



Effects of season and acoustic telemetry sample sizes on the detections and movements of potadromous common bream *Abramis brama* in a highly connected wetland system

Simone Cittadino · Ali Serhan Tarkan · Sadi Aksu · Rosalind M. Wright · Andrew M. Hinds · Steve Lane · Emily Winter · Jim Lyons · J. Robert Britton

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Abstract Acoustic telemetry is a powerful tool for understanding spatial and temporal fish movements in complex freshwater systems but determining appropriate sample sizes for measuring individual variability in movement metrics is challenging. Here, the movements of 170 common bream *Abramis brama* were measured over two years in the highly connected River Bure wetland system, eastern England.

Analyses of seasonal and spatial movement patterns revealed higher movement metrics in winter versus summer, with the extent of movements measured enabled by the high lateral connectivity of this wetland system, with bream often occupying the numerous off-channel lentic habitats present. Power analyses were then applied to this relatively large dataset to assess how changes in tagged fish number influenced the individual variability in the movement metrics. Although retaining 95% of the movement variability required relatively large samples, using 60 individuals retained 90% of individual variability, with only 20 fish needed to retain 80%. These results emphasise

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S. Cittadino (✉) · A. S. Tarkan · E. Winter · J. R. Britton
Department of Life and Environmental Sciences,
Bournemouth University, Poole BH12 5BB, UK
e-mail: scittadino@bournemouth.ac.uk

A. S. Tarkan
Faculty of Biology and Environmental Protection,
Department of Ecology and Vertebrate Zoology,
University of Lodz, Lodz, Poland

A. S. Tarkan
Department of Basic Sciences, Faculty of Fisheries, Muğla
Sitki Koçman University, Menteşe, Muğla, Türkiye

S. Aksu
Vocational School of Health Services, Eskişehir
Osmangazi University, Eskişehir, Türkiye

R. M. Wright
Environment Agency, Rivers House, Threshelfords
Business Park, Inworth Road, Feering CO5 9SE, UK

A. M. Hinds
Fishtrack Ltd, 2 South End Farm Cottages,
Beccles NR34 8TG, UK

S. Lane
Environment Agency, Dragonfly House,
Norwich NR3 1UB, UK

S. Lane
The Rivers Trust, Rain Charm House,
Kyl Cober Park, Stoke Climsland, Callington PL17 8PH,
UK

E. Winter
River Waveney Trust, Mill Ln, Pulham Market,
Diss IP21 4XL, UK

J. Lyons
Environment Agency, Trentside,
West Bridgford, Nottingham NG2 5FA, UK

the importance of high connectivity in wetlands to enable potadromous fish to access key functional habitats in all seasons. It also reveals relatively small sample sizes in acoustic telemetry can capture much of the movement variability measured across larger numbers of tagged fish.

Keywords Acoustic telemetry · Movement metrics · Sample size · Side channels · Wetlands

Introduction

Lowland wetland systems play a crucial role in maintaining the ecological integrity and biodiversity of aquatic ecosystems (Elosegi et al., 2010). High connectivity facilitates fish movements across the different habitats, allowing full expression of the phenotypic variation present between individuals (Schofield et al., 2018). Where this high connectivity has been maintained in freshwater systems, many fish populations express considerable inter-individual variation in their behaviours and movements in response to environmental cues and resource availability (Amat-Trigo et al., 2024; Cittadino, 2024). For example, individual roach *Rutilus rutilus* (Linnaeus 1758) repeatedly will migrate from lakes into connected streams during winter while others remain resident, with this associated with trade-offs between predation risk and foraging opportunities (Brodersen et al., 2014). High river connectivity promotes access to resource-rich areas for fish populations, potentially leading to the formation of semi-independent sub-populations that use different habitats outside of the reproductive periods but then share the same spawning areas (Kessel et al., 2018; Winter et al., 2021b). This process reduces inter- and intraspecific competition, but maintains gene flow (Turbek et al., 2018).

Several factors influence the short- and long-term movement patterns of potadromous fishes in riverine systems. The availability of functional habitats facilitates access to productive foraging habitats, spawning areas and nursery grounds (McLean et al., 2016). Habitat selection involves individuals selecting the environments that best meet their needs for survival, growth, and reproduction, which is based on a range of factors including prey availability, predation risk, and the prevailing abiotic conditions (Cooke et al., 2022). Seasonal differences, particularly in temperate

climates, can strongly shape habitat use, with mean temperatures often differing by over 15 °C between summer and winter (Amat-Trigo et al., 2024; Tarkan et al., 2025). Winter is a potentially critical season for freshwater fish communities, as reduced temperatures lower metabolic rates, swimming capacities, and foraging activity (Marsden et al., 2021; Sutton et al., 2021). These low temperatures are often combined with shortened daylight hours, ice cover, and/or elevated flow rates (including spates), all of which can further impact fish activity levels (Gutmann Roberts et al., 2019; Sutton et al., 2021). Many temperate freshwater fish can enter a quiescent state during winter, where activity and movements largely cease (Reeve et al., 2022). However, recent evidence from the highly fragmented lower River Severn, western Britain, revealed that the movement ecology of potadromous European barbel *Barbus barbus* (Linnaeus 1758) and common bream *Abramis brama* (Linnaeus 1758) was largely similar between summer and winter, with individuals continuing to make extensive movements during winter, including at water temperatures below 2 °C (Tarkan et al., 2025).

Acoustic telemetry is now a widely used tool for investigating fish movement ecology, providing insights into how movements correlate with environmental variables, physiological traits, seasons, and reproductive periods (Hussey et al., 2015; Mourier et al., 2025). Yet, despite technological improvements, the method can still represent a relatively expensive methodology, with sample sizes and receiver array resolutions often constrained by budget rather than being informed by prior assessments of the number of individuals needed to capture population movement variability (Lamb et al., 2023). There is thus limited knowledge on how sample sizes affect the statistical power of movement analyses and whether typical study designs are sufficient to generalise findings beyond the subset of tagged individuals.

Common bream (“bream”) represents a strong model species for understanding movements across different seasons and in freshwaters that are highly fragmented (e.g. Gardner et al., 2013; Tarkan et al., 2025), as well as those that have high connectivity (e.g. Winter et al., 2020; Winter et al., 2021a).

The species is encountered in many European lowland rivers and wetland areas, where individuals of up to ~600 mm can form relatively large aggregations that can comprise substantial proportions of

the fish biomass (Lyons & Lucas, 2002). Their potadromy means that individuals within populations can undertake relatively large pre-spawning migrations of over 60 km across short periods (Lucas and Baras, 2000), with individuals then regularly moving shorter distances between discrete foraging habitats in non-spawning periods (Kafemann et al., 2000). Tracking studies have also revealed regular seasonal habitat shifts that are coupled with distinct and repeated migrations to specific off-channel spawning areas (Lucas and Baras, 2000; Skov et al., 2011; Gardner et al., 2013).

The River Bure wetland system in eastern England is a highly connected wetland network comprising the Rivers Bure, Ant, Thurne, and associated broads, where bream populations show clear spatial structuring outside the spawning season but converge on shared upstream spawning sites during reproduction (Winter et al., 2021a,b). While previous studies have focussed primarily on pre-spawning migrations, comprehensive assessments of their full-year movement patterns, particularly the influence of season on their movement ecology and habitat use, is missing. Accordingly, we apply the extensive acoustic telemetry dataset of Winter et al. (2020; 2021a) to firstly investigate the effect of season on individual bream movements and habitat use, where the emphasis is on differences between winter and summer periods (as Winter et al., 2020, 2021a already assessed pre-spawning migrations). We posit that due to the tendency of bream to reduce their movements in very cold water, winter movement metrics will be substantially reduced compare with summer. We then apply this relatively large acoustic telemetry dataset to explore how the measured individual variability in the movement metrics is a function of sample size, using posteriori analyses to identify how reducing acoustic telemetry sample sizes affects the extent of this individual movement variability.

Methods

Study area

The study area includes the northern part of the Broads National Park, situated in Eastern England, with a focus on the lower River Bure and its main tributaries, the Rivers Ant and Thurne (Fig. 1). The

study area is characterised by high lateral and longitudinal connectivity, with the main rivers intersected by a dense network of lateral small lakes (broads) and dyke systems (Fig. 1). The main rivers are generally slow flowing with average water velocities ranging between 0.2 and 0.6 m/s under typical conditions. With distance downstream, the main River Bure transitions to semi-artificial open grazing marsh fringed with reeds, with the water becoming more brackish due to groundwater interaction with seawater, plus an increasing influence of the tide (Winter et al., 2021b). The lateral connections, that include secondary channels and numerous dyke systems, are even more weakly flowing, with velocities typically below 0.2 m/s and often just a few centimetres per second. Across the study area, there is high heterogeneity in macrophyte composition and coverage, which reflect the landscape pattern and habitat typologies. The low-lying and relatively homogeneous topography of the landscape means the wetland system is prone to saline intrusion during large spring tides and storm surges in winter where, during severe saline incursion episodes, the salt wedge can reach 50,000 microS/cm and has the potential to penetrate more than 10 km inland (Clarke, 1990; Winter et al., 2020).

Fish capture, acoustic transmitter implantation and receiver network

Bream were captured for the study using rod and line angling, which was considered the most effective method for capturing large-bodied, free-swimming fish in these open habitats. Between November 2017 and September 2018, a series of fish capture events were conducted in the Rivers Bure, Ant, and Thurne, resulting in a total of 181 bream being tagged (Table S1).

Following their capture, fish were held in keep cages and/or aerated tanks prior to their tagging, with no fish held for more than 12 h before their processing and release. Processing involved each bream being implanted with an acoustic transmitter, which began with their immersion in an anaesthetic bath (MS-222, Tricaine methanesulfonate; $\sim 0.10 \text{ g l}^{-1}$) until the fish reached a state of general anaesthesia, indicated by loss of equilibrium and/ or a lack of response to external stimuli. The fish were then removed, measured (fork length, nearest millimetre), scale and pelvic fin samples taken, and an acoustic transmitter implanted

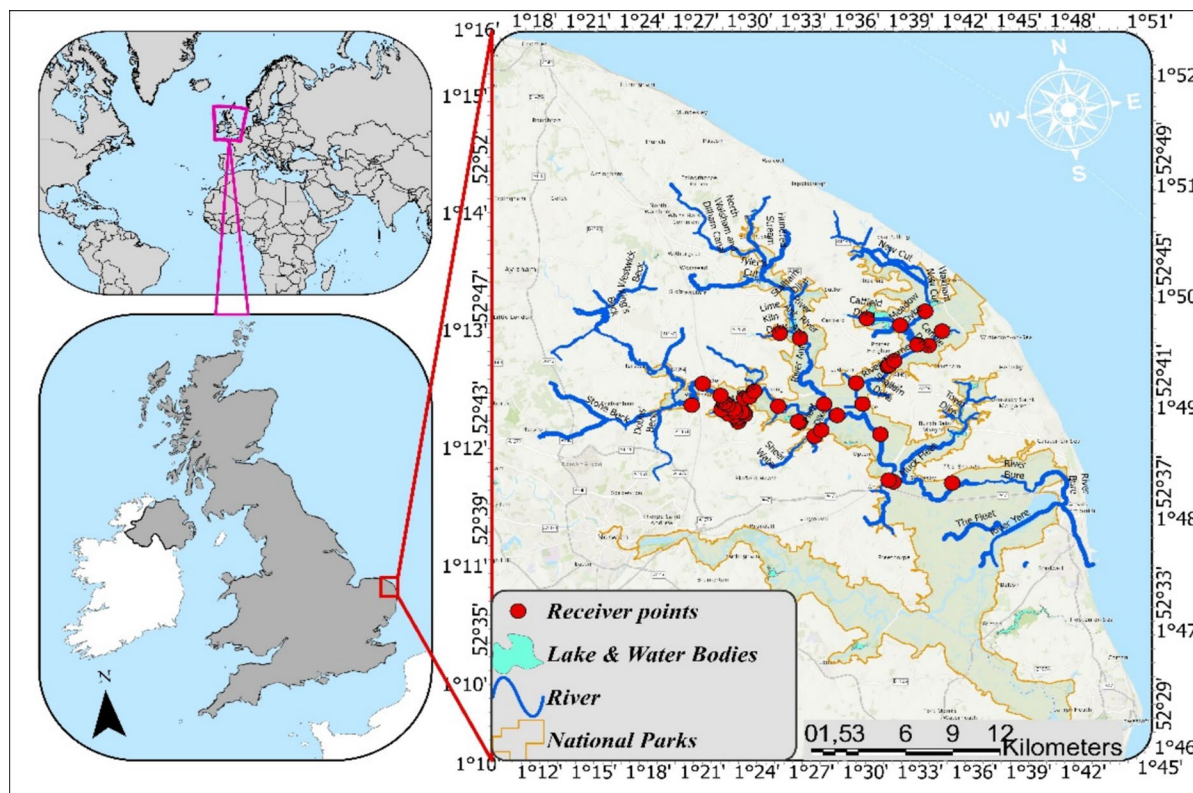


Fig. 1 Map depicting the study area within Broadlands National Park, specifically within the Bure system, shows the placement of acoustic receivers marked by red circles

into the body cavity. The acoustic transmitters were Vemco V13 (L x D: 36 × 13 mm, 6.0 g mass in water, $n=148$) and V9 (27.5 × 9 mm, 2.7 g mass in water, $n=9$), and Thelma Biotel ID-LP13 (28 × 13 mm, 5.5 g mass in water, $n=24$). The acoustic transmitter was implanted via a lateral, ventral incision into the body cavity, with a 23 mm passive integrated transponder (PIT) tag also inserted to enable both individual identification of recaptured fish and detection on PIT detection antennas in the wetland system (Winter et al., 2020). All transmitters were programmed on a random transmission interval of approximately 90 s, providing an estimated battery life between 900 and 1200 days. Following implantation, the incision was closed using a single suture and wound sealer, and the fish was then placed in recovery tanks filled with river water. Following their return to normal behaviour (maintenance of body equilibrium, responses to external stimuli, usually within 2 min), they were released back near their capture sites within two

hours. All surgeries were performed by the same surgeon under UK Home Office project license 70/8063 (granted under the Animals (Scientific Procedures) Act (1986)) and following ethical approval.

To detect the fish movements via their transmitters, a network of 54 Vemco VR2W acoustic receivers was deployed across the rivers and their connected wetland areas. These receivers were strategically positioned on permanent structures, navigation posts, or floating objects at mid-water depths (approximately 1.0–1.5 m) to ensure optimal detection during tidal fluctuations and avoid air exposure. Detection data were downloaded every four months, and receiver batteries were replaced annually. Movement data of the fish were recorded from 2017 to 2020. Despite variability in detection efficiency influenced by environmental factors such as water temperature and precipitation, the receiver network provided reliable long-term monitoring of the tagged bream (Winter et al., 2021b). The placement and maintenance of

receivers ensured high spatial and temporal coverage, critical for accurate tracking of fish movements (Winter et al., 2021b).

Movement metrics

Data were downloaded from receivers using VUE software (version 2.7.0), and subsequent data manipulation was conducted using the Vtrack R package (Campbell et al., 2012), which enables the detection data of Vemco acoustic transmitters to be assimilated across all receivers and then analysed appropriately (Udyawer et al., 2018). Prior to data analyses, the detection records were processed using the *actel* R package to eliminate false detections, such as those caused by transmitter code collisions (Flávio & Baktoft, 2021). The movement metric selected for analysis was the mean daily distance moved (MDD), calculated following the methodology of Gutmann Roberts et al. (2019) to assess individual-level residency and movement patterns. MDD was defined as the mean distance moved between receivers within a 24-h window, with days without movement excluded to prevent overestimation (Craig, 2008; Acolas et al., 2017). Although detection data for some individual bream were available from late 2017 to 2020, to provide consistency in the time periods when most bream were tracked, their movement metrics were calculated using detection data for the 24 months between January 2018 and December 2019.

To assess seasonal effects on movements, the bream detections were grouped into: “Winter” (October 1—March 31), “Spawning” (April 1—June 30), and “Summer” (July 1—September 30) periods (Winter et al., 2020, 2021a; Amat-Trigo et al., 2024). Although Winter et al. (2020; 2021a) have already assessed spawning movements in the dataset, they were included here as these movements separate the winter and summer periods, and thus the location of the tagged individuals was able to be tracked continuously across these groups. MDD was computed for each season of each year to assess variation in bream movement behaviour. Additionally, the number of fish detected in each season was recorded. To then assess how the tagged bream used different habitat typologies across the study area, the receiver locations were categorised into three groups: “main” river (including the Bure mainstem and the Ant and Thurne tributaries), “broads” (the shallow, connected

lentic habitats), and “lateral” (the ditch and dyke systems), with the number of fish and the number of detections determined for each habitat type and season. Kernel density estimation (KDE) was then applied to delineate the primary areas of bream spatial occupancy within the study area and displayed as heat maps. This method involved computing the density of point features surrounding each output raster cell. A continuous, smoothly curved surface was then fitted over each point, with the surface exhibiting its highest value at the point’s location. This value gradually decreases as the distance from the point increases, eventually tapering off to zero at a distance equal to the specified search radius (Cantrell, 2018). KDE was performed by dividing detections according to the season. These analyses were all conducted in ArcMap version 10.8.2, which enabled the generation of heat maps as the final step in the process.

Data analyses

For statistical analysis, only bream individuals detected for more than 10 days in each season of both 2018 and 2019 were included. Out of the initial sample of 181 tagged bream, 170 met these criteria and were retained in the final dataset used for modelling (*cf.* Results). Given the potential spatial and temporal biases arising from differences in both the lengths of each season (with winter considerably longer) and receiver density (with the Bure mainstem holding a greater number of receivers than the Ant or Thurne tributaries), a preliminary generalised linear mixed model (GLMM; Gamma distribution) using the *glmTME* package in R was constructed to explicitly test whether the number of receivers per river (“Density”) and the number of days per season (“Duration”) significantly influenced detection number (as the response variable). Habitat (as main river, lateral channels, and broads) and season (winter/ spawning/ summer) were the fixed predictors. As both receiver density and the number of days per season did not have significant effects on the dependent variables, “Density” and “Duration” were excluded from all subsequent analyses (Table S2).

To then investigate patterns in bream movement behaviour and habitat use, two sets of GLMMs were constructed. The first model examined the relationship between the number of individual detections and the predictors: macrohabitat type (“Habitat”) and

season (summer/ winter/ spawning). The final, best-fitting model was identified through backward selection using the Akaike Information Criterion (AIC), with a threshold of $\Delta AIC \leq 2$. To account for the number of individuals detected, the number of bream detected was incorporated as a random factor as well as the river (Bure/Ant/Thurne) and the receiver ID. Although fish lengths ranged from 286 to 527 mm and could potentially be an important predictor, it was never significant in the models and so was not included in final models. Prior to model fitting, all datasets underwent thorough exploratory data analysis following the protocol outlined by (Ieno and Zuur, 2015), which covered checking for missing values, identifying outliers in both response and explanatory variables, assessing homogeneity and zero inflation in the response variable, evaluating collinearity between explanatory variables, ensuring balance in categorical variables, and examining the nature of relationships between the response and explanatory variables. All candidate models were subsequently validated using the DHARMA package in R (Hartig & Lohse, 2022). The *simulateResiduals* function in the package simulated the standardised residuals of fitted models, enabling model assumptions to be checked by examining whether the residuals exhibited patterns that would indicate deviations from key model assumptions (homogeneity of variance, normality of residuals, and the presence of outliers). Additionally, *plotQQunif* function generated a Q-Q plot, allowing evaluation of the normality of residuals. Tests for model dispersion and the presence of outliers were also conducted during this step.

The second model analysed movement patterns across the different seasons, using the R package sdmTMB for geostatistical spatial and spatiotemporal analyses, which extends the capabilities of mixed-effects models by incorporating spatial and spatiotemporal Gaussian Markov random fields (GMRFs) through a stochastic partial differential equation (SPDE) approach. The package constructs a mesh based on receiver locations and integrates the "Time" object to account for temporal components to the data (Anderson et al., 2022). The model investigated differences in movement patterns across season and habitat type, where mean daily distance moved (MDD) was the response variable, while an interaction term between season and macrohabitat was used to determine the seasonal effect on habitat use, with FishID

used as a random factor to account for individual variation in movement behaviour, and *Year* (2018 and 2019) was incorporated within the "Time" object to control for temporal effects.

Power analyses

To evaluate how the extent of individual variation in the movement analyses was affected by sample size, two post-hoc power analysis (PA) quantified the minimum number of tagged individuals required to capture variance across a range of power thresholds (40 to 95%). The first set of analyses focussed on the complete detection dataset to identify the minimum number of tagged bream needed to retain a given proportion of the variance observed in detection frequencies. The second set of analyses was based on the mean daily distance moved (MDD) metric from the entire dataset, with calculation of the smallest subset of tagged fish needed to explain the variability in MDD. Both sets of analyses were based on a bootstrap variance coverage approach, where a resampling routine was applied within each group to assess the proportion of total variance captured as a function of sample size (Lamb et al., 2023). To identify the optimal transmitter subset, a greedy selection algorithm was applied, iteratively selecting individuals that maximised explained variance (Kumle et al., 2021). The analyses were implemented in R (version 4.2.2) using custom scripts, with iterative functions relying on the purr package. The results of both sets of power analysis were visualised by plotting the variance threshold versus tagged fish number.

After identifying the minimal sufficient sample sizes to explain 90% of the variance, the two GLMMs with response variables of the number of detections and MDD were re-run using the reduced datasets to compare outputs before and after the power analysis, thus assessing whether the conclusions drawn from the full datasets could be reliably generalised from smaller, optimally selected samples.

Results

Of 181 tagged bream, 170 individuals between lengths of 286 to 527 mm (mean: 406 ± 47 mm) generated movement data suitable for analyses, which in 2018 and 2019 were detected over 7 million times.

Most bream detections were recorded in the areas in and around the River Bure rather than the River Ant and Thurne, with the Bure section of the study area also having the highest number of tagged individuals and higher density of receivers. Bream detections counts were higher during winter than summer (Fig. 2). Seasonal heat maps suggested some shifts

in the areas of highest detection density, but with the core habitat use in the upper area of the study reach remaining relatively stable across seasons (Fig. 3). Most bream detections were on receivers deployed in the “Broads” habitat type (45% in all seasons), with lateral habitats then having a higher proportion of detections than receivers in the main river (Fig. 4).

Fig. 2 The number of detections recorded daily between January 2018 and January 2020 in the three main rivers Ant (black), Bure (grey) and Thurne (light grey). Dashed vertical lines indicate the seasonal divisions used in the analyses: winter (October–March), spawning (April–June), and summer (July–September)

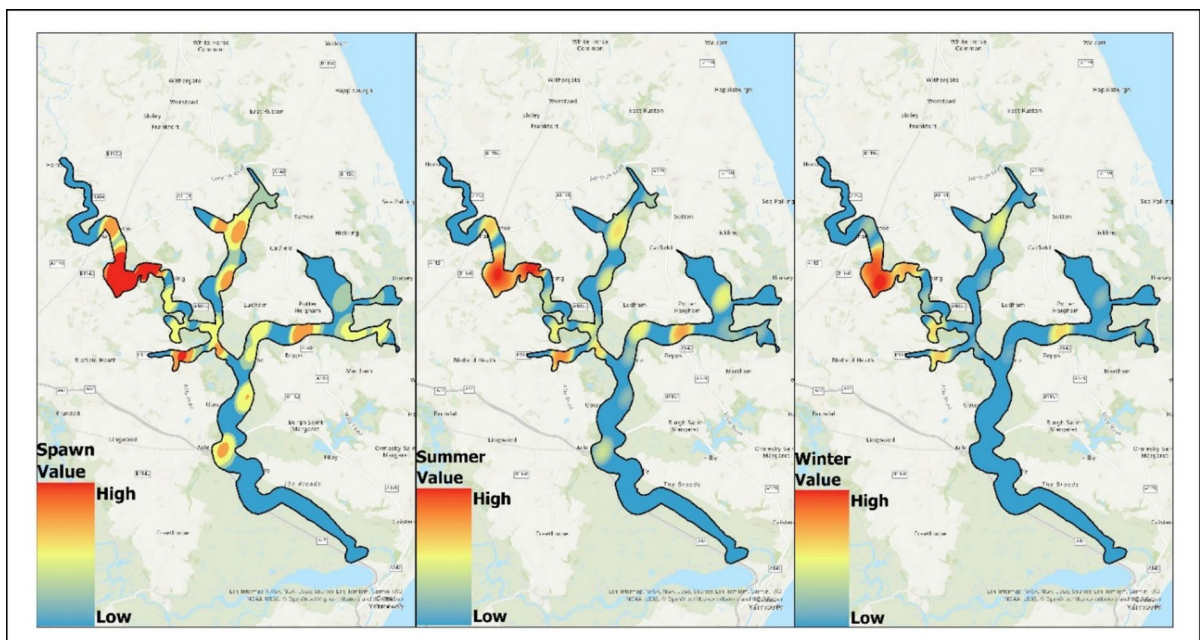
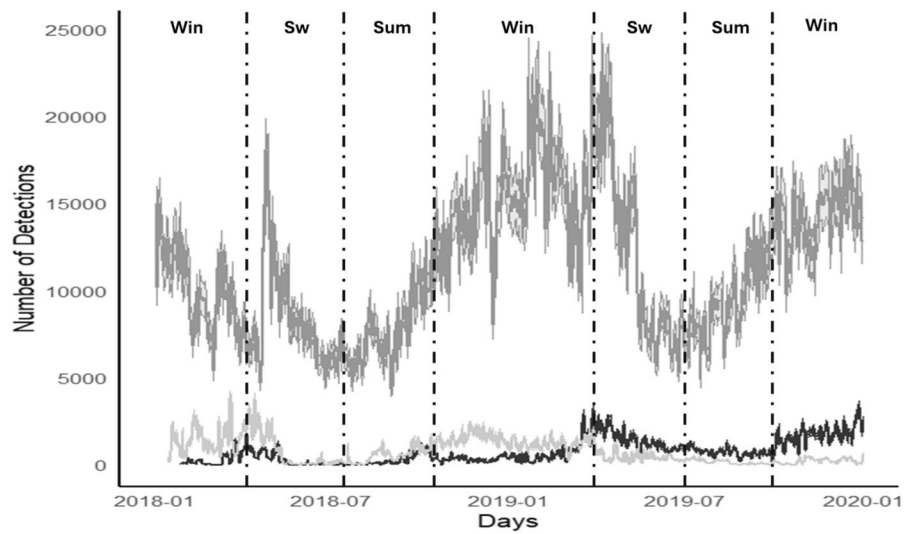
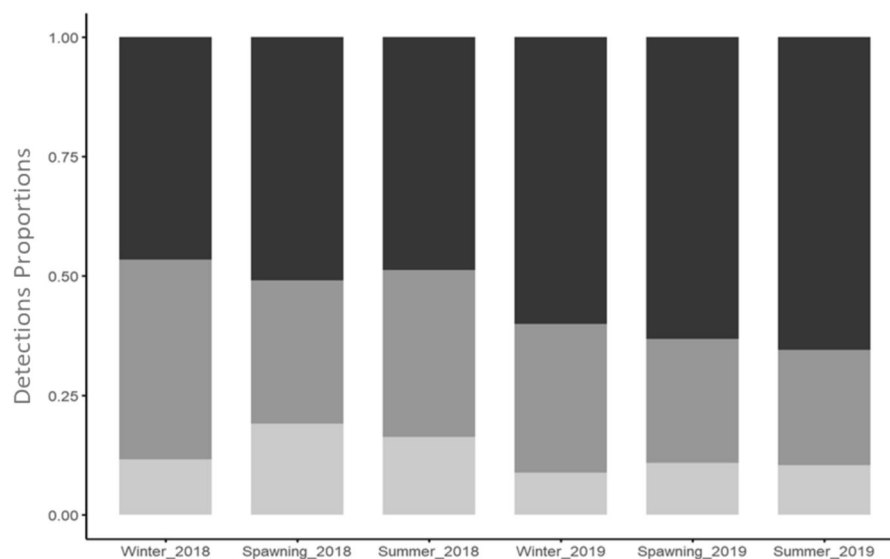


Fig. 3 Density maps displaying the spatial distribution of bream detections across the river system during the winter (left), spawning (middle), and summer (right) seasons. Areas of high activity density are shown in red, while blue areas indicate lower activity levels

Fig. 4 Comparison of detections proportions across macrohabitats, broads (black), lateral (grey), and main (light grey) per season between 2018 and 2019



The GLMMs revealed that season and habitat type significantly influenced the number of bream detections, with winter having a positive effect and summer and spawning having a negative. Detections were significantly higher in broad habitats ($p < 0.001$), corresponding to approximately a tenfold increase compared with the main river and with lateral habitats having slightly, but not significantly, higher detections than the main river (Table 1). The use of random intercepts by receiver in the model indicated substantial variability in detections across individual receivers but no influence of the river (Table 1).

Season and habitat were significant predictors of MDD, highlighting clear seasonal and habitat-related variations (Table 2). MDD was significantly lower in summer compared to winter, with a decrease of approximately 22%. Both the broad habitats and the lateral habitats had a significant lower daily distanced moved versus the main section of the river (respectively -54% and -27%). Importantly, the interaction terms highlighted partial compensatory effects in summer, with positive interactions observed in both broad (coefficient = +0.30, SE = 0.07) and lateral (coefficient = +0.22, SE = 0.07) habitats, compared to the same habitats in winter (Table 2). The model

Table 1 Results of three generalised linear mixed models (GLMM) evaluating the influence of season (spawning, summer and winter) and habitat (broad, lateral and main) on the number of detections. The receiver identification number and the number of bream detected were added as random factors. P-values in bold indicate statistically significant effects

Detections ~ Season + Habitat + (1 ReceiverID) + (1 Bream detected) Detections			
Predictors	Estimates	CI	P
(Intercept)	9845.92	4973.44 – 19,491.96	< 0.001
Habitat [Broad]	10.24	3.86 – 27.17	< 0.001
Habitat [Lateral]	1.76	0.66 – 4.67	0.26
Season [Spawning]	0.48	0.33 – 0.70	< 0.001
Season [Summer]	0.44	0.28 – 0.68	< 0.001
<i>Random Effects</i>			
Bream Detected	0.32		
River	0.01		
ReceiverID	1.76		
Observations	244		
Marginal R ² / Conditional R ²	0.313 / 0.738		

P-values in bold indicate statistically significant effects

Table 2 Model output of a generalised linear model implemented in the sdmTMB package, showing the mean daily distance (MDD) as the response variable. The interaction between Season (Spawning, Summer, and Winter) and Habitat (Broad, Lateral, and Main) is used as predictor, with FishID included as a random factor to account for dependency. Estimates are presented with standard errors and 95% credible intervals (CrI). A value was considered statistically important and highlighted in bold if zero did not fall within the range of the lower and upper CrIs

MDD ~ Season * Habitat + (1 FishID)		Mean Daily Distance	
Predictors	Estimate	Std. Error	CrI
Intercept	7.51	0.04	7.43, 7.59
Season [Spawning]	0.07	0.05	-0.03, 0.17
Season [Summer]	-0.09	0.04	-0.17, -0.01
Habitat [Broad]	0.67	0.07	0.53, 0.8
Habitat [Lateral]	0.97	0.05	0.87, 1.07
Season [Spawning] × Habitat [Broad]	-0.09	0.09	-0.26, 0.08
Season [Summer] × Habitat [Broad]	-0.15	0.06	-0.26, -0.08
Season [Spawning] × Habitat [Lateral]	-0.22	0.08	-0.27, -0.03
Season [Summer] × Habitat [Lateral]	0.05	0.05	-0.05, 0.15
Random Effects			
FishID (Std. Dev.)	0.18		
Dispersion Parameter	5.07		
Spatiotemporal AR1 Correlation	-0.66		
Matérn Range	0.03		
Spatial SD	2.23		
Spatiotemporal Marginal AR1 SD	0.17		
ML Criterion at Convergence	17,820.006		

also revealed a moderate negative spatiotemporal AR1 correlation of -0.66, indicating inverse movement trends between consecutive years (Table 2).

Power analyses of movement variance

The results of the power analysis series assessed the number of transmitters required to retain decreasing proportions of the total variance in the detection dataset and the MDD dataset (Fig. 5). While substantial numbers of transmitters were needed to retain 95% of the total variance in both sets of analyses, retaining 90% of the variance only required ~60 individuals, which reduced to ~20 when the threshold was lowered to 80%, with very low tagged fish numbers needed to capture 50% of variance (<5; Fig. 5).

Comparison of the GLMM of habitat use based on all data (N=170) versus data capturing 90% of the variance (n=58) revealed the effect of the broad habitats remained strong and significant in both models. However, seasonal effects differed: in the pre-PA model, both the spawning (-0.74, SE=0.19, $p < 0.001$) and summer (-0.83, SE=0.23, $p < 0.001$) periods showed significant reductions in detections compared to winter, whereas in the post-PA model, although the coefficients remained negative, these seasonal effects were no longer statistically

significant (Table 3). For the GLMM of MDD analysis, the 90% PA model used 56 tagged fish, with the post-PA sdmTMB model showing similar patterns to the pre-PA model (Table 4). Habitat effects remained strong, with broad habitats showing a slightly larger reduction in movements post-PA (Table 4).

Discussion

The analysis of the movements of 170 bream over 2 successive years revealed strong temporal and spatial patterns in their movement behaviour. Bream detections were concentrated within the off-channel lentic habitats specifically in the broads, where the highest detection densities were recorded consistently across all seasons. Seasonal comparisons indicated that, contrary to prediction, detection rates were significantly higher during the winter months compared to summer, with bream frequently recorded at receivers distributed across the system in winter, including the main river channel. MDD in the main river was higher during winter and spawning season when compared to summer. This dataset also enabled the application of power analyses to measure the effects of sample size on measured movement variance, with sample sizes of approximately 60 individuals sufficient to

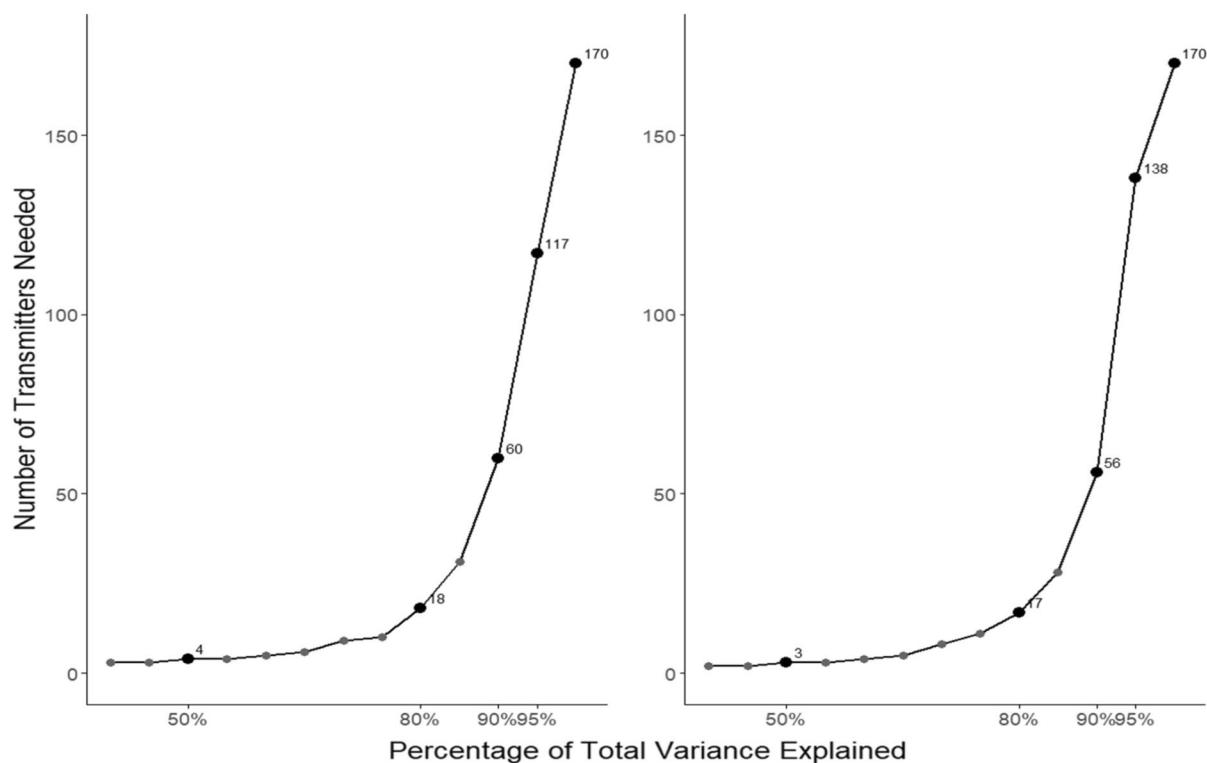


Fig. 5 Power analysis results for (A) mean daily distance moved (MDD) and (B) detection count datasets. Each curve shows the number of transmitters needed to retain increasing percentages of the total variance, from 40 to 100%

Table 3 Summary of the negative binomial generalised linear mixed models (GLMM) evaluating the influence of habitat type (Broad, Lateral, Main) and season (Spawning, Summer, Winter) on the number of detections, comparing the full dataset (pre-power analysis, PrePA) and the reduced dataset

(post-power analysis 90%, PostPA). The models include random intercepts for receiver and the number of breem detected to account for receiver-level variability and individual detection frequency. Estimates and standard errors (StdError) are reported on the log scale, with associated p values (p)

Detections ~ Season + Habitat + (1 Receiver) + (1 Breem detected)							Detections
Predictor	Estimate PrePA	StdError PrePA	p PrePA	Estimate PostPA	StdError PostPA	P PostPA	
Intercept	9.19	0.35	< 0.001	8.64	0.41	< 0.001	
Habitat [Broad]	2.33	0.5	< 0.001	2.4	0.54	< 0.001	
Habitat [Lateral]	0.56	0.5	0.26	0.94	0.54	0.08	
Season [Spawning]	-0.74	0.19	< 0.001	-0.15	0.24	0.53	
Season [Summer]	-0.83	0.23	< 0.001	-0.34	0.26	0.19	

P-values in bold indicate statistically significant effects

explain 90% of measured variance, and only around 20 individuals were needed for 80% variance. These findings collectively suggest that modestly sized samples of acoustically tagged fish can effectively capture key behavioural patterns, particularly when using

metrics that inherently reduce individual-level variability (Chatterjee, 2024).

Although breem activity typically peaks during the spawning season, as described by Winter et al. (2020; 2021a), our results reveal that their activity

Table 4 Summary of the generalised linear mixed models (GLMM), evaluating the effects of habitat type (Broad, Lateral, Main) and season (Spawning, Summer, Winter), including their interactions, on the mean daily distance (MDD) moved by

bream. The models compare outputs from the full dataset (pre-power analysis 90%, PrePA) and the reduced dataset (post-power analysis, PostPA). Fish ID was included as a random intercept to account for repeated measurements of individuals

MDD ~ Season * Habitat + (1 FishID)				Mean Daily Distance
Predictor	Estimate PrePA	StdError PrePA	Estimate PostPA	StdError PostPA
Intercept	7.51	0.04	7.62	0.06
Season [Spawning]	0.07	0.04	-0.02	0.06
Season [Summer]	-0.25	0.05	-0.18	0.06
Habitat [Broad]	-0.77	0.04	-0.99	0.06
Habitat [Lateral]	-0.32	0.04	-0.34	0.06
Season [Spawning] × Habitat [Broad]	0.01	0.05	0.14	0.08
Season [Summer] × Habitat [Broad]	0.3	0.07	0.14	0.09
Season [Spawning] × Habitat [Lateral]	0.03	0.06	0.15	0.09
Season [Summer] × Habitat [Lateral]	0.22	0.07	0.12	0.1

levels were also high during the winter months, with consistently elevated detections in lateral habitats and notably higher MDD, especially in the main river. In contrast, detection rates dropped sharply during the summer season. Common bream typically show this activity peak during the spawning period where the rise in water temperature and changes in photoperiod are the primary factors triggering the onset of spawning migrations (Gardner et al., 2013), with responses to these changes also seen in other fishes of the Cyprinidae family (e.g. Gutmann Roberts et al., 2019). While temperature is a key driver of long-distance movements, high temperatures are not necessarily correlated with increased movement (Slavík et al., 2024). The bream in the Bure system demonstrated the capacity to sustain elevated activity levels even during the coldest winter months. This pattern may reflect the necessity for bream to undertake relatively long, temporally constrained movements between habitats in winter, potentially driven by localised resource scarcity (Tarkan et al., 2025). In contrast, such movements appear less essential in summer, when habitats such as the broads become highly productive and resource-rich, allowing individuals to meet their foraging needs within more confined spatial areas and reducing the need for long-distance displacement.

The consistent use of lateral habitats across all seasons in the Bure system underscores the significance of these functional habitats for bream as year-round foraging and refuge areas. This aligns with findings

from other European floodplain systems, such as the Rhône and Danube, where species such as roach and chub *Squalius cephalus* (Linnaeus 1758) exhibit prolonged occupation of floodplain lakes and backwaters beyond the reproductive period (Nunn et al., 2007; Bouloy et al., 2024). In these systems, off-channel areas provide stable conditions, food-rich environments, and protection from high-flow disturbances, supporting fish communities year-round. The second most frequented habitat type was the lateral channel network, while the main river consistently had the lowest detection rates. When considered alongside the observation that distances moved were highest in the main river, this suggests the river channel primarily serves as a corridor facilitating transitions between preferred habitats, rather than as a site for prolonged occupancy. Similar habitat partitioning has been reported in other species in this area, including *Esox lucius* Linnaeus 1758, which utilize lentic or low-flow backwaters for spawning and juvenile development but move through river channels for migration (Nilsson et al., 2014; Cittadino et al., 2024). Moreover, these occupancy patterns were not an artefact of the receiver density being uneven across the different habitats, as the preliminary GLMM indicated no significant effect of receiver density on bream detection rates by habitat.

Previous studies on the same bream sample revealed divergent spawning migration behaviours in the Bure, with some individuals remaining in the Upper Bure year-round and others migrating from

River Thurne to spawning areas that were ~25 km upstream in the Bure, before their return to the Thurne after the spawning was complete (Winter et al., 2020, 2021a). These repeated behavioural patterns suggest the presence of semi-independent subpopulations, potentially functioning as an adaptive strategy to reduce intraspecific competition and buffer against local environmental perturbations, thus supporting long-term population stability (Brodersen et al., 2019). The high lateral hydrological connectivity and extensive network of secondary channels and habitats observed in this system likely underpin these spatial dynamics, enabling fish to freely move between functionally diverse macrohabitats, including overwintering refugia, productive nursery grounds, and essential spawning areas (Winter et al., 2020, 2021a). Year-round access to these habitats is therefore crucial for fish populations. In winter, off-channel and lateral habitats provide vital refuge and foraging opportunities while the main river serves as a connection between different secondary habitats (Karchesky and Bennett, 2004; Huntsman & Falke, 2019). During summer, these habitats can act as resource-rich nursery grounds and recovery sites post-migration. Such uninterrupted connectivity enhances demographic stability, buffers against stressors such as salinity incursions, hypoxia, or harmful algal blooms, and promotes behavioural and phenotypic diversity (Holdway et al., 1978; Wagstaff et al., 2021; Davis et al., 2023; Cittadino et al., 2024). Moreover, this connectivity supports the formation of spatially structured populations, linked through shared spawning areas, establishing a metapopulation framework that mitigates local extinction risk and promotes population viability (Fagan, 2002; Banks et al., 2013; Tonkin et al., 2018; Stoffels et al., 2022). Maintaining these ecological connections is increasingly critical as climate change intensifies the frequency and severity of extreme events, potentially altering habitat complexity, reducing resource availability, and affecting fish movement patterns, so ultimately impacting genetic diversity and population health (Van Leeuwen et al., 2018; Ventura et al., 2023).

The application of post-hoc power analyses in our study indicated how sample size influences the extent of the measured inter-individual variance in fish movements. These analyses revealed that relatively small sample sizes were able to describe important bream movement metrics, an important outcome

given many acoustic telemetry studies on bream and similar species where sample sizes are often between 10 and 30 tagged individuals (e.g. Jacobsen et al., 2014; Gutmann Roberts et al., 2019; van Leeuwen et al., 2023). The power analyses indicated that these limited sample sizes can still explain approximately 80% of the variance in movement behaviour. Moreover, the use of summary movement metrics (such as mean daily distance), which inherently reduce short-term behavioural variability, further enhances the robustness of analytical outcomes. While larger samples are beneficial for capturing the full extent of population variance in movements, our findings suggest that even relatively modest sample sizes will generate useful movement information, including individual variability.

In conclusion, this study demonstrates that modest sample sizes can still provide substantial coverage of population-level behavioural variability in acoustic telemetry studies. The use of movement metrics, such as mean daily distance moved, enhances the robustness of the final inferences by inherently averaging out individual-level variability, thus reducing the necessary sample size without compromising the reliability of the results. Although acoustic telemetry research is frequently constrained by budget limitations and a priori power analyses can be challenging to perform, our findings indicate that even relatively small samples, when optimally selected, can yield robust and reliable insights into fish movement patterns.

Finally, winter was identified as a crucial period here, significantly affecting bream movement dynamics in the Bure system. Lateral connectivity and access to secondary habitats (especially broads) were found to be vital year-round. These habitats provide critical ecological functions that shift throughout the year, acting as refuge and foraging areas during winter, productive nursery sites and recovery habitats post-migration in summer. Consequently, from a conservation and management perspective, preserving the hydrological connectivity and ensuring continuous accessibility to these diverse habitats should be a primary goal. Such conservation measures should not be limited to spawning periods, when reproductive habitats are clearly indispensable, but extended throughout the year to sustain broader ecological functions essential for the resilience, stability, and long-term viability of fish populations.

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Data availability Raw data that are not already provided in the manuscript are available from the corresponding author upon reasonable request.

Declarations

Conflict of interests The authors declare no conflicts of interest.

Ethics approval All procedures involving fish were conducted in accordance with UK legislation (Animals [Scientific Procedures] Act 1986) under Home Office Project Licence 70/8063 and were approved by the institutional animal ethics committee prior to tagging.

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