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Movements of common bream *Abramis brama* in a highly connected, lowland wetland reveal sub-populations with diverse migration strategies

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Abstract

1. Studies suggest the migratory behaviours of potamodromous fishes can be highly variable in barrier-free systems, where differing movement types enable populations to exploit a wide range of food and space resources. This intra-population diversity in spatial and temporal resource use is important to our ecological understanding of fish distribution patterns and population structure. Despite this, freshwater ecosystems are increasingly characterised by high levels of fragmentation and degradation that restrict mobile fauna, and limit opportunities to study natural, unconstrained movement behaviour.
2. Common bream *Abramis brama* (*bream*) is a potentially strong model species for testing the importance of diverse migration patterns in lowland rivers, but existing studies have been largely restricted to spatially confined and/or anthropogenically modified systems. This study's principal focus was to examine the diversity of bream movement behaviour in a highly connected, lowland system using passive acoustic telemetry, which provided continuous, multi-year data on the movements of 181 bream across a tidally influenced, lowland wetland in eastern England (*c*. 60 km of continuous river length plus numerous interconnected shallow lakes and dykes). Tracked bream were grouped according to their initial location and timing of tagging.
3. Bream migratory behaviours varied considerably between tagging groups, but with greater consistency within groups. There was little mixing of groups outside of spawning periods, with season and tidal phase being significant predictors of movement. Rates of movement and swimming speeds were highest in spring, with movements also generally occurring in the direction of tidal flows.
4. For fish sampled just prior to spawning, there was considerable diversity in their post-spawning behaviour, with some remaining in the immediate vicinity of the sampling location and others that moved to areas *c*. 25 km away. These spatially discrete patterns remained until the following spawning period.

5. These results suggest that this lowland fish population is comprised of several distinct, semi-independent subpopulations that only share space resources in their spawning period. This indicates the importance of connectivity in lowland freshwater systems for enabling and maintaining high phenotypic diversity in the movement behaviours of potamodromous fishes.

KEYWORDS
barrier-free, behaviour, partial migration, phenotype, spawning

1 | INTRODUCTION

Knowledge of the spatial and temporal dynamics of fish population structures is fundamental to their sustainable management, and for predicting how they may respond to environmental change (Sih et al., 2011). Population structure can be driven by animal behaviour, including life history variability and differential movement strategies for maximising survival and fitness (e.g. residency vs. migration; Chapman et al., 2012). However, in modern freshwater landscapes, the extent of fish movement is often limited by widespread habitat fragmentation, a lack of functional habitat availability, and/or the loss of ecological diversity (Bisson et al., 2009; Grill et al., 2019; Jones et al., 2019). As such, there are now few opportunities to assess natural, unconstrained fish movement behaviour and its effects on the dynamics of population structure.

In unrestricted corridors, some potamodromous fishes undertake considerable migrations and/or habitat shifts during their lifecycle (e.g. migrations of more than 100 km in tropical *Prochilodus* spp.; Lucas & Baras, 2001). It is increasingly recognised that highly diverse behavioural phenotypes can exist in certain environments (Secor, 1999), with fish populations comprising a spectrum of movement types that allow individuals to exploit spatially and temporally discrete habitats and resources (Kessel et al., 2018). For example, in populations of the cyprinid fish roach *Rutilus rutilus*, individual migratory strategies can vary from lifelong lake-residents to recurring lake-stream migrants, or fish that may be more plastic in their movement behaviour, dependent on genetic and/or environmental conditions (Brodersen et al., 2014). In addition, behavioural variability may present as differences in the migration distance or destination habitat of migratory phenotypes (Gahagan et al., 2015). For example, in the Great Lakes of North America, lake sturgeon *Acipenser fulvescens* exhibit five behavioural phenotypes that vary in their phenology and duration of river and lake use (Kessel et al., 2018). By contrast, fish populations inhabiting degraded and fragmented landscapes may have already lost a degree of behavioural variation, and thus exhibit simplified population structures (Thompson et al., 2019). Understanding how optimal intra-population variability can be incorporated into management efforts to conserve and restore freshwater ecology is challenging (Lennox et al., 2019), but studies that explore the range of movement behaviours in barrier-free habitats can inform this process.

The common bream *Abramis brama* (*bream*) is a relatively large-bodied cyprinid fish (regularly attaining lengths >500 mm), found abundantly in lowland river systems across Europe and with capacity for partial and facultative spawning migration over distances of at least 60 km (Lucas & Baras, 2001), as well as foraging movements between both freshwater and brackish environments (Kafemann et al., 2000). Bream may be more nomadic (or arrhythmic) in their movement patterns (Brodersen et al., 2019; Schulz & Berg, 1987) versus other riverine cypriniformes, such as European barbel *Barbus barbus*, that exhibit more predictable homing behaviour (Britton & Pegg, 2011). Nevertheless, tracking studies have suggested that bream populations can also demonstrate regular seasonal habitat shifts and distinct spawning migrations, such as between main-stem and tributary or off-channel habitats (Gardner et al., 2013; Lucas & Baras, 2001; Molls, 1999; Skov et al., 2011). Notably, spring aggregations of bream may break down into smaller subpopulations with varying migratory tendencies following their spawning (Whelan, 1983). However, the broader ecological applicability of these bream tracking studies are potentially limited as they have been limited to small sample sizes (<10 individuals) and short durations (<1 year), and/or applied in either highly restricted spatial areas (<10 km; Molls, 1999; Lyons & Lucas, 2002; Skov et al., 2011; Brodersen et al., 2019), or in anthropogenically modified systems that could inhibit the expression of natural behaviours (Gardner et al., 2015). Thus, while bream have potential as a strong model species for testing the diversity of migratory behaviours within populations of lowland potamodromous fishes, the extent of their inter-individual variability within highly connected systems has yet to be described adequately.

The aim of this study was to examine the diversity of bream movement patterns and understand its influence on their spatial occupancy patterns and population structure. The approach used passive acoustic telemetry to provide continuous, multi-year measurements of the movements of a large sample of adult bream (181 individuals) in the northern Norfolk Broads (the *Broads*), an internationally important and protected wetland in eastern England (Natural England, 2020). The flooded peat diggings of the Broads were abandoned in the 14th century and, aside from localised biomanipulation projects that restrict fish access in some small areas (Moss et al., 1996), they have since remained largely free of physical barriers. Indeed, fishes in the Broads can freely move throughout

200 km of mainstem river/estuarine habitat, along with 100s km of connected lakes and dykes. A recent assessment of river fragmentation concluded that, on average, there was a barrier every 1.3 km in English rivers (Jones et al., 2019); therefore, it can be argued that the Broads system is highly connected on a relative scale. The objectives were to (1) describe the range of population-scale movements of bream within the River Bure wetland study system; (2) assess the influence of the timing and location of tagging, as well as abiotic factors, on bream movement patterns, including on the extent of their vagility and speed of movement; and (3) determine whether the diversity of movement patterns in this system suggests the bream population is comprised of several spatially discrete sub-populations.

2 | METHODS

2.1 | Study area

The focal study area was the River Bure wetland system that forms the northern area of the Broads National Park. This comprises the main River Bure, its two tributaries the rivers Ant and Thurne, plus numerous interconnected small shallow lakes (medieval peat diggings termed *broads*) and dykes (Figure 1). The Bure is 87 km in length, flows south-east towards Breydon Water estuary at Great Yarmouth, and has a mean discharge of 6 m^3/s into the North Sea. The Ant is 27 km in length and the Thurne is 11 km in length. The system is tidal and conductivity can reach 50,000 µS/cm (approx. 37 PSU dependent on water temperature; Fofonoff & Millard, 1983) at Acle (Figure 1), with major saline incursions often occurring during tidal surges and/or low river flows that have led to dramatic fish kills (BBC, 2014).

The River Bure study system encompassed approximately 60 km of river length (not including lateral connections; Figure 1) and was divided into four reaches, with differing habitats and saline influence: Upper Bure, Lower Bure, River Ant, and River Thurne (Table 1). The upper limit of saline incursion on the River Bure (Horning, Figure 1; Clarke, 1990) provided the boundary between the Upper Bure and the Lower Bure reaches. Bream spawning has been observed at Hoveton Great Broad in the Upper Bure reach (Figure 1), but probably also occurs elsewhere in the catchment. Channel widths across the upper limits of the study area are approximately 25 m wide with depths to 1.5 m, while in the lower reaches they increase to >40 m, with depths of 3–5 m.

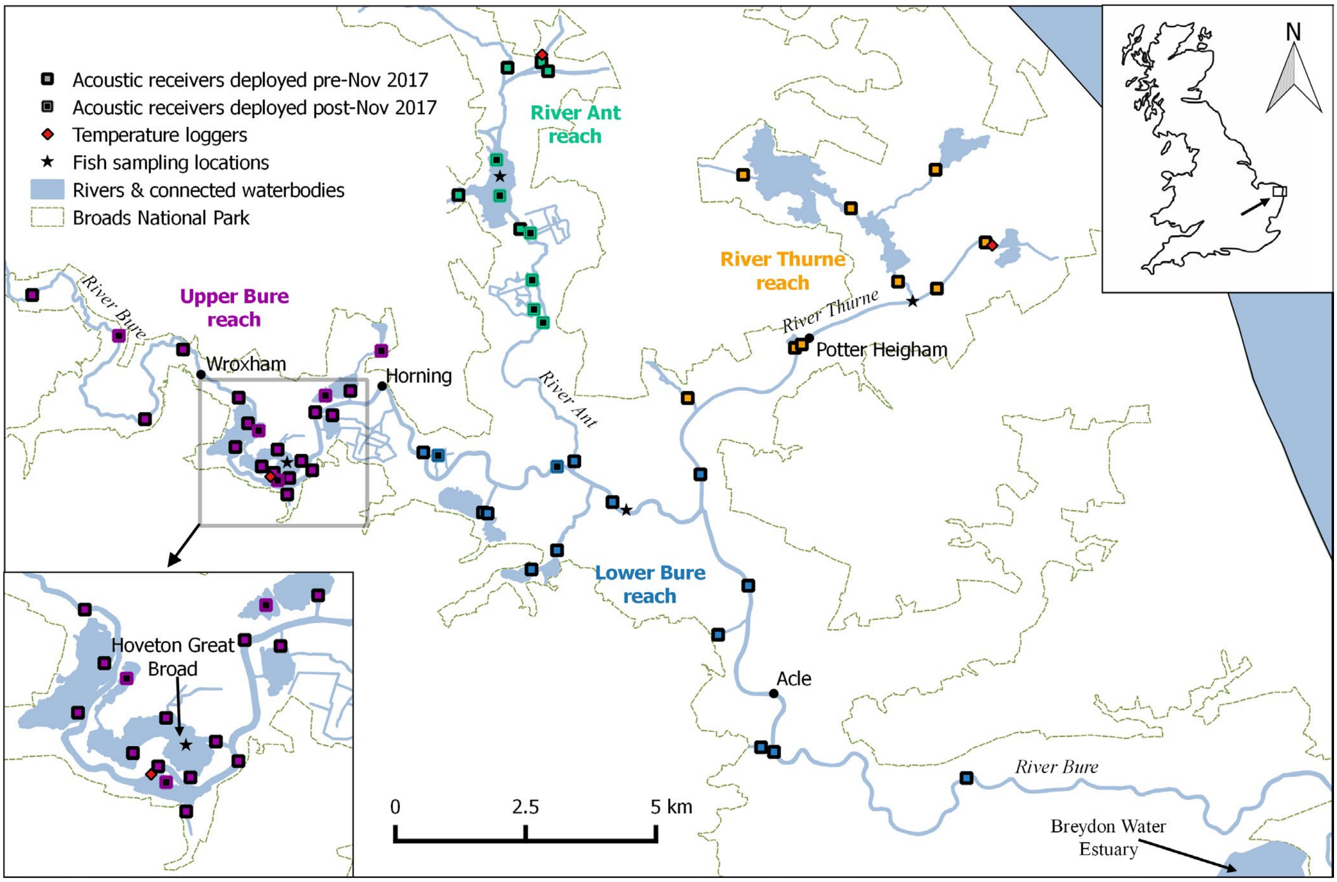

FIGURE 1 Map of the River Bure study system within the Broads National Park, showing the locations of acoustic receivers according to river reach (Upper Bure = purple; Lower Bure = blue; Ant = green; Thurne = orange) and date of deployment. General fish sampling locations, temperature loggers and points of interest are also shown [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Details of the predominant habitat, saline influence, and other impacts to fishes in the four reaches of the study system

Reach	Predominant habitat	Urbanised areas	Saline influence	Other impacts
Upper Bure	Banks of wet woodland (alder carr), small patches of reedbed. High density of laterally connected broads and dyke systems	Wroxham	Low	Potential future loss of lateral connectivity (Environment Agency, 2020)
Lower Bure	Semi-artificial landscape of open, reed-fringed grazing marshes	Horning	Medium–high (Clarke, 1990)	N/A
River Ant	Banks of wet woodland (alder carr), small patches of reedbed. Extensive marsh dyke systems	N/A	Low	N/A
River Thurne	Open marshland, abundant areas of reedbed. Features highest abundance and species richness of aquatic macrophytes (Broads Authority, 2019)	Potter Heigham	Medium–high (Pallis, 1911)	Blooms of toxic *Prymnesium parvum* (Holdway et al., 1978)

TABLE 2 Details of common bream sampling locations, tagging dates, and acoustic tracking duration by group in the River Bure study system

Group name	Sampling location	Tagging date(s)	Length (mm)	Tracking duration (days)	*N*
UB-1	Upper Bure	6 Nov 2017–8 Nov 2017	374–491 (435 ± 28)	0–725 (217 ± 198)	26
LB-1	Lower Bure	8 Nov 2017–9 Nov 2017	286–471 (362 ± 70)	25–524 (181 ± 173)	8
TH	Thurne	14 Jan 2018	341–471 (394 ± 32)	40–371 (132 ± 80)	17
AN	Ant	27 Jan 2018–29 Jan 2018	362–502 (406 ± 34)	28–645 (286 ± 235)	25
UB-2	Upper Bure	20 Apr 2018–23 Apr 2018	313–527 (413 ± 44)	18–562 (414 ± 217)	62
LB-2	Lower Bure	15 Sep 2018–18 Sep 2018	290–503 (389 ± 54)	2–414 (177 ± 147)	43

Note: Length and tracking duration are represented by the range of values, with mean ± *SD* in parentheses.

2.2 | Fish sampling and acoustic telemetry

A total of 181 fish were captured and tagged between November 2017 and September 2018, resulting in six distinct groups of tagged fish that varied by the date and location of tagging (Table 2). Due to heavy boat traffic and the inefficiency of general fish sampling methods (e.g. electric fishing, seine netting, fyke netting) in these large, open waterbodies (Radinger et al., 2019), all fish were captured by rod and line angling, where methods generally focused on fishing using swim-feeders containing groundbait mixes, with worms and/or maggots on the hook. Angling was conducted by boat and occurred at multiple sites within the four general fish sampling locations (Table 2; Figure 1). Anglers were predominantly active during the night and fish were held in keep cages and/or aerated tanks prior to their processing and tagging. No fish was held for more than 12 hr before their processing and release.

The tagging procedure initially involved the fish being measured (fork length; ±1 mm) and, where possible, sexed. Sex was determined by assessing secondary sexual characteristics, such as body shape and the presence of spawning tubercles on the head, where the latter indicates a male fish (Poncin et al., 2011). These features are most pronounced in bream close to their reproductive period, but may also be evident at other times of the year. Consequently, sex determination was considered most reliable for bream sampled just prior to spawning (Group UB-2; Table 2). Under general anaesthesia (Tricaine methanesulfonate, MS-222), each fish measuring ≥286 mm was then surgically implanted with an internal acoustic transmitter (*tag*) sourced either from Vemco (V13: length 36 mm × diameter 13 mm, 6.0 g mass in water, *N* = 148; V9: length 27.5 mm × diameter 9 mm, 2.7 g mass in water, *N* = 9) or Thelma Biotel (ID-LP13: length 28 mm × diameter 13 mm, 5.5 g mass in water, *N* = 24). Acoustic tags operated at 69 kHz and pulsed randomly every 60–120 s, ensuring that adjacent signals did not continuously overlap and cause interference. Tags were inserted ventrally and anterior to the pelvic fins and incisions were closed with a single suture and wound sealer. As this surgical process was completed quickly (<3 min), water was not supplied over the fish gills. Following their return to normal body orientation and swimming behaviour in oxygenated tanks, the fish were released close to their capture location. The movements of the tagged fish were then monitored within an array of receivers for up to 2 years (to 5 November

2019). All surgical techniques were completed under the U.K. Home Office project licence 70/8063 and after ethical review.

A fixed array of 43 acoustic receivers (Vemco, VR2W) was installed throughout the study system (Figure 1) in October 2017, prior to the first fish sampling and tagging event. A further 13 receivers were deployed in January 2018 ($N = 1$) and in March 2019 ($N = 12$) to expand the monitored area (Figure 1). Receivers situated in the mouths of the Rivers Ant and Thurne tributaries were categorised as *Lower Bure* due to their proximity to the Lower Bure reach (Figure 1). Receivers were placed in the channel margins at approximately mid-water depth (1–2 m). Data were downloaded every 3 months, while batteries were replaced annually. Detection range was highly variable according to local environmental conditions, but rarely fell below channel width distance (Winter et al., 2021). Distance measurements between receivers represented the mid-channel circuitous river length.

2.3 | Environmental data

Water temperature (±0.5°C) was recorded at hourly intervals by three data loggers (HOBO® Pendant; model MX2202, Onset Computer Corporation; Figure 1). Water temperatures recorded between 9 August 2018 and 7 November 2019 in the River Bure were highly correlated with those in the Rivers Ant and Thurne ($r > 0.99$ and $p < 0.001$ for all pairwise comparisons). Consequently, only River Bure temperature data were used in further analyses. Conductivity and river level data, recorded at 15-min intervals at Acle (Figure 1), were sourced from the Environment Agency. These data were offset by 30 min to account for the time difference between high tide at Acle and Horning/Potter Heigham (Figure 1).

2.4 | Data and statistical analyses

Movement data were initially explored and visualised using the package *actel* (Flávio, 2020) in R 4.0.2 (R Core Team, 2020), which enabled calculation of the daily number of bream from each group present in each reach, providing descriptive information on their general movement and reach occupancy patterns. Although the recovery of bream following acoustic tagging can be rapid (Le Pichon et al., 2015), all data collected in the first 7 days following tagging were excluded from analyses (in case the fish were demonstrating abnormal behaviours). Data were also excluded from stationary tags, which occurred due to fish death or tag expulsion within range of an acoustic receiver (Winter et al., 2021). The *seasonal range* of each fish in each season was estimated as the distance (in river km) between the furthest upstream and furthest downstream detections, and where this included two or more rivers, the distances were summed. Laterally connected lakes and dykes were not included in range estimates. A linear mixed-effects model tested the effect of season and group on fish range, with fish ID included as a random effect. Use of the *nlme* package (Pinheiro et al., 2020) enabled calculation of *p*-values.

Continuous-time multistate Markov models (CTMMs) then analysed fish movements between the reaches using the package *msm* (Jackson, 2011). CTMMs assessed the instantaneous rate of transition (i.e. the movement of fish) between discrete spatial states (reaches) in continuous time, whilst allowing for time-constant and time-dependent explanatory variables (Jackson, 2011). This relied on the Markov assumption that transition rate was dependent only on the current state and was independent of the movement history of an individual fish or the time it spent in previous states. Correspondingly, this meant that the staggered-entry of fish into the study (i.e. from the six discrete tagging events with different sampling dates) did not require left-censorship (whereby spatial states of the fish prior to tagging would be accommodated into the model). Incorporating movement history using second-, third- or X-order CTMMs impeded model convergence but was instead accommodated using the Group categorical variable (see below). Fish that were not detected within 3 months of the study end date were considered deceased or lost from the study and entered a *Lost* absorbing state within the model, immediately following their final acoustic detection. While the river reaches represented the discrete spatial states, the Ant and Thurne reaches were combined to aid model convergence. The previous descriptive information on reach occupancy compensated for this loss of accuracy in the model. The resulting states were *Upper Bure*, *Lower Bure*, *Tributaries*, and *Lost*. The time variable represented the number of days since the start of the study.

The time-constant covariates tested were fish length and sample group, while the time-dependent covariates tested were water temperature, conductivity, river level, tidal phase (high, ebb, low, flood), time of day (day, night), season, and year. Sex determination for 11 bream was considered unreliable and univariate CTMMs run on the reduced dataset did not always converge (Table S1), and so the covariate *sex* was excluded from this analysis. Detection data for CTMMs were converted into hourly records of fish locations (i.e. states) and combined with the corresponding environmental conditions for each time step (hourly means where necessary). Time of day was classified for each observation according to sunset and sunrise times for the study area, which were extracted from the package *suncalc* (Thieurmel & Elmarhraoui, 2019). Season was defined as: spring (1 March–31 May); summer (1 June–31 August); autumn (1 September–30 November); and winter (1 December to 28 February). Covariate effects (β) were explored only for movements between the river reaches and not for transitions between the reaches and the *Lost* state (see Winter et al., 2020 for an analysis of bream post-tagging survival). Hazard ratios (HR; $\exp(\beta)$) indicated the strength of covariate effects; $\text{HR} < 1$ indicated a negative effect, $\text{HR} = 1$ was no effect, and $\text{HR} > 1$ indicated a positive effect. The effect was considered significant if 95% confidence intervals (CI) did not overlap 1.0, or for categorical covariates, if the CIs did not overlap (Spruance et al., 2004).

The mean residency in each reach, plus the expected number of visits to each reach prior to transition into the *Lost* state, were calculated from the best-fitting CTMM. Selection of the best-fitting model followed the minimisation of Akaike information criterion (AIC) values, with models exhibiting ΔAIC ≤ 2 also awarded strong support, provided they were parsimonious (Burnham & Anderson, 2002; Richards et al., 2011). Initially, covariates were parameterised separately in univariate models, with those resulting in reduced AIC compared in multivariate models. Models containing both fish length and sample group as covariates were disregarded due to length differing significantly by group (ANOVA: $F_{5,175} = 5.71$, $p < 0.001$). Similarly, a significant relationship between some environmental variables and seasonality meant that they were not modelled together (Time of day ~season, $\chi^2_{(3,17,496)} = 883$, $p < 0.001$; ANOVA: Temperature ~season, $F_{3,17,492} = 17{,}123$, $p < 0.001$; Conductivity ~season, $F_{3,17,492} = 659$, $p < 0.001$; River level ~season, $F_{3,17,492} = 1{,}002$, $p < 0.001$). Where interdependencies arose, only the covariates resulting in the greatest reduction in AIC were retained for further comparison in multivariate models (Table 3).

The package *actel* (Flávio, 2020) also facilitated examination of the speed of movement for fish moving between reaches. Generalised additive mixed models were applied to testing the effect of fish length, sex, sample group, day of year (DOY; Julian day, representing seasonality), year, and route (i.e. between which reaches, irrespective of direction) on the speed of movement using the *gamm4* package (Wood & Scheipl, 2020). This was performed through the uGamm wrapper function from the package *MuMIn* (Barton, 2020) to allow automatic multi-model inference based on corrected AIC values. The data required a Gaussian family structure and identity link function, with a random effect of fish ID accounting for between-individual variation. A non-linear effect of DOY was modelled using a cyclic cubic regression spline as a smoothing function. The degrees of freedom of the smooth term were limited to a maximum of 3 to avoid overfitting. As above, fish length and sample group were not modelled together. Generalised additive mixed models incorporating and comparing the effects of fish sex were performed on reduced datasets due to missing data (as described above). Analysis of residual plots ensured model adequacy.

TABLE 3 The combinations of covariates tested in CTMM models that examined rate of movement of common bream between reaches in the River Bure study system

Model	ΔAIC
~ Group + Season + Tidal phase + Year	0.00
~ Group + Season + Tidal phase	25.51
~ Group + Season + Year	27.00
~ Group + Season	52.52
~ Group + Tidal phase + Year	250.75
~ Group + Tidal phase	255.95
~ Group + Year	277.74
~ Group	282.76
~ Season + Year + Tidal phase	442.56
~ Season + Year	469.47
~ Fish length[a]	472.27
~ Season + Tidal phase	476.25
~ Season	502.96
~ Light[a]	690.99
~ Tidal phase + Year	699.92
~ Temperature[a]	700.93
~ Tidal phase	710.70
~ Conductivity[a]	711.02
~ Year	726.80
~ River level[a]	727.77
~ Null	737.63

Note: Models are ordered by Akaike information criterion (AIC) values.
[a] Covariates not compared in multivariate models due to interdependency with another covariate exhibiting higher explanatory power.

3 | RESULTS

3.1 | Spatial occupancy by sampling group and river reach

The 181 tagged bream were tracked for between 0 and 725 days (Table 2). Eight fish were removed from further analyses due to tracking durations of less than 7 days. Of the remaining fish used in analyses, 116 transitioned to the *Lost* state during the study period (of which 2 bream emigrated from the monitored area), while 57 were detected within 3 months of the study end-date and therefore considered *living* at the end of the study. The loss rate was considered higher than expected from natural mortality alone; however, evidence suggested that acoustic tag expulsion contributed to the loss of some bream from the study (Winter et al., 2020). Bream were recorded at 53 of the 56 acoustic receivers in the study area, including all receivers placed in the mainstem Bure, Ant, and Thurne across approximately 60 km of river length (Figure 1). The seasonal range of individual fish varied from 0 (detected at only one receiver) to 26.7 km, being significantly largest during spring and greatest for bream from Group TH (Figure 2; Table 4). Example trajectories of individual fish are provided in Figure S1.

Bream from groups UB-1 and AN remained predominantly in their respective sampling reaches throughout the study and none of these fish were ever recorded in the River Thurne (Figure 3 and Figure S1). LB-1 and LB-2 bream had similar reach occupancy profiles, with the highest daily abundance in the Lower Bure reach, but with some overwintering presence in the River Thurne, and to a lesser extent the River Ant (Figure 3). The profile of the TH group indicated their fidelity to the River Thurne in summer and winter, but not in their spring spawning period when they moved mainly into the Upper Bure reach (Figure 3 and Video S1). This pattern was similar in a subset of UB-2 fish (24%); whilst they had been tagged in the Upper Bure in spring, they were then largely resident in the Thurne during summer and winter (Figure 3 and Figure S1). However, a large

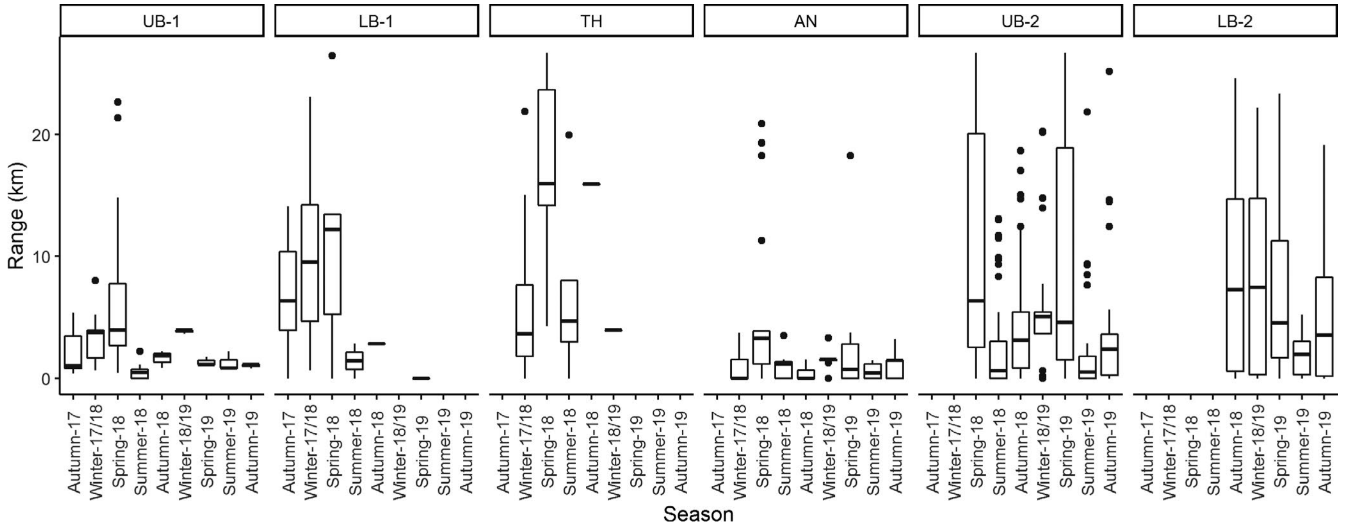

FIGURE 2 Seasonal range of common bream in the River Bure study system according to their tagging group and season

TABLE 4 Results of the linear mixed model predicting the fixed effects of group and season on the seasonal range of bream

Covariate	Estimate	t Value	p
(Intercept)	6.94 ± 0.98	7.05	<0.001
Season: Summer	−6.80 ± 0.58	−11.38	<0.001
Season: Autumn	−4.38 ± 0.55	−7.96	<0.001
Season: Winter	−3.81 ± 0.57	−6.66	<0.001
Group: LB-1	4.19 ± 1.88	2.23	0.027
Group: TH	6.33 ± 1.52	4.17	<0.001
Group: AN	−1.89 ± 1.33	−1.42	0.16
Group: UB-2	2.53 ± 1.09	2.33	0.02
Group: LB-2	4.33 ± 1.22	3.55	<0.001

Note: 'Spring' and 'UB-1' are represented by the intercept.

proportion of UB-2 fish (47%) remained resident in the Upper Bure throughout the study period, with the remaining proportion (29%) utilising the Lower Bure at various times of the year (Figure 3 and Figure S1). No fish from groups TH or UB-2 entered the River Ant during the study period. Furthermore, the reach occupancy profiles revealed almost no active fish from any of the groups were present in the River Thurne during the period of peak spawning activity.

3.2 | Continuous-time multistate Markov modelling of movement rates

The best-fitting CTMM describing the movements of 173 bream between river reaches retained tagging group, season, tidal phase, and year as explanatory variables (Tables 3, 5, 6). No other combinations of covariates had strong support under the selection criteria.

The effect of group revealed that bream in UB-1 and UB-2 had the lowest rates of transition from the Upper Bure to Lower Bure, while bream in LB-1 and LB-2 had the highest (Table 5). For movements from the Lower to Upper Bure, fish in UB-1 transitioned at a significantly higher rate than LB-1 and LB-2, suggesting fish tended to move more readily towards their tagging locations. The rate of upstream movement from the Lower Bure into the Tributaries was not significantly affected by group, although AN fish had a lower rate of downstream movement from the Tributaries into the Lower Bure than bream from UB-1 and LB-1 (Table 5). For the effect of season, transition rates between all reaches and in all directions were significantly higher in spring than in all other seasons, except for movements from the Lower Bure into the Tributaries, which occurred at a significantly higher rate during winter (Table 5). This is in line with results of the LMM showing that seasonal range was highest during spring (Figure 2; Table 4). In addition, upstream and downstream movements between the Upper and Lower Bure were significantly more frequent during winter than during summer.

The effect of tidal cycle revealed that downstream movements of fish from the Upper to the Lower Bure occurred at a significantly lower rate during a flooding (incoming) tide, while the rate of upstream movement from the Lower Bure into the Tributaries was significantly greater during a flooding tide. Furthermore, a high tide increased the rate of upstream movement from the Lower to the Upper Bure but decreased the rate of downstream movement from the Tributaries to the Lower Bure. The second year of study was associated with a *c*. 60% reduction in the rates of downstream movement between the Upper and Lower Bure, and upstream movement between the Lower Bure and Tributaries.

3.3 | Residency, number of visits per reach, and speed of movement

For all groups except UB-2, tagged bream were predicted to spend the longest time in their respective sampling reaches, with this particularly evident for groups UB-1 and AN, where average residency exceeded 150 days (Table 6). On average, UB-2 fish spent a similar amount of time in the Upper Bure and Tributaries reaches,

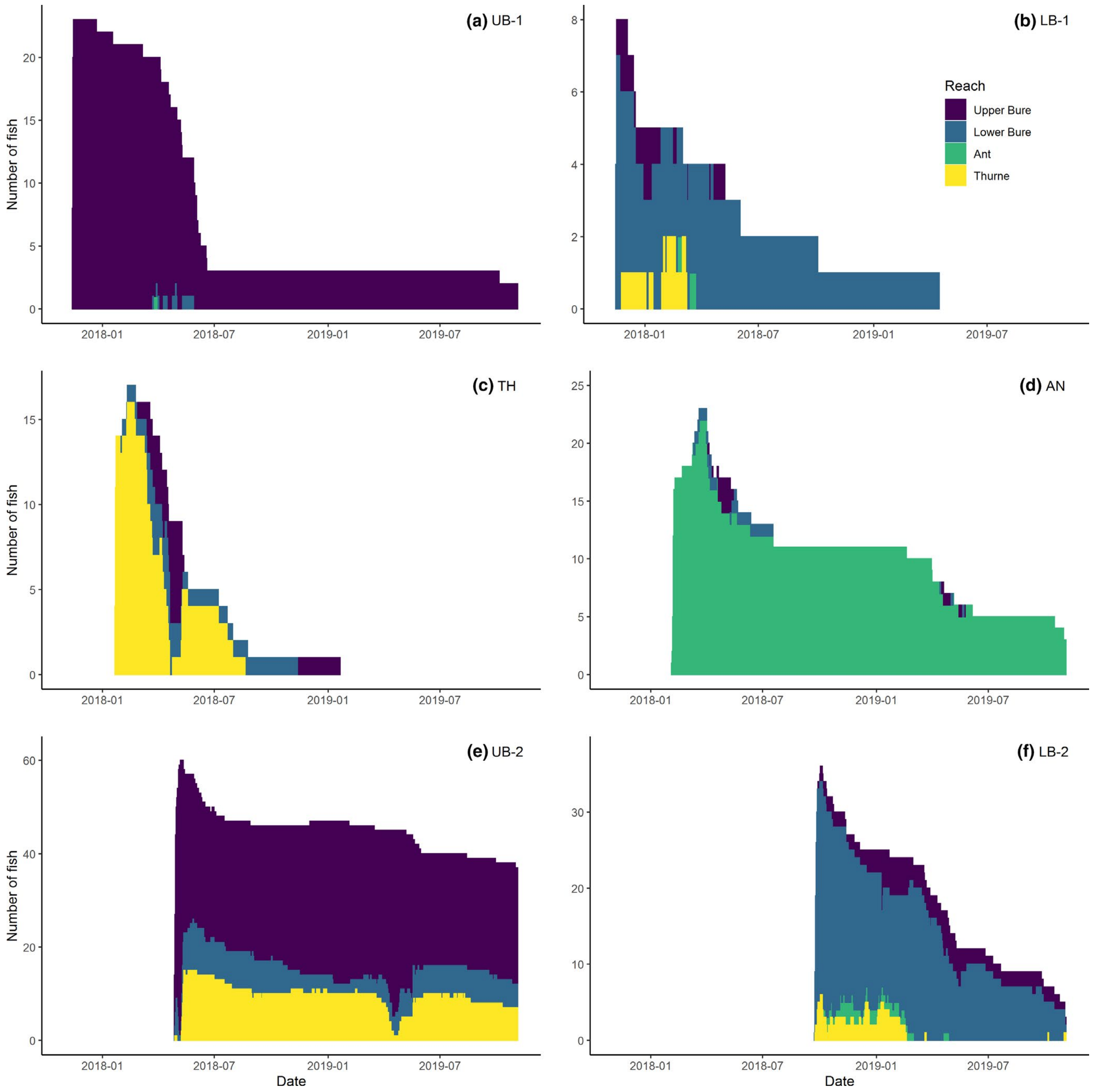

FIGURE 3 Occupancy profiles of common bream in the reaches of the River Bure study system according to tagging group [Colour figure can be viewed at wileyonlinelibrary.com]

which reflects the partially migratory nature of this group. Across the groups sampled outside the Upper Bure, TH spent the longest in the Upper Bure (20 days), but this was only significantly different to LB-2. Bream from UB-1 and AN had fewer visits to each reach than bream in UB-2, LB-1, LB-2, and TH, indicating lower levels of migratory activity (Table 6).

The best-fitting model predicting speed of movement between reaches retained an effect of route as well as a nonlinear effect of DOY (Table 7; Figure 4). Bream travelled significantly faster (by 0.10–0.13 m/s) when moving between the Thurne and Lower Bure reaches than between the Upper and Lower Bure or between the Ant and Lower Bure. In addition, speed of movement peaked during spring at Day 115 (25 April). A random effect of fish ID accounted for 39% of the residual variation. No other combinations of covariates were retained under the selection criteria.

4 | DISCUSSION

Acoustic telemetry revealed that the movement behaviour of bream in this highly connected wetland system varied considerably between the tagging groups, but was largely consistent within them,

TABLE 5 Hazard ratio estimates from the best-fitting continuous-time multi-state Markov models, indicating the covariate effects on the transition rates of common bream between reaches in the River Bure study system

	Movement/transition			
Covariate	**Upper Bure > Lower Bure**	**Lower Bure > Upper Bure**	**Lower Bure > Tributaries**	**Tributaries > Lower Bure**
Group				
UB-2	**7.44 (3.16, 17.51)**	0.58 (0.20, 1.70)	2.45 (0.33, 18.19)	0.19 (0.02, 1.74)
LB-1	**50.95 (17.13, 151.56)**	**0.14 (0.04, 0.48)**	0.64 (0.08, 4.89)	2.64 (0.28, 24.54)
LB-2	**51.36 (19.65, 134.21)**	**0.16 (0.05, 0.49)**	0.90 (0.12, 6.81)	1.50 (0.16, 14.28)
TH	**14.05 (5.10, 38.66)**	0.47 (0.15, 1.49)	2.27 (0.30, 17.09)	0.25 (0.03, 2.27)
AN	**34.61 (11.60, 103.29)**	1.22 (0.37, 4.11)	4.54 (0.57, 36.36)	**0.02 (0.002, 0.22)**
Season				
Summer	**0.06 (0.02, 0.15)**	**0.07 (0.03, 0.16)**	**0.23 (0.13, 0.39)**	**0.42 (0.24, 0.73)**
Autumn	**0.18 (0.10, 0.32)**	**0.35 (0.22, 0.56)**	**0.40 (0.25, 0.65)**	**0.28 (0.16, 0.49)**
Winter	**0.29 (0.17, 0.50)**	**0.53 (0.31, 0.91)**	**2.38 (1.58, 3.60)**	**0.49 (0.32, 0.76)**
Tidal phase				
Flood	**0.55 (0.37, 0.81)**	1.20 (0.79, 1.81)	**1.88 (1.35, 2.62)**	0.71 (0.50, 1.01)
High	0.65 (0.33, 1.30)	**2.79 (1.67, 4.64)**	1.10 (0.58, 2.09)	**0.40 (0.18, 0.93)**
Low	**0.43 (0.19, 0.99)**	1.64 (0.88, 3.03)	1.00 (0.51, 1.95)	1.02 (0.59, 1.76)
Year				
Year 2	**0.40 (0.25, 0.62)**	0.85 (0.54, 1.34)	**0.41 (0.26, 0.63)**	1.10 (0.68, 1.77)

Note: Effects are compared to baseline covariate values (Group = UB-1; Season = Spring; Tidal phase = Ebb; Year = Year 1). 95% confidence intervals are in parentheses and significant effects are in bold.

TABLE 6 Metrics calculated from the best-fitting continuous-time multi-state Markov model, showing mean residency of common bream and the expected number of visits to each river reach in the River Bure study system prior to a fish transitioning into the *Lost* state

	Reach		
Group	**Upper Bure**	**Lower Bure**	**Tributaries (Ant/Thurne)**
Mean residency (days)			
UB-1	198.12 (112.43–349.13)	10.87 (4.53–26.04)	7.99 (0.96–66.12)
LB-1	5.62 (2.56–12.37)	41.20 (27.36–62.04)	3.08 (1.77–5.34)
TH	19.94 (10.78–36.85)	13.17 (8.91–19.46)	29.66 (19.64–44.80)
AN	8.25 (3.91–17.37)	5.90 (3.56–9.80)	168.60 (118.13–240.65)
UB-2	36.63 (25.83–51.93)	11.49 (8.32–15.88)	38.22 (23.92–61.09)
LB-2	5.58 (3.13–9.97)	33.45 (23.06–48.52)	5.36 (2.87–10.00)
Expected number of visits			
UB-1	1.87	2.41	0.45
LB-1	2.93	7.14	3.27
TH	4.08	9.27	4.80
AN	1.86	3.61	1.67
UB-2	3.62	7.63	3.74
LB-2	3.14	8.38	4.35

Note: 95% confidence intervals are in parentheses. Estimates are presented for different values of the covariate *Group* (with tagging location in parentheses), while other covariate values were set to zero.

except for the fish tagged just prior to their spawning period. For fish tagged close to the spawning period, their movement behaviours were more divergent, including both year-round Upper Bure residents and migrants that predominantly resided in the brackish River Thurne, approximately 25 km away. Migratory behaviour in the latter group was characterised by a return movement between the Thurne and Upper Bure reaches during the reproductive period. These results suggest the bream population comprised several

TABLE 7 Results of the best-fitting generalised additive mixed model predicting the speed of movement of common bream between the reaches of the River Bure study system

	Estimate coefficient	*t* Value	*p*	Estimate *df*	*F* value	*p*
(Intercept)	0.227 ± 0.012	18.73	<0.001			
Route: Ant–Lower Bure	−0.036 ± 0.031	−1.16	0.25			
Route: Thurne–Lower Bure	0.097 ± 0.015	6.51	<0.001			
s(DOY)				1.81	555.9	<0.001

Note: The Upper Bure–Lower Bure route is represented by the intercept. Error margins are *SE*.

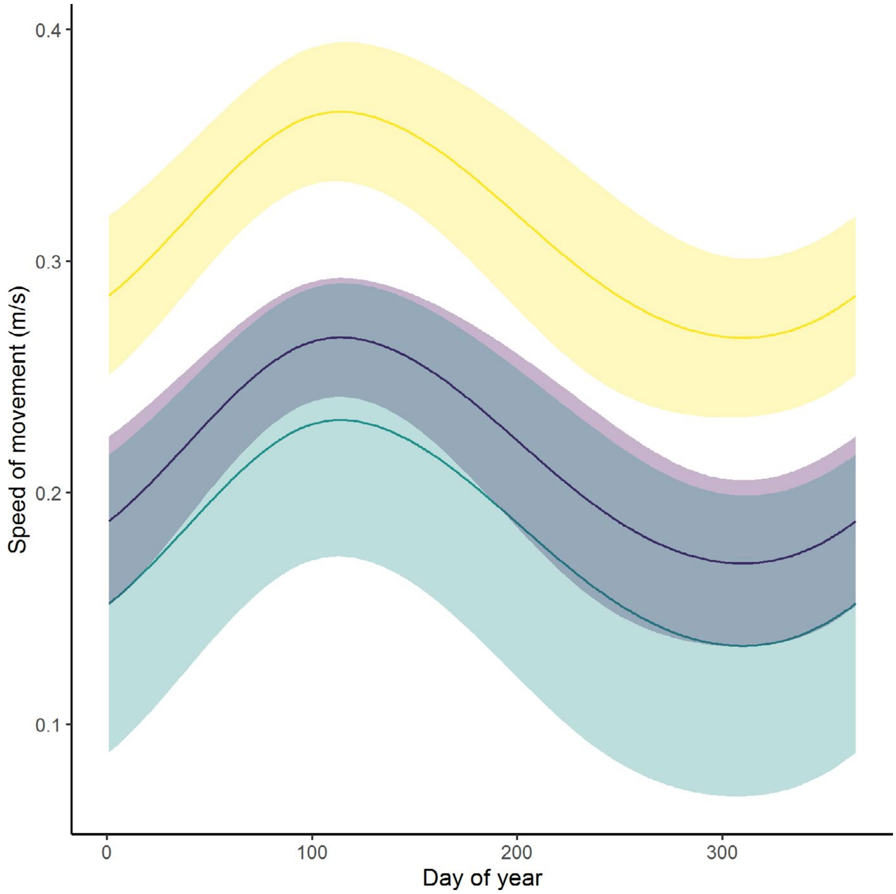

FIGURE 4 Predicted speed of movement of common bream between reaches of the River Bure study system as a function of day of year (Julian day) and travel route (purple = Upper Bure–Lower Bure; blue = Ant–Lower Bure; yellow = Thurne–Lower Bure) according to the best-fitting generalised additive mixed model. Shaded areas represent 95% confidence intervals. Random effect uncertainty is not accounted for [Colour figure can be viewed at wileyonlinelibrary.com]

semi-independent subpopulations that resided in spatially distinct areas outside of the annual spawning period, with the population as a whole exhibiting partial migration. Furthermore, bream tagged in the River Ant appeared to be more reproductively isolated, with limited exchanges of fish between this reach and the rest of the system during the spawning period.

These spatial differences in bream occupancy outside of the spawning season could relate to the brackish areas (such as the River Thurne and Lower Bure) potentially providing differential feeding opportunities for adult bream (Kafemann et al., 2000). The migration of some adults between these areas and lower salinity reaches probably reduces the population's dependence on more confined spawning/rearing habitats and stabilises the population through diversifying space and resource use. This could be increasingly important in future, given that the study area is already subject to episodes of saline intrusion that are likely to intensify with sea level rise due to climate change, coupled with blooms of toxic *Prymnesium parvum* that lead to fish mortalities (BBC, 2014; Holdway et al., 1978). The system also faces some loss of connectivity in upper reaches in the near future (planned installation of fish barriers at Hoveton Great Broad, Figure 1, Environment Agency, 2020). As such, there is a management requirement to identify how the expression of this phenotypic—and potentially genetic—variation within the bream population can be maintained in both the immediate and long-term future, given that this species supports a nationally important recreational fishery, while the connectivity of the system is important for the functionality of the ecosystem more widely (Blanchet et al., 2020; Thompson et al., 2019).

The study was effective in demonstrating phenotypic diversity in the movement patterns of bream in this system, with some individuals making relatively large movements in spring to access spawning grounds, while others were more limited in the extent of their movements. In respect of this diversity, and a possible link between movement and personality traits (Chapman et al., 2011), the reliance on angling as a capture method for the tagged fish could have potentially biased for the selection of specific behavioural phenotypes that are more susceptible to angler capture (Diaz Pauli et al., 2015). For example, resident fish can have increased spatial encounters with anglers that can increase their vulnerability to capture (Alós et al., 2012). However, responses may be species- and population-specific with, for example, studies on bluegill *Lepomis macrochirus* reporting conflicting results regarding susceptibility of both shy and sociable fish to angling (Louison et al., 2018; Wilson et al., 2011). Moreover, the results here revealed both low and high vagility of individuals, suggesting the tagged fish represented a range of phenotypes that were independent of the sampling method. A minimum fish size constraint for acoustic tagging could have also masked an effect of size on rate of movement, as no fish were tagged below 286 mm. Indeed, in small lake systems, the partial migration of bream into overwintering habitats has been associated with size and predation risk (Skov et al., 2011), and the Norfolk Broads' small dyke systems are typically dominated by juvenile and small-bodied cyprinid fishes (Tomlinson et al., 2010). However, documenting these small-scale movements to/from open water habitats was not the focus of this study and, at a larger scale, predation is considered unlikely to be driving fish movements between river reaches, given that piscivorous birds (e.g. cormorant *Phalacrocorax* spp.), fish (e.g. northern pike *Esox lucius*), and mammals (e.g. otter *Lutra lutra*) are present throughout the system. Finally, while it was shown that some bream that were tagged in the River Thurne and Lower Bure moved into the Upper Bure during the spawning period, it is not currently clear whether these groups of fish then mixed with residents and/or each other on spawning grounds. As such, the extent of gene flow between these sub-populations is currently unknown but represents an important next step to determine.

This study's relatively large sample size (at least compared to other bream studies; Gardner et al., 2013; Le Pichon et al., 2017; Lyons & Lucas, 2002) and continuous tracking for two years revealed both known and undescribed movement behaviours in bream. The results support the finding of Whelan (1983), who described divergent migration in bream in Ireland, where fish aggregated during spawning, before subsequently dispersing into smaller groups with differing migratory tendencies. Partial migration of bream into brackish environments has also been inferred through otolith isotopic chemistry (Kafemann et al., 2000). Seasonality was also important for both rate and speed of movement, which builds on work by Gardner et al. (2013) that identified predictable seasonal shifts of adult bream between mainstem and tributary habitats. The novel finding of a significant effect of tidal phase on movement indicated a tendency for bream to exploit natural flow variations for passive transport, probably to minimise the energetic costs of largescale movements (Taylor & Cooke, 2012). Elsewhere, flooding tides have been linked to increased feeding activity of bream in intertidal habitats (Le Pichon et al., 2017), but it remains unclear whether faster movement between the Thurne and Lower Bure reaches is the result of greater tidal flow in this area or simply represents elevated swimming speeds. It should be noted that the absence of a strong effect of sex on either rate or speed of movement could reflect poor reliability of the sex determination method for fish sampled outside of their reproductive period.

There is increasing evidence from multiple taxa (e.g. birds, mammals, fishes) that divergent migration strategies are an important form of life-history diversity that should be considered within management and conservation initiatives (Gilroy et al., 2016; Thompson et al., 2019; Tucker et al., 2018). In their entirety, these studies suggest that populations of species can no longer be considered as showing one common behavioural pattern but instead comprise groups of individuals that specialise according to their spatial use of the wider habitat. The potential implications of this within freshwater fishery management are far-reaching, with evidence not only informing the spatial scale at which conservation and restoration efforts should be targeted, but also directing the sustainable harvesting of populations (e.g. avoiding the selective capture of certain behavioural phenotypes) and/or guiding the effective manipulation of ecosystems (e.g. biomanipulation of lake systems by removal of fishes; Chapman et al., 2012). Phenotypic variation is key to maintaining species' adaptive potential in spatially and temporally heterogeneous environments (Mimura et al., 2017; Schindler et al., 2010), and may have already been lost from isolated fish populations in fragmented river systems (Thompson et al., 2019). Indeed, individual behavioural flexibility may be the key to species' successful adaptation to climate change and other anthropogenic stressors (Winkler et al., 2014). Furthermore, the suppression of intraspecific diversity through human disturbance potentially decreases the resilience of species to natural and anthropogenic threats, and should not be overlooked regarding models of environmental change (Blanchet et al., 2020; Schindler et al., 2010).

The high connectivity of the River Bure wetland system appears to have encouraged the use of a wide range of spatial resources within the bream population and has resulted in the formation of a series of spatially distinct sub-populations across the wider system. These results emphasise the importance of lateral and longitudinal connectivity, and habitat heterogeneity, for the expression of behavioural variability with respect to space and resource use in potamodromous fishes. They can be used to inform the future management of fish populations, including conserving the phenotypic diversity of migratory behaviours in connected systems, and assisting the restoration of suppressed populations in more fragmented systems.

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AUTHORS' CONTRIBUTIONS

E.W., A.H., S.L., and R.B. conceived the ideas, designed methodology and collected the data; E.W. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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