



The winter movements of two fish species in a temperate lowland river

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Abstract Winter involves long periods of low water temperatures, with the activities and movements of many temperate fish species being reduced compared with summer. In very cold periods, individuals can become winter quiescent. The extent to which the activities and movements of many fish species reduce in winter is unknown, including how these decrease in relation to environmental conditions. Acoustic biotelemetry was applied here to measure the body temperatures and movements of European barbel *Barbus barbus* (barbel) across winter 2020/2021 and 2021/2022, and common bream *Abramis brama* (bream) in winter 2022/2023 in the River Severn, western Britain. Body temperatures of barbel were measured from 1.9 to 11.3 °C and bream 0.4 to 12.8 °C. The tagged fish generally remained active throughout the winters, including when water

temperatures were at their lowest. The median total distance moved by bream was 106 km, which was higher than that measured in summer (103 km). Barbel moved less than bream and had total ranges that were similar in winter and summer (median range: 3.9 km in both seasons). These temperate fishes thus remained active throughout winter, did not become quiescent in the coldest periods, and their winter movements were similar to those measured in summer.

Keywords Acoustic biotelemetry · Common bream · European barbel · Total range · Winter dormancy

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Introduction

Winter is a potentially important season for freshwater fish communities given that reduced temperatures decrease their metabolic rates, swimming capacities and foraging rates (Marsden et al., 2021; Sutton et al., 2021). Low winter temperatures are also coupled with shortened day lengths, ice cover and/or elevated flow rates (including spates) that might further impact fish activity (Gutmann Roberts et al., 2019; Sutton et al., 2021). Some fishes express a quiescent state in winter, when their activity and movements largely cease (Reeve et al., 2022). This reduction in activity is associated with suppressed energy intake and expenditure compared to summer periods when water temperatures can be more than 20 °C warmer (Marsden et al., 2021; Sutton et al., 2021).

To withstand periods of cold winter temperatures, fishes have evolved tolerance and specialisation strategies (Shuter et al., 2012). Tolerance includes the pre-winter storage of energy for subsequent use, coupled with minimising physiological demands on that stored energy (e.g. by reducing their general activity) (Berg et al., 2009). Specialisation involves individuals continuing their energy acquisition during winter, although this tends to be restricted to cold-water species (Finstad et al., 2004). Accordingly, relatively warm-water species, such as largemouth bass *Micropterus salmoides* (Lacepède, 1802), usually demonstrate winter quiescence, whereas colder water species, such as white bass *Morone chrysops* (Rafinesque, 1820), remain active through the winter (Cooke et al., 2003). During periods of elevated food availability (especially if these are also periods of increasing temperature and flow), even quiescent fish can increase their activity, especially if their energy stores are becoming depleted (Brown et al., 2001; Block et al., 2020).

The winter conditions in many temperate rivers, characterised by brief periods of cold conditions and low flows interspersed with much warmer temperatures and high flow conditions, might mean the fish populations—irrespective of their thermal tolerances—do not enter a quiescent state as they have to respond frequently to the changing conditions (Weber et al., 2013). For example, in some lowland rivers, fishes, such as European barbel *Barbus barbus* (Linnaeus, 1758) ('barbel') and common bream *Abramis brama* (Linnaeus, 1758) ('bream'),

frequently experience temperature fluctuations of over 8 °C across periods of only several days, with flows also increasing substantially following periods of heavy precipitation (Babaeyan-Koopaei et al., 2002; Gutmann Roberts et al., 2019). Such conditions are unlikely to provide these fish populations with relatively benign conditions when the fish can express quiescence, but instead might provide episodic extreme conditions that strongly influence their individual behaviours, movements and even survival (Weber et al., 2013; Marsden et al., 2021).

In winter, barbel activity tends to decrease as temperatures decrease, with a shift to being more diurnal than crepuscular and auroral, coupled with increased shoaling and use of refugia, and individual movements cease below 4 °C (so becoming quiescent) (Baras, 1995). Whilst bream generally form large, relatively static shoals in winter, studies on lentic populations suggest they remain active all year, thus not entering a quiescent state, with this continued activity facilitated by their use of warmer, deep water areas and avoidance of shallow, colder waters (Jurajda et al., 2018). This suggests bream express some behavioural thermoregulation, where individuals actively move to warm-water refugia in winter to maintain their body temperatures and physiological activities (Amat-Trigo et al., 2023). Nevertheless, movement studies suggest that as water temperatures decrease below 10 °C, bream activities also reduce, with few fish detected moving at water temperatures below 5 °C (Gardner et al., 2013; Hansen et al., 2019).

Acoustic telemetry is capable of measuring fish movements over winter periods, with passive systems involving year-round receiver deployment providing opportunities to generate data to assess winter activity patterns across a range of ambient temperatures, so enabling movement comparisons across seasons (Colborne et al., 2019; Marsden et al., 2021). This is allied with the deployment of temperature sensors in acoustic transmitters that, when implanted internally into fish, enables measurement of their body temperatures, meaning their responses to the changing environmental conditions can be measured more directly (Amat-Trigo et al., 2024). The responses of fish to changing environmental conditions can include whether individuals express behavioural thermoregulation, such as their use of localised areas of warmer water (Amat-Trigo

et al., 2023). Accordingly, the aim here was to determine the movements of barbel and bream in the lower River Severn basin, western England, where barbel were tracked during the winters of 2020/2021 and 2021/2022, and bream during winter 2022/2023. We initially assessed fish body versus water temperatures to identify whether the fish expressed behavioural thermoregulation, before assessing the movements of the fishes in relation to changes in temperature and river flow. We then compared the movements of the tagged individuals between winter and summer (*cf.* Amat-Trigo et al., 2024).

Material and methods

Study area

The study area comprises the lower River Severn, including the main river channel and the contiguous River Teme tributary (Fig. 1). The main River Severn is impounded by four major weirs, which have been fitted with fish passes [three deep vertical slot passes and one bypass channel, designed for the passage of twaite shad *Alosa fallax* (Lacepède, 1803)]. The last pass to be completed was opened in April 2022 (Unlocking the Severn, 2023). The most downstream of these weirs is Diglis Weir whose deep vertical slot

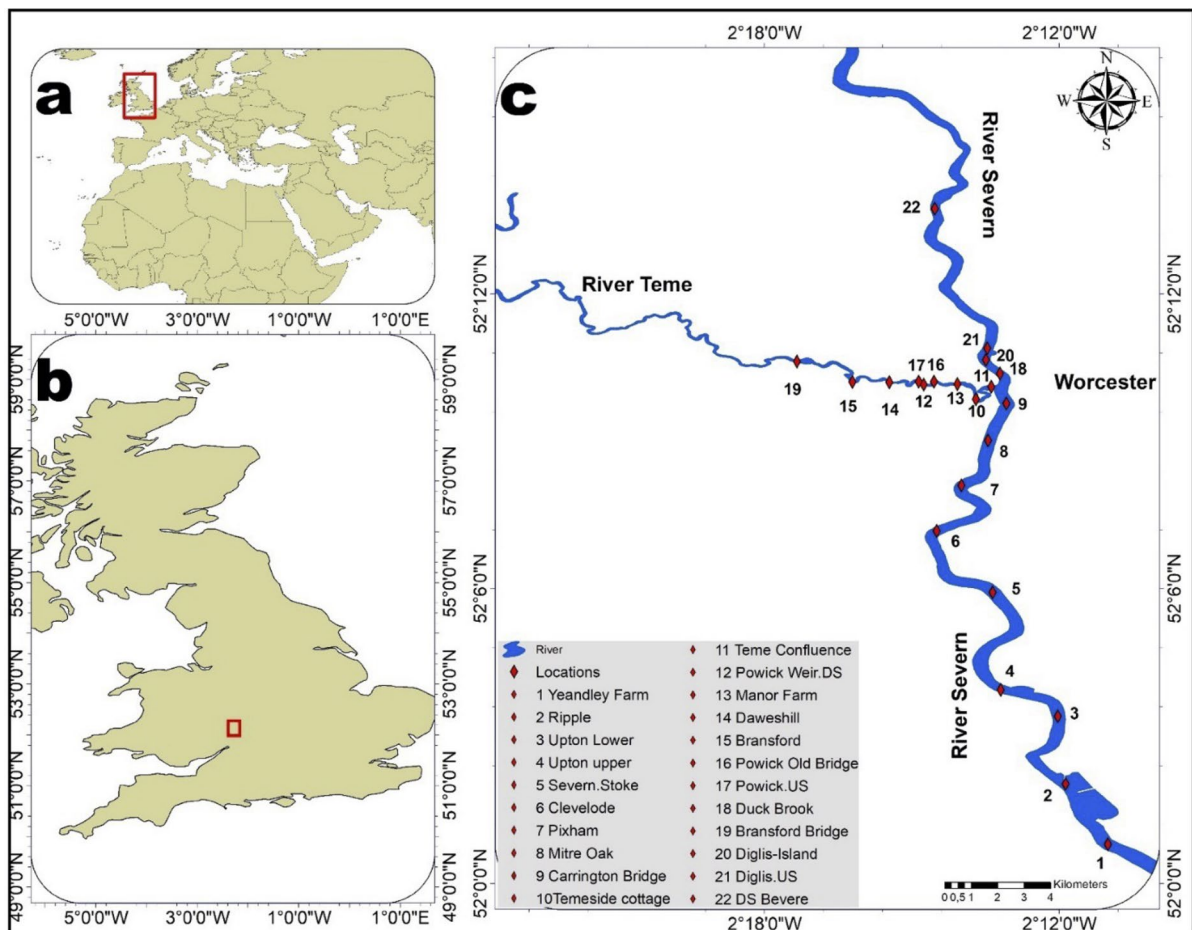


Fig. 1 Maps showing: **a** the position of the study country; **b** the study area within the UK **c** the core study area within the River Teme and Severn, with the 22 receiver locations with circles. In (c), the Teme flows from west to east and the Severn from north to south; the high density of receivers at the lower

end of the River Teme and around its confluence with the Severn mean that some receiver locations are obscured. Note that the modified Powick Weir on the Teme tributary is located between receivers 16 and 17, and Diglis Weir between receivers 20 and 21

fish pass was opened in April 2022, with this weir being largely impassable to barbel prior to fish pass construction (Gutmann Roberts et al., 2019). Compared with the main River Severn, the Teme provides a shallower habitat composed of pool and riffle sequences (Gutmann Roberts et al., 2019), with two weirs in the lower reaches that were modified in 2018 to increase fish passage rates (Antognazza et al., 2021). The study covered three winter periods, 2020/2021 and 2021/2022 (barbel) and 2022/2023 (bream), with the period of study in both winters being the 4-month period between 1st November (when water temperatures are decreasing) and 28th February. After this end date, fish movements could relate more to their pre-spawning movements than responses to changing abiotic conditions (even if water temperatures remain $< 10^{\circ}\text{C}$). Note that for both species, detections of their movements did continue on the receivers after 28th February.

Fish capture and transmitter implantation

The tagged barbel were captured by electrofishing and angling using rod and line. Electrofishing was completed from a boat in the lower River Teme on 30 September 2020, with angling then used on 11 and 12 March 2021 in the lower River Severn (500 m downstream of the Teme confluence) (Table 1). All bream were captured by angling and tagged in the lower River Severn on 12 and 13 March 2022 (Table 1). All captured fishes were held in large containers filled with river water, before being transferred to aerated holding tanks prior to tagging, where they were implanted with a Vemco V9T acoustic transmitter (manufactured and programmed by Innovasea, USA (<https://www.innovasea.com/>)). The transmitters were fitted with a temperature sensor (manufacturer information indicated temperature accuracy always within $\pm 0.5^{\circ}\text{C}$ of actual temperature and a resolution of 0.1°C when tested at temperatures between -4 and 20°C). Each transmitter was 9×37.5 mm, approximate weight 5 g (below 2% of fish body weight) and operated on 69 kHz. The transmitters were coded to enable individual identification and pulsed randomly once every 60–180 s, providing a battery life for each tag of a minimum of 13 months (but with some tags lasting considerably longer than this). Random repeat pulse rates allowed multiple individual fish to be monitored simultaneously within a given area and

without continuous signal overlap and risk of signal interference at the receivers. All transmitters were inserted into the peritoneal cavity via a mid-ventral incision that was closed with a single suture, whilst the fish was under general anaesthesia (tricaine methanesulfonate; MS-222) throughout. Following suturing, the fish were then transferred to recovery tanks containing aerated river water, held until normal swimming behaviour recommenced and then returned close to their area of capture (all fish were returned to the river within 30 min of their tagging). Additional information recorded for each fish was fork length (nearest mm) and method of capture (electrofishing/angling), but the fish were unable to be sexed due to the lack of external identification features.

Acoustic biotelemetry array

The movements of the tagged barbel and bream were detected in the study area using a fixed array of 22 acoustic receivers (VR2W, Vemco Ltd, Halifax, Nova Scotia, Canada) deployed in the core area (Fig. 1). The furthest upstream of these receivers for the River Teme was at Bransford Bridge, and for the River Severn, at Bevere Weir, with the furthest downstream receiver on the Severn being at Yeandley Farm (Fig. 1). This provided a total river distance covered by the receivers of 53 km in the Teme and 83 km in the River Severn. All receivers remained in situ throughout the study period. Water temperature loggers (a combination of Tiny TagTGP-4500 and HOBO Pendant Temperature loggers) were deployed in both rivers in the study period, with six deployed in the Teme and seven in the Severn, recording river temperatures every 15 min (to 0.1°C). These loggers were located within 0.5 m of the riverbed, and both rivers were considered as isothermic. In each river, temperature differences between the loggers at the times of recording were never more than 0.3°C (Teme) and 0.4°C (Severn). The loggers at Temeside Cottage (Teme) and Pixham (River Severn) were used exclusively to provide river temperatures, as these operated at all times in the study period, providing a continuous temperature record. These temperature data were then used to calculate daily mean temperature for each river. In addition, data on river flow (in $\text{cm}^3 \text{s}^{-1}$) were available for both rivers in the study reach from automated recording stations controlled by the Environment Agency (a public agency in England

Table 1 Fish length (L), sampling method (Method; as EF (electrofishing) and ANG (angling), detection data and movement metrics, including rivers occupied (S; Severn; T; Teme) for (A) European barbel between 1st November 2020 and 28th February 2021 (20/2021) and 1st November 2021 and 28th February 2022 (2021/2022), and (B) common bream between 1st November 2022 and 28th February 2023. All distances are estimated to the nearest metre

Fish	Winter	L (mm)	Method	Days from first to last detection	Days of detection	Number of detections	Number of receivers detected on	Receiver residency index	Array residency index	Linearity index	Total range	Total distance moved	Rivers occupied
(A)													
1361296	20/21	563	EF	73	25	39,471	2	0.21	0.62	0.09	655	7200	T
1361293	20/21	400	EF	100	27	9581	4	0.22	0.85	0.32	1106	3300	S/T
1361294	20/21	350	EF	118	50	25,792	3	0.42	1	0.05	3657	81,100	S
1362069	20/21	410	EF	118	19	4511	4	0.16	1	0.18	7225	39,500	S
1361292	20/21	365	EF	75	8	3642	3	0.07	0.64	0.51	7572	14,700	S
1361291	20/21	468	EF	101	18	8374	7	0.15	0.86	0.38	14,736	39,000	S/T
1362074	21/22	529	ANG	118	97	47,030	2	0.82	1	0.02	516	27,800	S/T
1362073	21/22	739	ANG	77	7	300	2	0.06	0.65	0.17	516	3000	S/T
1362062	21/22	800	ANG	118	11	612	3	0.09	1	0.66	2025	3000	S/T
1362068	21/22	576	ANG	49	3	1196	2	0.03	0.42	0.5	3904	7800	S
1361297	21/22	462	EF	74	8	4299	3	0.07	0.63	0.60	4716	7800	S
1362066	21/22	628	ANG	118	39	17,908	3	0.33	1	0.14	6933	49,400	S
1362072	21/22	804	ANG	118	28	5857	4	0.24	1	0.22	10,508	48,900	S/T
(B)													
1396540	490	ANG	93	10	3151	2	0.29	0.99	0.99	0.08	2271	15,800	S
1396541	525	ANG	117	64	11,605	10	0.54	0.99	0.99	0.04	8569	157,400	S/T
1396542	520	ANG	115	53	8359	12	0.45	0.98	0.98	0.05	12,251	236,100	S/T
1396533	530	ANG	108	29	2826	7	0.25	0.91	0.91	0.10	12,251	128,900	S
1396535	585	ANG	117	51	2692	10	0.43	0.99	0.99	0.08	13,890	166,700	S
1396536	472	ANG	113	48	9337	5	0.41	0.96	0.96	0.01	5376	40,070	S
1396537	563	ANG	115	28	13,443	7	0.24	0.98	0.98	0.15	8059	52,700	S
1396538	516	ANG	107	20	8081	9	0.17	0.91	0.91	0.22	12,323	57,000	S
1396539	545	ANG	113	20	1843	7	0.17	0.96	0.96	0.13	11,232	86,800	S
1396812	484	ANG	117	52	9824	8	0.44	0.99	0.99	0.07	11,232	152,300	S
1396814	520	ANG	116	50	8808	7	0.42	0.98	0.98	0.13	8569	69,200	S

Table 1 (continued)

Fish	L (mm)	Method	Days from first to last detection	Days of detection	Number of detections	Number of receivers detected on	Receiver residency index	Array residency index	Linearity index	Total range	Total distance moved	Rivers occupied
1396815	526	ANG	117	34	11,205	8	0.29	0.99	0.08	12,251	150,900	S
1396816	472	ANG	117	57	15,813	13	0.48	0.99	0.08	9625	125,253	S/T
1396817	505	ANG	8	3	4514	4	0.03	0.07	1	4868	4800	S
1396818	601	ANG	114	51	8224	7	0.43	0.97	0.16	7552	47,800	S
1396819	426	ANG	116	45	7563	11	0.38	0.98	0.09	15,903	180,400	S

with responsibilities including flood risk and hydrological management) and were used to determine mean daily flow rates. Both temperature and flow data were extracted and their mean daily data used for the study periods of winter 2020/2021, 2021/2022, and 2022/2023.

Upon reception of a signal from a V9T transmitter, the VR2W receivers identified its number by its unique coded transmission pattern and recorded its time of detection and temperature, where the transmitter temperature was assumed to be that of the fish body temperature (hence ‘fish body temperature’ hereafter). Detection distances of the VR2W receivers were generally 70–120 m in the River Teme (actual distances varied according to the location of the nearest riffle in both up- and downstream directions), and over 100 m in the River Severn (no riffles present due to impoundment) (Gutmann Roberts et al., 2019; Davies et al., 2024). A standardised detection distance of 100 m was thus utilised in subsequent analyses. In all cases, detection distances exceeded the width of the rivers, thus the receivers functioned as a gated array (Gutmann Roberts et al., 2019; Davies et al., 2024). Moreover, the receivers were located so there was no overlap in their detection fields, thus a fish detected on one receiver which was then detected subsequently on an adjacent receiver was able to be interpreted as that fish actively moving between these receivers (Amat-Trigo et al., 2024). At the conclusion of the study period, the receivers were all removed from the river and the data downloaded. All receivers remained operable throughout the study period and remained highly efficient in all winters (> 99%; assessed in the *explore* function of the *actel* R package; Flávio & Baktoft, 2021). Prior to any data analyses, the detection data were also processed in the *explore* function of the *actel* R package to remove any false detections (e.g. transmitter code errors caused by code collisions; see <https://hugomflavio.github.io/actel-website/manual-explore.htm> for details on how the *explore* function works) (Flávio & Baktoft, 2021).

Data and statistical analyses

There were 6 barbel tracked in winter 2020/2021, 7 barbel tracked in winter 2021/2022 and 16 bream tracked in winter 2022/2023 that generated data suitable for further analyses (Table 1). River and fish

body temperature data were used to calculate daily means over the study period (separately for Teme, Severn and each fish). The fish detection data were analysed in R (R Core Team, 2023), where movement data were analysed in the *detectionSummary* function of the *Vtrack* package, which enables the detection data of Vemco acoustic transmitters to be assimilated across all receivers and then analysed appropriately (Udyawer et al., 2018). The analyses completed here were a series of movement metrics as per Gutmann Roberts et al. (2019) (Table 2). To assess the residency of each fish within the receiver array, two indices were utilized: the residency index, which quantified the number of days the fish was detected as a proportion of the total study days, and the array residency index, which measured the number of days each fish remained within the spatial limits of the receiver array as a proportion of the total study days (Acolas et al., 2017). The total range of an individual fish was calculated as the sum of river length (both mainstream and tributary) used by that fish, determined by the distances between the receivers at the up- and downstream limits of their detection. Total distance moved by an individual was computed as the sum of all movement distances made between receivers, regardless of direction.

The relationship between the daily mean River Severn water temperatures (independent variable) and body temperatures of both species (dependent variable) was assessed using linear regression, with assessment of the 95% confidence limits of regression coefficients a and b identifying whether fish body temperatures deviated significantly from general river temperatures and so thus were expressing behavioural thermoregulation. The summer movements of these individual fish have already been measured (for 4 months, between July and October), where barbel

movements were assessed in summer 2021 and bream in summer 2022 (Amat-Trigo et al., 2024). Accordingly, for individuals where winter movement metrics were also available, the relationship between winter and summer movements was assessed in linear regression to identify whether individuals that were highly vagile in summer also moved frequently in winter, with Mann Whitney U tests then used to identify whether the extent of the distances moved between season was significantly different (as the data were not normally distributed).

To visually identify spatial occupancy of both species in the study area, the point density method was used (Silverman, 1986), using kernel density as the point density within the circle of a certain bandwidth radius (Aksu et al., 2021). In estimating kernel density (kernel density estimation, KDE), an intensity estimate was calculated based on the distance between each grid cell of an event and its centre (Hart & Zandbergen, 2013). The KDE technique used was a non-parametric technique that relied on few assumptions about the structure of the observed data and generated a density surface based on the receiver network (Silverman, 1986; Worton, 1989; O'Brien et al., 2012). This provided an expected distance between each receiver of approximately 750 m, providing an output raster of cells around receivers, enabling a neighbourhood around the centre of each cell to be defined. The number of points (detections) within that neighbourhood was then determined, with point density (low–high) representing the density ratio of each cell divided by the neighbourhood area (Amat-Trigo et al., 2024). These analyses were all conducted in ArcMap version 10.8.

The number of fish movements per day, where a movement of an individual fish was defined as when it was detected on at least two receivers that day,

Table 2 Overview of movement metrics calculated for each of the tagged European barbel and common bream for which movement data were available in each winter of study

Parameter	Equation—explanation
Residency Index	Number of days detected by at least one receiver/total number of study days
Linearity index	Total range/total movement
Residency within the array	Number of days that the fish was in the array/total number of study days
Total range (m)	Sum of river length between the most upstream and downstream receivers with detections
Total distance moved (m)	Sum of all upstream and downstream movements

was then calculated. For these days when a movement was detected as occurring within the receiver array, the distance moved by each individual was calculated (as 'daily distance moved'). To assess the influence of daily mean river flow and water temperature on a daily movement, generalized linear models (GLMs) were used, where it was assumed that the observed percentage of fish movements followed a beta distribution (i.e. beta regression), with models implemented in R using the *betareg* function from the *betareg* package (Cribari-Neto & Zeileis, 2010). Next, daily distances moved (excluded the days when no movement was detected, i.e. days when the distance moved was 0 m) were assessed against mean daily river temperatures and flows, plus their interaction (with winter period as a factor in the case of barbel), in Generalized additive models (GAMM), utilizing a Gamma distribution and log link function (Pedersen et al., 2019). In these GAMMs, individual fish identity was incorporated as a random variable to accommodate potential variations attributable to individual fish differences. This allowed the examination of individual-specific movement variations, with the number of knots set to 5 for all parameters included on balancing model flexibility and complexity whilst preventing overfitting. Before fitting the models, data exploration followed the protocol of Zuur et al. (2010), which involved checking for missing data, outliers in both response and explanatory variables, homogeneity, collinearity among explanatory variables, balance of categorical variables, and the nature of relationships between the response and predictors. Model validation was performed using the *DHARMA* package in R (Hartig & Lohse, 2022). The *simulateResiduals* function was used to generate standardized residuals for each fitted model, facilitating diagnostic checks of model assumptions. Residuals were plotted against fitted values to detect any systematic deviations, which could indicate potential misspecifications in model structure. Additionally, the *plotQQunif* function was used to produce a Q–Q plot, assessing the normality of residuals. Model dispersion and the presence of outliers were also examined as part of this validation process. In the results, when error is depicted around the mean, it signifies 95% confidence intervals and inter-quartile ranges are expressed around median values.

Results

Fish body temperatures versus river temperatures

All of the tagged fishes were tracked throughout the winter periods in which their movements were measured, indicating their full survival. The range of recorded barbel body temperatures in winter 2020/2021 was 1.9 to 11.8 °C (mean 6.5 ± 0.4 °C) and 3.3 to 11.3 °C (mean 6.9 ± 0.3 °C) in 2021/2022 (Figs. 2, 3). Recorded bream body temperatures in winter 2022/2023 were 0.4 to 12.8 °C (mean 6.7 ± 0.4 °C) (Figs. 2, 3). In all sampling years (2020/2021, 2021/2022 and 2022/2023), barbel and bream body temperatures and water temperatures were positively and significantly correlated (all $R^2=0.99$ and all $P<0.001$). In barbel, the 95% confidence limits of regression coefficient b for in both winters overlapped 1.0 (2020/2021: 0.97–1.0, 2021/22: 0.98–1.0), suggesting their body temperatures were similar to river temperatures (Fig. 3). In bream, however, there was some significant difference, as their 95% confidence limits of b were 0.94–0.98. Moreover, regression coefficient a of bream was significantly different from 0 (–0.54 to –0.23), suggesting their recorded body temperatures were consistently lower than those recorded in the river (mean difference across the entire winter was 0.65 ± 0.05 °C, with the transmitters recording temperatures to ± 0.5 °C of actual at a resolution of 0.1 °C) (Fig. 3). For barbel, the 95% confidence limits of regression coefficient a also overlapped 0 for barbel in 2020/2021, but did not in 2021/2022 (0.07–0.12, –0.34 to –0.14, respectively; Fig. 3).

Fish detections, general movements and winter versus summer movement metrics

Across both species, the tagged fish were detected as moving in the receiver array (i.e. at least one individual was detected on at least two receivers) throughout all winters, including periods of relatively cold temperatures and periods of high flow rates (Fig. 4). The movement of at least one barbel between at least two receivers occurred on 33 and 51% of days in winter 2020/2021 and 2021/2022, respectively; for bream, a movement of at least one individual between at least two receivers was detected on 73% of days in winter 2022/2023 (Fig. 4). On these days of movement,

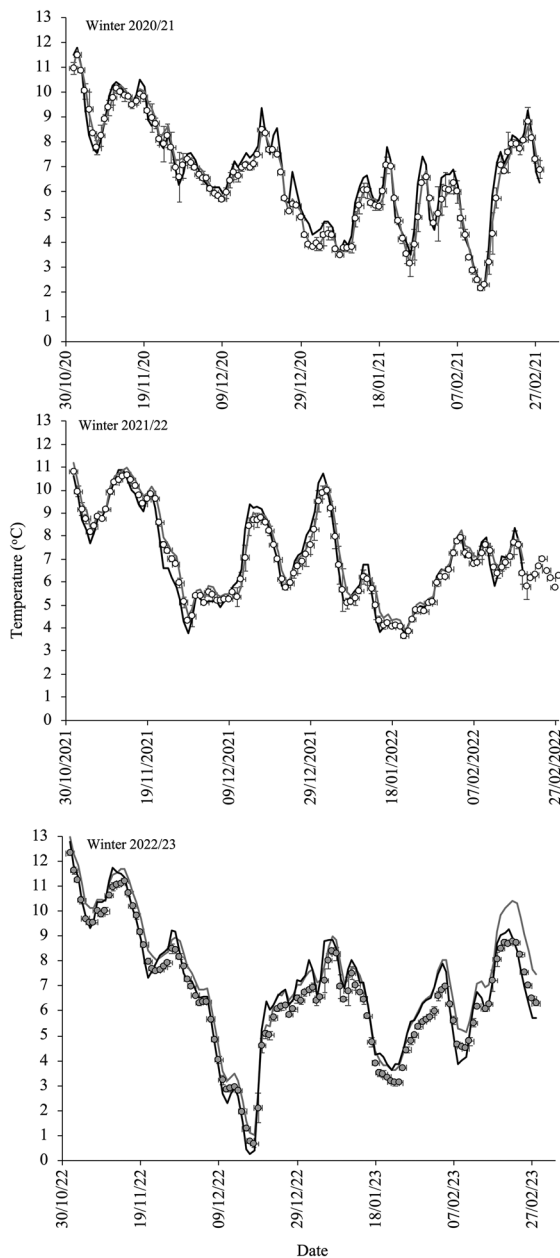


Fig. 2 Mean daily water temperatures for the River Severn (grey line) and Teme (black line) versus mean daily fish body temperatures (± 95 CI), where open circles are European barbel and grey circles are common bream, for winters 2020/2021, 2021/2022 and 2022/2023

individual barbel were detected on between 2 and 7 receivers across both winters, whereas individual bream were detected on between 2 and 13 receivers. Barbel were detected in both rivers, with individuals

also present in the Severn in areas upstream of Diglis weir (Table 1, Fig. 5). Bream were mainly present in the Severn, with one fish recorded as moving upstream of Diglis Weir where it remained for approximately four weeks (Fig. 5). There were also seven bream detected in the Teme tributary for part of the winter, including one fish that moved upstream of the modified Powick Weir (Fig. 5). These river occupancy patterns were reflected in the movement distances of both species, with individuals of moving considerable distances each winter (Table 1). Bream were, however, more vagile than barbel, with greater total distances moved (median barbel: 14,700 m (8200–39500 m); median bream: 106,027 m (51,475–153,575 m)), and total ranges (median barbel: 3781 m (993–7093 m); median bream: 10,429 m (7932–12,251 m)) (Table 1).

There were 16 individual bream where movement metrics were available in both winter and summer, with their total range being significantly and positively related ($R^2=0.58$, $F_{1,14}=19.28$, $P<0.001$) but not total distance moved ($R^2=0.20$, $F_{1,14}=3.58$, $P=0.08$) (Fig. 6). Neither bream total range (TR) nor total distance moved (TDM) differed significantly between summer and winter (TR: median winter vs summer: 10,429 m (7932–12,251) vs 8314 m (5376–12,251), Mann Whitney test, $Z=-0.70$, $P=0.48$; TDM: median winter vs summer: (106,027 m (51,475–153,575) vs 102,500 m (87,025–170,950); Mann Whitney test, $Z=-0.94$, $P=0.35$). There were 9 barbel with movement metrics from both winter and summer, with their relationships in TR and TDM not significantly related (TR: $R^2=0.14$, $F_{1,7}=0.12$, $P=0.74$; TDM: $R^2=0.07$, $F_{1,8}=0.56$, $P=0.48$) (Fig. 5). Although median barbel TDM was substantially lower in winter than summer (7,800 m (7,200–39,000)/46,200 m (19,500–56,500), the differences were not significant (Mann Whitney test, $Z=1.06$ $P=0.29$) (Fig. 6). Barbel TR was similar between winter and summer, with the differences also not significant (TR: median winter/summer: 3,904 m (655–6,933)/3,904 m (2,025–3,904), Mann Whitney test, $Z=0.57$, $P=0.57$).

Effects of river temperature and flow on fish movements and distances

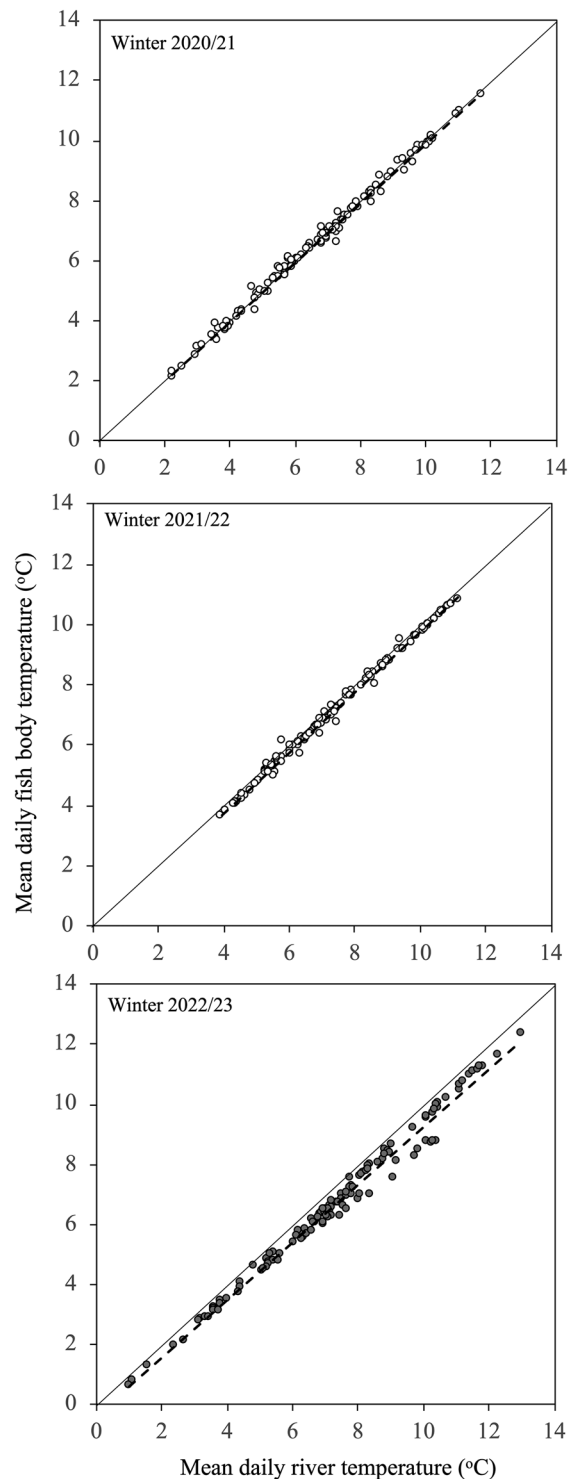
The lowest mean daily water temperature at which an individual bream was detected as moving between at

Fig. 3 Relationship of mean daily water temperatures for the River Severn versus fish mean daily body temperatures for barbel (clear circle) and common bream (grey circle) in winters 2020/2021, 2021/2022 and 2022/2023. The solid line represents the 1:1 relationship and the dashed line is the relationship according to linear regression (cf. Table 2)

least two receivers was 1.01 °C and was 2.23 °C for barbel, with both upstream and downstream movements detected throughout the winter periods (Fig. 4). Bream movements were detected across the entire range of flows recorded (33–448 m³s⁻¹), whereas barbel were only recorded moving in flows up to 317 m³s⁻¹ in a winter when the maximum flow was 472 m³s⁻¹ (Fig. 4). The GLM (beta distribution) assessing the influence of mean water temperature and river flow on movement was significant and negative for effect of flow on barbel, whereas temperature had a significant and positive effect on bream movement (Table 3). The GAMMs revealed that variance in the distances moved by both species was significantly and positively related to flow and temperature, their interaction and year of winter in barbel (Table 4). The effect of individual fish identification was also significant for both species (Table 4).

Discussion

Across the three winters, the lowest body temperature recorded of individual fish was 0.4 °C. The thermal optimum of both species is a minimum of 10 °C (Souchon & Tissot, 2012) and their activities have previously been suggested to largely cease at temperatures below 4 °C (barbel) and 5 °C (bream) (Baras, 1995; Gardner et al., 2013). Bream in lentic environments have also been recorded using relatively warm waters in winter, with active avoidance of shallow, colder littoral areas (Jurajda et al., 2018), suggesting behavioural thermoregulation in winter periods (Amat-Trigo et al., 2023). It was apparent that here, however, individuals were detected as moving between at least two receivers on the days of very low river temperatures (<3.5 °C). Despite water temperatures never exceeding 13 °C in any winter, individual total range sizes and total distances moved were similar to those recorded in the much warmer summer months (water temperatures up to 23 °C warmer; Amat-Trigo et al., 2024), with total distances moved by individual



bream to over 236 km. These results thus suggest that rather than these individual barbel and bream entering periods of quiescence in winter, they instead

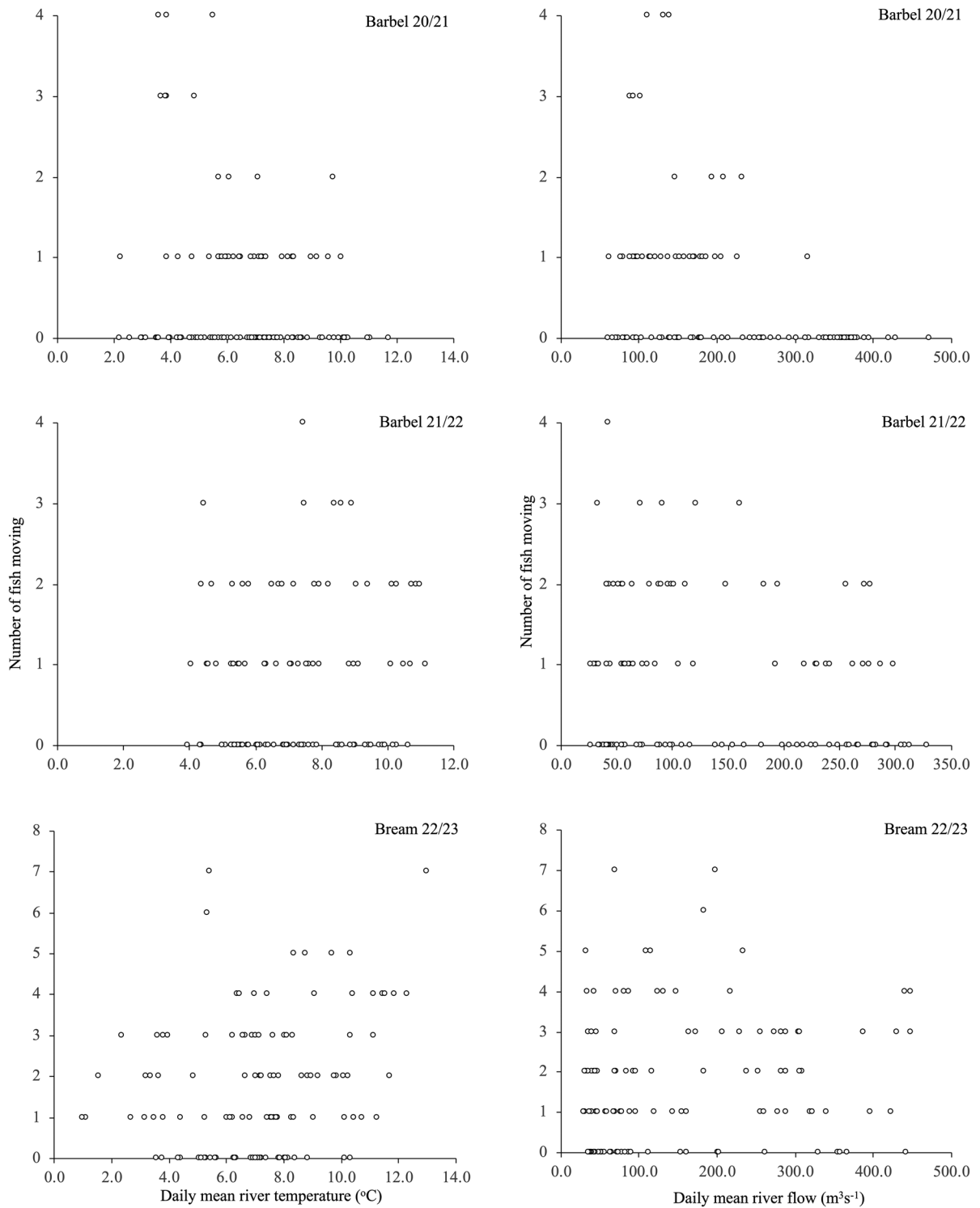


Fig. 4 Daily mean River Severn temperatures and flow rates versus the number of barbel and common bream detected as moving between at least two receivers on those days in winters 2020/2021 to 2022/2023

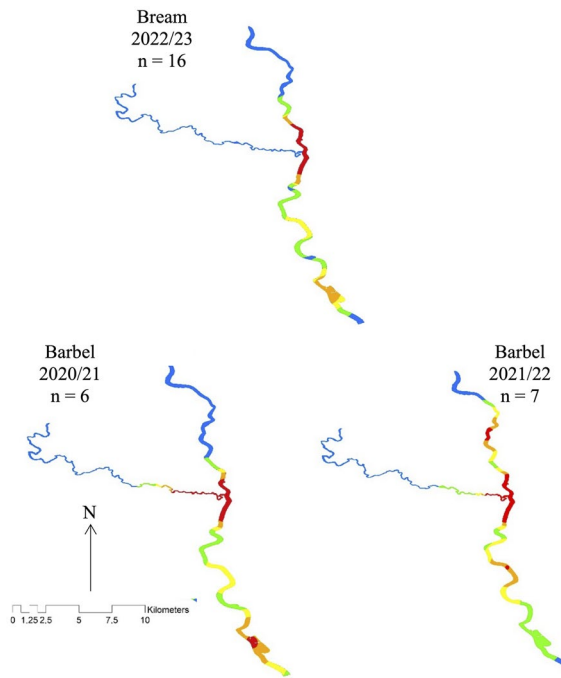


Fig. 5 Heat map showing probability of occupancy (density) of the study area (cf. Fig. 1) by common bream in winter 2022–2023 and European barbel in winter 2020–2021 and 2021–2022, where blue–green–yellow–orange–red represents a gradient of low through to high density. The direction of river flow is generally north to south in the main River Severn and west to east in the River Teme tributary

maintained some activity throughout, even when temperatures were $< 5^{\circ}\text{C}$. This is a contrast to other studies on these species, where movements largely ceased at these low temperatures (Baras, 1995; Jurajda et al., 2018).

Species with relatively warm-water thermal preferences often inhabit areas of warmer water in winter, such as in and around warm-water discharges (Ross & Winter, 1981). However, our results provided no evidence that individual fish were moving into warmer waters in cold periods, suggesting the fish were not expressing behavioural thermoregulation by seeking areas of relatively warm water when water temperatures were low (or such areas of warm water were absent in the river and thus not available to the fish) (Souchon & Tissot, 2012; Amat-Trigo et al., 2023). Although some individuals used the area of river around the confluence of the Teme tributary and River Severn mainstream, there was no evidence to indicate this enabled them to access warmer water.

In rivers where winter conditions are prone to rapid changes, including episodes of relatively extreme conditions, the fish populations in such rivers might be highly reactive to these changes, resulting in their sustained activity throughout winter (Weber et al., 2013). These results are important, as whilst the tagged fishes remained active even in very cold periods, the productivity of rivers in winter can be assumed to be much lower than in summer due to, for example, sustained periods of low temperatures ($< 10^{\circ}\text{C}$) and shorter day lengths ($< 8\text{ h}$ light) (Studd et al., 2021). In these conditions, prey availability can also be assumed to be reduced, thus the fish must maintain their energetic requirements in periods of low productivity, especially as the spawning period of these fishes follows soon after in spring and early summer. Moreover, these species form part of a popular catch-and-release fishery on the River Severn, with the behaviours and movements outlined here indicating that the capturing individuals throughout the winter could be possible (Britton & Nolan, 2021; Gutmann-Roberts et al., 2025), with capture less likely to be as physiologically stressful in winter versus the warmer summer period (Pinder et al., 2019).

There could be a number of reasons why the tagged fishes continued to maintain their activity throughout the winter periods. It might have been simply that the periods when temperatures reduced to levels where their activity and movements might cease were of too short duration for the fish to develop winter quiescence. For example, less than 2% of the entire winter 2021/2022 had water temperatures below the previously recorded 4°C activity threshold recorded for barbel by Baras (1995). However, more extended colder periods were encountered in 2020/2021, when the proportion was 15% of days $< 4^{\circ}\text{C}$, and in 2022/2023, 24% of the winter period had temperatures below the 5°C threshold when bream activity has been noted as largely ceasing (Gardner et al., 2013). The high flow rates encountered in the river during winter could also be potentially important drivers of movement here, where GAMMs indicated that the distances moved by both species were significantly and positively related to flow and temperature, with this also seen in riverine populations of other species. For example, the winter movements of brown trout *Salmo trutta* Linnaeus, 1758, white sucker *Catostomus commersonii* (Lacepède, 1803) and common carp *Cyprinus carpio* Linnaeus, 1758 in

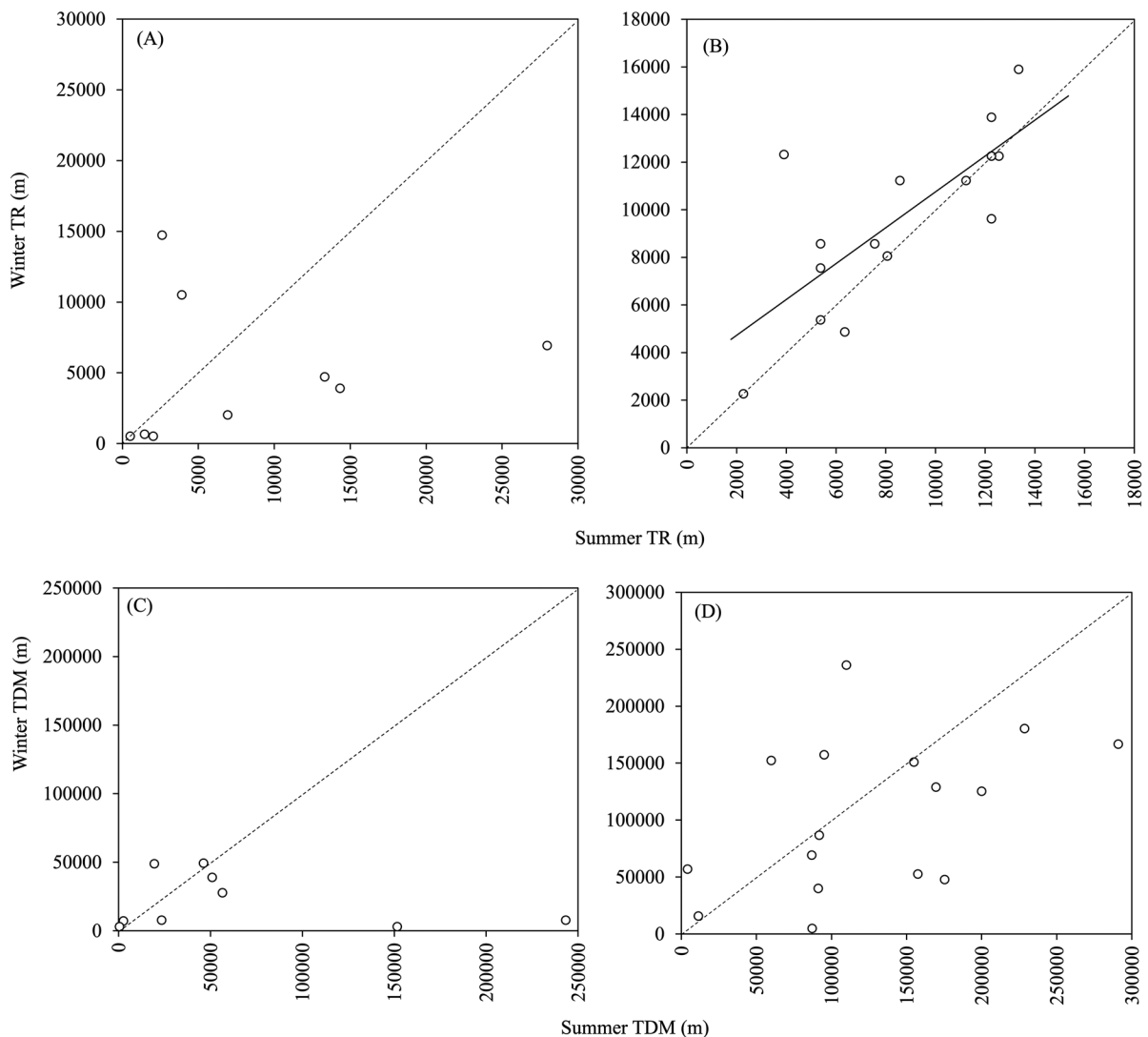


Fig. 6 Relationships of summer versus winter total range (TR) and total distance moved (TDM) in barbel (**A, C**) and bream (**B, D**). The dashed line represents the 1:1 relationship and

the solid line is the significant relationship according to linear regression ($P < 0.01$)

the Grand River, Ontario, were minimal other than in high flow periods, with floods resulting in both suckers and carp moving relatively long distances, albeit mostly downstream (Brown et al., 2001). Moreover, periods of elevated river flow rates generally result in non-salmonid fishes making larger and/or more frequent non-migratory movements, including upstream movements, indicating a general pattern that episodic changes in flow conditions modulate fish behaviours (Taylor & Cooke, 2012). These findings are thus consistent with our results that revealed significant

influences of changes in the abiotic conditions on the movements of the tagged fishes. Bream are known to exhibit different responses to flow compared to barbel, with some individuals showing reduced activity or avoidance in higher flow conditions (Winter et al., 2021). We thus suggest that the relatively high activity patterns and movements detected in these fishes across all winter periods were at least in part a function of the flow regime of the river, both in terms of the winter periods being characterised by relatively high flows but also that these flows often changed

Table 3 Coefficient estimates, standard errors, *z* scores and their significance from results of the generalised linear models (binomial distribution) testing the binary response of days when a fish was detected as moving between at least two receivers (1) versus days of no detected movement (0) versus daily mean water temperature and water flow for (A) European barbel in winter 2020–2021; (B) European barbel in winter 2021–2022; and (C) common bream in winter 2022–2023

	Estimate	Std. error	<i>z</i> -value	<i>P</i> -value
(A)				
Intercept	1.45	0.69	2.09	0.04
Temperature	0.05	0.08	– 1.81	0.07
Flow	– 0.01	0.01	– 4.96	< 0.01
(B)				
Intercept	– 0.89	0.63	– 1.40	0.16
Temperature	0.08	0.08	0.95	0.34
Flow	– 0.04	0.01	– 2.12	0.03
(C)				
Intercept	– 2.14	0.25	– 8.44	< 0.01
Temperature	0.07	0.03	2.71	< 0.01
Flow	0.01	0.01	1.44	0.15

Table 4 Results of generalised additive models for (A) European barbel (B) common bream on daily movement (only for days when a movement of at least one fish was detected between at least two receivers; Fig. 4), where edf is the effective degrees of freedom for the smoothing function (*s*) and a

rapidly, such as an increase from 170 to 374 m³s^{–1} in a 48 h period in winter 2020/2021.

Bream is generally a lentic fish species and, when encountered in lotic systems, tends to be found in deep, slow flowing areas (Huet, 1959; Lasne et al., 2007). Consequently, the tagged bream were expected to remain within the main River Severn channel throughout the winter (where they had spent the previous summer period; Amat-Trigo et al., 2024). However, seven bream moved at least 1.5 km into the Teme during winter 2022/2023, with one individual moving several km upstream, including passing the modified weir at Powick. Individual bream were also detected as moving above Diglis Weir on the Severn in periods of relatively low flow and thus most likely through the newly installed fish pass. Barbel were also detected as moving upstream of these obstacles on both rivers. These results demonstrate the importance of river connectivity to enable these movements, with the modification of otherwise largely impassable barriers through lowering their height and/or installing fish passes, allows for increased freedom of movement, albeit not entirely unrestricted, even among

tensor product smooth (te), where higher values indicate more complex relationships, and Ref.df is the reference degrees of freedom (the initial degrees of freedom before model fitting, providing a reference point for comparing with the effective degrees of freedom)

	Estimate	Std. error	<i>t</i> -value	<i>P</i> -value
(A)				
Intercept	3.73	0.23	16.31	< 0.0001
Winter_Year	– 0.33	0.27	– 1.21	0.023
	edf	Ref.df	<i>F</i>	<i>P</i> -value
s(Temperature)	4.80	9	3.79	< 0.0001
s(Flow)	0.01	9	0.01	< 0.001
te(Temperature, Flow)	1.32	22	29.35	< 0.001
s(Fish_ID)	8.65	11	15.05	< 0.0001
	Estimate	Std. error	<i>t</i> -value	<i>P</i> -value
(B)				
Intercept	4.64	0.16	29.83	< 0.0001
	edf	Ref.df	<i>F</i>	<i>P</i> -value
s(Temperature)	6.80	9	3.33	< 0.0001
s(Flow)	6.05	9	3.46	< 0.0001
te(Temperature, Flow)	7.94	22	1.30	< 0.01
s(Fish_ID)	13.23	15	10.23	< 0.0001

non-salmonid fishes (Benitez et al., 2015; Silva et al., 2018). It also emphasises the individual variability often seen in the movements of tagged fishes and that these individuals occasionally move into areas that are contrary to expectation, as with bream moving into relatively shallow and fast flowing tributary habitats.

Conclusion

The acoustic telemetry data from individuals of the two fishes across these winter periods revealed that their movements were detected at all recorded water temperatures (as low as 1 °C), with their movements perhaps being maintained due to the overriding influence of river flow rates. Nevertheless, the fish did move greater distances in warmer temperatures. With individual total range sizes to almost 16 km and fish moving total distances to over 236 km in a single winter, these data indicated that these fishes remained highly active throughout winter, with movements similar to those recorded in much warmer periods in summer. As the importance of this winter activity in barbel and bream to their subsequent reproductive effort and summer movements remains unknown, then further work is needed to understand the biological significance of winter to these populations.

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Author contributions JRB, FAT, DA and PG conceived the study; JRB, FAT, CGR, JB and MY collected field data; AST, SA and JRB analysed data; JRB and AST wrote the manuscript; and all authors contributed to editing the manuscript. All authors approved manuscript submission.

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Data availability Any raw data used in the manuscript that are not already provided are available from the corresponding author at reasonable request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Ethical approval All aspects of data collection were completed following ethical approval and were licenced under the U.K. Animals (Scientific Procedures) Act (1986) (project licence number: PPL PA2C7C4E6).

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References

- Acolas, M. L., C. Le Pichon & E. Rochard, 2017. Spring habitat use by stocked one year old European sturgeon *Acipenser sturio* in the freshwater-oligohaline area of the Gironde estuary. *Estuarine, Coastal and Shelf Science* 196: 58–69. <https://doi.org/10.1016/j.ecss.2017.06.029>.
- Aksu, S., S. Başkurt, Ö. Emiroğlu & A. S. Tarkan, 2021. Establishment and range expansion of non-native fish species facilitated by hot springs: the case study from the Upper Sakarya Basin (NW, Turkey). *Oceanological and Hydrobiological Studies* 50: 247–258. <https://doi.org/10.2478/oandhs-2021-0021>.
- Amat-Trigo, F., D. Andreou, P. K. Gillingham & J. R. Britton, 2023. Behavioural thermoregulation in cold-water freshwater fish: Innate resilience to climate warming? *Fish and Fisheries* 24: 187–195. <https://doi.org/10.1111/faf.12720>.
- Amat-Trigo, F., A. S. Tarkan, D. Andreou, S. Aksu, J. D. Bolland, P. K. Gillingham, C. Gutmann Roberts, M. A. Yeldham & J. R. Britton, 2024. Variability in the summer movements, habitat use and thermal biology of two fish species in a temperate river. *Aquatic Sciences* 86: 65. <https://doi.org/10.1007/s00027-024-01073-y>.
- Antognazza, C. M., J. R. Britton, V. De Santis, K. Kolias, O. A. Turunen, P. Davies, L. Allen, E. A. Hardouin, C. Crundwell & D. Andreou, 2021. Environmental DNA reveals the temporal and spatial extent of spawning migrations of European shad in a highly fragmented river basin. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 2029–2040. <https://doi.org/10.1002/aqc.3601>.
- Babaeyan-Koopaei, K., D. A. Ervine, P. A. Carling & Z. Cao, 2002. Velocity and turbulence measurements for two over-bank flow events in River Severn. *Journal of Hydraulic*

- Engineering 128: 891–900. [https://doi.org/10.1061/\(ASCE\)0733-9429\(2002\)128:10\(891\)](https://doi.org/10.1061/(ASCE)0733-9429(2002)128:10(891)).
- Baras, E., 1995. Seasonal activities of *Barbus barbus*: effect of temperature on time-budgeting. *Journal of Fish Biology* 46: 806–818. <https://doi.org/10.1111/j.1095-8649.1995.tb01603.x>.
- Benitez, J.-P., B. Nzau Matondo, A. Dierckx & M. Ovidio, 2015. An overview of potamodromous fish upstream movements in medium-sized rivers, by means of fish passes monitoring. *Aquatic Ecology* 49: 481–497. <https://doi.org/10.1007/s10452-015-9541-4>.
- Berg, O. K., A. G. Finstad, Ø. Solem, O. Ugedal, T. Forseth, E. Niemelä, J. V. Arnekleiv, A. Lohrmann & T. F. Næsje, 2009. Pre-winter lipid stores in young-of-year Atlantic salmon along a north–south gradient. *Journal of Fish Biology* 74: 1383–1393. <https://doi.org/10.1111/j.1095-8649.2009.02193.x>.
- Block, B. D., J. D. Stockwell & J. E. Marsden, 2020. Contributions of winter foraging to the annual growth of thermally dissimilar fish species. *Hydrobiologia* 847: 4325–4341. <https://doi.org/10.1007/s10750-020-04428-2>.
- Britton, J. R. & E. T. Nolan, 2021. Comparative angler catch rates of native versus alien piscivorous fish in an invaded river fishery. *Fisheries Research* 240: 105970. <https://doi.org/10.1016/j.fishres.2021.105970>.
- Brown, R. S., G. Power & S. Beltaoa, 2001. Winter movements and habitat use of riverine brown trout, white sucker and common carp in relation to flooding and ice break-up. *Journal of Fish Biology* 59: 1126–1141. <https://doi.org/10.1111/j.1095-8649.2001.tb00180.x>.
- Cribari-Neto, F. & A. Zeileis, 2010. Beta regression in R. *Journal of Statistical Software* 34: 1–24.
- Colborne, S. F., D. W. Hondorp, C. M. Holbrook, M. R. Lowe, J. C. Boase, J. A. Chiotti, T. C. Wills, E. F. Roseman & C. C. Krueger, 2019. Sequence analysis and acoustic tracking of individual lake sturgeon identify multiple patterns of river–lake habitat use. *Ecosphere* 10: e02983. <https://doi.org/10.1002/ecs2.2983>.
- Cooke, S. J., E. C. Grant, J. F. Schreer, D. P. Philipp & A. L. Devries, 2003. Low temperature cardiac response to exhaustive exercise in fish with different levels of winter quiescence. *Comparative Biochemistry and Physiology Part a: Molecular & Integrative Physiology* 134: 157–165. [https://doi.org/10.1016/S1095-6433\(02\)00240-4](https://doi.org/10.1016/S1095-6433(02)00240-4).
- Davies, P., J. R. Britton, D. Andreou, C. Crundwell, J. R. Dodd, O. Lepais, A. D. Nunn, S. Sabatino, R. Veltero & J. D. Bolland, 2024. Tracking repeat spawning anadromous fish migrations over multiple years in a fragmented river suggests philopatry and sex-linked variation in space use. *Aquatic Sciences* 86: 34. <https://doi.org/10.1007/s00027-024-01048-z>.
- Finstad, A. G., O. Ugedal, T. Forseth & T. F. Næsje, 2004. Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 61: 2358–2368. <https://doi.org/10.1139/f04-213>.
- Flávio, H. & H. Baktoft, 2021. *actel*: Standardised analysis of acoustic telemetry data from animals moving through receiver arrays. *Methods in Ecology and Evolution* 12: 196–203. <https://doi.org/10.1111/2041-210X.13503>.
- Gardner, C. J., D. C. Deeming & P. E. Eady, 2013. Seasonal movements with shifts in lateral and longitudinal habitat use by common bream, *Abramis brama*, in a heavily modified lowland river. *Fisheries Management and Ecology* 20: 315–325. <https://doi.org/10.1111/fme.12014>.
- Gutmann Roberts, C., A. M. Hindes & J. R. Britton, 2019. Factors influencing individual movements and behaviours of invasive European barbel *Barbus barbus* in a regulated river. *Hydrobiologia* 830: 213–228. <https://doi.org/10.1007/s10750-018-3864-9>.
- Hansen, J. H., J. Brodersen, H. Baktoft & C. Skov, 2019. Relationship between bream (*Abramis brama*) activity and water turbidity in a shallow lake under different season conditions. *Journal of Limnology* 78: 259–269. <https://doi.org/10.4081/jlimnol.2019.1883>.
- Hartig F, Lohse L 2022. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models.
- Hart, T. C. & P. A. Zandbergen, 2013. Reference data and geocoding quality. *Policing: An International Journal of Police Strategies & Management* 36: 263–294. <https://doi.org/10.1108/13639511311329705>.
- Huet, M., 1959. Profiles and biology of Western European streams as related to fish management. *Transactions of the American Fisheries Society Taylor & Francis* 88: 155–163. [https://doi.org/10.1577/1548-8659\(1959\)88\[155:PABOWE\]2.0.CO](https://doi.org/10.1577/1548-8659(1959)88[155:PABOWE]2.0.CO).
- Jurajda, P., K. Roche, K. Halačka, M. Mrkvová & J. Zúkal, 2018. Winter activity of common bream (*Abramis brama* L.) in a European reservoir. *Fisheries Management and Ecology* 25: 163–171. <https://doi.org/10.1111/fme.12275>.
- Lasne, E., B. Bergerot, S. Lek & P. Laffaille, 2007. Fish zonation and indicator species for the evaluation of the ecological status of rivers: example of the Loire basin (France). *River Research and Applications* 23: 877–890. <https://doi.org/10.1002/rra.1030>.
- Marsden, J. E., P. J. Blanchfield, J. L. Brooks, T. Fernandes, A. T. Fisk, M. H. Futia, B. L. Hlina, S. V. Ivanova, T. B. Johnson, N. V. Klinard, C. C. Krueger, S. M. Larocque, J. K. Matley, B. McMeans, L. M. O'Connor, G. D. Raby & S. J. Cooke, 2021. Using untapped telemetry data to explore the winter biology of freshwater fish. *Reviews in Fish Biology and Fisheries* 31: 115–134. <https://doi.org/10.1007/s11160-021-09634-2>.
- Muhawenimana, V., J. R. Thomas, C. A. M. E. Wilson, J. Nefjodova, A. C. Chapman, F. C. Williams, D. G. Davies, S. W. Griffiths & J. Cable, 2021. Temperature surpasses the effects of velocity and turbulence on swimming performance of two invasive non-native fish species. *Royal Society Open Science* 8: rsos.201516. <https://doi.org/10.1098/rsos.201516>.
- O'Brien, S. H., A. Webb, M. J. Brewer & J. B. Reid, 2012. Use of kernel density estimation and maximum curvature to set Marine Protected Area boundaries: Identifying a Special Protection Area for wintering red-throated divers in the UK. *Biological Conservation* 156: 15–21. <https://doi.org/10.1016/j.biocon.2011.12.033>.
- Pinder, A. C., A. J. Harrison & J. R. Britton, 2019. Temperature effects on the physiological status and reflex impairment in European grayling *Thymallus thymallus* from

- catch-and release angling. *Fisheries Research* 21: 169–175. <https://doi.org/10.1016/j.fishres.2018.11.014>.
- Pedersen, E. J., D. L. Miller, G. L. Simpson & N. Ross, 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ* 7: e6876. <https://doi.org/10.7717/peerj.6876>.
- R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reeve, C., L. E. Rowsey & B. Speers-Roesch, 2022. Inactivity and the passive slowing effect of cold on resting metabolism as the primary drivers of energy savings in overwintering fishes. *Journal of Experimental Biology* 225: p.jeb243407.
- Roberts, C. G., A. S. Tarkan, M. E. Hanley & J. R. Britton, 2025. Angler catch data as a monitoring tool for European barbel *Barbus barbus* in a data limited recreational fishery. *Fisheries Research* 28: 107224. <https://doi.org/10.1016/j.fishres.2024.107224>.
- Ross, M. J. & J. D. Winter, 1981. Winter movements of four fish species near a thermal plume in Northern Minnesota. *Transactions of the American Fisheries Society* 110: 14–18. [https://doi.org/10.1577/1548-8659\(1981\)110%3c14:WMOFFS%3e2.0.CO;2](https://doi.org/10.1577/1548-8659(1981)110%3c14:WMOFFS%3e2.0.CO;2).
- Shuter, B. J., A. G. Finstad, I. P. Helland, I. Zweimüller & F. Hölker, 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences* 74: 637–657. <https://doi.org/10.1007/s00027-012-0274-3>.
- Silva, A. T., M. C. Lucas, T. Castro-Santos, C. Katopodis, L. J. Baumgartner, J. D. Thiem, K. Aarestrup, P. S. Pompeu, G. C. O'Brien, D. C. Braun, N. J. Burnett, D. Z. Zhu, H. Fjeldstad, T. Forseth, N. Rajaratnam, J. G. Williams & S. J. Cooke, 2018. The future of fish passage science, engineering, and practice. *Fish and Fisheries* 19: 340–362. <https://doi.org/10.1111/faf.12258>.
- Silverman, B. W., 1986. Density estimation for statistics and data analysis. Monographs on Statistics and Applied Probability. Chapman and Hall, London.
- Souchon, Y. & L. Tissot, 2012. Synthesis of thermal tolerances of the common freshwater fish species in large Western Europe rivers. *Knowledge and Management of Aquatic Ecosystems* 405: 03. <https://doi.org/10.1051/kmae/2012008>.
- Sutton, A. O., E. K. Studd, T. Fernandes, A. E. Bates, A. J. Bramburger, S. J. Cooke, B. Hayden, H. A. L. Henry, M. M. Humphries, R. Martin, B. McMeans, E. Moise, A. M. O'Sullivan, S. Sharma & P. H. Templer, 2021. Frozen out: unanswered questions about winter biology. *Environmental Reviews* 29: 431–442. <https://doi.org/10.1139/er-2020-0127>.
- Studd, E. K., A. E. Bates, A. J. Bramburger, T. Fernandes, B. Hayden, H. A. Henry, M. M. Humphries, R. Martin, B. C. McMeans, E. R. Moise & A. M. O'Sullivan, 2021. Nine maxims for the ecology of cold-climate winters. *BioScience* 71: 820–830. <https://doi.org/10.1016/j.fishres.2024.107224>.
- Taylor, M. K. & S. J. Cooke, 2012. Meta-analyses of the effects of river flow on fish movement and activity. *Environmental Reviews* 20: 211–219. <https://doi.org/10.1139/a2012-009>.
- Udyawer, V., R. G. Dwyer, X. Hoenner, R. C. Babcock, S. Brodie, H. A. Campbell, R. G. Harcourt, C. Huveneers, F. R. A. Jaïne, C. A. Simpfendorfer, M. D. Taylor & M. R. Heupel, 2018. A standardised framework for analysing animal detections from automated tracking arrays. *Animal Biotelemetry* 6: 17. <https://doi.org/10.1186/s40317-018-0162-2>.
- Unlocking the Severn, 2023. Our Fish Passes. Retrieved from <https://www.unlockingthesevern.co.uk/our-fish-passes/>. Last accessed 20/12/2023
- Weber, C., C. Nilsson, L. Lind, K. T. Alfredsen & L. E. Polvi, 2013. Winter disturbances and riverine fish in temperate and cold regions. *BioScience* 6: 199–210. <https://doi.org/10.1525/bio.2013.63.3.8>.
- Winter, E. R., A. M. Hindes, S. Lane & J. R. Britton, 2021. Movements of common bream *Abramis brama* in a highly connected, lowland wetland reveal sub-populations with diverse migration strategies. *Freshwater Biology* 66: 1410–1422. <https://doi.org/10.1111/fwb.13726>.
- Worton, B. J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168. <https://doi.org/10.2307/1938423>.
- Zuur, A. F., E. N. Ieno & C. S. Elphick, 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecology and Evolution* 1: 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.

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