Dual-isotope isoscapes for predicting the scale of fish movements in lowland rivers

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Abstract. Assessments of patterns of animal movements are important for understanding their spatial ecology. Geostatistical models of stable isotope (SI) landscapes (isoscapes) provide a complementary tool to telemetry for assessing and predicting animal movements, but are rarely applied to riverine species. Often single-isotope gradients in freshwater environments are insufficiently variable to provide high isoscape resolution at relatively fine spatial scales. This is potentially overcome using dual-isotope assignment procedures, and thus, the aim here was to apply single (δ^{13}C) and dual (δ^{13}C and δ^{15}N) isoscapes to assigning riverine fish to origin and predicting their movements. Using the River Bure, England, as the study system, the foraging locations of a small-bodied lowland river fish (roach *Rutilus rutilus*) of low vagility were predicted using their SI data and those of a common prey item (amphipods). These foraging locations were then compared to their capture locations, with the distance between these being their predicted displacement distance. The results indicated significant enrichment of δ^{13}C and δ^{15}N with distance downstream in roach fin tissue and amphipods; roach bivariate isotopic niches were spatially variable, with no niche overlap between upstream and downstream river reaches. Furthermore, the dual-isoscape assignment procedure resulted in the lowest predicted displacement distances for roach, therefore enhancing model performance. The dual-isoscape approach was then applied to determining the predicted displacement distance of individual common bream *Abramis brama*, a larger, more vagile species, with these data then compared against the subsequent spatial extent of their movements recorded by acoustic telemetry. When using a high probability density threshold for isotope assignment, the predicted displacement distance of common bream was a significant predictor of the spatial extent of their subsequent movements recorded by acoustic telemetry, although it was less able to predict the direction of displacement. This first probabilistic assignment to origin for riverine species using a dual-isotope isoscape technique demonstrated that where the required spatial resolution of animal movements in freshwater is moderately broad (5–10 km), dual-isotope isoscapes can provide a reliable alternative or complementary method to telemetry.

Key words: *Abramis brama*; acoustic telemetry; geographic assignment; isotopic landscape; *Rutilus rutilus*; stable isotope ecology.

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INTRODUCTION

Documenting and understanding the scales of animal movements can be inherently challenging, yet inter- and intra-specific variation in movement distances can provide essential information on the availability and utilization of functional habitats (Mayor et al. 2009). While electronic tags provide

the opportunity to directly measure animal movements (Hussey et al. 2015), issues remain regarding their application in the aquatic environment, including the limited battery life of transmitters, the adverse physiological and/or behavioral effects of tagging on individuals, elevated study costs, and the limited detection range of transmitters across broad spatial scales (Brownscombe et al. 2019).

An alternative to telemetry is the inference of movements using intrinsic chemical markers, such as contaminants, inorganic trace elements, and/or isotopes (Hobson and Wassenaar 2008). Individuals acquire distinct chemical profiles according to their geographic location, which can be permanently retained in metabolically inert tissues (e.g., hair, feathers, fish otoliths; Gillanders 2005, Hobson and Wassenaar 2008). When associated with the timescales of exposure, these chemical data can be used to reconstruct animal movements. For example, otolith strontium:calcium (Sr:Ca) ratios are widely used as a proxy for salinity gradients to examine freshwater-marine habitat shifts of fishes (Gillanders 2005, Quinn et al. 2014). Also, in freshwaters, strontium isotope ratios (^{87}Sr:^{86}Sr) are commonly used to classify organisms to a watershed origin due to their association with the underlying geology (Kennedy et al. 2005, Duponchelle et al. 2016).

The chemical profiles of metabolically active tissues, such as muscle, can also provide information regarding an animal's geographic location through their representation of diet over varying timeframes (Hobson and Wassenaar 2008). Typically, the stable isotope ratios of light elements, such as carbon ^{13}C:^{12}C (i.e., δ^{13}C) and nitrogen ^{15}N:^{14}N (i.e., δ^{15}N), are employed as intrinsic markers that reflect geochemistry, as well as trophic dynamics (Peterson and Fry 1987). In fishes, stable isotope analysis (SIA) has utilized a multitude of tissue types, from mucus (Winter et al. 2019) to eye lenses (Wallace et al. 2014), with those sampled nonlethally providing a marked advantage in situations where lethal methods are either not permitted or are undesirable.

The successful application of chemical tracers to inferring animal movements requires detailed knowledge of the specific elemental/isotopic variation in the environment. For stable isotopes (SI), geostatistical models of isotopic landscapes

(isoscapes) can be developed to assign tissue SI values to their most probable geographic source (Vander Zanden et al. 2018). This isotopic tracking technique has been routinely applied to birds (Bowen et al. 2005) and, increasingly, to terrestrial mammals, insects, and marine fauna (Trueman et al. 2012, Voigt et al. 2012, Hobson et al. 2018). However, its use is rare for freshwater species (but see Brennan and Schindler 2017), perhaps due to relatively poor resolution of single isotopes at moderately fine spatial scales. The development of multi-isotope isoscapes has helped overcome this for terrestrial and marine tracking, enabling more spatially explicit predictions of movements and so advancing the geographic assignment process (Hobson et al. 2012, Vander Zanden et al. 2015a). Nevertheless, the use of multi-isotope isoscapes to predict fish movements is rare, with the only example being a dual isoscape (δ^{18}O and δ^{13}C) for assessing Atlantic salmon *Salmo salar* movements in the Baltic Sea (Torniainen et al. 2017).

Within river basins, there tends to be a gradual enrichment in δ^{13}C with distance from the source to sea (Peterson and Fry 1987). This geochemical gradient is reflected in the tissues of locally foraging organisms and has been applied to infer the foraging ranges of fishes using simple regression statistics (Cunjak et al. 2005, Rasmussen et al. 2009, Bertrand et al. 2011). In contrast, δ^{15}N tends to be less spatially variable, although enrichment can occur along salinity gradients (Quinn et al. 2014) and due to disturbance from anthropogenic activities (Harrington et al. 1998, Kennedy et al. 2005). Correspondingly, the combined application of δ^{13}C and δ^{15}N can reveal distinct isotopic niches within freshwater habitats (Kennedy et al. 2005) and these isotopic markers could potentially be used in dual isoscapes for predicting finer scale movements of vagile species.

Isoscape-derived predictions can then be complemented by movement data available from telemetry methods, as demonstrated by Seminoff et al. (2012) in their assessment of movements of leatherback sea turtles *Dermochelys coriacea* in the Pacific Ocean. As recapturing tagged animals can be difficult in many environments, the complementary use of isoscapes and telemetry can be reliant on stable isotope data collected from animals at the time of tagging, providing the

opportunity for testing whether isotope data collected at the time of tagging can be a good predictor of the subsequent movements of individuals (Harrison et al. 2017). This approach assumes sampling and tagging procedures have a minimal effect on the behavior of animals, such that pre- and post-tagging movements are comparable. For fishes, this is reasonable given previous studies have found few long-term behavioral impacts of tagging, including for one of the focal species studied here (Gardner et al. 2015, Hondorp et al. 2015), although comparisons to pure control groups in the wild are rarely logistically feasible (Wilson et al. 2017).

The aim here was to apply isoscape models to predicting the movements of two lowland river fish species. Firstly, single-isoscape ($\delta^{13}C$) and dual-isoscape ($\delta^{13}C$ and $\delta^{15}N$) models predicted the foraging locations of a small-bodied lowland river fish of relatively low vagility, based on their SI data and that of a common prey resource. Post hoc measurements of the predicted displacement distance to capture location were used to assess model performance. The dual-isoscape models were then applied to predicting the foraging locations of a larger-bodied species of relatively high vagility in the same system. As these fish were sampled nonlethally for their SI data, the predicted displacement distances to capture locations were then compared with their actual movements, as detected using acoustic telemetry over a 12-month post-sampling period. Thus, these data also enabled evaluation of the extent to which SI data collected at the time of tagging predict the spatial extent of subsequent fish movements.

METHODS

Study species

Roach (*Rutilus rutilus*), a common lowland river fish of the Cyprinidae family found across Eurasia, that rarely exceeds lengths of 300 mm (Tarkan and Vilizzi 2015, Ruiz-Navarro et al. 2016), was the small-bodied fish of relatively low vagility used in the study. The larger-bodied fish was common bream (*Abramis brama*), a cyprinid that has a similar natural range to roach, but with individuals regularly attaining lengths >450 mm (Lyons and Lucas 2002). Although zooplanktivorus in juvenile life stages, the diets

of riverine populations of both fishes tend to be dominated by macro-invertebrates as their body size increases (Persson and Brönmark 2002, Hjelm et al. 2003). For roach, other than during spawning in spring when populations can move considerable distances to spawning grounds, the spatial extent of habitat use rarely exceeds 5 km (Baade and Fredrich 1998). By contrast, common bream are more vagile, performing both spawning and seasonal habitat shifts of up to 60 km (Whelan 1983, Gardner et al. 2013).

Study system

The study system was the River Bure in eastern England. It is 87 km in length, flows south-east toward Breydon Water estuary at Great Yarmouth, and has a mean discharge of 6 m^3/s into the North Sea (Fig. 1). The Bure and its tributaries, the Rivers Ant and Thurne, form the northern area of the Broads National Park, a wetland of significant ecological importance (Natural England 2020; Fig. 1). The area is characterized by multiple small shallow lakes termed Broads (medieval peat diggings) <40 ha in size. As the landscape is generally flat, the catchment is tidal for approximately 45 km inland, with water levels fluctuating daily by about 10 cm toward the upstream limit of the study area (Fig. 1). At Acle, approximately 18 km from the river mouth (Fig. 1), conductivity (as a measure of salinity) can fluctuate between 1000 and 50,000 µS/cm, with major saline incursions occurring during tidal surges and/or low flows, generally in winter (Clarke 1990). As the upper limit of saline incursion is believed to be at Horning (Fig. 1; Clarke 1990), this location was used as the boundary between the upper (minimal saline influence) and lower (stronger saline influence) river reaches within the study area. The upper river reach was approximately 25 m wide with depths to 1.5 m, while in the lower reach, channel widths increased to >40 m, with depths of 3–5 m. Depths of the connected lakes were typically ~1.5 m and did not exceed 3 m. Across the two reaches, the fish assemblage has limited diversity, being dominated by roach and common bream.

A fixed array of 36 acoustic receivers (VR2W; Vemco, Halifax, Nova Scotia, Canada) was installed throughout the River Bure prior to fish sampling. These were distributed over 37 km of
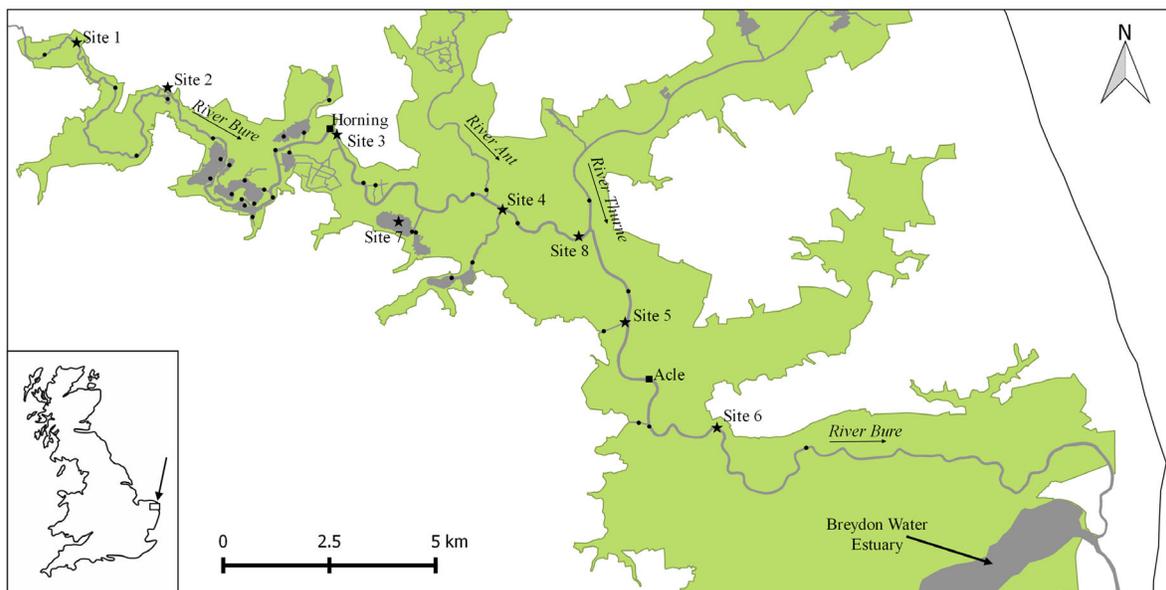
Fig. 1. Map of the River Bure study system, eastern England, showing sample sites (stars), points of interest (squares), and locations of acoustic telemetry receivers (circles). The boundary between the upper and lower river reaches is at Horning. The area of the Broads National Park is shaded green. All waterways pictured are tidal. Channel width not to scale.

main river channel and associated off-channel habitats (Fig. 1), and continuously monitored fish movements for the duration of the study. Receivers were placed in the channel margins at approximately mid-water depth. Detection ranges were variable, dependent on environmental conditions (Winter et al., *in press*), however very rarely fell below channel width distance.

Fish sampling and acoustic tagging

The sampling period was 11 September–3 October 2018, toward the end of the summer growth season for both fishes in the river. Roach and their putative prey resources were sampled across two sites in the upper river reach (sites 1 and 2) and four sites in the lower reach (sites 3–6; Fig. 1). Roach sample sizes were a minimum of nine fish per site ($N = 60$). In addition, 19 common bream were sampled from three sites in the lower river reach (sites 4, 7, and 8; Fig. 1). Due to heavy boat traffic, sampling by typical fish capture methods (e.g., electric fishing, seine netting) was not feasible and angling was used as an alternative. All captured fish were identified to species, measured (fork length, nearest mm) and

a biopsy of the pelvic fin taken and frozen for storage. Captured roach were of lengths 85–223 mm (mean ± standard deviation [SD] = 145 ± 32 mm) and common bream 321–503 mm (mean ± SD = 411 ± 47 mm). At these sizes, the diet of both fishes tends to focus on macro-invertebrates, including amphipods (Persson and Brönmark 2002, Hjelm et al. 2003). Amphipods also dominated samples of macro-invertebrates collected from littoral habitats, including the invasive *Dikerogammarus villosus*. Thus, amphipods were used as the putative prey of both fishes in subsequent analyses.

The sampled common bream were then surgically implanted with internal acoustic tags, sourced from Vemco (V13; 69 kHz; length 36 mm × diameter 13 mm; 6.0 g weight in water; random transmission interval around 120 s; estimated battery life 1200 d; $N = 11$) and Thelma Biotel (ID-LP13; 69 kHz; length 28 mm × diameter 13 mm; 5.5 g weight in water; random transmission interval around 120 s; estimated battery life 1400 d; $N = 8$). Surgical instruments were disinfected in iodine solution prior to each procedure, and fish scales were

removed from the incision site to aid scalpel and suture entry. Tags were inserted ventrally and anterior to the pelvic fins, and incisions were closed with a single suture and wound sealer. All regulated procedures were performed, while the fish were under general anesthesia (tricaine methanesulfonate, MS-222), according to the UK Home Office license 70/8063 and after ethical review. All fish were returned alive to the river following their postoperative recovery and return to normal behavior.

Stable isotope analysis

Fish and amphipod samples were rinsed in distilled water, dried at 60°C to constant weight, and then analyzed for $\delta^{13}C$ and $\delta^{15}N$ (‰) at the Cornell University Stable Isotope Laboratory, New York, USA, where they were ground to powder and weighed precisely to 1000 μg in tin capsules. The samples were analyzed on a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA) interfaced to a NC2500 elemental analyzer (CE Elantech, Lakewood, New Jersey, USA). The equipment was verified for accuracy against internationally known reference materials and calibrated against the primary reference scales for $\delta^{13}C$ and $\delta^{15}N$ values. Analytical precision of the $\delta^{13}C$ and $\delta^{15}N$ sample runs was estimated against an internal standard sample of animal (deer) material that was analyzed every 10 samples, with the overall SD estimated at 0.08‰ and 0.04‰, respectively. Ratios of C:N were generally between 3.5 and 4.0; their relationship with $\delta^{13}C$ was not significant (linear regression $R^2 < 0.01$; $F_{1.57} = <0.01$, $P = 0.92$). This suggests that any patterns of $\delta^{13}C$ enrichment in the fish were not associated with their C:N ratios. Moreover, mathematical lipid normalization of roach $\delta^{13}C$ (Kiljunen et al. 2006) did not alter their $\delta^{13}C$ enrichment patterns in the river; lipid normalization merely enriched the roach $\delta^{13}C$ values across the six sites by a mean of 1.17‰ per site (range 1.10–1.24‰). Consequently, non-lipid normalized SI data were used in subsequent analyses.

For macro-invertebrates, amphipods of the family Gammaridae were the main group analyzed as these dominated the samples. One SI sample was comprised of up to five individuals and a minimum of four samples were collected for each site ($N = 29$), except for site 2 where sampling for Gammaridae was unsuccessful. For SIA, *D. villosus* were kept separate from *Gammarus* spp. Where *Gammarus* spp. and *D. villosus* were sampled from the same site, isotopic differences between the groups were not significant for $\delta^{13}C$ (t test; site 4 $t_6 = 1.31$, $P = 0.24$; site 5 $t_5 = 0.47$, $P = 0.66$). For $\delta^{15}N$, there was no difference at site 5 ($t_5 = 1.29$, $P = 0.25$), but a significant difference occurred at site 4 ($t_6 = 2.80$, $P = 0.03$), although the difference of 0.84‰ was not considered biologically relevant in the context of $\delta^{15}N$ fractionation between consumer and prey being in the region of 3.0–3.4‰ (Post 2002). Thus, for subsequent analyses, *Gammarus* spp. and *D. villosus* SI data were combined as amphipods.

Data analyses

Bivariate isotopic niches for the amphipod and roach samples from each site and reach were visualized using 95% confidence ellipses of the bivariate means, corrected for small sample sizes, using the R package SIBER (Jackson et al. 2011). Then, the R package IsoriX (Courtiol et al. 2019) was used to create isoscape models for expected $\delta^{13}C$ and $\delta^{15}N$ of amphipod and roach fin tissue in the river using the SI data from sites 1 to 6. The geostatistical mean model was a linear mixed-effects model (LMM), with linear river distance (km from source; DIST) and biotic group (amphipod/roach; GRP) as fixed effects, plus sample site as a random effect. To account for spatial autocorrelation, an additional Matérn correlation function (Matérn 1986) was included in the mean model as a random effect. A dendritic approach to geostatistics (Brennan and Schindler 2017) was not considered appropriate due to the tidal nature of this system, which buffers the downward transport of organic matter, including at tributary junctions. In a further gamma generalized LMM (GLMM; the residual dispersion model), the variance of the residual error in the mean model was assumed to be spatially structured according to the random effects of sample site and a Matérn correlation structure. A detailed account of the model structure is available in Courtiol and Rousset (2017). The inclusion of an interaction term (DIST × GRP) in the best-fitting mean models for $\delta^{13}C$ and $\delta^{15}N$ was determined by the minimization of conditional Akaike's information criterion values

(cAIC; Vaida and Blanchard 2005), provided by the AIC function in package IsoriX (Courtiol et al. 2019).

The single and dual isoscapes were generated for amphipods and roach using a structural raster of the study system (approximate cell resolution = 8 m^2), containing linear river distance data (distance from source) measured to the nearest km. For each raster cell (r), the predicted mean and residual variance for $\delta^{13}C$ (μ_C; σ_C^2) and $\delta^{15}N$ (μ_N; σ_N^2) were derived directly from the mean model outputs. To assign the single-isotope ($\delta^{13}C$) value of a test sample with its predicted foraging location, a spatially explicit univariate normal probability density function was calculated according to

$$f(x|r) = \frac{1}{\sqrt{2\pi}\sigma_{C_r}}\exp\left(-\frac{(x-\mu_{C_r})^2}{2\sigma_{C_r}^2}\right).$$

Alternatively, to assign the dual-isotope ($\delta^{13}C$ and $\delta^{15}N$) values of a test sample with its predicted foraging location, a spatially explicit bivariate normal probability density function was calculated according to

$$f(x,y|r) = \frac{1}{2\pi\sigma_{C_r}\sigma_{N_r}\sqrt{1-\rho^2}}\exp\left(-\frac{z}{2(1-\rho^2)}\right)$$

where

$$z = \frac{(x-\mu_{C_r})^2}{\sigma_{C_r}^2} - \frac{2\rho(x-\mu_{C_r})(y-\mu_{N_r})}{\sigma_{C_r}\sigma_{N_r}} + \frac{(y-\mu_{N_r})^2}{\sigma_{N_r}^2}.$$

In the equations, x and y denote the $\delta^{13}C$ and $\delta^{15}N$ values of the test sample, respectively, while r, μ_C, σ_C^2, μ_N, and σ_N^2 are as defined previously. The correlation of x and y is defined by ρ and was obtained from the mean correlation of $\delta^{13}C$ and $\delta^{15}N$ at each sample site.

The predictive power of single- and dual-isotope values in identifying fish foraging areas was assessed using a fivefold cross-validation technique. Data were split into five mutually exclusive subsets, each containing 12 fish (20%), with stratified sampling from each sample site used to account for the hierarchical data structure (Koper and Manseau 2009). With each fold, four subsets were used as training data to fit the roach isoscape models and one as testing data to predict the foraging locations of each fish. Due to the fine-scale resolution of the rasters, the resultant

probability density surfaces were comprised of very small values for each raster cell. For ease of comparison, the surfaces were rescaled relative to their largest density value, such that all surfaces comprised values ranging between 0 and 1 (Wunder 2010). For each assignment method (single- or dual-isotope), the predicted displacement distance represented the linear river distance between an individual fish's capture location and the nearest raster cell containing a density value greater than a given threshold (nearest value of r for which $f(x|r)$ or $f(x, y|r) \geq$ threshold; Campbell et al. 2020). To assess uncertainty in the geographic assignment procedure, three threshold density values were chosen (0.6, 0.8, 1.0). Predicted displacement distance was summarized across roach sampling groups using the mean and variance.

As the ecological niches of adult roach and common bream overlap considerably, the roach dual isoscape was assumed a suitable baseline for the geographic assignment of bream. Diet-tissue isotopic fractionation was also assumed to be similar for the two fishes, such that a rescaling of the baseline was not required. Bream were assigned to their predicted foraging locations using the method above, with the predicted displacement distance from their respective capture sites also calculated as per roach, using threshold probability density values of 0.6, 0.8, and 1.0. In addition, acoustic telemetry data were collected for up to one year from 25 September 2018 (7 d post-release). Analyses utilized individual fish that were detected for at least nine months post-release (Appendix S1: Table S1), as this enabled their movements to be tracked up to and during their 2019 growth season and compared to isoscape-based movement predictions which represented the 2018 growth season. Any individual spending substantial time (>50%) outside of the study area (e.g., in tributaries; Fig. 1) was removed from the analysis. Nevertheless, the study area included connected lakes, as these were considered to be in isotopic equilibrium with the River Bure due to their shallow depth (~1.5 m), close proximity to the river (generally <1 km), and the constant tidal flux of water throughout the wetland system. Weighted linear regressions assessed whether isotopic displacement could predict the scale and directionality of fish movements the following year, measured as the maximum displacement

from the capture site evidenced by acoustic telemetry, and weighted according to the proportion of time spent within 8 km (see *Results*) of this location. Standard linear regressions examined whether fish length was a factor determining $\delta^{13}C$, $\delta^{15}N$, or maximum displacement recorded by telemetry. All analyses were conducted in R 3.5.3 (R Core Team 2019).

RESULTS

Stable isotope data of amphipods and roach

The isotopic values of amphipods and roach revealed a similar range and enrichment pattern ($\delta^{13}C$ amphipods −32.4‰ to −26.8‰; $\delta^{13}C$ roach −32.0‰ to −23.8‰; $\delta^{15}N$ amphipods 11.0–15.2‰; $\delta^{15}N$ roach 12.3–19.1‰). Using 95% confidence ellipses of the bivariate means, dual-isotopic profiles ($\delta^{13}C$ and $\delta^{15}N$) sampled across sites 1 to 6 revealed varying levels of niche overlap, with an overall enrichment of both isotopes with distance downstream for both biotic groups (Fig. 2a, b). When grouped into the upper and lower river reaches, the ellipses did not overlap (Fig. 2c, d).

Isoscapes and predicted roach foraging areas

In the geostatistical models, the best-fitting $\delta^{13}C$ mean model retained both river distance and biotic group as fixed effects, with a predicted enrichment of 0.08‰ per km and an amphipod-roach fractionation of 1.56‰ (Table 1a). Similarly, the best-fitting $\delta^{15}N$ mean model retained both river distance and biotic group as fixed effects, with a predicted enrichment of 0.06‰ per km and an amphipod-roach fractionation of 2.93‰ (Table 1b). Interaction terms were not retained in either of the best models predicting $\delta^{13}C$ and $\delta^{15}N$. The isoscapes resulted from joint predictions stemming from both fixed and random effects (Fig. 3). Residual variance was greatest in the upper reaches of the river for both $\delta^{13}C$ and $\delta^{15}N$ isoscapes (Fig. 3).

Based on the single- and dual-isoscape models, individual fish were geographically assigned to their most probable foraging locations (Fig. 4). Cross-validation of the univariate and bivariate probability density functions revealed the proportion of roach that were assigned to within 5 km of their capture locations increased as threshold density values decreased from 1.0 to 0.6 (Fig. 5). With a threshold probability density value of 1.0, mean predicted displacement distance, irrespective of directionality, was 11.4 km using a single-isotope value vs. 8.2 km using dual-isotope values, although this varied spatially (Table 2). This decreased to 3.7 km using a single-isotope value vs. 2.7 km using dual-isotope values for a threshold density value of 0.6 (Table 2). Overall, variance was lowest for the dual-isotope assignment procedure (Table 2).

Common bream tracking and predicted foraging areas

Bream were acoustically tracked from 12 to 365 d (mean ± 95% CI = 242 ± 51 d), with eight individuals detected for at least nine months (274 d), including two captured at site 4, three captured at site 7, and three captured at site 8 (Appendix S1: Table S1, Fig. S1). The tracking data revealed that seven of these fish remained exclusively in the River Bure and associated off-channel habitats for the duration of the tracking period, while one individual occupied the River Ant tributary for 19% of its time. When using a threshold probability density value of 1.0, the scales of isoscape-predicted displacement distance and maximum displacement distance measured by telemetry were significantly positively correlated ($R^2 = 0.45$, $F_{1,6} = 6.77$, $P = 0.04$; Fig. 6 a), with the gradient not significantly different to 1.0 (95% CI 0.61–1.36), but when using lower thresholds the relationship was not significant (threshold of 0.8, $R^2 = 0.39$, $F_{1,6} = 5.45$, $P = 0.06$; threshold of 0.6, $R^2 = 0.39$, $F_{1,6} = 5.38$, $P = 0.06$). In addition, the isotopic data were unable to predict the directionality of displacement (upstream or downstream), as indicated by the relationship being non-significant at a density threshold of 1.0 ($R^2 = -0.10$, $F_{1,6} = 0.38$, $P = 0.56$; Fig. 6b), as well as at thresholds of 0.8 ($R^2 = -0.17$, $F_{1,6} = 0.001$, $P = 0.97$) and 0.6 ($R^2 = -0.16$, $F_{1,6} = 0.02$, $P = 0.89$). Standard linear regressions confirmed there was no relationship between fish length and $\delta^{13}C$, $\delta^{15}N$ or maximum displacement distance recorded by telemetry ($R^2 \leq 0.30$, $F_{1,6} \leq 2.55$, $P \geq 0.16$).

DISCUSSION

The study revealed predictable enrichment in $\delta^{13}C$ and $\delta^{15}N$ with distance downstream for both roach and amphipods (a putative food
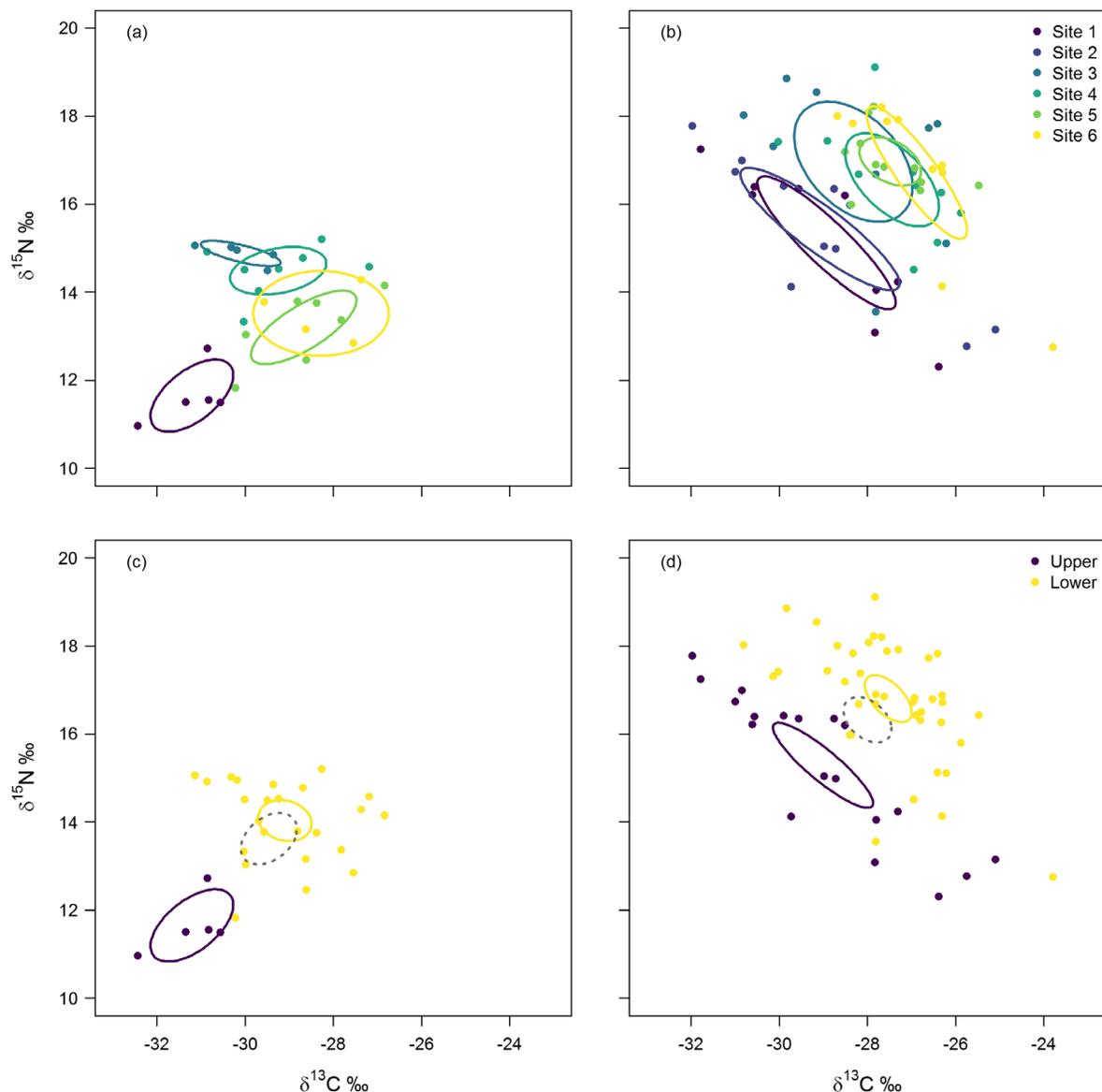
Fig. 2. Stable isotope biplots and associated 95% confidence ellipses of the bivariate means for amphipod (a, c) and roach (b, d) subpopulations grouped according to sample site (a, b) and river reach (c, d). The ellipses for all data combined for each biotic group are given in (c) and (d) as dark gray dotted lines.

resource of roach) in the study river. This geographic variation in $\delta^{13}C$ and $\delta^{15}N$ was successfully modeled using isoscapes and, subsequently, the dual-isotope assignment procedure of roach was the most reliable in assigning the predicted foraging locations in relatively close proximity to their capture location. The application of this dual-isoscape procedure to common bream then

demonstrated that the extent of their isotopic disequilibrium with resources at their capture location was a significant predictor of the spatial extent of their subsequent movements.

The lack of an interaction term in either the $\delta^{13}C$ or $\delta^{15}N$ isoscape models indicated the downstream enrichment patterns of amphipods closely matched those of roach, suggesting

Table 1. Linear mixed-effects model coefficient estimates (± standard error) for the geostatistical mean model fixed effects predicting δ^{13}C (a) and δ^{15}N (b).

Model	Intercept	DIST	GRP:Roach	DIST × GRP:Roach	ΔcAIC
(a) δ^{13}C					
1	−33.43 ± 0.82	0.08 ± 0.01	1.56 ± 0.30		0.00
2	−34.33 ± 1.46	0.09 ± 0.03	2.83 ± 1.73	−0.02 ± 0.03	1.44
(b) δ^{15}N					
1	9.94 ± 2.40	0.06 ± 0.05	2.93 ± 0.27		0.00
2	10.35 ± 2.72	0.06 ± 0.05	1.89 ± 1.54	0.02 ± 0.03	1.53

Notes: DIST, linear river distance; GRP, biotic group. Estimates for the amphipod category are represented by the intercept.
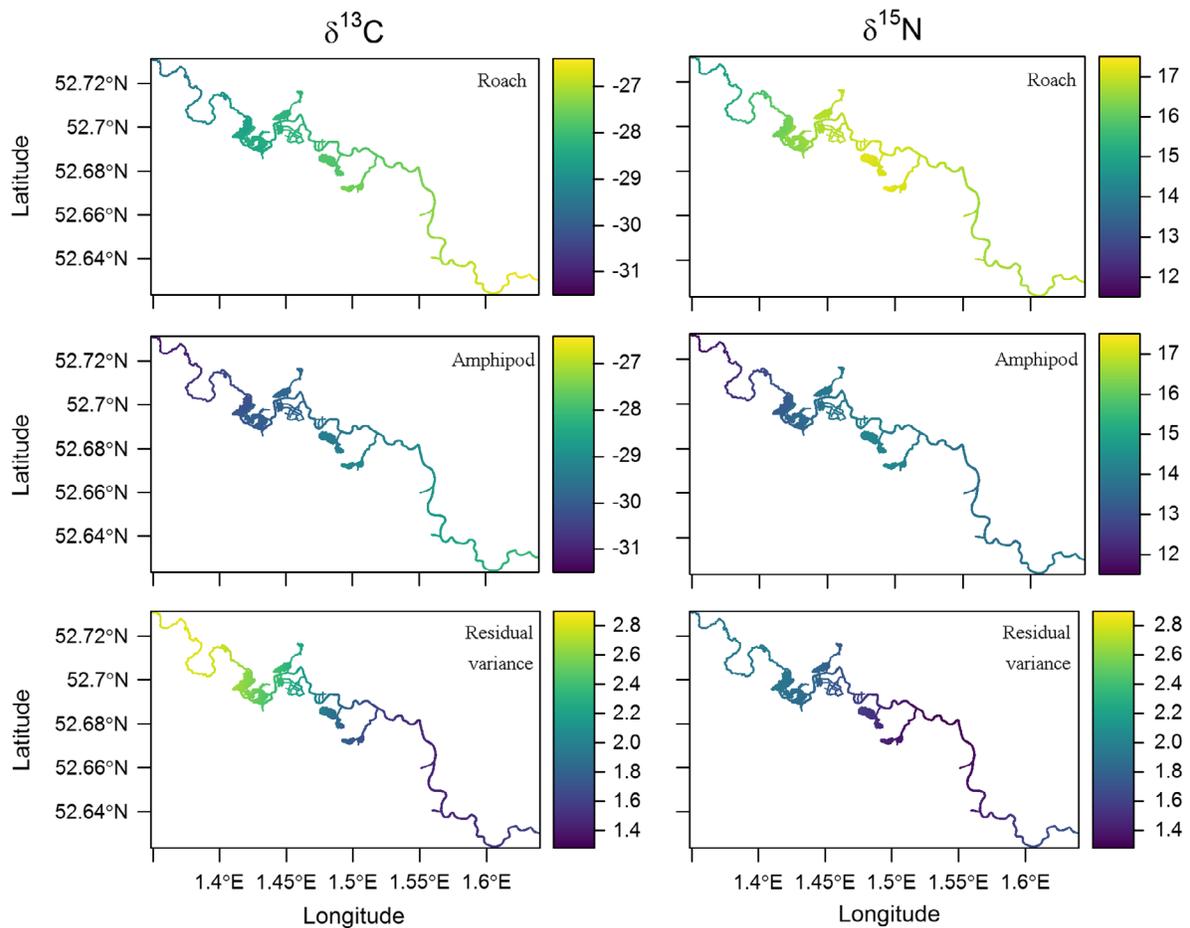
Fig. 3. δ^{13}C (left) and δ^{15}N (right) isoscapes based on best-fitting linear mixed-effects models for roach fin tissue (top) and amphipods (middle) in the River Bure. Residual variance (bottom) is also displayed. Channel width not to scale.

localized roach foraging behavior that contrasted to studies on more vagile species (*S. salar*; Rasmussen et al. 2009). Considering the dietary flexibility of roach (Hayden et al. 2014), this also suggested that longitudinal variation in roach δ^{13}C and δ^{15}N was a result of isotopic changes in the baseline geochemistry and, thus, in their food resources rather than site-specific differences in
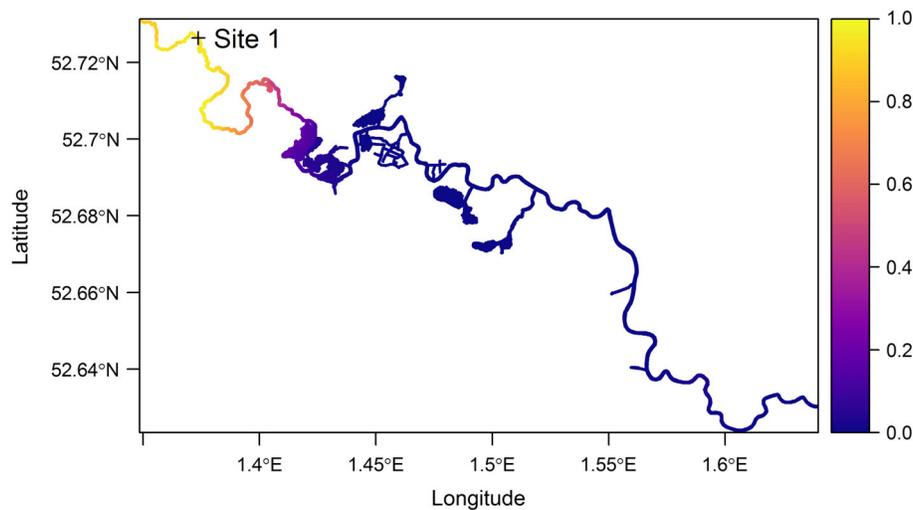
Fig. 4. A bivariate (δ^{13}C and δ^{15}N) probability density surface for an example roach captured at site 1, with values rescaled to between 0 and 1.

prey choice. Isotopic niches of the upper and lower river reaches did not overlap, with site 3, although situated on the reach boundary, being isotopically similar to the lower reach, likely due to this being the limit of saline influence (Clarke 1990).

The single-isotope (δ^{13}C only) assignment method was the least effective at assigning roach foraging locations close to capture locations and was likely compromised by a high level of residual variation that, in some locations, was as large as the average difference in δ^{13}C at the extremities of the study system. When using threshold probability densities of 0.8 and 0.6, mean foraging displacement predicted by the dual-isotope assignment method was within the expected vagility of roach outside of the spawning period and in the absence of in-stream barriers (<5 km; Lucas et al. 1998). For example, in the River Spree, Germany, the wide-range habitat use of roach (based on 90% of locations determined by radio-tracking) did not exceed 3.8 km (Baade and Fredrich 1998). Nonetheless, at a higher threshold density value of 1.0, mean predicted displacement distance exceeded 5 km. However, such model error can be considered small when the accuracy of endogenous chemical tracers is usually measured at watershed or geographically regional scales (Brennan and Schindler 2017, Vander Zanden et al. 2018). Ultimately, the

spatial resolution of intrinsic markers is dependent on the degree of elemental/isotopic variation in the environment, which in freshwater varies from distinct ^{87}Sr:^{86}Sr profiles of whole drainage basins encompassing very large spatial areas (e.g., >10^6 km^2; Duponchelle et al. 2016) to separate ^{87}Sr:^{86}Sr and δ^{15}N profiles of tributaries separated by relatively short distances (<100 km; Harrington et al. 1998, Kennedy et al. 2005). Indeed, Rasmussen et al. (2009) recorded error of only ~2 km when predicting the scale of *S. salar* movement, due to a steep δ^{13}C gradient existing across a relatively small study area. Where isotopic gradients are less variable, this study demonstrates that isoscape assignment accuracy can be improved by use of multiple isotopic markers.

The dual-isoscape assignment for common bream predicted the extent of their foraging displacement from capture locations, which, when using a high probability density threshold, was a significant predictor of the scale of their subsequent movements, though not of the directionality of these movements. This suggests a high level of repeatability of bream general activity (functional habitat use, extent of movements) between years and offers complementary information to previous tracking studies on this species, given individual bream have rarely been monitored for more than one year (Gardner et al.
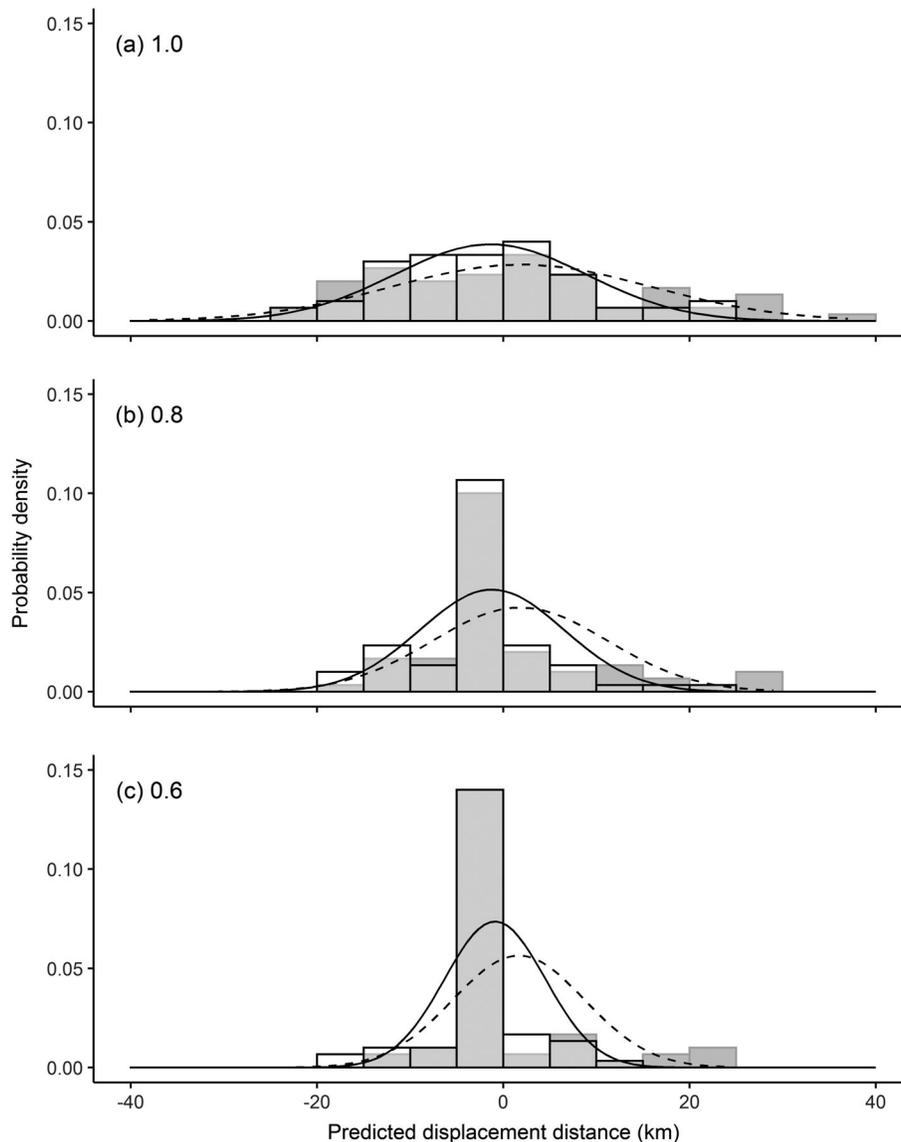
Fig. 5. Probability densities of predicted displacement distances for roach using single (shaded bars) and dual isoscapes (white bars), and calculated using threshold assignment density values between 1.0 and 0.6 (a–c). Normal probability density functions are displayed for single-isotope (dashed lines) and dual-isotope methods (bold lines).

2013). Thus, for species exhibiting predictable unidirectional migrations, such as juvenile anadromous salmonid fishes, the dual-isoscape technique offers high potential for determining distance travelled. However, for species that are more variable in their use of functional habitats, especially in non-linear, heterogeneous environments, then the method may be less robust in its predictions. Elsewhere, biotelemetry has been used to validate the isoscape tracking of birds and reptiles (Jaeger et al. 2010, Vander Zanden et al. 2015*a*), but has also highlighted the limitations of isoscape tracking where SI signatures may not be spatially defined (Coffee et al. 2020). Nonetheless, isoscape tracking can be effective in environments with measurable isotopic

Table 2. Mean predicted displacement distances (km) (± standard deviation) following the single-isotope (δ^{13}C) and dual-isotope (δ^{13}C and δ^{15}N) geographical assignment procedures for roach, based on threshold probability density values ranging from 0.6 to 1.0.

Location	Single-isotope method			Dual-isotope method		
	1.0	0.8	0.6	1.0	0.8	0.6
Site 1 (Upper reach)	15.4 ± 13.6	10.4 ± 11.7	7.8 ± 9.6	4.3 ± 3.7	1.9 ± 3.2	1.1 ± 2.3
Site 2 (Upper reach)	12.5 ± 9.5	7.5 ± 10.4	5.2 ± 9.5	7.0 ± 6.6	3.9 ± 6.6	0.9 ± 2.5
Site 3 (Lower reach)	14.0 ± 6.1	7.0 ± 5.2	3.4 ± 3.3	10.9 ± 7.3	6.2 ± 6.8	4.0 ± 4.4
Site 4 (Lower reach)	11.2 ± 6.8	5.0 ± 6.2	3.0 ± 4.3	10.2 ± 4.4	5.9 ± 5.1	2.9 ± 4.2
Site 5 (Lower reach)	6.5 ± 4.1	1.8 ± 2.9	0.6 ± 1.8	5.1 ± 4.8	2.4 ± 4.1	1.6 ± 4.3
Site 6 (Lower reach)	9.9 ± 6.9	4.3 ± 5.2	2.8 ± 4.8	12.3 ± 6.9	9.8 ± 7.1	5.8 ± 7.9
All sites	11.4 ± 8.4	5.9 ± 7.6	3.7 ± 6.3	8.3 ± 6.3	5.0 ± 6.0	2.7 ± 4.8

Note: Results are both grouped by sample site and combined across the study system.
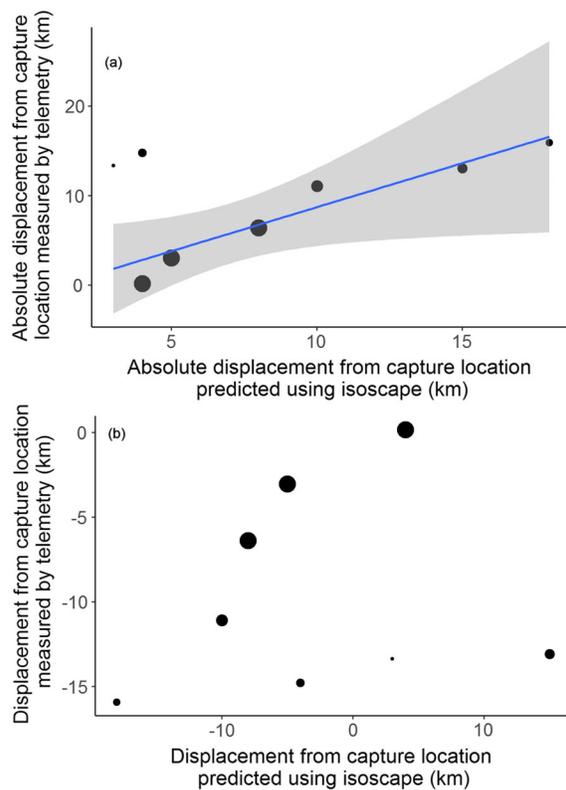
Fig. 6. Relationship between absolute (a) and directional (b) isoscape-predicted displacement distances and telemetry-observed displacement distances of common bream from capture locations. Predicted displacement distance was calculated using a probability density threshold of 1.0. Data were weighted according to time spent within 8 km of maximum displacement recorded by telemetry, represented by point size.

gradients, even at relatively fine spatial scales, as demonstrated here.

Due to varying rates of isotopic turnover in fish tissues, the isoscape assignment results likely reflect the foraging locations of fish at several weeks or months prior to their capture. Studies have revealed that the SI turnover rate (as its half-life) of fin tissue varies between species, being 13 d in juvenile rainbow trout *Oncorhynchus mykiss* (Heady and Moore 2013), 26 d in juvenile Japanese seabass *Lateolabrax japonicus* (Suzuki et al. 2005), 95 d in juvenile barbel *Barbus barbus* (Busst and Britton 2018), and 133 d in juvenile Colorado pikeminnow *Ptychocheilus lucius* (Franssen et al. 2016). Despite this variability in half-lives between species, these figures suggest that the data in the present study reflect resources accumulated over the summer foraging period that occurred just prior to fish sampling. Given the potential for fish movement and foraging over isotopically variable environments during this time, isotopic data derived from fin tissue could represent a blending of signatures from multiple areas within the study system. While home ranges of bream in the Bure system generally contract during summer (the authors, *unpublished data*), short-term habitat shifts could be masked when predicting foraging displacement using the methods here. The use of tissues with more rapid rates of isotopic turnover, such as mucus (Ibarz et al. 2019, Winter et al. 2019), could facilitate isoscape tracking with greater temporal, and therefore spatial, resolution.

In the Bure study system, seasonal variability in isoscapes potentially occurs due to cyclic patterns of algal productivity (Moss and Balls 1989, Torniainen et al. 2017), as well as considerable tidal surges and saline intrusions in winter (Clarke 1990). This is likely to result in a steeper gradient in $\delta^{13}C$ between the upper and lower river reach in winter than was demonstrated here. Moreover, increased winter precipitation and seasonal agricultural practices can also impact isotopic baselines (Finlay and Kendall 2007). Nevertheless, given that the two model species were both cyprinids that rarely grow at temperatures <12°C (Britton 2007), their SI data in winter would likely still represent their summer diet (Perga and Gerdeaux 2005), and thus, winter-based isoscapes might be less suitable for predicting the extent of their movements. However, seasonal variability in SI data may be more apparent in other species where over-winter growth is more likely to occur, such as in *S. salar* (Simmons et al. 2020), or in apex predators such as Northern pike *Esox lucius* that can assimilate resources over a longer time period (Vander Zanden et al. 2015*b*). Should the isoscape tracking technique be applied to other species, then it may be appropriate to combine multiple seasonal isoscapes, where samples of putative food resources are taken for SI analyses at repeated intervals.

For many freshwater systems, downstream hydrological transport is likely to influence the spatial variability of isotopes, for example, abrupt changes at tributary junctions or point sources of pollution. Given the tidal nature of the River Bure study system, this was not considered problematic, but elsewhere it may need accounting for in both sample collection and data analyses. Brennan and Schindler (2017) successfully applied a combination of dendritic and traditional Euclidean modeling approaches to strontium isoscapes in a North American river system, to reconstruct the freshwater movement patterns of Chinook salmon, *Oncorhynchus tshawytscha*. This technique may play a significant role in the development of future riverine isoscape applications. Indeed, combining multiple-isotope isoscapes with the dendritic modeling approach offers a novel avenue for further freshwater research.

In summary, this is the first probabilistic assignment to origin for riverine species using dual-isotope isoscapes. The study demonstrated that a dual-isotope assignment procedure is preferential for determining the extent of foraging movements of lowland river fish at moderately fine spatial scales. The increased application of this procedure (over single-isotope tracking) to movement studies is recommended, particularly where telemetry is deemed unsuitable, or can only be applied to limited numbers of animals.

Acknowledgments

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