RESEARCH ARTICLE

Variability in the summer movements, habitat use and thermal biology of two fish species in a temperate river

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Abstract

The ability of fish to cope with warm water temperatures in summer depends on factors including their thermal traits and the ability of individuals to access cool-water refugia. Knowledge is highly limited on the in situ responses of many fishes to elevated summer temperatures, including whether they express behavioural thermoregulation. The responses of two riverine species to summer water temperatures were tested here using the movement metrics, spatial habitat use and body temperatures of individual European barbel *Barbus barbus* ('barbel') and common bream *Abramis brama* ('bream') versus river temperatures. Acoustic biotelemetry was applied in the lower River Severn basin, western Britain, in summer 2021 (barbel) and 2022 (bream), where individuals could move across > 150 km of river, including a tributary of cooler water. Across all individuals, bream occupied 37 km of river length (mainstem only), with low inter-individual variability in their spatial habitat use, movements and body temperatures. In contrast, barbel occupied 62 km of river (main river/tributary), with relatively high inter-individual variability in spatial habitat use, movements and body temperatures, with higher variation in body temperatures as river temperatures increased (maximum mean daily temperature difference between individuals on the same day: 4.2 °C). Although warmer individuals generally moved more, their activity was greatest at relatively low temperatures and higher flows, and neither species revealed any evidence of behavioural thermoregulation during elevated temperatures. Enabling phenotypically diverse fish populations to express their natural behaviours and thermal preferences in summer water temperatures thus requires maintaining their free-ranging in thermally heterogenous habitats.

Keywords *Barbus barbus* · *Abramis brama* · Acoustic telemetry · Thermal phenotype · Phenotypic diversity · Climate change

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Introduction

Temperature plays a key role in defining the spatial distributions, temporal activity patterns and bodily functions of ectothermic organisms (Cossins and Bowler 1987; Huey and Kingsolver 1993). With climate change already driving periods of extreme weather, such as drought and heat-wave events (Gudmundsson et al. 2021), the ability of ectotherms to cope with these changes depends on their inherent thermal traits and tolerances, acclimation capacity and ability for evolutionary adaptation (Morgan et al. 2020).

Heat stress from episodic warming can negatively impact fish communities, including via physiological stress (Magel et al. 2020; Amat-Trigo et al. 2023). The extent to which species might be affected by elevated temperatures can be informed by metrics such as their thermal optima and critical thermal maxima (CTM), with the

latter often used to infer the acute upper thermal tolerances of fishes (Deforges et al. 2023). CTM is also frequently applied to predicting how species might respond to warming temperatures and for formulating climate change adaptation actions (Radtke et al. 2022; Deforges et al. 2023). These actions are potentially important as the ability of climatically vulnerable freshwater fishes to move to cooler waters at higher latitudes and/or altitude can be inhibited by the physical boundaries of river basins (Comte and Grenouillet 2013; Núnez-Riboni et al. 2019). This means the population responses of freshwater fishes to warming events must generally occur in situ (McDonnell and Chapman 2015; González del Pliego et al. 2020).

Although CTM can inform predictions of how freshwater fish species might respond to elevated water temperatures, these laboratory-based predictions are unlikely to account for the extent to which individuals might be able to access local cool-water refugia via behavioural thermoregulation (Amat-Trigo et al. 2023). For example, in thermally heterogeneous riverine environments, considerable reductions in instream temperatures can occur in areas of groundwater upwelling and/or riparian shading, with incoming tributaries into main river channels also often providing rapid access to cooler waters (Broadmeadow et al. 2011; Ritter et al. 2020; Hare et al. 2021). Thus, in warm periods, riverine fishes can potentially move into these cool-water refugia to maintain their body temperatures at physiologically optimum levels, providing their ability to access them is not inhibited by anthropogenically constructed barriers, such as weirs and dams (Grill et al. 2019).

The resilience of freshwater fishes to elevated water temperatures might also be influenced by intra-population variability in their behavioural and thermal traits. Within
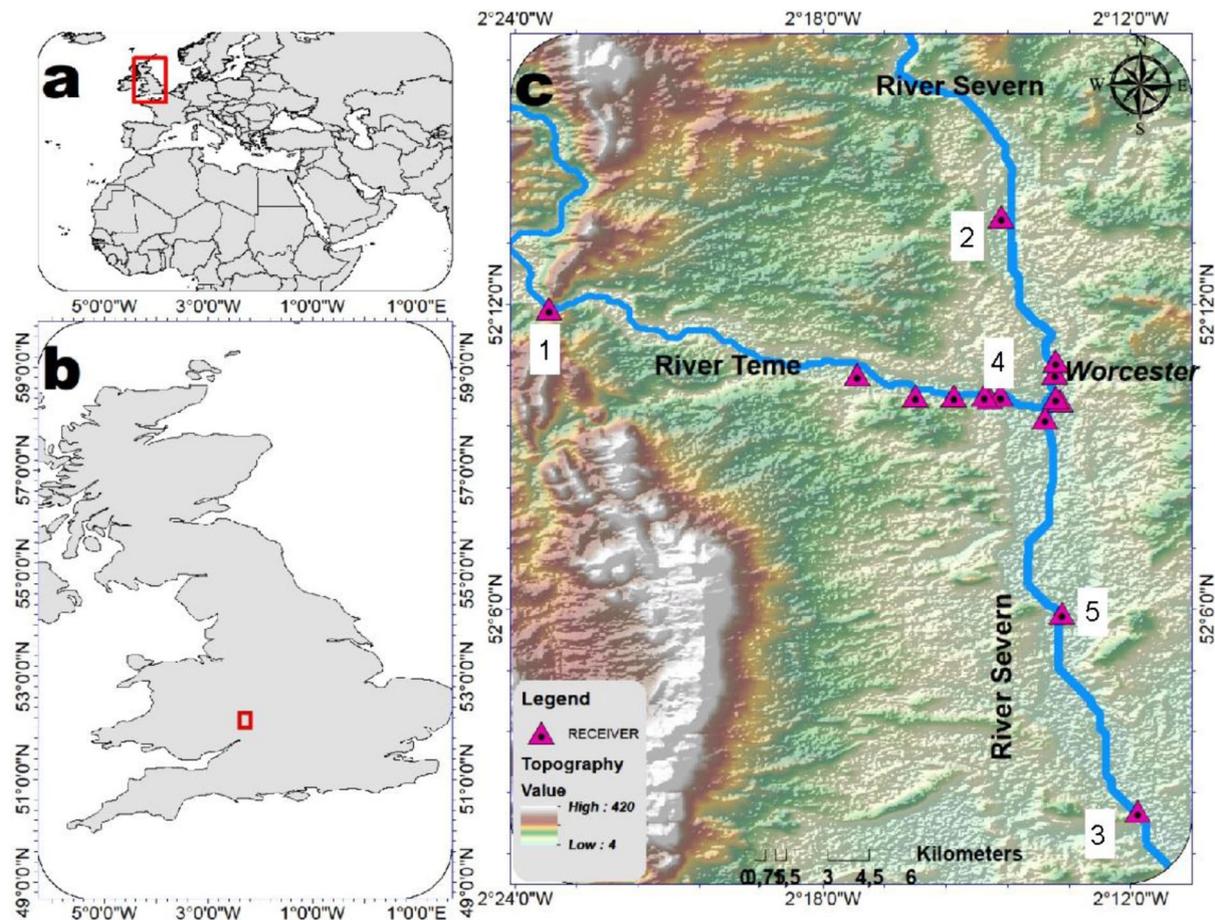

Fig. 1 Maps showing **a** the position of the study country; **b** the study area within the UK; (**c**) the core study area within the Rivers Teme and Severn, with the 17 receiver locations shown with triangles. In (**c**), the Teme flows from west to east and the Severn from north to south; the high density of receivers at the lower end of the River Teme and around its confluence with the Severn mean that some receiver locations are obscured; (1) River Teme upstream limit of core study area downstream of Knightwick Weir; (2) River Severn upstream limit located downstream of Bevere Weir; (3) downstream limit of the core study area at Severn Stoke; (4) location of the temperature logger in the River Teme at Temeside Cottage; and (5) location of the temperature logger in the River Severn at Pixham

Table 1 Fish length (L), sampling method [method; as EF (electric fishing) or ANG (angling)], detection data and movement metrics (cf. Table S1) for (A) European barbel between 1 July and 31 October 2021, and (B) common bream between 1 July 2022 and 31 October 2022.

Fish	L (mm)	Method	Days from first to last detection	Days of detection	Number of detections	Number of receivers detected	Receiver residency index	Array residency index	Total range	Total distance moved	Mean daily distance	Rivers occupied
(A)												
1362069	410	EF	108	101	443	1	–	–	–	–	–	Teme
1362063	560	ANG	106	2	11	1	–	–	–	–	–	Severn
1362064	652	ANG	85	63	20,543	1	–	–	–	–	–	Severn
1362067	700	ANG	115	5	803	3	0.04	0.94	2079	2700	15	Teme
1362072	804	ANG	116	104	21,830	4	0.71	0.82	3904	19,500	119	Severn
1362074	529	ANG	122	96	7446	4	0.74	1	2025	56,500	19	Severn/Teme
1362073	739	ANG	119	106	15	4	0.01	0.01	516	500	516	Severn/Teme
1361296	563	EF	101	44	5137	6	0.19	0.75	1457	2600	78	Teme
1362065	575	ANG	119	118	31,214	7	0.84	0.93	5200	78,000	170	Severn
1361291	468	EF	122	89	15,136	7	0.51	0.93	2615	50,900	19	Severn/Teme
1362062	800	ANG	122	115	15,561	8	0.62	1	6933	151,600	207	Severn
1362070	555	ANG	115	41	8780	10	0.2	0.86	7776	18,600	53	Severn/Teme
1362068	576	ANG	122	96	29,574	11	0.71	0.94	14,331	243,300	216	Severn
1361297	462	EF	111	32	6719	11	0.11	0.9	13,322	23,400	52	Severn/Teme
1361295	514	EF	108	33	2327	12	0.13	0.77	4403	6200	12	Teme
1362066	628	ANG	118	88	19,718	16	0.65	0.94	27,961	46,200	216	Severn/Teme
(B)												
1396540	490	ANG	108	15	860	2	0.12	0.89	2271	11,300	37	Severn
1396538	516	ANG	192	7	309	3	0.06	0.75	3904	4000	22	Severn
1396813	568	ANG	111	13	895	4	0.11	0.91	7572	26,000	62	Severn
1396536	472	ANG	122	93	16,578	5	0.76	1	5376	91,100	57	Severn
1396814	520	ANG	122	95	29,762	5	0.78	1	5376	86,800	63	Severn
1396818	601	ANG	122	103	22,801	5	0.84	1	5376	175,300	59	Severn
1396541	525	ANG	118	64	7188	6	0.53	0.97	7552	95,100	81	Severn
1396812	484	ANG	84	21	893	6	0.17	0.69	11,232	59,800	108	Severn
1396537	563	ANG	122	95	20,011	6	0.78	1	8059	157,500	76	Severn
1396533	530	ANG	122	90	26,582	7	0.74	1	12,551	169,500	137	Severn
1396539	545	ANG	117	30	11,258	7	0.25	0.96	8569	91,800	77	Severn
1396817	505	ANG	118	45	7481	7	0.37	0.97	6347	87,100	77	Severn

Table 1 (continued)

Fish	L (mm)	Method	Days from first to last detection	Days of detection	Number of detections	Number of receivers detected	Receiver residency index	Array residency index	Total range	Total distance moved	Mean daily distance	Rivers occupied
1396535	585	ANG	122	102	27,338	8	0.84	1	12,251	291,000	72	Severn
1396542	520	ANG	122	56	4006	8	0.46	1	12,251	109,900	98	Severn
1396815	526	ANG	122	83	25,027	8	0.68	1	12,251	154,800	76	Severn
1396816	472	ANG	113	102	27,536	8	0.84	0.93	12,251	199,900	89	Severn
1396819	426	ANG	118	76	13,645	9	0.62	0.97	13,347	228,500	132	Severn

All distances are estimated to the nearest metre

populations, individuals are often categorised into personality types of 'proactive' (active coping or bold), 'intermediate' (more flexible individuals) and 'reactive' (passive coping or shy) (MacKay and Haskell 2015). Individuals within these personality categories show consistent behaviours, such as in their rates of exploration, activity and socialness (Rey et al. 2013; Villegas-Ríos et al. 2018). These individual personalities have also been strongly associated with thermal preferences where, for example, proactive zebra fish *Dani rerio* have stronger preferences for warmer water than reactive individuals (Rey et al. 2015), individual Nile tilapia *Oreochromis niloticus* that prefer warmer water were also proactive in behavioural tests (Cerqueira et al. 2016), and juvenile coral fishes that were more active at warmer temperatures were also bolder and aggressive (Biro et al. 2010). There are, however, considerable knowledge gaps between the laboratory derived thermal metrics of freshwater fishes (e.g. thermal optima, CTM) and their actual spatial and thermal habitat use in the wild, including how their habitat use during warming events is affected by the presence of cool-water refugia, barriers and intra-population trait variability.

Accordingly, the aim here was to apply acoustic biotelemetry to assessing the movements and thermal habitat use in summer periods of individuals of two fish species in a thermally heterogenous lowland river system. The objectives were to assess the variability in the movement metrics and thermal habitat use of individuals of the two species, quantify the spatial differences in river temperatures in the study area, and evaluate the results in the context of phenotypic diversity and future climate warming and adaptation strategies. It was posited that both species would exhibit considerable intra-species variability in their movement metrics and temperature preferences, and that during periods of elevated water temperatures which were close to, or exceeded, the thermal optima of the species, individual fish would respond by moving into cooler waters.

Materials and methods

Study species

The two study species were European barbel *Barbus barbus* ('barbel') and common bream *Abramis brama* ('bream'). Barbel is an aggregative riverine fish with a range that extends from southern to northern Europe (Britton and Pegg 2011) and a thermal optimum at adult life stages of 10 to 24 °C (generated in the River Rhone, France), with a CTM of 32 °C (laboratory generated) (Souchon and Tissot 2012). They show high intra-population variability

in movements (Penaz et al. 2002; Britton and Pegg 2011), where populations comprise 'resident' and 'mobile' fish (Gutmann Roberts et al. 2019). For example, in the middle reaches of the River Severn, western England, over 85% of tagged fish remained within 5 km of their release point, but some were recorded up to 34 km away (Hunt and Jones 1974). More recently, an acoustic telemetry-based study in the lower River Severn basin revealed that a high proportion of barbel had total ranges below 5.5 km, while others had ranges greater than 12 km (Gutmann Roberts et al. 2019). Bream is also an aggregative species, but tends to prefer slow-moving waters to barbel, and with thermal optima reported up to 26 °C and an upper lethal temperature of 36 °C (after acclimation at 26 °C), but with extreme temperatures generally tolerated to 28 °C (Souchon and Tissot 2012). Compared to barbel, telemetry studies have suggested more consistent behaviours in bream, with some fidelity to specific river reaches and with larger scale movements for spawning (e.g. > 20 km; Winter et al. 2021).

Study area

Individual barbel and bream of the lower River Severn basin were assessed here for their spatial and thermal habitat use (Fig. 1). In the study area, the main channel of the River Severn is characterised by impoundment from four major weirs, with each having a fish pass fitted and operational in the last three years (Unlocking the Severn 2023). The study area also encompassed a major tributary, the River Teme (Fig. 1), which provided a shallower, cooler habitat (Gutmann Roberts et al. 2019), and whose weirs in the lower reaches were modified to increase fish passage in 2018 (Antognazza et al. 2021). These fish passes and weir modifications mean that, in entirety, the fishes could move relatively freely over 150 km of river.

The core study area was downstream of Knightwick Weir on the River Teme, through to its confluence with the River Severn, and then in the River Severn between Bevere Weir (upstream) and Severn Stoke (downstream) (Fig. 1). The River Severn was characterised by impounded sections of relatively slow flowing water, with widths to 40 m and depths to > 5 m. Within the study area, the River Teme was characterised by sequences of large pools and riffles within a river channel of up to 15 m width and depths < 2 m (Gutmann Roberts et al. 2019). Overhanging trees (primarily *Salix* spp.) were abundant in the riparian zone.

The study ran between July (to avoid fish movements associated with spawning behaviours; Gutmann Roberts and Britton 2020) and October (to avoid movements more associated with dispersal to overwintering habitats) in 2021 (barbel) and 2022 (bream). Peak summer air temperatures in the region generally occur in July and early August, with maximum air temperatures of the Central England Temperature (which includes data collected from Malvern, which is < 10 km from the study area) recorded in the two study years of 29.2 °C (22 July 2021) and 37.3 °C (19 July 2022). The warmest river temperature recorded in July 2021 was 24.9 °C, with river temperatures in 2022 always below 23 °C (cf. Results).

Acoustic biotelemetry array and water temperature recording

The movements of barbel and bream were measured in the study area using acoustic biotelemetry, with a fixed array of 17 acoustic receivers (VR2, Vemco Ltd, Halifax, Nova Scotia, Canada) deployed in the core area (Fig. 1), but with an additional 17 receivers located outside of these boundaries to track fish movements should the fish leave the core area. The furthest upstream of these receivers for the River Teme was at Tenbury (approximately 48 km from Powick Weir), and for the River Severn, at Shrewsbury (approximately 100 km from Bevere Weir), with the furthest downstream receiver on the Severn being at Ripple (approximately 5 km from Severn Stoke; Fig. 1). All receivers remained in situ throughout the study period. Water temperature loggers (a combination of Tinytag TGP-4500 and HOBO Pendant temperature loggers) were deployed in both rivers in the study period, with six deployed in the Teme and seven in the Severn, recording river temperatures every 15 min (to 0.1 °C). Within each river, temperature differences between the loggers at the times of recording were never more than 0.3 °C (Teme) and 0.4 °C (Severn). Some loggers were also exposed to air for short periods (due to reducing river level), which resulted in their recording of air temperatures rather than water temperatures (air temperatures are considerably higher than water temperatures, and more variable over 24 h periods). Consequently, the loggers at Temeside Cottage (Teme) and Pixham (River Severn) were used exclusively to provide river temperatures (Fig. 1), as these loggers remained submerged at all times between 1 July 2021 and 18 October 2021, and 1 July 2022 and 31 October 2022, so provided a continuous water temperature record in these periods. These temperature data were then used to calculate daily mean temperature for each river. The data analyses of fish movements were then focused on these two summer periods. In addition, data on river flow (in cm^3 s^{-1}) were available for both rivers in the study reach from automated recording stations controlled by the Environment Agency and were used to determine mean daily flow rates.

Fish sampling and tagging procedures

Both barbel and bream were implanted with acoustic transmitters during the study, with data suitable for movement analyses during the study period for 16 barbel

and 17 bream (Table 1). Two methods were used to sample the barbel, electric fishing and angling using rod and line. Electric fishing was completed from a boat in the lower River Teme on 30 September 2020. Although angling was also used on 29 and 30 September 2020 in both the lower Teme and downstream of its confluence with the Severn, no barbel were captured, likely due to low and clear river conditions. Consequently, angling was repeated on 11 and 12 March 2021 in the lower River Severn (500 m downstream of the Teme confluence) under higher river conditions that were more conducive to capturing barbel using bait, resulting in barbel capture (Table 1). For bream, electric fishing in September 2021 was not able to proceed due to logistical constraints imposed by local fuel shortages. Consequently, all bream were captured using angling in the lower River Severn on 12 and 13 March 2022 (Table 1). All captured barbel and bream were held in large water-filled containers before being transferred to aerated holding tanks prior to tagging.

The fish were then all implanted with a Vemco V9T acoustic transmitter fitted with a temperature sensor (hereafter referred to as 'acoustic tags'), with each tag measuring 9×37.5 mm with an approximate weight of 5 g and operated at 69 kHz. The tags were coded to allow individual fish identification and pulsed randomly once every 60 to 180 s, providing a battery life for each tag of approximately 13 months. Random repeat pulse rates allowed multiple individual fish to be monitored simultaneously within a given area and without continuous signal overlap and risk of signal interference at the receivers. The tags were inserted into the peritoneal cavity via a mid-ventral incision that was closed with a single suture, with the fish under general anaesthesia

Table 2 Results of generalised additive models for (A) European barbel and (B) common bream, where edf is the equivalent degrees of freedom [effective degrees of freedom for the smoothing function (te(Temperature,Flow) and s(Fish_ID), where higher values indicate more complex relationships], and Ref.df is the reference degrees of freedom (the initial degrees of freedom before model fitting, providing a reference point for comparison with the effective degrees of freedom)

	Estimate	Std. error	*t*-value	*P*-value
(A)				
Intercept	3.94	0.46	8.49	<0.0001
	edf	Ref.df	*F*	*P*-value
te(Temperature,Flow)	3.54	22	75.74	<0.001
s(Fish_ID)	9.88	10	89.80	<0.0001
(B)				
Intercept	4.25	0.17	25.43	<0.0001
	edf	Ref.df	*F*	*P*-value
te(Temperature, Flow)	14.71	24	47.42	<0.0001
s(Fish_ID)	14.91	16	6.01	<0.0001

(tricaine methanesulfonate (*MS-222*), dose 0.04 g l^{-1}) throughout. The fish were then transferred to recovery tanks containing river water, held until normal swimming behaviour recommenced and then returned within 500 m of their capture site. Additional information recorded for each fish was fork length (nearest mm) and method of capture (electric fishing/angling). The mean fork length barbel was 596 ± 57 mm (range 410–804 mm), and those captured by electric fishing (EF) (tagged in September 2020) were significantly smaller than those captured by angling (ANG) in March 2021 (EF: 483 ± 51 mm; ANG: 647 ± 59 mm; Mann–Whitney *U* test, $Z = -2.95$, $P < 0.01$; Table 1). The bream were between 426 and 601 mm in length (Table 1). All surgical procedures were completed following ethical approval, were licenced under the U.K. Animals (Scientific Procedures) Act (1986) (project licence number: PPL PA2C7C4E6), and were undertaken by a licensed, competent and experienced practitioner.

Upon receipt of a signal from a V9T tag, the VR2 receivers identified the tag number by its unique coded transmission pattern and recorded its time of detection and temperature, where the tag temperature was assumed to be that of the fish body temperature (hence 'fish body temperature' hereafter). Detection distances of the VR2 receivers were 70 to 120 m in the River Teme (actual distances varied according to the location of the nearest riffle in both up- and downstream directions), and over 100 m in the River Severn (no riffles present due to impoundment). A standardised detection distance of 100 m was thus utilised in subsequent analyses. In all cases, detection distances exceeded the width of the rivers, and so the receivers functioned as a gated array (Gutmann Roberts et al. 2019). At the conclusion of the study period, the VR2 receivers were all removed from the river and the data downloaded. All receivers remained operable in the study period.

Fish movement metrics and analyses

All of the 17 tracked bream and 13 of 16 tracked barbel had movement data suitable for determining movement metrics (Table 1). Three barbel were not suitable for these analyses due to their detection on only one receiver during the study period. For fish where movement metrics were calculated, their movement data (calculated from downloaded receiver data and expressed as distance of river length (m) moved) were initially manipulated within the software 'Vtrack' (Campbell et al. 2012), a package written within the R programming language (R Core Team 2017), prior to being analysed for a series of relevant movement metrics as per Gutmann Roberts et al. (2019). For indices of the extent of the residency of each fish in the receiver array, the residency index measured the number of days when the fish was detected as a proportion of the total number of study
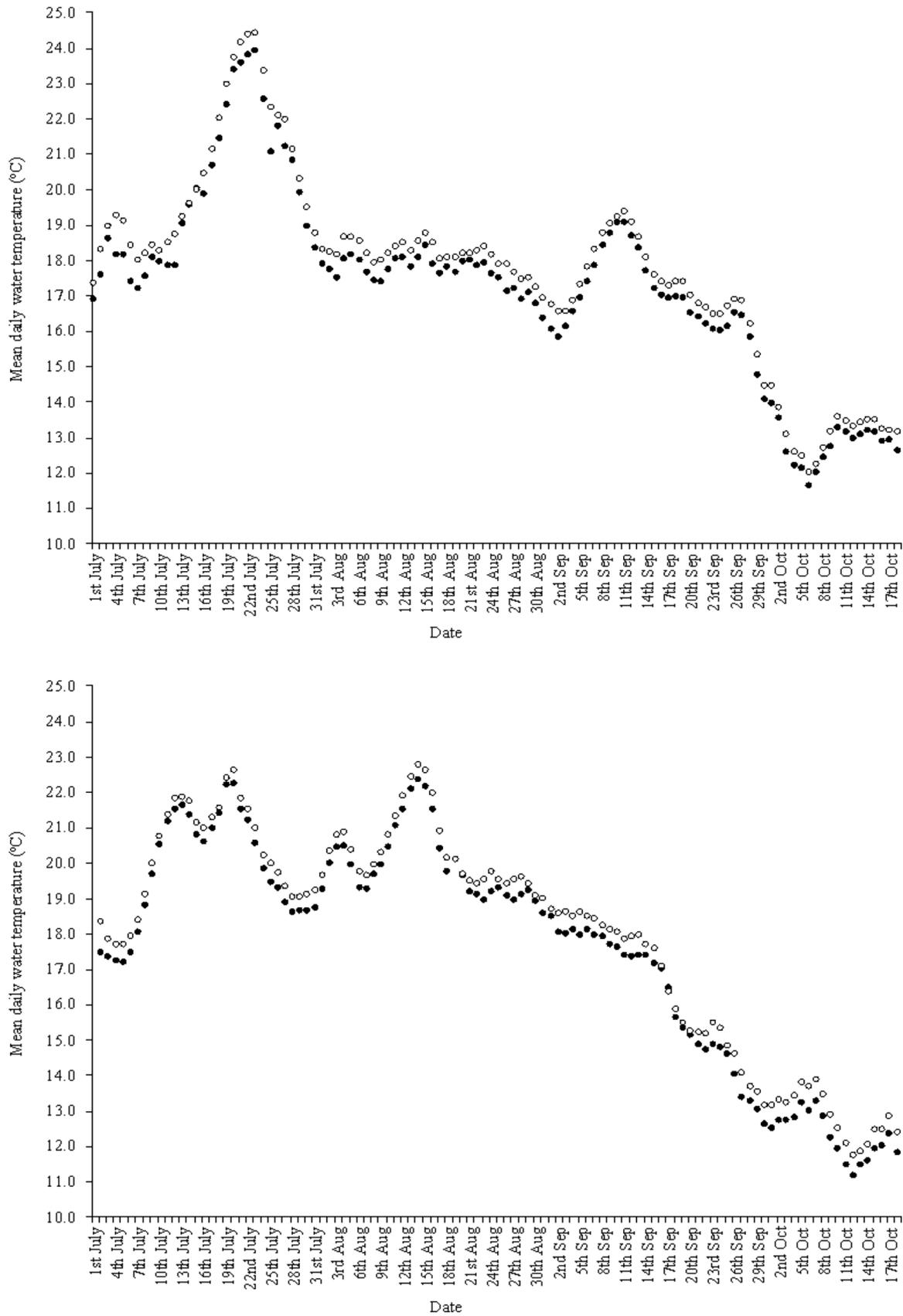
Fig. 2 Mean daily river temperature for the River Severn (clear circle) and the River Teme (filled circle) in 2021 (top) and 2022 (bottom), between July and October

Table 3 The regression coefficients a and b (and their 95% confidence limits) and the results of the linear regression test (F values omitted for brevity) for the relationship for individual barbel (A) and common bream (B) between the mean daily River Severn temperature and fish mean daily temperature, using data only on days when that fish was detected (cf. Table 1)

Fish	a	95% CL a	b	95% CL b	R^2	P
(A)						
1362066	−0.53	−1.20 to 0.14	1.02	0.98 to 1.06	0.99	<0.01
1362062	−0.52	−0.75 to −0.28	1.02	1.00 to 1.03	0.99	<0.01
1362072	−0.60	−0.80 to −0.40	1.03	1.01 to 1.03	0.99	<0.01
1362073	−0.63	−0.78 to −0.49	1.01	1.00 to 1.02	0.99	<0.01
1362065	−0.91	−1.08 to −0.74	1.04	1.03 to 1.05	0.99	<0.01
1362068	−0.38	−0.62 to −0.14	1.00	0.98 to 1.01	0.99	<0.01
1362074	0.81	0.18 to 1.44	0.92	0.88 to 0.95	0.97	<0.01
1362064	−0.24	−0.45 to 0.03	0.99	0.98 to 1.00	0.99	<0.01
1361291	0.95	0.50 to 1.41	0.90	0.88 to 0.93	0.98	<0.01
1361295	−0.40	−1.25 to 0.47	0.96	0.91 to 1.00	0.98	<0.01
1362070	1.22	0.59 to 1.86	0.89	0.85 to 0.92	0.99	<0.01
1361297	0.40	−0.48 to 1.28	0.91	0.87 to 0.96	0.98	<0.01
1361296	−0.43	−1.09 to 0.24	0.95	0.91 to 0.99	0.99	<0.01
1362069	0.36	−0.29 to 1.02	0.87	0.84 to 0.91	0.96	<0.01

Fish	a	95% CI a	b	95% CI b	R^2	P
(B)						
1396542	−0.99	−1.25 to −0.73	1.03	1.02 to 1.04	0.99	<0.01
1396541	−0.80	−1.06 to −0.54	1.01	1.00 to 1.03	0.99	<0.01
1396540	−1.57	−2.24 to −0.90	1.07	1.04 to 1.11	0.99	<0.01
1396814	−0.71	−0.87 to −0.54	1.01	1.00 to 1.02	0.99	<0.01
1396812	−0.90	−1.21 to −0.59	1.03	1.01 to 1.05	0.99	<0.01
1396813	−0.73	−1.32 to −0.15	1.02	0.99 to 1.05	0.99	<0.01
1396815	−1.01	−1.29 to −0.73	1.03	1.02 to 1.05	0.99	<0.01
1396816	−0.93	−1.13 to −0.73	1.02	1.01 to 1.04	0.99	<0.01
1396817	−0.87	−1.14 to −0.60	1.03	1.01 to 1.04	0.99	<0.01
1396818	−0.79	−0.99 to −0.60	1.01	1.00 to 1.02	0.99	<0.01
1396819	−1.01	−1.28 to −0.74	1.03	1.02 to 1.05	0.99	<0.01
1396533	−1.00	−1.18 to −0.81	1.03	1.02 to 1.04	0.99	<0.01
1396535	−0.87	−1.05 to −0.69	1.03	1.02 to 1.04	0.99	<0.01
1396536	−0.67	−0.91 to −0.42	1.01	1.00 to 1.03	0.99	<0.01
1396537	−0.69	−0.88 to −0.51	1.02	1.01 to 1.03	0.99	<0.01
1396538	−0.72	−1.19 to −0.25	1.01	0.99 to 1.04	0.99	<0.01
1396539	−1.01	−0.79 to −1.23	1.03	1.04 to 1.02	0.99	<0.01

days, and the array residency index measured the number of days when each fish remained within the spatial limits of the receiver array as a proportion of the total number of study days (Acolas et al. 2017). The total range of an individual fish was taken as the sum of river length (both mainstem and tributary) used by that fish, measured as the distances between the receivers at the up- and downstream limits of their detection (where the fish was detected in both rivers, the sum of the two distances was taken). An individuals's total distance moved was the sum of the distances of all movements made between receivers, irrespective of whether the movements were in an up- or downstream direction. For both total range and total distance moved, the distance between the VR2 receivers was determined as the river length (m) to the nearest 100 m (as the standardised detection range). Daily movement of an individual was calculated as the total distance moved by an individual on each day of detection (i.e. days when that fish was detected on at least two receivers) and was used to calculate the mean daily distance moved per individual fish. In calculating mean daily distances, each day of movement could not be initially treated as independent of the movement on the following or previous day. Accordingly, the movement (m) time-series data were tested for temporal autocorrelation

using a Box–Pierce test, from package 'tseries' (Trapletti et al. 2017). As all tested fish revealed non-significant results ($P = 0.22$–0.90), the data were not considered auto-correlated and so could be analysed without further treatment.

The river occupied by each fish was taken as the Severn (the individual was only ever detected on receivers in the Severn mainstem), the Teme (the individual was only ever detected on receivers in the Teme tributary) or Severn/Teme (the individual was detected in receivers in both the Severn mainstem and Teme tributary). The spatial occupancy of both species in the study area was then visually demonstrated by the construction of heat maps that showed the probability of occupancy of the river across all individuals by species. The maps were constructed using the Kernel density method (Silverman 1986), which calculated the density of point features surrounding each cell in the output raster, so defining a neighbourhood around the centre of each raster cell and determining the number of points within that neighbourhood. This count was then divided by the area of the neighbourhood to obtain the point density (low–high). These analyses were all conducted in ArcMap version 10.8.2.

The relationships between daily movements of each species (as the river length distance) and the mean daily water temperature and river flow (and their interaction) were tested for each species in generalised additive models (GAM; gamma distribution, log link function (Pedersen et al. 2019)). To account for potential unexplained variability due to individual differences among fish, the individual fish were included as a random variable, enabling testing of individual-specific variations in movement, with the number of knots set to 5 to avoid overfitting. Model fitting processes were followed to find the smooth tasks that best fitted the data while balancing the functions' goodness of fit and smoothness. GAMs were run in the mgcv R package (Wood et al. 2017).

River and fish body temperature data and analyses

River temperature data were used to calculate daily means over the study period (Teme tributary and Severn mainstem). The significance of differences in mean daily river temperatures between the two rivers were tested in a paired t-test. The daily mean body temperature of each fish on their days of detection were then calculated, with box plots used to compare the distribution of the mean daily river and fish body temperatures. Fish body temperatures were only available on days when the individual fish was detected on a receiver, whereas mean river temperatures were available for all study days (cf. Results). As a result, testing the relationship of river versus body temperature for each individual fish in linear regression used daily mean data only from the actual days when the fish was detected on at least

one receiver. The river temperatures used in these regression models were from the Pixham logger on the River Severn (Fig. 1), with the reasons for this being twofold. Firstly, the Severn mainstem was the warmer river; thus any movement into the Teme tributary by an individual fish would represent a movement into cooler water (cf. Results). Secondly, bream were only ever recorded in the Severn mainstem; thus the temperatures in the Teme tributary were not relevant for the species (Table 1). The results of the regression models were the significance of the relationship between fish and River Severn temperatures, and their regression coefficients *a* and *b*, with these coefficients then tested against the fish median body temperatures in a linear model to identify the extent to which they were predictors of the temperature variability across the individuals.

A principal components analysis (PCA) was then completed to summarise data of fish length, total range, median body temperature, mean daily distance, and the regression coefficients *a* and *b* using the *prcomp* function in R. The outputs of the PCA were the extent of variability explained on axes PC1 and PC2 (and the contributions of each variable to this variability), with the scores retained for each individual fish on PC1 and PC2 and used to visualise their distribution in a plot using the *ggbiplot* function in the ggbiplot package in R.

Results

Fish movement metrics

Across the 16 barbel, six were only ever detected in the Severn, four only in the Teme, and six in both rivers (Table 1; Supplementary material, Fig. S1). Three of these barbel were also detected upstream of Diglis Weir on the Severn (most likely passing the weir via the new fish pass), and four were detected upstream of at least one modified weir on the Teme, resulting in an occupancy of river length of 62 km across all barbel (Fig. S1). Conversely, bream were only ever detected as being in the main River Severn, with none recorded as moving upstream of any weir, resulting in their overall occupancy of 37 km of river length (Fig. S1).

In the individual barbel where movement metrics could be calculated, there was relatively high variability in their total ranges (1457–27,961 m) and mean daily distances (12–516 m) when compared with bream (total ranges: 2271–13,347 m; mean daily distances: 22–132 m) (Table 1). The high individual variability in the barbel metrics meant, however, that differences in total range and mean daily distances between the species were not significant (Mann–Whitney *U* test: total range, $Z = 1.66$, $P = 0.10$; mean daily distance, $Z = 0.87$, $P = 0.43$). GAMs revealed that variance in the daily distances moved by both species
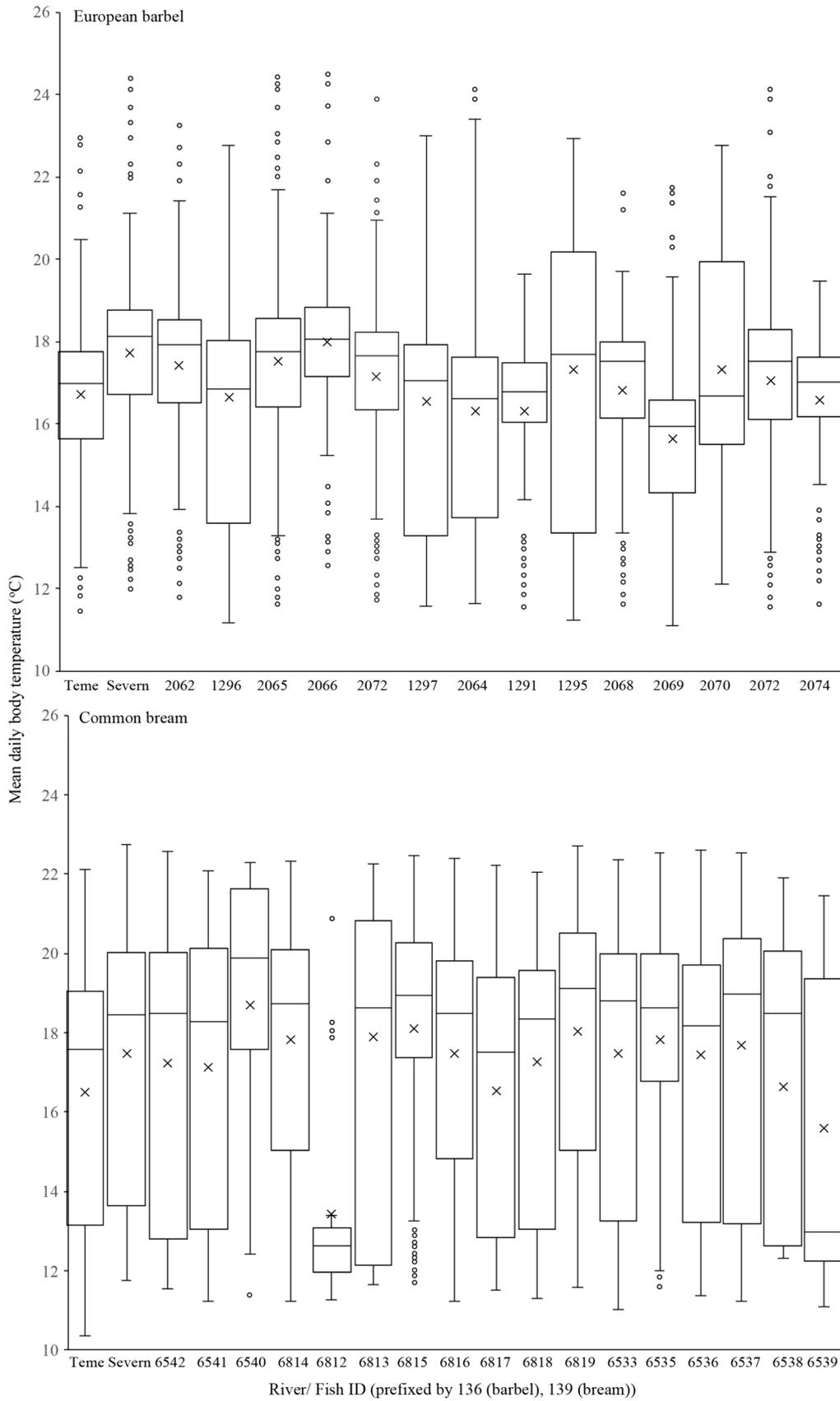
◀ **Fig. 3** Box plots of mean daily temperatures in summer 2021 for the River Teme and Severn, and European barbel (top) and summer 2022 for the River Teme and Severn, and common bream, where horizontal lines represent the 10th, 25th, median, 75th and 90th percentiles, clear circles are outliers, and x is the mean

was significantly related to the interaction of flow and river temperature, where movements were generally higher on days of lower temperatures and higher flow, with the effect of individual fish identification also significant (Table 2; Fig. S2).

River versus fish body temperatures

The River Severn was significantly warmer than the Teme across both summers (paired t-test: 2021: $t = 30.82$, df $= 109$, $P < 0.001$; 2022: $t = 20.06$, df $= 121$, $P < 0.001$; Fig. 2). The mean daily temperature of the Teme was 16.7 ± 0.5 °C in 2021 and 16.5 ± 0.6 in 2022, while in the Severn it was 17.7 ± 0.5 °C in 2021 and 17.5 ± 0.6 °C in 2022 (Table 3). The warmest river temperatures were recorded in late July 2021 (Severn maximum: 24.9 °C; Teme maximum: 24.0 °C), with river temperatures in 2022 not exceeding 23 °C (Fig. 2).

Recorded barbel body temperatures in summer 2021 ranged between 11.0 and 24.8 °C, with the highest differences in mean daily body temperatures between individuals occurring in the warm period of late July 2021 (Fig. 2), where the maximum range in the mean daily temperatures across all detected barbel was 4.2 °C. For common bream, recorded bream body temperatures in summer 2022 ranged between 10.9 and 23.0 °C. In a warm period between 17 and 22 July 2022, when mean daily river temperatures were between 21.3 and 22.6 °C (Fig. 2), mean daily bream body temperatures were between 20.5 and 22.7 °C, with the maximum difference between individual bream being 1.2 °C. In these warmer periods, no fish of either species made a movement from the Severn mainstem (warmer) to the Teme tributary (cooler). Percentiles of fish mean daily body temperatures revealed some variability between individuals of both species (Fig. 3). The common bream ID of 1396812 and 1396539 both had very low median temperature values, which was due to most of their detections occurring in October, when the river temperatures were reduced compared with July to September (Table 1, Fig. 3).

The linear relationships of mean daily body temperatures of each fish and the mean daily water temperatures of the Severn mainstem only on days when the individual fish was detected were all highly significant (linear regression, $P < 0.01$; Table 4; Figs. S3, S4). The relationships of regression coefficients a and b versus median fish body temperatures (omitting bream 1396812 and 1396539 for reasons outlined above) revealed a significant and negative relationship for a ($R^2 = 0.64$, $F_{1,27} = 47.97$, $P < 0.01$), and significant

and positive for b ($R^2 = 0.66$, $F_{1,27} = 52.59$, $P < 0.01$) (Fig. 4). In the PCA, PC1 explained 45.7% and PC2 26.3% of the variability in the dataset comprising median body temperatures, regression coefficients a and b, fork length, total range and mean daily distance (data combined for both species). PC1 described the thermal variability of the fish (a and b had the largest contributions for both species), and PC2 described the variability in their movement metrics (total range and mean daily distance had the largest contributions for both species) (Table 4). Compared with bream, barbel had greater differentiation in their individual scores when plotted in the space of PC1 and PC2 (Fig. 5). The scores of barbel that were only ever detected in the Severn mainstem were relatively close to those of bream and were also distinct from barbel only detected in the Teme tributary (Fig. 5). The barbel that were detected in both the Severn and Teme were more variable in their scores versus those only detected in the single rivers (Fig. 5).

Discussion

Barbel expressed relatively high individual variability in their movement metrics and body temperatures when compared with bream, with barbel that moved more having relatively higher body temperatures, with this result for barbel thus consistent with the prediction (but not for bream). There was no indication that any of the tagged fish had moved from the warmer Severn mainstem into the cooler waters of the Teme tributary during periods of elevated water temperatures, such as during July 2021 when barbel body temperatures were measured to 24.8 °C. This absence of behavioural thermoregulation in both species was contrary to the prediction. The relatively high intra-specific variability in barbel was facilitated by their use of the modified weirs in the Teme tributary and fish passes on weirs on the Severn mainstem, which enabled their use of 62 km of river length. The relatively low intra-specific variability in bream was due to their use only of the Severn mainstem that restricted their use of only 37 km of river length, with no individual bream entering the Teme tributary or moving upstream of a weir via a fish pass during the study period. However, following completion of the study period, some of the bream were subsequently detected upstream of weirs in both the Teme tributary and Severn mainstem (unpublished data).

This individual variability of barbel is consistent with other barbel movement studies on this river (Hunt and Jones 1974; Gutmann Roberts et al. 2019) and elsewhere (e.g. Penaz et al. 2002). Individual differences in behaviour have also been shown to affect the thermal habitat use by other fishes. For example, in a study to investigate how the personality of wild cod *Gadus morhua* affected their spatial

Table 4 Scores on PC1 (45.7% of variance explained) and PC2 (26.3%) by species for median fish body temperatures (MBT), regression coefficients a and b, fork length (FL), total range (TR) and mean daily distance (MDD)

Species/axis	MBT	a	b	FL	TR	MDD
Barbel/PC1	0.45	−0.48	0.52	0.43	0.01	0.31
Bream/PC1	−0.48	0.58	−0.57	0.26	−0.13	−0.16
Barbel/PC2	−0.02	−0.01	0.07	0.13	−0.95	−0.27
Bream/PC2	0.20	−0.10	0.20	0.20	−0.70	−0.70

responses to temperature change, Villegas-Ríos et al. (2018) completed behavioural assays to categorise fish into personality types (proactive/reactive) before tracking their movements, revealing that as sea temperatures increased, the total range of only the reactive individuals decreased. Although the telemetry data here did not allow quantification of barbel

Fig. 4 Relationships of the regression coefficients a (top) and b (middle) from the linear relationships of River Severn mean daily temperature and fish body temperature versus median fish body temperatures (species combined), and the relationship of regression coefficient a versus b (bottom) for common bream (squares) and European barbel, where black symbols are fish only detected in the Severn mainstem, white symbols are fish only detected in the Teme tributary, and grey symbols are fish detected in both rivers. Dashed lines represent significant regression relationships ($P < 0.01$) (color figure online)

personality types, the fish travelling higher mean daily distances were most likely expressing a personality type that was pro-active or intermediate, whereas those of relatively low activity were considered likely to be reactive (MacKay and Haskell 2015).

The range of the mean daily barbel body temperatures increased as river temperatures increased, but this was not apparent in bream. At the highest river temperatures in late July 2021, differences in water temperatures between the lower reach of the River Teme and contiguous Severn were up to 1.5 °C, yet the largest daily range in body temperatures across individual barbel was 4.2 °C. The barbel with the lowest body temperature during this period had moved from the River Severn into the River Teme prior to the study commencing, continued upstream for approximately 50 km (most likely for spawning), and remained in that area throughout the study period. All barbel were able to move relatively freely across this entire area during the study period due to the recent weir modifications in the Teme and the construction of fish passes on Severn weirs. Indeed, seven tagged barbel were detected as moving upstream of these weirs in summer 2021, whereas before fish pass construction, barbel only passed weirs on the Teme when flows were at least Q_{50}, and none were recorded passing weirs on the Severn, despite approaches (Gutmann Roberts et al. 2019). During the study period, no bream were detected as moving upstream over the modified weirs and through the fish passes. However, bream did move upstream through fish passes in subsequent spawning periods (unpublished data).

Behavioural thermoregulation provides thermally stressed fish with the opportunity to move to waters of more optimum temperatures in order to maintain their normal physiological functioning (Amat-Trigo et al. 2023). Movements of salmonid fishes from main rivers to tributary streams have resulted in fish lowering their experienced water temperatures by up to 10 °C (Kaya et al. 1977; Chiaramonte et al. 2016). A recent meta-analysis of behavioural thermoregulation in freshwater fish revealed that the mean reduction in water temperatures achieved through these movements was 4.7 °C (Amat-Trigo et al. 2023). Given that the mean daily body temperatures of barbel here differed between individuals by up to 4.2 °C, the fish with higher body temperatures could have demonstrated
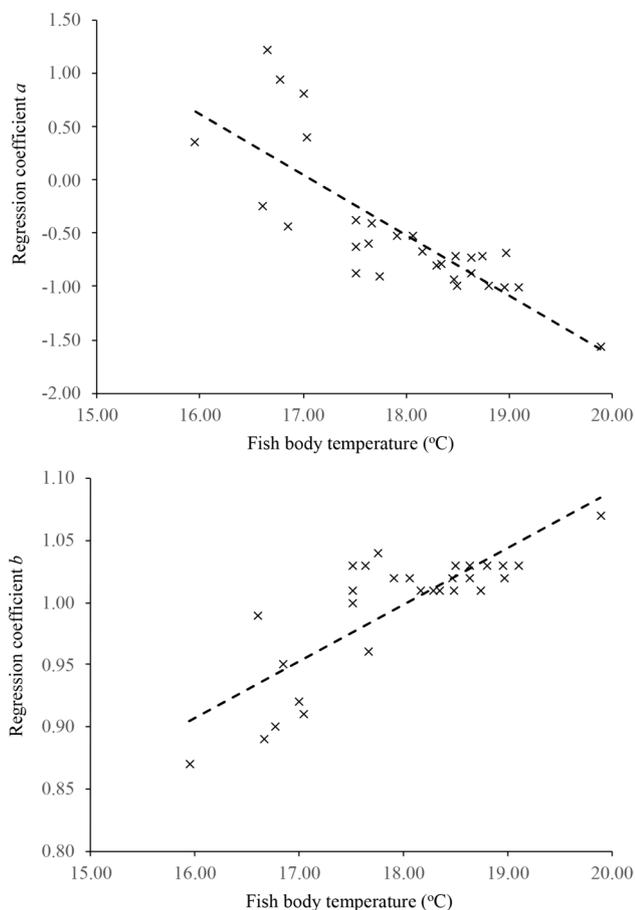
Fig. 5 Position of individual fish by species along principal components 1 and 2, where black squares are bream (detected only in Severn), black circles are barbel detected only in the Severn mainstem, clear circles are barbel detected only in the Teme tributary, and grey circles are barbel detected in both the Severn and Teme. Arrows depict variable contributions to principal components, where *MBT* is the median body temperatures of fish, *a* and *b* are regression coefficients, *FL* is fork length, *TR* is total range, *MDD* means daily distance (color figure online)
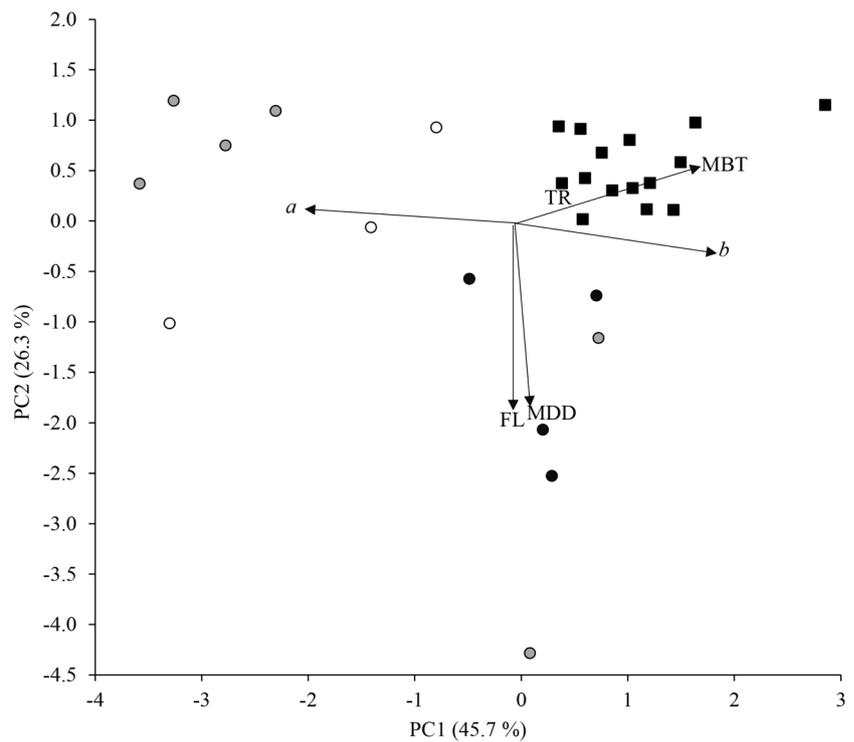
behavioural thermoregulation through deliberate movements from the warmer (Severn) to cooler waters (middle reaches of the Teme). However, there was no evidence in either species of movements to cooler waters during periods of elevated water temperatures (contrary to the prediction). This lack of behavioural thermoregulation could have been due to the maximum water and body temperatures rarely exceeding the published thermal optimum of barbel and never for bream (Souchon and Tissot 2012). These water and body temperatures were also below the reported CTMs for the species (Souchon and Tissot 2012). Thus, the risk of physiological stress and mortality from these warming events could have been negligible. However, these thermal optima and CTM values of both species were drawn from published values completed on more southerly populations in Europe (Souchon and Tissot 2012), and so the values of these thermal metrics for the lower River Severn populations could be lower. If the tagged fishes had been thermally stressed in these warmer periods then the costs of searching for cooler habitat, especially if located some distance away, might have been too high for individuals to risk (i.e. their lack of upstream movement could have been a response to increased thermal stress).

Although it can only be speculated as to why some of the fish did not move into cooler waters during the warm water periods, it was nevertheless apparent that the presence of the cooler waters of the River Teme could become more important for maintaining these fish populations in future, especially barbel. This is because predictive models suggest

that for every 2 °C increase in air temperature through climate warming, there will be an increase in river temperature of approximately 1.5 °C, with this warming already being recorded in North American rivers (Hardenbicker et al. 2017; Isaak et al. 2017). With air temperatures potentially warming by over 4 °C in some emission scenarios and a concomitant increased risk of extreme heat waves and associated fish deaths (Till et al. 2019), then it is likely that further warming of the main River Severn could result in the warm water-tolerant barbel responding by increasing their occupancy of the lower River Teme, with fish that tend to occupy the lower Teme responding by moving further upstream into cooler waters in its middle reaches. With bream not using the River Teme in the summer period, then their responses to elevated temperatures might need to occur within the warmer main River Severn.

An inherent issue with the results of this study is that they were derived from a relatively small sample of tagged fishes, which was further reduced by some tagged barbel having tracking data that were insufficient for calculating movement metrics. However, the focus here was on individual responses to water temperature changes rather than investigating population-level responses. Moreover, individual-level data gained from relatively small sample sizes using telemetry methods have been applied to answering other contemporary questions on thermoregulation strategies, including how sharks cope with temperature extremes when diving from the surface into deep waters ($n < 10$; Royer et al. 2023). Moreover, the sample size of barbel here was sufficient to

capture high variability in fish spatial habitat use and a wide range of body temperatures, with the individual variability in movement metrics being similar to that in other studies (e.g. Gutmann Roberts et al. 2019). The relatively low variability in individual bream behaviours was also consistent with other studies indicating that their movements are generally predictable, with high fidelity to specific river areas (e.g. Winter et al. 2021).

In summary, there was considerable individual variation in the movement metrics and spatial habitat use of the tagged barbel, with both of these aspects then reflected in the body temperatures of the fish. This individual variation was less evident in the tagged bream, with more consistency in their spatial and thermal habitat use. There was no evidence to suggest that short-term behavioural thermoregulation was a strategy used by either species, despite periods of elevated water temperatures in both study periods and the presence of a cool-water refugium in the study area (River Teme), where barbel had much lower body temperatures than those in the Severn on the same day. These results suggest that for ectothermic populations of high phenotypic diversity, maintaining thermally heterogenous habitats and ensuring that individuals can move freely between these habitats will be important in ensuring that individuals can express their natural behaviours across all thermal conditions.

Declarations

Conflict of interest The authors declare no conflict of interest.

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

References

Acolas ML, Le Pichon C, Rochard E (2017) Spring habitat use by stocked one year old European sturgeon *Acipenser sturio* in the freshwater-oligohaline area of the Gironde estuary. Est Coast Shelf Sci 196:58–69

Amat-Trigo F, Andreou D, Gillingham PK, Britton JR (2023) Behavioural thermoregulation in cold-water freshwater fish: Innate resilience to climate warming? Fish Fish 24:187–195

Antognazza CM, Britton JR, De Santis V et al (2021) Environmental DNA reveals the temporal and spatial extent of spawning migrations of European shad in a highly fragmented river basin. Aquat Conserv 31:2029–2040

Biro PA, Beckmann C, Stamps JA (2010) Small within-day increases in temperature affects boldness and alters personality in coral reef fish. Proc Roy Soc B 277:71–77

Britton JR, Pegg J (2011) Ecology of European barbel *Barbus barbus*: implications for river, fishery, and conservation management. Rev Fish Sci 19:321–330

Broadmeadow SB, Jones JG, Langford TEL, Shaw PJ, Nisbet TR (2011) The influence of riparian shade on lowland stream water temperatures in southern England and their viability for brown trout. Riv Res Appl 27:226–237

Campbell HA, Watts ME, Dwyer RG, Franklin CE (2012) V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Mar Freshw Res 63:815–820

Cerqueira M, Rey S, Silva T, Featherstone Z, Crumlish M, MacKenzie S (2016) Thermal preference predicts animal personality in Nile tilapia *Oreochromis niloticus*. J Anim Ecol 85:1389–1400

Chiaramonte LV, Ray RA, Corum RA, Soto T, Hallett SL, Bartholomew JL (2016) Klamath river thermal refuge provides juvenile salmon reduced exposure to the parasite *Ceratonova shasta*. Trans Am Fish Soc 145:810–820

Comte L, Grenouillet G (2013) Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography 36:1236–1246

Cossins AR, Bowler K (1987) Temperature biology of animals. Chapman and Hall, New York

Desforges JE, Birnie-Gauvin K, Jutfelt F et al (2023) The ecological relevance of critical thermal maxima methodology for fishes. J Fish Biol 102:1000–1016

González-del-Pliego P, Scheffers BR, Freckleton RP et al (2020) Thermal tolerance and the importance of microhabitats for Andean frogs in the context of land use and climate change. J Anim Ecol 89:2451–2460

Grill G, Lehner B, Thieme M, Geenen B et al (2019) Mapping the world's free-flowing rivers. Nature 569:215–221

Gudmundsson L, Boulange J, Do HX et al (2021) Globally observed trends in mean and extreme river flow attributed to climate change. Science 371:1159–1162

Gutmann Roberts C, Britton JR (2020) Spawning strategies in cypriniform fishes in a lowland river invaded by non-indigenous European barbel *Barbus barbus*. Hydrobiologia 847:4031–4047

Gutmann Roberts C, Hindes AM, Britton JR (2019) Factors influencing individual movements and behaviours of invasive European barbel *Barbus barbus* in a regulated river. Hydrobiologia 830:213–228

Hardenbicker P, Viergutz C, Becker A, Kirchesch V, Nilson E, Fischer H (2017) Water temperature increases in the river Rhine in response to climate change. Reg Environ Change 17:299–308. https://doi.org/10.1007/s10113-016-1006-3

Hare DK, Helton AM, Johnson ZC, Lane JW, Briggs MA (2021) Continental-scale analysis of shallow and deep groundwater contributions to streams. Nat Comms 12:1–10

Huey RB, Kingsolver JG (1993) Evolution of resistance to high temperature in ectotherms. Am Nat 142:21–46

Hunt PC, Jones JW (1974) A population study of *Barbus barbus* (L.) in the River Severn, England: II. Movements J Fish Biol 6:269–278

Isaak DJ, Wenger SJ, Peterson EE et al (2017) The NorWeST summer stream temperature model and scenarios for the western US: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. Wat Resource Res 53:9181–9205

Kaya CM, Kaeding LR, Burkhalter DE (1977) Use of a coldwater refuge by rainbow and brook trout in a geothermally heated stream. Prog Fish Cult 39:37–39

MacKay JR, Haskell MJ (2015) Consistent individual behavioral variation: the difference between temperament, personality and behavioral syndromes. Animals 5:455–478

Magel JM, Dimoff SA, Baum JK (2020) Direct and indirect effects of climate change-amplified pulse heat stress events on coral reef fish communities. Ecol Appl 30:e02124

McDonnell LH, Chapman LJ (2015) At the edge of the thermal window: Effects of elevated temperature on the resting metabolism, hypoxia tolerance and upper critical thermal limit of a widespread African cichlid. Conserv Physiol 3:cov050

Morgan R, Finnøen MH, Jensen H, Pélabon C, Jutfelt F (2020) Low potential for evolutionary rescue from climate change in a tropical fish. Proc Nat Acad Sci 117:33365–33372

Núnez-Riboni I, Taylor MH, Kempf A, Püts M, Mathis M (2019) Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (*Gadus morhua*) under climate change. ICES J Mar Sci 76:2389–2403

Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7:e6876

Penaz M, Barus V, Prokes M, Homolka M (2002) Movements of barbel, *Barbus barbus* (Pisces: Cyprinidae). Folia Zool 51:55–66

R Studio Team (2017) R Studio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/

Radtke G, Wolnicki J, Kapusta A, Przybylski M, Kaczkowski Z (2022) Critical thermal maxima of three small-bodied fish species (Cypriniformes) of different origin and protection status. Euro Zool J 89:1351–1361

Rey S, Boltana S, Vargas R, Roher N, MacKenzie S (2013) Combining animal personalities with transcriptomics resolves individual variation within a wild-type zebrafish population and identifies underpinning molecular differences in brain function. Mol Ecol 22:6100–6115

Rey S, Digka N, MacKenzie S (2015) Animal personality relates to thermal preference in wild-type zebrafish, *Danio rerio*. Zebrafish 12:243–249

Ritter TD, Zale AV, Grisak G, Lance MJ (2020) Groundwater upwelling regulates thermal hydrodynamics and salmonid movements during high-temperature events at a montane tributary confluence. Trans Am Fish Soc 149:600–619

Royer M, Meyer C, Royer J et al (2023) "Breath holding" as a thermoregulation strategy in the deep-diving scalloped hammerhead shark. Science 380:651–655

Silverman BW (1986) Density estimation for statistics and data analysis. Chapman and Hall, New York

Souchon Y, Tissot L (2012) Synthesis of thermal tolerances of the common freshwater fish species in large Western Europe rivers. Know Man Aquat Sci 405:03

Till A, Rypel AL, Bray A, Fey SB (2019) Fish die-offs are concurrent with thermal extremes in north temperate lakes. Nat Clim Change 9:637–641

Trapletti A, Hornik K, LeBaron B, Hornik MK (2017) Package 'tseries'.

Unlocking the Severn (2023). Our fish passes. https://www.unlockingthesevern.co.uk/our-fish-passes/. Last accessed 22/12/2023

Villegas-Ríos D, Réale D, Freitas C, Moland E, Olsen EM (2018) Personalities influence spatial responses to environmental fluctuations in wild fish. J Anim Ecol 87:1309–1319

Winter ER, Hindes AM, Lane S, Britton JR (2021) Movements of common bream *Abramis brama* in a highly connected, lowland wetland reveal sub-populations with diverse migration strategies. Freshw Biol 66:1410–1422

Wood SN, Li Z, Shaddick G, Augustin NH (2017) Generalized additive models for gigadata: modelling the UK black smoke network daily data. J Am Stat Assoc 112:1199–1210. https://doi.org/10.1080/01621459.2016.1195744