assessed using acoustic telemetry in the upper River Thames estuary, southeast England. Analyses revealed that individual pikeperch were capable of moving relatively long distances in a short time (e.g., speeds up to 70 m min^{-1}), with movement patterns associated more with tidal state and elevation at the water surface (both assumed to relate to changes in salinity) than diurnal changes. There were no recorded movements of any pikeperch into the more saline, downstream waters of the estuary where salinity levels were recorded to over 40‰, with the mean salinity in the most downstream area where pikeperch were detected being 1.39‰ (range of logger: 1.22–1.71). The results suggest that these pikeperch did not use high salinity waters when less saline waters were available, and thus the risk that they will use to move through high salinity areas to expand their invasive range appears low. Accordingly, efforts to minimize risks of the further dispersal of invasive pikeperch populations can focus on control and containment programmes within fresh waters.

KEYWORDS
acoustic telemetry, direction traveled, distance traveled, tidal state, zander

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[†] Deceased.

1 | INTRODUCTION

The ability of newly introduced non-native species to establish, disperse, and colonize new areas is fundamental to their invasion success (Andrew & Ustin, 2010; Britton et al., 2023; Dominguez Almela et al., 2022). The rate at which non-native species disperse in a novel environment is a function of their biological traits, including their dispersal abilities, coupled with the abiotic characteristics of the environment, especially habitat connectivity (Andrew & Ustin, 2010). The natural dispersal of non-native freshwater fishes requires fluvial connectivity (Gozlan et al., 2010), with intra-catchment dispersal rates dependent on the extent to which the river network has been fragmented (Mari et al., 2014), with multiple barriers, such as dams, weirs, and culverts, being encountered in many rivers (Belletti et al., 2020). These barriers both inhibit the spread of invasive species (Daniels & Kemp, 2022) and prevent the free ranging of native species (Meixler et al., 2009).

Limiting and preventing the dispersal of alien fish species into novel environments are important for protecting native freshwater biodiversity from the impacts of their invasions (Britton et al., 2023; Dudgeon et al., 2006; Reid et al., 2019). Efforts to prevent the dispersal of freshwater non-native species thus include the construction of physical, electric, chemical, and acoustic barriers (Jones et al., 2021). The use of chemical barriers is analogous to the natural salinity gradients encountered in lower river reaches and estuaries that usually prevent the further downstream dispersal of most non-native freshwater fishes (Brown et al., 2007). However, the relatively high salinity tolerances of euryhaline alien fishes potentially enable their movements across salinity gradients, with non-native fishes such as the Ponto-Caspian round goby *Neogobius melanostomus* being invasive in both freshwater and brackish waters (Kornis et al., 2012; Puntila-Dodd et al., 2021). For invasive euryhaline fishes, the presence of strong salinity gradients in the tidal reaches of rivers might thus be insufficient to prevent their downstream dispersal, raising the possibility of their spread between river catchments through estuarine and inshore areas (Brown et al., 2007).

The euryhaline pikeperch (or zander) *Sander lucioperca* (L.) is a popular angler target species in Europe, which has resulted in its introduction across much of Western Europe, with invasive populations present in countries, including France, Spain, Portugal, and Great Britain (Elvira & Almodóvar, 2001; Gago et al., 2021; Kopp et al., 2009). In Britain, pikeperch was introduced in 1878 into enclosed waters in the East of England (Copp et al., 2003), with subsequent translocations into rivers occurring during the 1960s (Wheeler, 1974), with these later releases leading to the species establishing and invading open waters (Copp et al., 2003; Hickley, 1986; Linfield & Rickards, 1979). The capture of pikeperch was subsequently reported by anglers from other catchments throughout the 1970s (Wheeler, 1974; Hickley, 1986), with self-sustaining populations now present throughout eastern, central, and western England (Copp et al., 2003; Nunn, 2007; Smith et al., 1998). Despite occasional reported sightings, there are not yet any confirmed reports of self-sustaining pikeperch populations in northern and southwest England (Nolan & Britton, 2019).

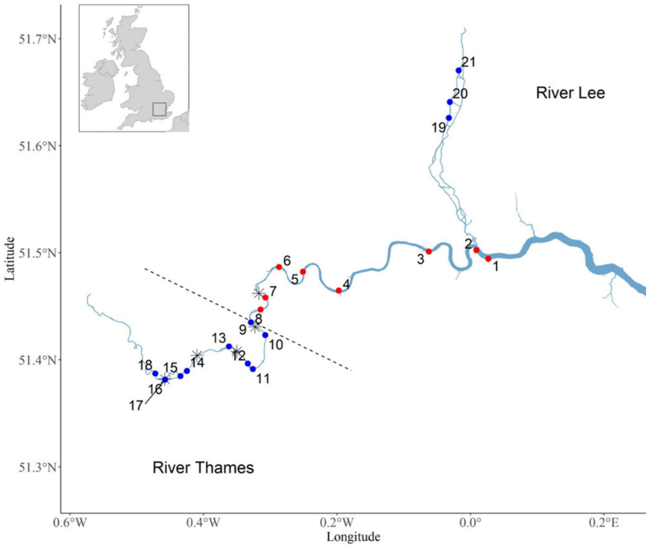

FIGURE 1 Map showing the location of the study area in the UK (inset) and the study locations on the rivers Thames and Lee, with labels that correspond to those in Table 1. Blue circles represent freshwater sites, and red circles represent tidal sites. Asterisks (*) show the locations of barriers that likely inhibit pikeperch movement at certain times. The black dashed line bisects the River Thames at the tidal limit at Teddington Lock and Weir (WGS84 latitude, longitude: 51.430123, −0.321107). Note that the receivers and loggers were sometimes used in multiple locations throughout the study; for example, two loggers were used at Hambhaugh Island, Weybridge Lock (labels 16 and 17).

With pikeperch now present at the tidal limits of some major river systems within their current range in England, such as in the rivers Thames, Severn, Trent, and Great Ouse, their euryhaline traits suggest that there is a possibility of their spread into neighboring, uninvaded river catchments via dispersal through brackish or saltwater bridges (Brown et al., 2007). Movements across saltwater bridges could have already occurred in other European countries, given the species is present in the lower salinity regions of the Baltic Sea, the Kiel Canal, and many European estuaries (Brown et al., 2007). Non-native fish legislation and regulations in England and Wales aim to control and contain pikeperch populations where, for example, control is through fish removals to reduce abundance, and containment aims to limit their distribution to its current range (Hickley & Chare, 2004; Nolan et al., 2019). Consequently, should pikeperch disperse naturally in England from their current range into uninvaded river catchments via saltwater bridges, then this would be contrary to these regulatory aims. However, the actual risk of pikeperch dispersing naturally in this manner remains highly uncertain (Brown et al., 2007).

Therefore, the aim here was to characterize the dispersal and movement patterns of non-native pikeperch in the lower River Thames, southeast England, and assess their movements across a gradient of salinity to identify their potential to disperse between river catchments via saltwater bridges (Scott et al., 2008). Specifically, pikeperch movements were tracked using acoustic telemetry to quantify their home range, movement distances, and speeds, particularly in

TABLE 1 Names and coordinates of the study sites on the rivers Thames and Lee, together with their receiver and logger code, and an indicator of whether they were tidal.

Label	Station	Longitude	Latitude	Receiver	Logger	Tidal	Median salinity (‰) [range]	Number of fish detected
1	Riverside, New Charlton, Thames Barrier	0.027	51.494	5177	1795	Yes	6.65 [0–44.8]	0
2	North Greenwich Pier, Millennium Dome	0.009	51.503	5175	1773	Yes	6.4 [2.14–11.88]	0
3	Cherry Garden Pier, Tower Bridge	−0.062	51.501	4834	1772	Yes	0.01 [0.01–0.54]	0
4	Hurlingham Harbor, Putney Bridge	−0.198	51.465	4833	1800	Yes	0.02 [0–0.27]	0
5	Chiswick Pier, Corney Reach Way	−0.251	51.482	5176	1787	Yes	1.39 [1.22–1.71]	4
6	Thames Path, Kew Bridge	−0.287	51.487	4825	1788	Yes	1.22 [0.9–1.64]	4
7	Buccleuch Passage, Richmond Bridge	−0.307	51.458	4831	1792	Yes	1.47 [1.28–1.96]	0
8	Twickenham Ferry	−0.314	51.447	4832	1777	Yes	2.58 [2.55–2.6]	0
9	Strawberry Vale, Teddington	−0.329	51.435	4824	1793	No	1.1 [0.88–1.45]	10
10	Teddington Tamesis Sailing Club	−0.307	51.423	4829	1791	No	2 [1.75–2.56]	1
11	Ferry Rd Thames Ditton	−0.326	51.391	4833	1787	No	1.57 [1.24–1.87]	0
12	Alexandra Rd, u/s of Thames Ditton Island	−0.334	51.397	4831	1792	No	1.72 [1.58–1.95]	9
13	Hampton Ferry Boat House	−0.362	51.413	4835	1778	No	0.71 [0.49–1.05]	2
14	Felix Lane, Shepperton Marinas	−0.425	51.390	4832	1777	No	2.14 [1.77–2.67]	3
15	Thames Meadow, u/s of Walton Bridge	−0.435	51.385	4830	1772	No	0.01 [0–0.01]	3
16	Hambhaugh Island, Weybridge Lock	−0.458	51.382	4826	1782	No	2.01 [1.62–2.4]	3
17	Hambhaugh Island, Weybridge Lock	−0.458	51.382	4826	1800	No	0.01 [0.01–0.01]	3
18	Dockett Eddy, Chertsey	−0.472	51.387	4827	1782	No	1.61 [1.36–2.1]	0
19	Alfie's Lock, Pickets Lock Lane, Edmonton	−0.032	51.626	4829	1791	No	2.21 [1.88–2.4]	0
20	South Island Marina, d/s of Ponders Lock	−0.031	51.641	4829	1791	No	2.86 [2.03–3.17]	0
21	Refuges, Government Row/Smeaton Rd	−0.018	51.670	4830	1772	No	0.01 [0.01–0.01]	0

Note: Each site is associated with a label that corresponds to Figure 1.

relation to salinity gradients and barriers, including locks and weirs, that potentially impede their movements.

2 | MATERIALS AND METHODS

2.1 | Application of acoustic telemetry to pikeperch movements in the lower Thames basin

The study area used for acoustic telemetry was the lower section of the River Thames (hereafter *lower Thames*) that runs through London (Figure 1), receiving inputs from several tributary streams up- and downstream of its upper tidal limit at Teddington Lock and Weir (WGS84 latitude, longitude: 51.430123, −0.321107). A network of 18 VR2W, single-channel, acoustic receivers (Vemco, Canada; hereafter *receivers*) was deployed along the lower river between the town of Chertsey and the Thames Barrier, Royal Borough of Greenwich, as well as along the lower River Lee where it represents the eastern borders of the London boroughs of Enfield and Haringey (Figure 1; Table 1; Supplementary Material: Table S1). Twelve conductivity data loggers (hereafter *loggers*) were deployed between 20 receivers (Figure S1) to provide a surrogate measure of water salinity.

Field studies began in April 2005, when pikeperch were captured for tagging using continuous electrofishing in the lower sections of the rivers Thames ($n = 20$, 246–765 total length [TL]) and Lee ($n = 4$; 525–640 mm TL) using a generator-powered unit in a small boat (Table 2). The care and use of the captured pikeperch complied with the regulations of the UK Home Office under the Animals (Scientific Procedures) Act 1986 and was completed following ethical review and under project license. Accordingly, the captured pikeperch selected for tagging were anaesthetized (0.4–0.5 mL L^{-1} solution of 2-phenoxyethanol) and implanted internally with the acoustic transmitter by making an incision (10–12 mm) in the area between the pelvic fins and vent, with the incision closed with a single suture (coated

TABLE 2 Details of the pikeperch tagged, including the "Tagging site" where they were tagged and their "Home range," calculated as the total distance it ranged during the study (those with no home range estimate were recorded only at a single location).

Acoustic transmitter	Total length (mm)	Age	Sex	Tagging site	Date	UK National Grid reference	Latitude	Longitude	Home range (m)
1	675	7	Male	Weybridge Lock River Thames	March 24, 2005	TQ074658	51.381	−0.458	4799.695
2	705	7	Female	Weybridge Lock River Thames	March 24, 2005	TQ074659	51.381	−0.458	1694.647
3	735	8	Female	Young Mariners Marina River Thames	May 3, 2005	TQ164724	51.439	−0.326	7108.770
4	715	7	Male	Young Mariners Marina River Thames	May 3, 2005	TQ164724	51.439	−0.326	7108.770
5	625	6	Female	Young Mariners Marina River Thames	May 3, 2005	TQ164724	51.439	−0.326	7108.770
6	715	7	Female	Teddington Lock River Thames	May 31, 2005	TQ166714	51.430	−0.323	
7	765	8	Female	Teddington Lock River Thames	June 1, 2005	TQ166714	51.430	−0.323	
8	640	7	Unknown	Picket Lock River Lee	June 27, 2005	TQ363938	51.627	−0.032	
18	246	1	Juvenile	Teddington Lock River Thames	November 11, 2005	TQ166714	51.430	−0.323	
26	435	3	Male	Young Mariners Marina River Thames	May 3, 2005	TQ164724	51.439	−0.326	7108.770
27	425	3	Female	Young Mariners Marina River Thames	May 3, 2005	TQ164724	51.439	−0.326	7108.770
28	425	3	Male	Young Mariners Marina River Thames	May 3, 2005	TQ164724	51.439	−0.326	
30	592	5	Female	Teddington Lock River Thames	November 11, 2005	TQ166714	51.430	−0.323	
46	595	5	Male	Weybridge Lock River Thames	March 24, 2005	TQ074660	51.381	−0.458	9875.070
47	585	5	Male	Young Mariners Marina River Thames	May 3, 2005	TQ164724	51.439	−0.326	7108.770
48	590	5	Female	Young Mariners Marina River Thames	May 3, 2005	TQ164724	51.439	−0.326	7108.770
49	605	5	Male	Teddington Lock River Thames	May 31, 2005	TQ166714	51.430	−0.323	7108.770
50	595	5	Unknown	Picket Lock River Lee	June 27, 2005	TQ363939	51.627	−0.032	
51	525	4	Unknown	Picket Lock River Lee	June 27, 2005	TQ363940	51.627	−0.032	
52	550	5	Unknown	Picket Lock River Lee	June 28, 2005	TQ362936	51.625	−0.033	
57	528	4	Male	Teddington Lock River Thames	November 10, 2005	TQ166714	51.430	−0.323	
63	665	6	Male	Teddington Lock River Thames	November 10, 2005	TQ166714	51.430	−0.323	
64	547	4	Female	Teddington Lock River Thames	November 10, 2005	TQ166714	51.430	−0.323	
65	537	4	Female	Teddington Lock River Thames	November 10, 2005	TQ166714	51.430	−0.323	

Note: "Tagging site" differs from receiver "Location name," and the table has been ordered by the "Date" of tagging.

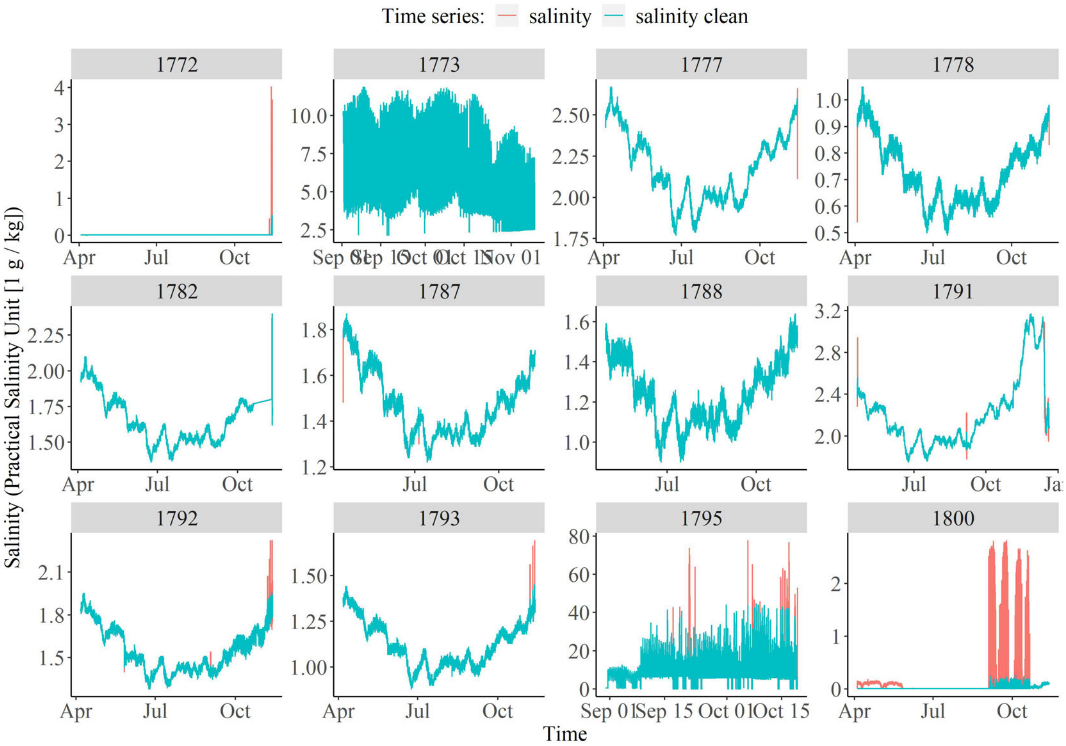

FIGURE 2 Plot showing the original and cleaned salinity measurements recorded at each logger. Cleaned salinity measurements were treated for statistical outliers. Even after cleaning, measurements taken on loggers 1772, 1795, and 1800 were considered unusable.

Vicryl), and the wound then treated with a mixture of Orahesive and Cicatrin (see Moore et al. [1990] and Stakėnas et al. [2009] for details). The acoustic transmitters were all Vemco V8SC–1 (8 mm diameter, 26 mm length, 4.2 g). The period of anaesthesia and surgery lasted 3–6 min. Following recovery to normal behavior, the fish were released at their point of capture. Detection data from the receivers were downloaded every 3 months.

2.2 | Data analyses

Information about receivers, together with their detections, was compiled into a single database joined by *Location name*, accounting for their deployment and recovery timings at different locations (using R package data. table; Barrett et al., 2023; Table S1). Distances between locations along the river course were calculated from river data cleaned and reprojected to the Transverse Mercator projection (using R packages sf and riverdist; Tyers [2023]; Pebesma and Bivand [2023]) and used to calculate *Distance traveled* (*m*) between consecutive detections for all individual movements (using the riverdistance function in R package riverdist). Additional potentially useful explanatory variables were calculated and added to the database, including the *Time of day of departure* that was classified as day or night depending on whether the detection was after sunrise and before sunset at the specific location (using function getSunlightTimes in R package suncalc; Thieurmel & Elmarhraoui, 2022), and *Acoustic transmitter* number used to group movements by pikeperch in subsequent analyses (Figures S2 and S3). These data were used to calculate *Home range* for each pikeperch detected on more than one occasion, as the maximum distance traveled between two detections and their movement *Speed* (m min^{-1}), as the time taken (in minutes) to travel between locations of two consecutive detections (in meters).

Measures of the aquatic environment were calculated for use as covariates in the models. Salinity measurements from loggers revealed regular spatial and temporal variations but were incomplete records, including occasional unusual recordings (Figure 2). To reduce the effect of likely spurious/erroneous salinity measurements on subsequent analyses, a cleaned version of the salinity measurements was prepared in which statistically outlying measurements taken at loggers at specific sites, that is, those that were outside the 25th–75th interquartile range of seasonally adjusted measurements, were replaced with a linearly interpolated value using the tsoutliers function in R package forecast (Hyndman & Khandakar, 2008). Visual inspection suggested that the resulting cleaned salinity time series were useable, except time series from loggers 1772, 1795, and 1800, which were excluded from subsequent analyses (Figure 2). Tide state, that is, whether the tide was in flood (rising water surface elevation) or ebb (falling water surface elevation), was estimated as peaks and troughs of water surface elevation measured at Sheerness (available at https://www.bodc.ac.uk/data/hosted_data_systems/sea_level/uk_tide_gauge_network/) using the findpeaks function in R package gsignal (van Boxtel et al., 2021).

Distances traveled (*m*) data were then joined with aquatic environment data by the *Date and time* of each movement departure *Location*

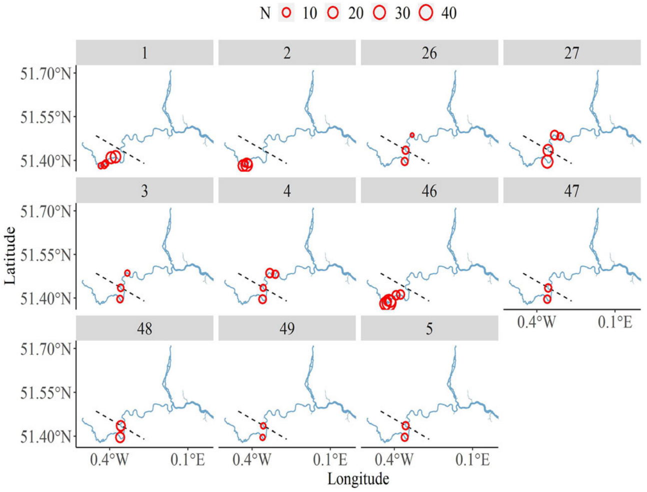

FIGURE 3 Counts (*N*) and locations of pikeperch detections in the study area for each individual tagged fish. The black dashed line bisects the River Thames at the tidal limit at Teddington Lock and Weir (WGS84 latitude, longitude: 51.430123, −0.321107).

name, allowing the calculation of water *Salinity at departure* and *Tide state at departure*, which were added to the database. In addition to these variables, the *Direction traveled* was inferred from consecutive detections and recorded in the database as either upstream or downstream.

The response variables *Distance traveled* (m) and *Direction traveled* were then selected for further analyses. *Distance traveled* was left-skewed, which was improved using a natural log transform, and was analysed using a linear mixed model assuming log-normal errors and including *Acoustic transmitter* as a grouping variable to account for repeat measurements on an individual. *Direction traveled* was analysed using a generalized linear model assuming binomial errors. These models were fit using R package lme4 (Bates et al., 2015) and base (R Core Team, 2023), respectively. For each response variable, multiple candidate models were fitted, and their fits were compared using AIC corrected for small sample size (AICc; Burnham and Anderson [2003]); the candidate model best explaining variations in the response variable was taken to be the one with the smallest AICc value, although models within 2 δAICc points of that model were also considered parsimonious descriptions of the observed data (Burnham and Anderson, 2003). Marginal effects of explanatory variables were plotted for each response variable to help the interpretation of the model fits using R package ggplot2 (Wickham, 2016). All code for the analysis is provided in the GitHub repository at https://github.com/CefasRepRes/pikeperch-homerange-salinity.

3 | RESULTS

3.1 | Overview of pikeperch movement data

Pikeperch tagged on the River Lee (acoustic transmitters 8, 50, 51, and 52) were recorded only at the receiver closest to their point of release and nowhere in the River Thames (Figure 3). Of the fish tagged in the River Thames, movements by most tagged pikeperch were in the form of regular down- and upstream movements (Figure 3; Table 3), often associated with an in-river structure. For example, the pikeperch with Acoustic transmitter 46 made 50 repeated and regular movements among three stations in April 2005, which were mostly upstream from Walton bridge in the Thames Meadow (Receiver 4830; Table S1) to Weybridge Lock at Hambhaugh Island (Receiver 4826; Table S1) and back downstream to Walton bridge.

The prevalence of these regular down- and upstream movements was reflected in measures of tagged pikeperch home ranges and movement speeds. Although the smallest and largest home ranges were ~1.5 and 10 km, respectively, the home ranges of most fish were ~7 km and centered around acoustic receivers near the tidal limit at Teddington Lock and Weir (receivers 4824 and 4831). Similarly, there were some notably fast (>70 m min^{-1}) and slow (<1 m min^{-1}) pikeperch movements, but with most movement speeds between 15 and 30 m min^{-1} and with no difference between the speeds of movements in upstream and downstream directions (mean m min^{-1} ± SD; downstream: 25.15 ± 15.95; upstream: 25.06 ± 14.27). For some tagged pikeperch, no home ranges and speeds could be calculated because they were detected on too few occasions (Table 3).

Across the study area, median salinities were recorded by loggers up to 6.65 (range of logger: 0‰–44.80‰; Table 1). However, no pikeperch was recorded in an area where the median salinity was higher than 2.14 (range of logger: 1.77–2.67; Figure 2; Table 1). Among the tagged pikeperch, only four moved to locations downstream of the tidal limit. Of these, one seemed to make only a single journey from the fresh water to the tidal zone at *Thames Path, Kew Bridge* (Acoustic transmitter 26; Figure 4), whereas another seemed to make that same journey twice (Acoustic transmitter 3). The two remaining tagged pikeperch (acoustic transmitters 27 and 4) made seven and four journeys to the tidal zone, including movements to *Thames Path*, *Kew Bridge* and *Chiswick Pier*, *Corney Reach Way*, respectively. Of these, the movements between two receivers in fresh water tended to last longer than movements between a receiver in the fresh water and tidal zone or between two in the tidal zone (Figure 4). In most cases, these movements appear to be a discrete movement to the tidal zone that started and ended in the fresh water, albeit that tagged pikeperch detected at *Chiswick Pier*, *Corney Reach Way* could also be detected at *Thames Path*, *Kew Bridge*. There were, however, a few cases in which a tagged pikeperch seemed to move repeatedly between receivers in the tidal zone, the longest of which was seven repeated movements in the tidal zone over 19 days (Figure 5).

3.2 | Influence of tidal state on pikeperch movements

The model best describing *Distance traveled* (m) by pikeperch included both *Direction traveled* and *Salinity at departure* (to the power of 2) and suggested that distances traveled downstream

TABLE 3 Summary of acoustic tag detections and distances traveled by month.

Acoustic transmitter	Period	Number stations	Days detected	Number of downstream movements	Average distance traveled downstream (m)	Average speed downstream (m min^{-1})	Number of upstream movements	Average distance traveled upstream (m)	Average speed upstream (m min^{-1})
1	2005-03	2	2	0			1	8197.876	0.499
	2005-04	4	4	6	1974.303	23.892	3	1215.981	16.448
	2005-05	2	12	9	2144.126	54.223	9	2144.126	50.776
	2005-06	2	15	10	2144.126	32.192	11	2144.126	28.228
	2005-07	2	2	1	4799.695	0.279	0		
2	2005-04	3	14	13	1308.032	31.114	14	1335.647	16.727
	2005-05	3	9	5	1562.109	22.378	5	1466.387	17.609
	2005-06	3	12	8	1634.820	23.016	8	1694.647	30.187
	2005-10	2	2	1	1694.647	8.662	1	1694.647	27.488
3	2005-05	3	7	3	10,468.269	6.734	3	12,837.859	15.188
	2005-06	2	4	2	7108.770	19.084	2	7108.770	18.383
4	2005-06	3	5	2	11,405.587	76.014	2	11,405.587	28.277
	2005-07	4	12	6	10,493.027	30.162	6	9060.755	39.880
	2005-08	4	8	4	5055.510	22.542	4	7203.918	10.423
5	2005-06	2	4	1	7108.770	43.701	2	7108.770	22.078
	2005-07	2	6	2	7108.770	23.817	2	7108.770	42.543
	2005-08	2	2	1	7108.770	38.988	1	7108.770	42.031
	2005-09	2	1	1	7108.770	28.141	0		
26	2005-05	2	2	1	8593.634	2.787	0		
	2005-08	3	5	3	7108.770	32.923	4	9257.178	22.260
	2005-09	2	4	2	7108.770	10.082	1	7108.770	21.421
27	2005-06	3	9	6	11,405.587	35.317	6	11,405.587	72.850
	2005-07	4	16	12	8572.758	26.926	11	9352.100	29.889
	2005-08	4	16	9	7759.432	31.303	10	7694.365	25.799
	2005-09	2	4	2	7108.770	13.609	1	7108.770	13.689
46	2005-04	3	21	25	1407.447	19.424	25	1407.447	18.214
	2005-05	4	17	17	1374.100	16.820	20	1317.256	16.004
	2005-06	6	13	13	1849.838	28.958	10	1865.683	16.432
	2005-07	2	2	2	2144.126	7.483	1	2144.126	46.815
	2005-11	2	2	1	7730.944	1.983	0		
47	2005-06	2	4	1	7108.770	4.684	2	7108.770	3.980
	2005-07	2	8	4	7108.770	29.337	3	7108.770	26.677
	2005-08	2	2	1	7108.770	10.500	1	7108.770	14.311
48	2005-06	2	4	2	7108.770	32.355	2	7108.770	28.905
	2005-07	2	19	7	7108.770	32.650	7	7108.770	23.914
	2005-08	2	11	4	7108.770	32.107	4	7108.770	24.376
49	2005-07	2	3	2	7108.770	51.445	2	7108.770	14.624

Note: Absence of an "Acoustic transmitter" or "Period" indicates that no movement was recorded. "Number stations" is the number of stations with at least one "Day detected" during the study period. Details of the movements are given in up- and downstream movements.

increased as the salinity at departure increased, and distance traveled upstream increased up to a certain salinity (1‰) and then decreased thereafter, both irrespective of the tide state (Figure 6a and S4). This model explained 36% (marginal R^2; Table 4) of the variation in the distances traveled by tagged pikeperch and had substantially more empirical support (although < 2δAICc points) than the next most parsimonious model, which also included an effect of tide state.

Analyses of *Direction traveled* were inconclusive, with the best-fitting model including *Tide state at departure*, suggesting that the probability of upstream movement was higher when the tide was flooding versus ebbing (Figure 4b and S5). This model explained only 1.3% (marginal R^2; Table 4) of the variation in the direction that pikeperch chose to travel and did not provide substantially more empirical support than the null model. Model coefficient estimates (Tables S3 and S4), diagnostic plots, and the R session info are provided in the supplementary materials.

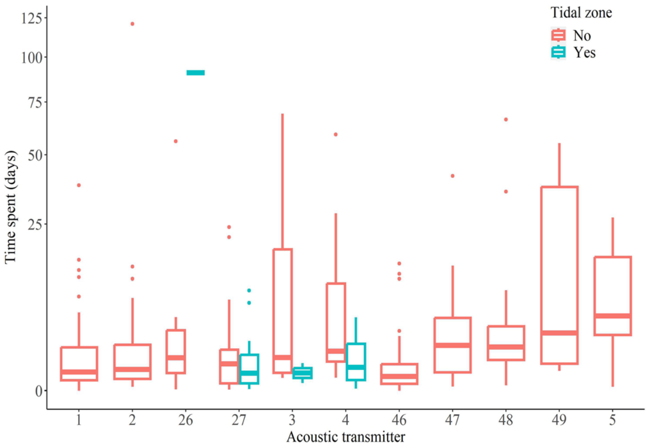

FIGURE 4 Duration of movements between receivers by tagged pikeperch, grouped by whether or not the receiver was in the tidal zone, that is, downstream of the tidal limit. Note that the *y*-axis is on a square root scale. Note the outlier of fish implanted with Acoustic transmitter 26 was a single movement of that pikeperch to the tidal zone where the fish remained for ~90 days.

4 | DISCUSSION

The application of acoustic telemetry to this freshwater pikeperch population revealed individual variability in their movements, with some having home ranges as small as 1.5 km and some as large as 10 km. These home range differences were consistent with the findings of Fickling and Lee (1985) and Aarts and Breukelaar (2017), who both detected two components within pikeperch populations, one that tended to remain resident in specific areas and the other that was more mobile. The movements of those pikeperch were not related to the speed of their movements or body size (Fickling & Lee, 1985), with this also the case here. The largest home ranges reported here are in line with some other movement studies on pikeperch (e.g., Poulet et al., 2005), but with other studies indicating home ranges of 40 km can be typical and where individuals migrate across distances of 200 km (Aarts & Breukelaar, 2017).

Populations of pikeperch are frequently encountered in waters of relative high salinity. For example, pikeperch make seasonal migrations into the Lithuanian coastal waters of the Baltic Sea where salinity levels are generally between 4.9‰ and 6.8‰ (Ložys, 2004), but with Baltic pikeperch generally restricted to coastal areas of relatively low salinity that are also eutrophicated (Lehtonen et al., 1996). Pikeperch egg survival is, however, highest at 0.7‰ and decreases linearly to 6.7‰ where egg mortality is total (Klinkhardt & Winkler, 1989). In a radio-tracking study in Denmark, pikeperch revealed downstream movements in winter where some individuals were detected in a fjord where salinity levels were recorded to 30‰ (Koed et al., 2002). Physiological experiments suggest freshwater pikeperch might resist salinity changes by manipulation of their nitrogen metabolism (Sadok et al., 2004). Despite this apparent salinity tolerance, pikeperch in the River Thames here were only recorded in reaches of river where the maximum salinity recorded to 2.67‰, with only four moving into

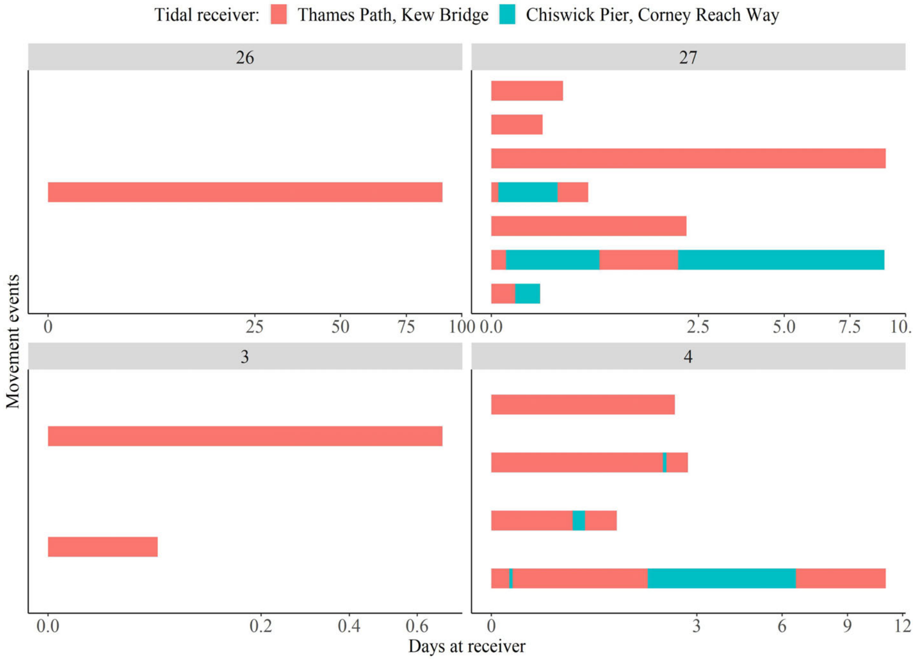

FIGURE 5 Plot showing the time spent at different receivers in the tidal zone on which the four tagged pikeperch were detected. Note that the *x*-axis is on a square root scale and differs for each panel.

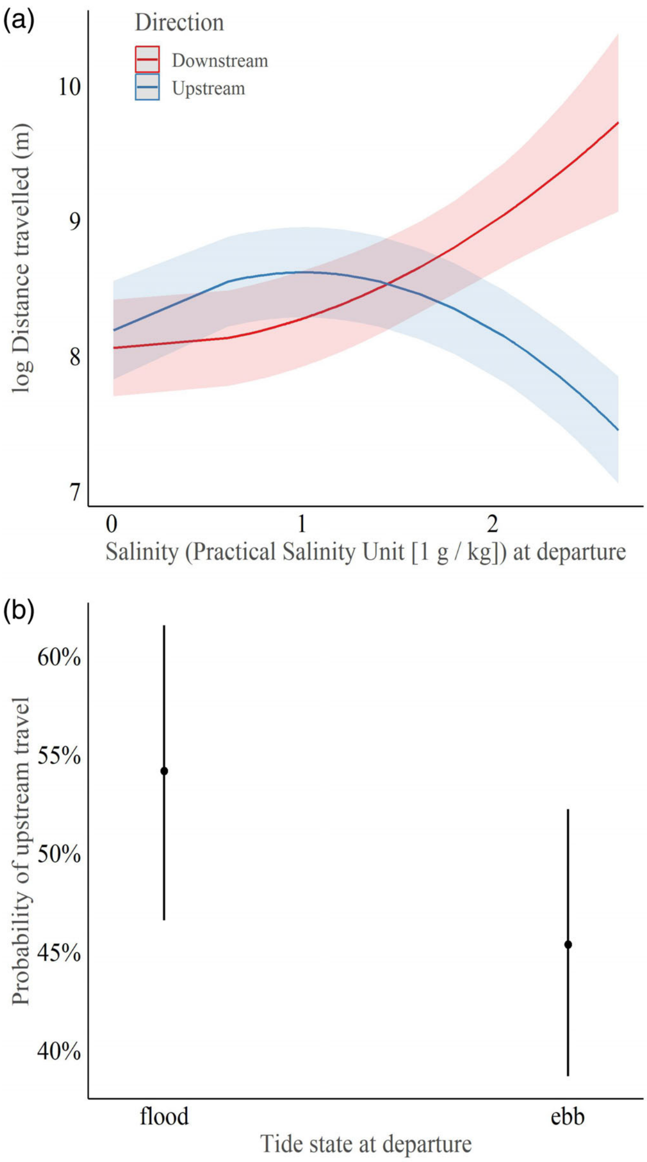

FIGURE 6 Marginal effects of salinity depending on direction (a) on distance traveled (in meters) in a single journey and the tide state at departure (b) on the probability of traveling upstream (compared to downstream).

tidal areas and with these tidal movements generally starting and ending in fresh water. Although the best-fitting model for distance traveled suggested that movements downstream increased as the salinity at departure increased, the effect was primarily measured across 1‰–2‰ and the models had relatively low values of explanatory value (as adjusted R^2). Accordingly, these downstream movements might have not necessarily been related to salinity but were perhaps driven by factors unable to be measured here, such as increased prey availability in downstream areas that resulted from movements with changes in the tidal state, although this can only be speculated.

The best-fitting and most parsimonious models did not include time of day as a significant predictor of movement, with this generally contrary to studies suggesting pikeperch activity is highest at dusk (e.g., Poulet et al., 2005), and Aarts and Breukelaar (2017) indicating swimming activity was highest in darkness in a Dutch lowland river. Although Poulet et al. (2005) discussed that pikeperch activity may be the result of trade-offs between physiological requirements of temperature and light, the satisfaction of energy needs, and avoidance of predators. In tidal rivers, the osmoregulatory costs relating to regular salinity changes might also need to be considered in these trade-offs (Sadok et al., 2004). In Aarts and Breukelaar (2017), movements of pikeperch to the seaward side of a dam from fresh water did occur, but with fish either returning to the freshwater side after foraging or dying if they remained there in periods of high salinity.

It has been outlined that the tagged pikeperch in the River Thames never moved into areas of relatively high salinity. However, some non-tagged pikeperch have been observed in areas of high salinity outside of this study. For example, one author of this study (S.S., *personal communication*) captured a 90-mm pikeperch on July 26, 2006, in a seine net (35 m length with 2.5 m drop and a 5-mm fine knotless mesh center) at London Yard, Millwall, Isle of Dogs (51.494666, −0.030080), upstream of logger 1773 cf. Table S2, when the salinity at that location at that time was 7.62‰ at 23.5°C. Moreover, in the Fumemorte Canal, France, salinity in summer can reach 5‰, with pikeperch present throughout the waterbody (Poulet et al., 2005), Ložys (2004) recording pikeperch in the Baltic at 6.8‰. Thus, the euryhaline traits of pikeperch suggest that their invasive populations could disperse into new areas via movements across brackish or saltwater bridges (Brown et al., 2007). Indeed, such movements across saltwater bridges have already been outlined to occur between fresh water and brackish water in the Baltic (at least into salinities of 6.8‰) (Ložys, 2004). In our study on River Thames pikeperch, we have no supporting evidence that movements across salinity gradients and salt bridges provide their invasive populations with a dispersal mechanism. However, we cannot definitively say it cannot happen, given such large-scale dispersal events might occur during episodic floods that cause both displacement of fish and reduced salinity levels (Williamson, 2006), with these conditions not occurring during our study period.

In summary, the movements of the tagged pikeperch in the tidal River Thames did not suggest a propensity for moving into habitats with relatively high salinity levels, with no movements into areas with salinities above 2.67‰, despite the species being generally capable of tolerating higher salinities, often having large home ranges (to 40 km), and being able to undertake large-scale movements across seasons (especially for spawning, e.g., to 200 km) (Aarts & Breukelaar, 2017; Koed et al., 2000). Although this suggests that the risk of their dispersal across a salt-bridge in the Thames specifically appears low, this has a caveat that some non-tagged individuals were encountered in areas of higher salinity. The movements of the tagged pikeperch indicated some variability among individuals, especially in relation to home range and speed of movement, with this consistent with other studies suggesting that their populations comprised resident and mobile individuals. Accordingly, it might be these more mobile individuals that present the higher risk of dispersing through salt-bridges, but the results of this study suggest that this risk is low. Thus, control and

TABLE 4 Candidate models, their performance, and their selection statistics.

Response variable	Model description	Number of parameters	AICc	δAICc	Cumulative weight	Conditional R^2	Marginal R^2
Distance traveled (m)	$D \times H^2$	8	202.329	0.000	0.492	0.838	0.364
	$S + D \times H^2$	9	204.051	1.722	0.700	0.833	0.385
	$D \times H^2 + L + X$	10	205.102	2.773	0.823	0.819	0.214
	$S \times D \times H^2$	14	206.112	3.783	0.898	0.812	0.232
	$S + D \times H^2 + L + X$	11	206.850	4.522	0.949	0.832	0.386
	$T + S \times D \times H^2$	15	208.103	5.774	0.976	0.828	0.371
	$S \times D \times H^2 + L + X$	16	209.029	6.701	0.994	0.790	0.331
	$T + S \times D \times H^2 + L + X$	17	211.048	8.719	1.000	0.789	0.325
	$T \times S \times D \times H^2$	26	222.703	20.374	1.000	0.811	0.233
	$T \times S \times D \times H^2 + L + X$	28	226.079	23.750	1.000	0.807	0.217
	$S + H^2$	6	262.208	59.879	1.000	0.764	0.164
	$S \times H^2$	8	263.520	61.191	1.000	0.764	0.158
	$D + H^2$	6	263.531	61.202	1.000	0.791	0.321
	$S + D + H^2$	7	263.563	61.234	1.000	0.790	0.312
	$S + H^2 + L + X$	8	264.816	62.488	1.000	0.828	0.371
	$D + S \times H^2$	9	265.198	62.869	1.000	0.788	0.322
	$D + H^2 + L + X$	8	266.132	63.803	1.000	0.766	0.155
	$S \times H^2 + L + X$	10	266.177	63.849	1.000	0.766	0.145
	$S + D + H^2 + L + X$	9	266.193	63.864	1.000	0.807	0.217
	$D + S \times H^2 + L + X$	11	267.878	65.549	1.000	0.763	0.156
	$S + D \times H$	7	269.086	66.757	1.000	0.825	0.150
	$S + D \times H + L + X$	9	271.992	69.663	1.000	0.824	0.150
	$S \times D \times H$	10	274.828	72.500	1.000	0.822	0.110
	$S \times D \times H + L + X$	12	277.815	75.486	1.000	0.821	0.110
	$S + D + H$	6	302.261	99.933	1.000	0.818	0.029
	$D + S \times H$	7	303.801	101.473	1.000	0.818	0.029
	$S + D + H + L + X$	8	305.115	102.786	1.000	0.820	0.008
	$D + S \times H + L + X$	9	306.681	104.352	1.000	0.820	0.008
	Null	3	323.291	120.963	1.000	0.802	0.000
Direction traveled	S	2	518.189	0.000	0.349		0.013
	Null	1	519.032	0.843	0.578		0.008
	$S + T$	3	520.105	1.916	0.711		0.013
	$S \times T$	4	520.438	2.249	0.825		0.008
	T	2	521.033	2.844	0.909		0.008
	$S + L + X$	4	522.203	4.014	0.956		0.000
	$S + T + L + X$	5	524.111	5.923	0.974		0.008
	$S \times T + L + X$	6	524.514	6.325	0.988		0.000
	$T + L + X$	4	524.989	6.801	1.000		0.000

Note: There is no conditional R^2 for the "Direction traveled" models because they did not include random terms.
Abbreviations: D, direction traveled; H, salinity at departure; L, total length (in millimeters); S, tide state at departure; T, time of day of departure; X, sex.

containment programmes that aim to reduce their ecological impacts and prevent their further dispersal should be sufficient as species-specific invasion management strategies.

AUTHOR CONTRIBUTIONS

Saulius Stakėnas, Keith J. Wesley, and Gordon H. Copp conceived the ideas; Saulius Stakėnas, Keith J. Wesley, and Gordon H. Copp designed the methodology and collected the data. Saulius Stakėnas, Stephen D. Gregory, j. Robert Britton, Jessica E. Marsh, and Ali Serhan Tarkan conducted statistical analyses, and led the writing of the manuscript. All authors contributed critically to the drafts and approved for publication. The authors declare no competing interests.

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