Received: 29 June 2020 | Accepted: 14 August 2020
DOI: 10.1111/jfb.14504

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Predicting the factors influencing the inter- and intraspecific survival rates of riverine fishes implanted with acoustic transmitters

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Funding information
EW of the EU LIFE+ Nature and Biodiversity Programme, Grant Number: LIFE14NAT/UK/000054; Environment Agency

Abstract

Biotelemetry is a central tool for fisheries management, with the implantation of transmitters into animals requiring refined surgical techniques that maximize retention rates and fish welfare. Even following successful surgery, long-term post-release survival rates can vary considerably, although knowledge is limited for many species. The aim here was to investigate the post-tagging survival rates in the wild of two lowland river fish species, common bream *Abramis brama* and northern pike *Esox lucius*, following their intra-peritoneal double-tagging with acoustic transmitters and passive integrated transponder (PIT) tags. Survival over a 2-year period was assessed using acoustic transmitter data in Cox proportional hazards models. Post-tagging survival rates were lowest in the reproductive periods of both species, but in bream, fish tagged just prior to spawning actually had the highest subsequent survival rates. Pike survival was influenced by sex, with males generally surviving longer than females. PIT tag detections at fixed stations identified bream that remained active, despite loss of an acoustic transmitter signal. In these instances, loss of the acoustic signal occurred up to 215 days post-tagging and only during late spring or summer, indicating a role of elevated temperature, while PIT detections occurred between 18 and 359 days after the final acoustic detections. Biotelemetry studies must thus always consider the date of tagging as a fundamental component of study designs to avoid tagged fish having premature end points within telemetry studies.

KEYWORDS

common bream, mortality, northern pike, PIT tag, tag retention, tracking

1 | INTRODUCTION

Biotelemetry has developed into a central tool for fisheries management, providing valuable information on population dynamics, fish behaviours and movements, habitat connectivity, and even inter-specific relationships (*e.g.*, Halfyard *et al.*, 2017; Hussey *et al.*, 2015). The technology of tracking devices has advanced considerably in recent decades, from simple, passive, externally attached markers to active, internally implanted transmitters, or "tags", that can broadcast a multitude of information over large distances (Hussey *et al.*, 2015; Lucas & Baras, 2001). As a result, the interpretation of telemetry data has become increasingly complex, requiring consideration of several limitations, such as signal interference (Simpfendorfer *et al.*, 2008), detection range/efficiency (*e.g.*, Huveneers *et al*., 2016) and the effects of tagging on study animals (Bridger & Booth, 2003).

The implantation of transmitters into fish (and other animals) requires refined surgical techniques completed by experienced practitioners to minimize the adverse effects on the welfare of the animal (Bolland *et al*., 2019; Skov *et al*., 2020). This should ensure that the survival of the tagged animal is not compromised and that it also returns to normal behaviour relatively quickly (Cooke *et al*., 2011; Moore *et al*., 1990). More fundamentally, the tagged individuals should be representative of the wider, untagged population (Bridger & Booth, 2003), yet many studies evidence inter- and intraspecific variation in post-tagging success. For example, intracoelomic tag implantation maximizes survival and recovery of fusiform fishes when compared to external tag attachment (Bégout Anras *et al*., 2003; Cooke *et al*., 2011; Jepsen *et al*., 2002), but can result in poorer survival and altered behaviour in flatfishes such as the European flounder (*Platichthys flesus*, L.) (Neves *et al*., 2018). Within species, tagging success may be dependent on body size relative to tag size (Welch *et al*., 2007). It can also vary by sex, with some studies reporting lower survival and tag retention in females (Jepsen *et al*., 2002; Šmejkal *et al*., 2019). Furthermore, environmental factors can influence fish responses to tagging, particularly water temperature, with elevated temperatures tending to reduce survival and welfare (Walsh *et al*., 2000; Yasuda *et al*., 2015).

Ultimately, research objectives, study design, and data interpretation are driven by knowledge of the impacts of tagging on fish survival and behaviour (Donaldson *et al*., 2014). This includes the planning of sampling and release protocols, tagging procedures and timeframes of subsequent telemetry (Bolland *et al*., 2019). However, of studies that apply acoustic telemetry to aquatic ecology/behavioural research, around 50% fail to account for or acknowledge the mortality of the study species (Klinard & Matley, 2020), and a standardized method for identifying the fates of tagged fish (*e.g*., survival, natural mortality, fishing mortality) has only recently been developed (Villegas-Ríos *et al*., 2020). Consequently, as the diversity of tracking technologies and tracked fish species expands, including a wider range of fish sizes and morphologies, such as Anguillids and flatfish (Neves *et al*., 2018; Thorstad *et al*., 2013), knowledge gaps surrounding the effects of telemetry are potentially widening. This can be especially problematic for researchers studying species where information is more limited, as it constrains their ability to optimize tagging procedures in relation to maximizing fish welfare and survival or draw robust conclusions from the resulting data.

The aim of this study was thus to investigate the survival rates of two lowland river fish species following their intraperitoneal double-tagging with acoustic transmitters and passive integrated transponder (PIT) tags, and their subsequent release back into the wild. The two species were common bream (*Abramis brama*, L., "bream" hereafter), a cyprinid that often dominates the biomass of lowland river fish assemblages in north-west Europe (Lyons & Lucas, 2002), and northern pike (*Esox lucius*, L., "pike" hereafter), an apex predator (Beaudoin *et al*., 1999). Survival within the study was assessed using data from the acoustic transmitters, with survival over a 2-year post-tagging period requiring the fish to remain alive, stay within the study area and continue to transmit acoustic signals *via* their tags. As a result of the multimethod, double-tagging approach, PIT tag data were then used to categorize fish that had not "survived" into those that had actually died and those that remained active, but whose acoustic signals had been lost. The study objectives were thus to (a) assess the survival rates of the two fishes in relation to their individual characteristics, and the timing and location of tagging; and (b) for those fish that did not survive within the study, assess their fate (death, leaving the study area, or loss of the acoustic tag signal, such as through tag failure or tag expulsion).

2 | MATERIALS AND METHODS

2.1 | Study system and telemetry equipment

The study system was the River Bure in eastern England, along with its tributaries the Rivers Ant and Thurne, plus associated small shallow lakes (medieval peat diggings termed "Broads") and dykes, which form the northern area of the Broads National Park (Figure 1). The Bure is 87 km in length, flows south-east towards Breydon Water estuary at Great Yarmouth and has a mean discharge of 6 $m^3\ s^{-1}$ into the North Sea (Moss, 1977). By contrast, the Ant is 27 km in length and the Thurne is just 11 km in length. Conductivity (as a measure of salinity) can fluctuate between 1000 and 50,000 $\mu S\ cm^{-1}$ at Acle (Figure 1), with major saline incursions often occurring during spring tides in winter and early spring (Environment Agency, unpublished data). Channel widths towards the upper limits of the study area were approximately 25 m wide with depths to 1.5 m, while in the lower reaches they increased to >40 m, with depths of over 3 m. Across the study area, bream tend to spawn in late April and throughout May, and pike in late March to mid-April.

A fixed array of 43 acoustic receivers (Vemco, VR2W) was installed throughout the study system (Figure 1) in October 2017, prior to the first fish sampling and tagging event. A further 13 receivers were deployed in January 2018 (n = 1) and March 2019 (n = 12) to expand the monitored area (Figure 1). Receiver coverage was optimized to monitor longitudinal riverine movements to at least 6 km resolution, as well as finer-scale lateral movements. Data were downloaded every 3 months onto a laptop, while battery replacements and receiver maintenance occurred annually. This enabled the tracking of fish implanted with acoustic transmitters until the study end in November 2019. Receivers were placed in the channel margins at approximately mid-water depth (1.0–1.5 m) to optimize detection efficiency. Range testing revealed some variability in detection distances that correlated to changes in environmental conditions (E. Winter, unpublished data), but which rarely fell below channel width distance.

Acoustic telemetry was deemed inappropriate for tracking fish in the small marshland drainage channels of the study system, but utilizing multimethod telemetry can be useful for monitoring fish movements at varying spatial scales (*e.g*., Tummers *et al*., 2016). Thus, six stream-width, swim-through half-duplex (HDX) radio-frequency

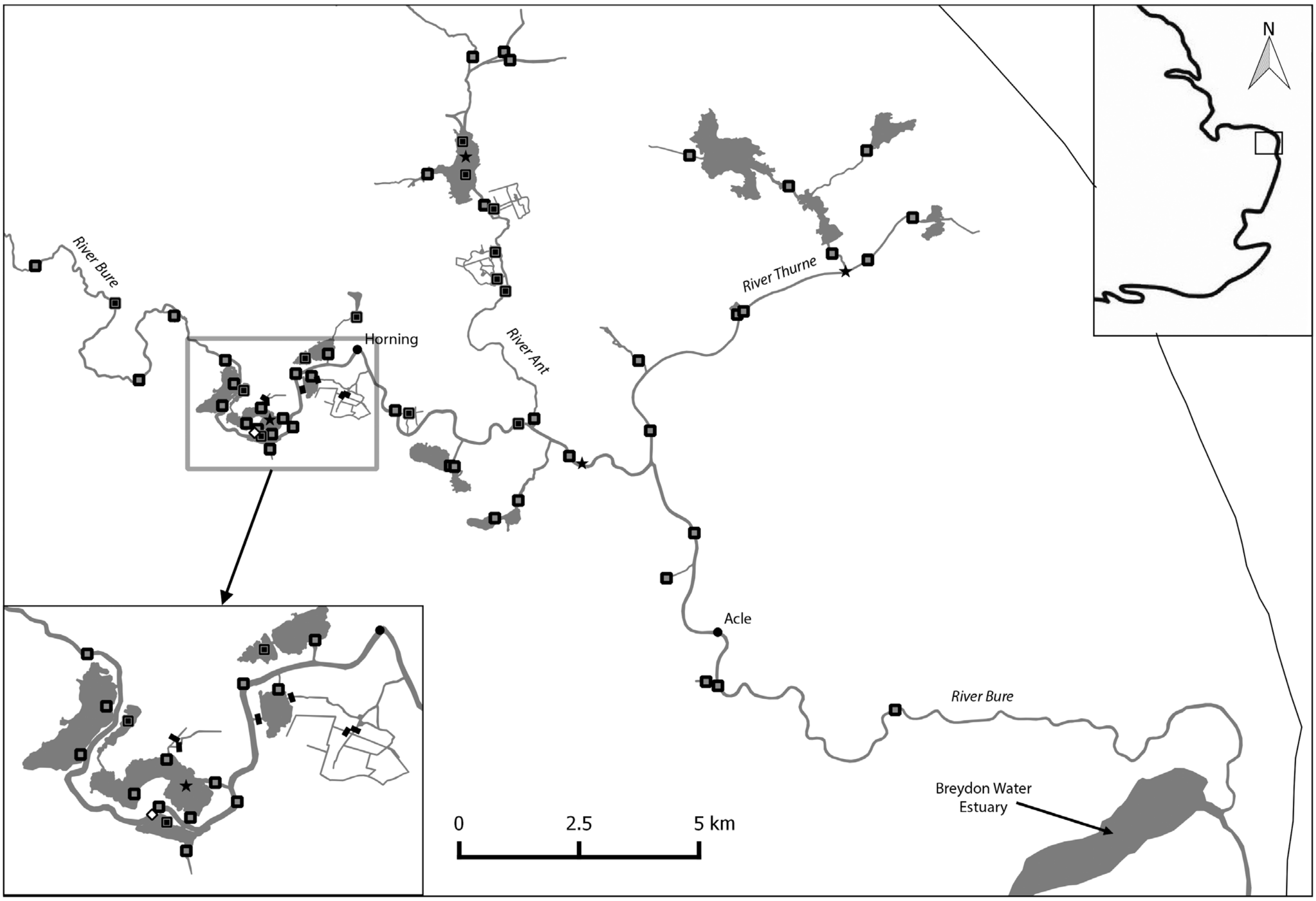

FIGURE 1 Map of the River Bure study system, eastern England, showing sampling locations, acoustic receivers, PIT antennae and temperature logger. Channel width not to scale. (★) approx. sampling location; (◇) temperature logger; (——) PIT antenna; (▣) deployed post-Nov 2017; (■) deployed pre-Nov 2017

identification (RFID) PIT antennae (15–30 m circumference), with remote, telemetric, web-based data logging systems (Wyre Micro Development, Bungay, Suffolk, UK) were constructed and installed in dykes in March 2018 (Figure. 1). PIT tags were detected by readers (model WMD-HDX-DEC-MK5) that interrogated the loops continually and recorded tag presence 10 times per second. Data were transmitted to a cloud-based server *via* a multiband roaming sim modem (model WMD-MC-GPRS/GSM) and accessed remotely. Minimum horizontal detection range for 23 mm tags (see below) was measured at installation (approx. 40 cm) and the tuning frequency of each loop was maintained using a digital dynamic antenna tuning unit (model WMD-DDATU). The RFID PIT detector systems were powered by 2 × 12 V 120 A batteries (wired in parallel) which were charged *via* solar arrays and maintained by a configurable charge controller and power supply filter that limited noise (models WMD-MSC-45, WMD-PS-F). Each PIT antenna was operational for between 37% and 68% of the study period; periods of nonoperation were at least partly due to inconsistent power supply (*e.g.*, due to failure to keep solar panels clear of undergrowth or damage to equipment by boats), which were identified using half-hourly records of battery status and antenna frequency.

In addition, water temperature (±0.5°C) was recorded at hourly intervals by a data logger (HOBO® Pendant; model MX2202, Onset Computer Corporation, Bourne, MA, USA; Figure 1).

2.2 | Fish sampling and tagging

The study area was divided into four sampling locations: Upper Bure, Lower Bure, River Ant and River Thurne. The upper limit of saline incursion on the River Bure (Horning, Figure 1; Clarke, 1990) provided the boundary between the Upper Bure and the Lower Bure. Several fish sampling and tagging events occurred between November 2017 and September 2018, and details of their timing and location are shown in Table 1. Water temperature during the November 2017 and January 2018 tagging events was 5.0–9.4°C, while during the April 2018 and September 2018 events it was 15.0–17.8°C. Fish were then tracked for up to 2 years to 5 November 2019. In all sampling, bream and pike were caught by rod and line angling, as sampling by methods such as electric fishing, seine netting and fyke netting were too inefficient in these large waterbodies (Radinger *et al.*, 2019). Bream were captured using ledger rods and monofilament lines, with groundbait

TABLE 1 Details of common bream (a) and pike (b) tagging dates, fish lengths, acoustic tracking durations and proportion of days detected, grouped by sampling location

Sampling location	Tagging date(s)	Length (mm)	Tracking duration (days)	Proportion of days detected	*n* total	*n* lost to study	*n* detected on PIT antennae
(a) Bream							
Upper Bure	6 Nov 2017–8 Nov 2017	374–491 (435 ± 11)	0–725 (217 ± 76)	0.84 ± 0.04	26	23	2
Upper Bure	20 Apr 2018–23 Apr 2018	313–527 (413 ± 11)	18–562 (414 ± 54)	0.56 ± 0.07	62	22	14
Lower Bure	8 Nov 2017–9 Nov 2017	286–471 (362 ± 47)	25–524 (181 ± 120)	0.56 ± 0.18	8	8	0
Lower Bure	15 Sep 2018–18 Sep 2018	290–503 (389 ± 16)	2–414 (177 ± 44)	0.53 ± 0.07	43	34	0
Thurne	14 Jan 2018	341–471 (394 ± 15)	40–371 (132 ± 38)	0.44 ± 0.08	17	17	1
Ant	27 Jan 2018–29 Jan 2018	362–502 (406 ± 13)	28–645 (286 ± 92)	0.22 ± 0.07	25	20	1
(b) Pike							
Upper Bure	6 Nov 2017–8 Nov 2017	583–1014 (780 ± 64)	4–727 (477 ± 144)	0.54 ± 0.16	15	7	0
Lower Bure	8 Nov 2017	776	124	0.81	1	1	0
Lower Bure	16 Jan 2018 & 28 Jan 2018	682–859 (774 ± 100)	422–644 (563 ± 139)	0.69 ± 0.16	3	1	0
Lower Bure	16 Sep 2018	590	413	0.20	1	0	0
Thurne	13 Jan 2018–15 Jan 2018	590–1143 (766 ± 69)	13–659 (434 ± 143)	0.37 ± 0.09	14	6	0
Ant	27 Jan 2018–28 Jan 2018	570–935 (758 ± 76)	5–645 (373 ± 143)	0.26 ± 0.12	11	7	0

Note: Length of fish and tracking duration are represented by the range of values, with mean ± 95% CI in parentheses, while P_d represents the mean ± 95% CI. *n* total, sample size; *n* lost to study, number lost due to disappearance from the acoustic array or a signal becoming stationary. Numbers of fish detected on the PIT antennae are also presented.

mixes in swim-feeders and worms or maggots presented on hooks close to the substrate. Pike were captured using specialist rods, braided fishing line (>40 lbs breaking strain) and wire traces to prevent the fish biting through the line, and used with either dead-bait (marine and freshwater fishes) or spinners, spoons and lures (hard and soft bodied artificial fishes). Each captured fish was measured (fork length ±1 mm; Table 1) and, where possible, sexed. Sex determination in both species involved inspecting the shape of the urogenital opening (*e.g*., Casselman, 1974). For bream sampled during the spawning season (April 2018), other characteristics also informed sex determination, such as body shape, the presence of spawning tubercles on the head and the production of milt when lightly pressing the abdomen (when the fish were under general anaesthesia).

Each fish was surgically implanted with an internal acoustic transmitter ("tag") sourced from Vemco (V13: length 36 mm × diameter 13 mm, 6.0 g mass in water, *n* = 193; V9: length 27.5 mm × diameter 9 mm, 2.7 g mass in water, *n* = 9) or Thelma Biotel (ID-LP13: length 28 mm × diameter 13 mm, 5.5 g mass in water, *n* = 24). Acoustic tags operated at 69 kHz and were set to pulse randomly every 60 to 120 s, providing battery lives of between 29 and 46 months, depending on transmitter type. Random transmission intervals ensured adjacent signals did not continuously overlap and cause interference. Noise quotients, calculated from summary data stored by the receivers (Simpfendorfer *et al*., 2008), revealed interference due to tag collisions at some receivers, but this was not a strong predictor of acoustic detection efficiency (E. Winter, unpublished data). All fishes were additionally tagged with an internal passive integrated transponder (PIT) tag (Wyre Micro Developments: model WMD-HDX-GL-BAR, length 23.0 mm × diameter 3.35 mm, 0.6 g mass in air, 134.2 kHz), suited for use with fixed monitoring stations (Lucas & Baras, 2000; Zydlewski *et al*., 2001). All regulated procedures were performed by the same surgeon whilst the fish were under general anaesthesia (tricaine methanesulfonate, MS-222), under the UK Home Office project licence 70/8063 and after ethical review. Iodine solution was used to disinfect surgical instruments and scales were removed from the incision site to aid scalpel and suture entry. Both acoustic and PIT tags were inserted ventrally and anterior to the pelvic fins, at the same incision site, with incisions then closed using a single suture and wound sealer. All fish were returned alive to the river following their postoperative recovery and return to normal body orientation and swimming behaviour.

2.3 | Survival analysis (acoustic transmitter data)

Factors affecting bream and pike survival were examined using semiparametric Cox proportional hazards (CPH) regression (Cox, 1972), the rationale being that this method allows for the analysis of time-varying covariates without making assumptions about the relationship between the hazard, or instantaneous rate of loss, and time (Therneau & Grambsch, 2000). The hazard function $h(t)$ at time t was determined for a set of k covariates (x_1, x_2, …, x_k) according to Murray (2006):

$$h(t) = h_0(t) \times \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k)$$

where the coefficients β indicate the relative covariate effects and $h_0(t)$ is the nonparametric baseline hazard when the covariate vector x_I = (0, 0, …, 0). The hazard ratio, $h_i(t)/h_j(t) = \exp(\beta)$, is assumed to be independent of time.

The time-to-event interval represented time since release, and the event of interest was the last recorded acoustic detection or the last recorded detection prior to a signal becoming stationary, which indicated fish death or tag expulsion within range of a receiver. Individuals were right-censored from analyses if the last detection occurred within 3 months (for bream) or 6 months (for pike) of the study end date (*i.e*., their final detections were not recorded as losses). These species-specific censoring periods were necessary given the interspecific behavioural differences of the fish, with bream tending to have much larger home ranges and higher vagility than pike (Gardner *et al*., 2013; Koed *et al*., 2006), and thus having greater probabilities of detection. Given these substantial differences in the behaviours of the two species, their data were also modelled separately. The time-constant predictors tested were fish length (cm, at capture), fish sex, sampling location (Upper Bure, Lower Bure, Thurne, Ant) and tagging date (Julian day of tagging). The time-varying covariates tested were water temperature, year and day of year (Julian day, representing seasonality). Nonlinear relationships between the hazard and day of year, as well as tagging date, were accommodated using the pspline() function within the coxph() function of R's *survival* package (Therneau, 2020). This allowed for smoothing using a "p-spline" basis, while degrees of freedom were optimized by minimizing the corrected Akaike's Information Criterion (AIC) value (Hurvich *et al*., 1998, included in the package). In addition, robust variances were computed by clustering daily observations according to fish ID.

Covariates were initially parameterized separately in univariate models and compared to the "null model" using AIC. Any covariates resulting in a reduction in AIC were retained for further comparison in multivariate models (Supporting Information Table S1). Models incorporating and comparing the effects of fish sex were performed on reduced datasets due to missing data (as sex determination for 11 bream and one pike was considered unreliable; Supporting Information Table S1). Given that fish sampling was not randomized in time and space, sampling location and tagging date were not modelled together to avoid collinearity. Bream length also differed significantly by sampling location (ANOVA: $F_{3,177} = 6.84$, $P < 0.001$; Table 1) and was thus modelled separately from sampling location and tagging date. Models incorporating the effects of both temperature and day of year were also disregarded. Models with ΔAIC ≤2 were considered to have strong support alongside the best-fitting (ΔAIC = 0) model (Burnham & Anderson, 2002), provided they were not more complex versions of nested models with greater AIC support (Richards *et al*., 2011). The proportional hazards assumption was verified for the best-fitting models by visual inspection of the Schoenfeld residual plots for departures from a horizontal (uncorrelated) trend. All statistical analyses were conducted using R 3.6.2 (R Core Team, 2019).

2.4 | Proportion of days detected (acoustic transmitter data)

The proportion of days detected was calculated for each fish by dividing the number of days on which acoustic detections were recorded by either the total number of days between the release date and the final detection (if fish were lost from the acoustic array) or by the total number of days between the release date and the study end date (if fish were right-censored from analyses).

2.5 | Fate of fish lost from the acoustic array (PIT data)

An additional application of the multimethod, double-tagging approach was the interrogation of PIT data to identify any active fish that had been lost from the acoustic array. PIT-detected fish were classified according to their acoustic telemetry status (ATS), "Active" or "Lost". "Active" fish were detected by their PIT tag prior to disappearing from the acoustic array. "Lost" fish were detected by their PIT tag after they had been considered as lost due to inactive or stationary acoustic signals. Binomial generalized linear models tested the effects of fish length (cm, at capture) and sex on ATS ("Active" = 0, "Lost" = 1), with models compared to the null using AIC.

3 | RESULTS

3.1 | Survival analysis (acoustic transmitter data)

A total of 181 bream were acoustically tracked for between 0 and 725 days (Table 1a), with 124 lost to the study. Of these, only two bream (1%) moved outside the monitored area (last detected at receivers on the edge of the array). The surviving 57 bream were detected within 3 months of the study end-date and were therefore right-censored in statistical analyses. On average, bream were detected on 22– 84% of days, with those sampled and released in the River Ant detected the least frequently (Table 1a).

The predicted cumulative probability of bream survival to 1 year post-release was 0.61 [95% confidence interval (CI) 0.48–0.78; Figure 2]. All covariates in the bream CPH univariate models, except fish sex, resulted in reduced AIC compared to the null model (Supporting Information Table S1). The best-fitting CPH model predicting bream survival (ΔAIC = 0) retained nonlinear effects of tagging date and day of year, as well as a linear effect of year (Table 2a). The relative hazard (rate of loss) of bream was 7 to 21 times lower for individuals sampled in April than those sampled during the autumn or winter (Figure 3a). In addition, the hazard peaked at day 156 (6 June in the calendar), at approximately 64 times the rate at day 0 (1 January) (Figure 3b). Although year 2 was associated with an increased rate of loss compared to year 1 ($\beta > 0$; Table 2a), uncertainty was high, with the confidence interval of the estimated hazard ratio ($\exp(\beta)$) overlapping 1.0 (HR = 2.40, 95% CI 0.67–8.63). Furthermore, under the selection criteria, the model incorporating nonlinear effects of day of year and tagging date, but without year, received strong support (ΔAIC = 0.85; Supporting Information Table S1), indicating year was a relatively weak predictor of bream survival (Supporting Information Table S2 and Figure S1).

There were 45 pike that were acoustically tracked for between 4 and 727 days (Table 1b). Of these, 22 were lost to the study, with only two (4%) having moved outside the monitored area. Thus, 23 pike were right-censored due to detections within 6 months of the study end-date. Pike were detected on 20–81% of days, with mean values for each sampling location generally similar to those for bream (Table 1).

The overall cumulative probability of pike survival to 1 year post-release was predicted at 0.80 (95% CI 0.66–0.96; Figure 2). In the pike CPH models, fish sex and a nonlinear effect of day of year improved model fit relative to the null model, and both covariates were retained in the best model (Table 2b and Supporting Information Table S1). Relative rate of loss reached a maximum at day 89 (31 March), at approximately 18 times the rate at day 0 (Figure 3c).

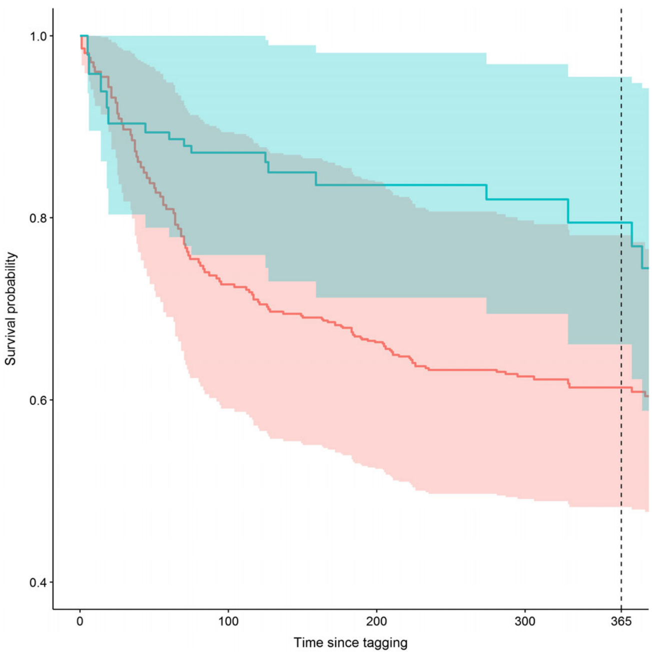

FIGURE 2 Predicted annual survival rates from bream *Abramis brama* (red/light grey curves) and pike *Esox lucius* (blue/dark grey curves) CPH models. Shaded regions represent 95% CIs

A second, smaller peak was observed at day 290 (18 October), although confidence intervals widened towards the end of the year. In addition, male pike had a reduced rate of loss compared to females ($\beta < 0$; Table 2b), equating to a hazard ratio of 0.15 times that of females, although the confidence intervals for this value overlapped 1.0 (95% CI 0.02–1.18).

3.2 | Fate of fish lost from the acoustic array (PIT tag data)

The PIT antennae detected a total of 18 bream (Table 1). Of these, six fish (33%) had previously been classified as "Lost" from acoustic tracking (Table 3), providing evidence against their mortality. Half of those classified "Lost" were due to stationary acoustic signals, suggesting acoustic tag expulsion rather than a transmission failure. The duration of acoustic tracking of "Lost" fish, prior to a signal becoming inactive or stationary, ranged from 37 to 215 days, and final detections all occurred during late spring or early summer (Table 3), which corresponds with the trend described in the bream CPH model (Figure. 3b). The delay between the final acoustic detection and the first PIT detection ranged from 18 to 359 days and during that period "Lost" fish travelled between 1 and 24 km (Table 3). Fish length was a poor predictor of acoustic telemetry status (increased AIC), but sex improved model fit compared to the null model (Table 4), with male bream more likely to be classified as "Lost". The PIT antennae did not detect any pike that had been implanted with an acoustic transmitter.

4 | DISCUSSION

The study revealed that post-tagging survival rates varied according to the time of year for both species, with rates of loss peaking during and following their respective spawning periods. The results also demonstrated an effect of tagging date on the survival of bream, with fish tagged just prior to their spawning period (April) having the highest survival rate. In contrast, the date of tagging did not influence pike survival, and pike have been successfully implanted with transmitters

TABLE 2 Coefficient estimates (β ± robust S.E.) for relevant covariates retained in the best-fitting CPH models predicting bream (a) and pike (b) survival

Parameter	β	Wald's χ^2	d.f.	*P*
(a) Bream				
Tagging date (linear)	−0.0002 ± 0.0012	0.12	1.00	0.73
Tagging date (nonlinear)		76.21	2.53	< 0.0001
Day of year (linear)	−0.0037 ± 0.0016	13.28	1.00	< 0.001
Day of year (nonlinear)		132.56	2.78	< 0.0001
Year	0.88 ± 0.70	1.80	1.00	0.18
(b) Pike				
Day of year (linear)	0.0037 ± 0.0086	14.66	1.00	0.0001
Day of year (nonlinear)		94.12	2.77	< 0.0001
Sex: male	−1.89 ± 1.03	3.25	1.00	0.071

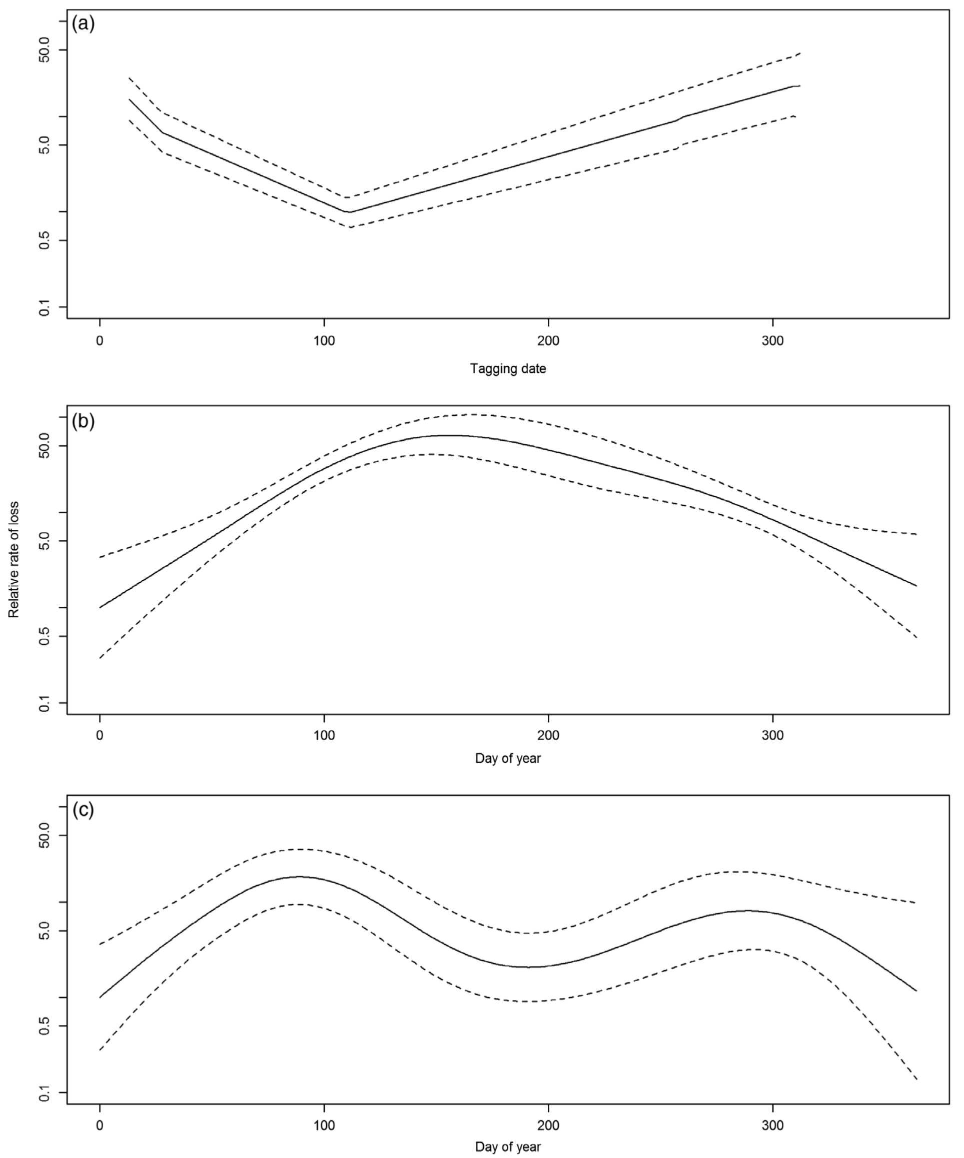

FIGURE 3 Nonlinear effects ("p-spline" smoothing) of tagging date (a) and day of year (b) and (c) on the rate of loss of bream *Abramis brama* (a) and (b) and pike *Esox lucius* (c) from the acoustic telemetry study according to the best-fitting CPH models. Hazards are relative to day = 109 (a) and day = 0 (b) and (c). The *x* axes represent time in Julian days

TABLE 3 Acoustic and PIT tracking details of common bream "Lost" from the acoustic array, but subsequently detected on PIT antennae

Fish ID	Location and timing of sampling	Acoustic tracking duration (days)	Date of final acoustic detection	Date of first PIT detection	Delay (days)	Distance travelled (km)
3811	Upper Bure, April 2018	37	27 May 2018	17 May 2019	355	22
27,268	Upper Bure, April 2018	73	2 July 2018	15 May 2019	317	1
28,576	Upper Bure, November 2017	215	8 June 2018	2June 2019	359	1
28,577	Upper Bure, November 2017	206	30 May 2018	17 June 2018	18	4
30,036	Upper Bure, April 2018	87	15 July 2018	18 May 2019	307	24
30,039	Upper Bure, April 2018	56	14 June 2018	18 May 2019	338	14

Note: Delay and distance travelled represent the period between the final acoustic detection and the first PIT detection.

in their pre-spawning period in other studies (Jepsen *et al*., 2000), although this was not attempted here. However, sex was an important determining factor for pike, with males generally surviving longer than females.

4.1 | Timing of tagging

Tagging fish during their reproductive periods is generally avoided, as it reduces the risk of damage to internal organs, which may be

TABLE 4 Estimated regression parameters (±S.E.), *z* values and *P* values for the best binomial Generalised Linear Model predicting the acoustic telemetry status (ATS) of common bream

	Estimate	*z*	*P*
Intercept	−2.08 ± 1.06	−1.96	0.050
Sex: male	2.30 ± 1.26	1.84	0.067

Note: The model resulted in a reduction in AIC of 2.3 compared to the null model.

enlarged, and prevents unnecessary stress during a period characterized by higher energy costs (Jepsen *et al*., 2002; Krams *et al*., 2017). For example, tagging success was reduced in gravid female channel catfish (*Ictalurus punctatus*, Rafinesque) when compared to spent females and males (irrespective of their reproductive state) (Marty & Summerfelt, 1986). Consequently, it was considered counterintuitive that survival rates were greater for bream sampled from spawning aggregations than those sampled during autumn or winter, especially given that immune systems in another cyprinid fish, roach (*Rutilus rutilus*, L.) are compromised during reproduction (Krams *et al*., 2017). Nevertheless, tagging of roach during spawning also did not appear to cause adverse effects (Hulthén *et al*., 2014). This highlights the need for evaluations of fish recovery and healing to be conducted in different environments, and in relation to testing across internal (*e.g*., hormonal) and external (*e.g*., seasonal) gradients (Cooke *et al*., 2011).

4.2 | Fate of bream

For bream that did not survive within the study (annual probability of 0.39), few individuals left the monitored area, but PIT data revealed some lost their acoustic transmitter signal. As the spatial and temporal coverage of the PIT monitoring stations was relatively low in the study area, the contribution of acoustic signal loss to overall loss of bream from the study could have been under-represented. Natural mortality rates (in the absence of fishing pressure) for bream populations in northern Europe and China have been estimated at 0.13 to 0.26 year^{-1} (Ding *et al*., 2019; Kompowski, 1988). Although these estimates are not directly comparable to the rate here, they do suggest the rate of loss of tagged bream was higher than what might be expected by natural mortality alone.

The process by which bream were lost from the acoustic array but remained active on the PIT antennae is uncertain. Possible explanations for the loss of an acoustic signal include transmission failure and/or detection failure. The stationary tags provide some evidence against transmission failure. While acoustic shadows and interference may cause temporary fluctuations in detection efficiency (Huveneers *et al*., 2016; Simpfendorfer *et al*., 2008), detection failure over prolonged periods of time (confirmed fish survival up to 359 days after acoustic signal loss) and across large sections of the receiver network (confirmed fish movement up to 24 km after acoustic signal loss) is also considered unlikely, especially given successful detection of conspecifics throughout this time and space. One further consideration is the possibility of tag expulsion. This was not observed directly, but in other species tags are often lost through the incision site or *via* a lesion in the body wall (Jepsen *et al*., 2002). Both mechanisms could have occurred here, although with increasing time since surgery wound healing should be further advanced, making surgical loss unlikely and the latter more likely (*e.g*., bream tracked for >200 days prior to signal loss).

Other fish species, including the cyprinid common carp (*Cyprinus carpio*, L.), are particularly susceptible to loss of acoustic and radio transmitters (Daniel *et al*., 2009; Marty & Summerfelt, 1986). Yet tag expulsion has not been previously considered in common bream, despite several completed studies using these methods (*e.g*., Brodersen *et al*., 2019; Gardner *et al*., 2013, 2015). The estimate of the proportion of bream losing their acoustic tag signal was dependent on bream retaining their PIT tag and therefore could be an underestimate if some individuals expelled both tags. However, PIT tag retention is generally high in cyprinid fishes (Bolland *et al*., 2009; Skov *et al*., 2005), especially for males (Šmejkal *et al*., 2019), but with some exceptions, such as topmouth gudgeon (*Pseudorasbora parva*, Temminck & Schlegel) (Stakėnas *et al*., 2009). For bream confirmed active by PIT telemetry, loss of acoustic signals occurred up to 215 days (>6 months) post-tagging, but all incidents occurred in late spring or summer, suggesting some role of spawning activity and/or elevated temperatures, as also suggested for tag losses in common carp (Daniel *et al*., 2009). In addition, male bream were more likely to experience acoustic signal loss that was then followed by a PIT tag detection, emphasizing the need for long-term tag retention studies in this species. When conducted over a range of naturally fluctuating environmental conditions, these should be more insightful than studies focusing only on the initial days and weeks post-tagging and/ or which operate under artificial laboratory conditions. However, any wild study would require consideration of the need to recapture individuals to determine the mechanisms driving acoustic signal loss.

4.3 | Fate of pike

The annual probability of pike loss due to mortality, acoustic signal loss or fish leaving the study area was estimated as 0.20 (from a survival probability of 0.80). In the literature, estimates for the natural mortality rate of adult pike vary widely and may exceed 0.50 year^{-1}, with males having similar or greater mortality compared to females (Haugen *et al*., 2007; Kipling & Frost, 1970). While results here suggested a greater loss of females, prediction error was wide. A possible explanation is that male pike exhibit greater vagility than females (Haugen *et al*., 2007) and subsequently the survival of females may have been underestimated due to their relatively sedentary behaviour (Koed *et al*., 2006). Nevertheless, the rate of loss of tagged pike appeared relatively low, indicating minimal impact of the tagging process.

No pike were detected *via* their PIT tags, therefore the proportion that died *versus* those that lost their acoustic signals (through tag failure, tag expulsion *etc*.) could not be estimated. However, other studies have suggested tag loss in the species is low. For example, Jepsen and Aarestrup (1999) found no expulsion of internal radio tags after1 year, and several recent studies that have utilized acoustic or radio telemetry to measure pike movements (for up to 18 months) have not reported evidence of tag loss (*e.g*., Birnie-Gauvin *et al*., 2019; Jacobsen *et al*., 2017; Pauwels *et al*., 2017). If the reason for signal loss was tag expulsion then differences in rates between the two species may be due to differences in morphology, where pike are more fusiform, with a wider body cavity than the laterally compressed bream. Consequently, pressure on internal organs and at the incision site might have been lower in pike, limiting tag loss (Cooke *et al*., 2011; Jepsen *et al*., 2002). Notwithstanding, there was complete retention of dummy acoustic tags in the laterally compressed bloater (*Coregonus hoyi*, Milner) (Klinard *et al*., 2018), suggesting that generalizing about tag losses across morphological, taxonomic or behavioural groups should be done with caution.

4.4 | Interpretation of survival

One fate not considered here is the possible consumption of tagged fish by aquatic predators (*e.g*., pike, otters), with the acoustic tags still appearing active in the study system. Elsewhere, this is typically identified by uncharacteristic changes in depth or horizontal space use (Klinard & Matley, 2020; Villegas-Ríos *et al*., 2020), but given the nature of the study system (*i.e*., shallow and relatively spatially confined), the movements of bream or pike and their predators were considered difficult to distinguish. The use of new telemetry technology designed to definitively identify predation events (Halfyard *et al*., 2017) has revealed acoustic transmitters may be retained for a substantial time in the guts of piscivorous predators (>150 days; Klinard *et al*., 2019), meaning survival may have been overestimated here. In addition, ghost tags (due to fish mortality or tag expulsion) can also travel independently within river systems, especially PIT tags during high flow events (Bond *et al*., 2019), although some may remain relatively stationary for long periods (Šmejkal *et al*., 2020). In the tidal River Bure system, while these movements could mask a mortality or tag loss event, the high flows that would be required to transport a tag are unlikely, usually being buffered by the wetland nature of the system that generally prevents large and sudden influxes of floodwater.

In summary, the results here demonstrate that the survival of fish that undergo intraperitoneal implantation of transmitters varies by species, and within species it can vary by sex and the date of tagging. They also suggest that where fish failed to survive during the study period, this could be due to the loss of the acoustic tag signal (*e.g*., due to tag loss or tag failure), rather than actual mortality, with the additive mortality caused by the procedure and subsequent tag burden appearing negligible considering natural mortality rates. Moreover, the double-tagging approach was instrumental in revealing the subsequent activity of fish that had lost their acoustic signal. This method of distinguishing mortality from tag loss/failure appears original, with no mention in a recent review of mortality assessments in acoustic telemetry research (Klinard & Matley, 2020). However, it should always be considered in future fish tagging studies to assist assessments of post-tagging survival.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support for EW of the EU LIFE+ Nature and Biodiversity Programme: LIFE14NAT/UK/000054, as well as funding and resource support from the Environment Agency. Thanks also to Jo-anne Pitt (Environment Agency) for her preliminary review of the manuscript.

CONTRIBUTIONS

E.W., A.H., S.L. and R.B. conceived and designed the investigation. E. W., A.H., S.L. and R.B. performed field work. E.W. analysed the data and wrote the paper.

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SUPPORTING INFORMATION

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

How to cite this article: Winter ER, Hindes AM, Lane S, Britton JR. Predicting the factors influencing the inter- and intraspecific survival rates of riverine fishes implanted with acoustic transmitters. *J Fish Biol*. 2020;97:1209–1219. https://doi.org/10.1111/jfb.14504