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Under what circumstances does the capture and tagging of wild Atlantic salmon *Salmo salar* smolts affect probability of return as adults?

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Adult return rates for wild Atlantic salmon *Salmo salar* smolts captured in a rotary screw trap and tagged with coded wire (CW) tags were compared with a control group, using detections from passive integrated transponder (PIT) antennae systems over 7 years in a small chalk stream in southern England, U.K. Compared with control smolts, capture and CW-tagging of experimental smolts affected detected return rates only under certain conditions, with a decreased return probability for smolts caught and tagged following mild winter river temperature anomalies and during the night. Similarly, analysis of the experimental smolts revealed that capture and CW-tagging following mild winters decreased their probability of return as adults. There were also marginal positive effects of length at PIT-tagging as parr and length at CW-tagging as smolts, on individual probability of return as adult. The results support the hypothesis that the effect of procedures involving the capture and tagging of migrating wild *S. salar* smolts will vary with the circumstances under which they are performed. The implications of the findings are considered in the context of ongoing investigations to derive and report marine return rates for *S. salar* in support of national and international stock assessments and in developing best practice.

KEYWORDS

assessment, coded wire tag, marine survival, marking, passive integrated transponder, salmonids

1 | INTRODUCTION

The marking or tagging of animals is a fundamental technique that has been widely used in research for more than a century. It allows groups or individuals to be recognised when re-encountered, enabling researchers to measure information on population size, survival, growth rates, exploitation, migratory behaviour and habitat use. Marking or tagging has been applied to different species including birds (Calvo & Furness, 1992), fish (McFarlane & Wydoski, 1990), mammals (Twigg, 1975), reptiles (Ferner & Plummer, 2016), amphibians (Heard *et al*., 2009) and invertebrates (Haddaway *et al*., 2011). Various marking techniques have been used, including branding, staining, clipping of appendages and the attachment of tags (Murray & Fuller, 2000).

To provide information on the natural behaviour of the studied animal, marking should not compromise the animal in any way. Techniques have been refined considerably over the years, partly in response to concerns about their effect on the study animals. For fish, early studies often involved the use of commercially made plastic or metal tags, which were inexpensive, easy to apply, highly visible and had high retention rates (Murray & Fuller, 2000). Many of these tags were subsequently found to result in adverse effects in laboratory and field investigations, including infection at the tagging site and reduced growth and survival, particularly in smaller fish (Berg & Berg, 1990; Bergman *et al*., 1992; Hansen, 1988; Morgan & Roberts, 1976; Nielsen, 1992). Factors influencing the invasiveness of a marking technique include the location of the marking site (Murray & Fuller, 2000),

the nature of any associated wound and its ability to heal (Mourning et al., 1994) and the size and weight of the tag relative to the fish (Jepsen et al., 2005). Fish marking methods thought to be more benign have since been developed, such as coded wire (CW) tags, passive integrated transponder (PIT) tags and elastomer visible implants (EVI). Such marks are small and light, do not result in healing problems and are widely reported to have negligible effect on variables such as survival and growth, even for small fish (Hohn & Petrie-Hanson, 2013; Moser et al., 2017). However, the effects of marking are not only attributable to the presence of the tag itself, but to the whole tagging process, that often involves fish capture, handling, anaesthesia, recovery and release. It is, therefore, important that researchers and fishery managers consider the combined effects of the whole tagging process they are using, particularly when studying a species or life-history stage in an environment or condition where the absence of negative consequences has not been clearly demonstrated.

The recent decline in stocks of Atlantic salmon *Salmo salar* L. 1758 has been largely attributed to poor survival in the marine environment (Friedland et al., 1998; ICES, 2017). Evidence for this change is generally provided by estimates of return rates for populations, i.e. the proportion of the out-migrating smolts that survive to return to their river of origin as adults, derived from monitored rivers (Potter & Crozier, 2000). Such data are reported annually to the International Council for the Exploration of the Seas (ICES) North Atlantic Salmon Working Group (ICES, 2017) and used as a proxy for marine survival. The capture and tagging of migrating wild smolts and an assessment of the subsequent return of this tagged cohort as adults is widely used to derive these return rate estimates. However, it has been reported that such techniques may have a negative effect on smolt physiology, behaviour and survival (Hansen, 1988; Hansen & Jonsson, 1988; Moffett et al., 1997; Riley et al., 2007; N. Lower, W. D. Riley, T. Ellis, & A. Moore, unpubl. data). Indeed, Crozier and Kennedy (2002) reported that over a 13 year study period wild S. salar smolts CW-tagged on the River Bush, Northern Ireland, U.K., displayed significantly poorer return rates (range 1.6–10.3%) relative to untagged fish (range 4.5–15.1%), in each year of study, with, on average, tagged fish surviving at a rate of 43.6% relative to the control group.

Improving the understanding of the effect of smolt capture, handling, anaesthesia, tagging, recovery and release back to the wild on subsequent survival is, therefore, important in the context of utilizing return-rate estimates in management and in developing best practice for tagging programmes.

For S. salar, the timing of smolt migration appears to be crucial for survival, to the extent that when the physiological and behavioural "smolt window" (McCormick et al., 1998) for migration (i.e., controlled by photoperiod, temperature and flow etc.) coincides with optimum environmental conditions, adult return rates are high. Other behavioural strategies, e.g. nocturnal migration, are generally accepted to be predator avoidance tactics (Solomon, 1978). It seems reasonable, therefore, to suggest that environmental conditions preceding, during, or post capture and tagging may affect smolt condition, behaviour, vulnerability to predation and thus survival following release.

This study used a long-term and individual-based dataset collected to measure the detected return rates of S. salar on the River Frome, Dorset, U.K. A robust experimental design compared the detected adult return rates of smolts captured in a rotary screw trap (RST) and CW-tagged with that for smolts that were not captured or CW-tagged, for thousands of individuals monitored over 7 years. This information was used to test two hypotheses: first, the capture and CW-tagging of S. salar smolts has a negative effect on detected adult return rates compared with a control group; second, the effect of the whole tagging process on return probability will vary with the circumstances under which it takes place.

2 | MATERIALS AND METHODS

2.1 | Study area

The River Frome is a chalk stream in southern England (Figure 1). It rises at Evershot (50.50.24° N; 02.36.12° W) at an elevation of 160 m a.s.l. It is c. 70 km long from its source to the tidal limit near Wareham Bypass Bridge (50.40.38° N; 02.07.30° W) and its lower estuary forms an arm of Poole Harbour (50.41.16° N; 02.04.42° W). It is a lowland, low gradient river that derives most of its discharge directly from a Cretaceous chalk aquifer and man-made bore holes. Consequently, the river is infrequently subject to sudden spates and has a relatively stable temperature regime. Historic use of the river for milling and agriculture has resulted in a braided, regulated system, with many sluice gates controlling both the level and flow in the main river channel, flood relief channels and numerous cross channels.

In such chalk streams and their tributaries, it has been reported that the majority of juvenile S. salar spend 1 year in fresh water before migrating to the sea in the spring as smolts (Solomon, 1978; Riley et al., 2012). Previous studies on the migration patterns of juvenile S. salar on the River Frome have also demonstrated that a substantial number (c. 25% of the spring smolt run in absolute terms) of the population migrate downstream to the lower reaches of the river during the autumn with the peak movement occurring during October and November (Pinder et al., 2007; Ibbotson et al., 2013). A number of these autumn migrating parr have been documented as subsequently returning as adults (Riley et al., 2009).

Returning adult S. salar stock estimates have been monitored on the River Frome since 1973 using a resistivity counter (Beaumont et al., 2007). Return rates (from a capture–mark–recapture experiment) have been reported annually to ICES North Atlantic Salmon Working Group since 2002 (ICES, 2017).

2.2 | Parr capture and PIT-tagging

In September 2005 to 2011 inclusive, S. salar parr were caught using electric fishing, anaesthetised (2-phenoxy-ethanol), measured for fork length (L_F, mm), had their adipose fin removed and were PIT-tagged (Ibbotson et al., 2013). Following recovery, all fish were returned to the same 100 m section of river from which they had been captured. Age was allocated from L_F-frequency histograms. Parr were PIT-tagged throughout the spawning range for adult S. salar upstream from East Stoke (50.40.47° N; 02.11.2° W; Figure 1) to minimise any possible site-specific effects. The total number of S. salar parr PIT-tagged each year is given in Table 1.
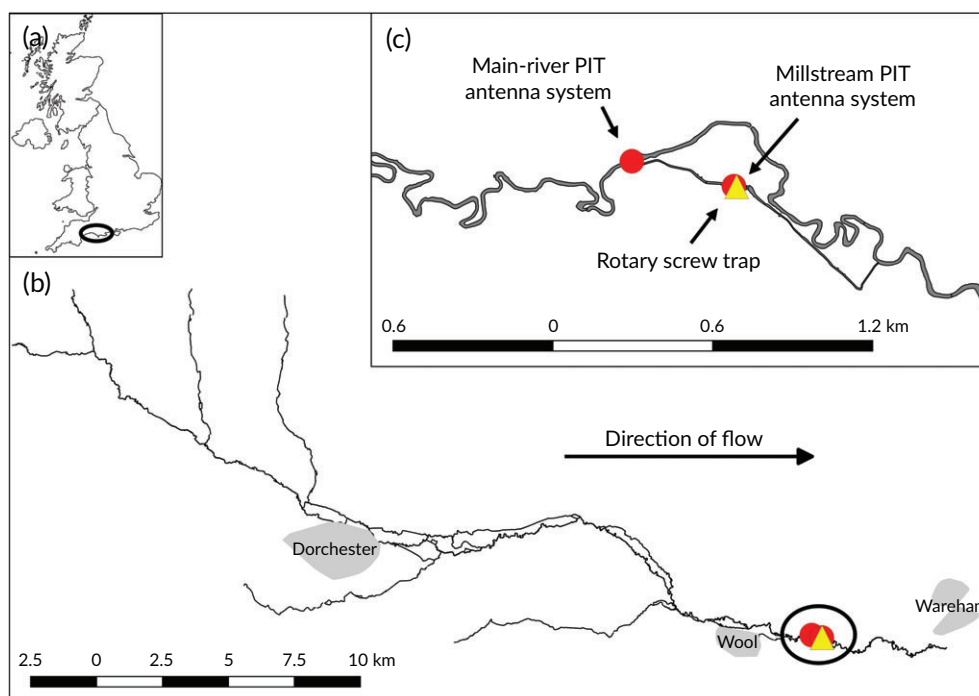
FIGURE 1   (a). Location of the River Frome, Dorset, U.K. (b) Location of the *Salmo salar* monitoring site at East Stoke on the River Frome. (c) Locations of the main-river and millstream passive integrated transponder (PIT) antenna systems and the rotary screw trap at East Stoke

2.3 | Smolt PIT-tag detection, capture and CW-tagging

Each spring between 2006 to 2012 inclusive, an acoustic bubble curtain (Welton *et al.*, 2002) located at East Stoke (8.6 km above the tidal limit) diverted downstream migrating *S. salar* smolts (including those previously PIT-tagged as parr in September) into a millstream that runs parallel to the main-river (Riley *et al.*, 2014; Figure 1) and past PIT-antenna detection systems (Wyre Micro Design Ltd.; www.wyremicrodesign.co.uk) installed in the millstream channel. [For a full description of the PIT-antenna systems used in this investigation see Welton *et al.* (2002) and Ibbotson *et al.* (2004, 2011)].

Following detection, a proportion of the PIT-tagged smolts were captured immediately downstream of one of these PIT-antenna

TABLE 1   Numbers of *Salmo salar* parr marked with individual passive integrated transponder (PIT) tags each autumn; PIT-tagged smolts detected (control group) each spring; PIT-tagged smolts intercepted by rotary screw trap and tagged with coded-wire tags (experimental group) each spring

Year Parr / smolt	PIT-tagged parr (*n*)	PIT-tagged smolts (*n*)		Smolt run PIT tagged (%)
		Control	Experimental	
2005/2006	11,494	969	325	17.4
2006/2007	10,882	693	604	10.8
2007/2008	10,712	718	402	10.8
2008/2009	10,031	621	447	11.3
2009/2010	10,835	557	363	7.9
2010/2011	10,496	476	247	8.1
2011/2012	5,851	210	244	9.1
Totals	70,301	4,244	2,632	Mean *c.* 10.8

systems using a RST (Riley *et al.*, 2010). PIT-tagged smolts captured by the RST, henceforth referred to as the experimental group, were anaesthetised (2-phenoxy-ethanol), measured, weighed (*M*, 0.1 g), CW-tagged (Jefferts *et al.*, 1963) and following full recovery from anaesthesia, returned to the millstream 50 m downstream within 1 h of capture.

PIT-tagged smolts not captured by the RST or those not deflected by the acoustic bubble curtain and detected by a PIT-antenna system (Wyre Micro Design) installed in the main-river (Figure 1) were used as the comparison group (henceforth referred to as the control group) in this investigation.

Differences in apparent survival between the experimental and control groups were determined based on the detected adult return rate of the two groups recorded by the main-river PIT-antenna system (Figure 1). The number of PIT-tagged smolts in the control group, the number of PIT & CW-tagged smolts in the experimental group and an estimate of the percentage of the total smolt run that carried PIT-tags each year are given in Table 1.

2.4 | Experimental design

Simulations indicated that *c.* 10,000 *S. salar* parr PIT-tagged each September for 5 years would provide enough spring smolt PIT-tag detections and RST interceptions to measure a 40% difference in control and experimental adult return detection rates with a high statistical power. The simulations were guided by the effects reported by Crozier & Kennedy (2002) and based on low over-winter survival (< 15%) for parr on the River Frome (Centre for Ecology and Hydrology, unpubl. data), RST capture rates of 10–25% and a proportion of control smolts detected returning to the river as adults of 7, 5 and 2.5% (updated after initial adult returns).

TABLE 2 Dates that the rotary screw trap was operational each year

	Rotary screw trap operation		
Smolt year	Start	End	Days
2006	1 April	9 May	38
2007	2 April	9 May	37
2008	31 March	9 May	39
2009	1 April	7 May	36
2010	2 April	20 May	48
2011	1 April	10 May	39
2012	1 April	5 May	34

To minimise bias between experimental and control groups, RST smolt capture and CW-tagging in the spring extended over most of the duration of the smolt run (Table 2) and only PIT-tagged smolts detected during the period of RST operation were included in the analysis. The RST was generally run continuously during the period of operation and was continuously manned when in use. To minimise any disruption to smolt migration, the RST was checked frequently (every 30 min) for captured smolts that were processed immediately. In addition, the individual-based dataset ensured that any undetected PIT-tagged smolts and fish moving downstream outside the period of RST operation (*e.g.* autumn migrating parr) were not mistakenly included as control group returning adults during statistical analysis.

Nevertheless, it is acknowledged that control group smolts did not behave identically to the experimental group (*i.e.*, they were not caught in the RST, which was part of the treatment) and were, in effect, self-selected. To some extent this was highlighted in the first year of study, when it was determined from PIT-antenna system detection data that day migrating PIT-tagged smolts were less likely to be captured by the RST than those migrating at night. However, this potential bias was removed from spring 2007 by using additional screening, installed upstream on either side of the RST, to increase daytime smolt capture.

2.5 | Environmental data collection

A variety of proximate environmental triggers, including threshold and cumulative river temperature, river discharge and turbidity, and the onset of darkness have been correlated with the intensity and timing of *S. salar* smolt migrations (McCormick *et al.*, 1998). Furthermore, release timing for wild *S. salar* smolts, following capture and tagging, has recently been reported to affect subsequent survival (Vollset *et al.*, 2017). Therefore, the environmental conditions under which the experimental group were captured could influence their behaviour following release. Similarly, smolt condition may be influenced by environment conditions prior to smoltification in the spring and preceding winter. Therefore, river temperature and discharge at time of release (experimental group) or detection (control group) and the mean daily river temperature and discharge anomalies during the preceding winters (December to March, inclusive) were included as variables for analysis.

River temperature was measured in the main-river at East Stoke, *c.* 300 m upstream of the RST site, using a Grant Instruments data logger (www2.grantinstruments.com) connected to in-river and in-air

TABLE 3 Variables used in models to explain observed variation in the response variable detected adult *Salmo salar* return rate

Variable name	Short	Analysis	Description	Type
Detected adult return	Return	Control & experimental; experimental-only	Whether the smolt was detected returning as an adult (0 = no, 1 = yes)	Binary response
Smolt year	Year	Control & experimental; experimental-only	Year that the smolt migrated to sea	Categorical random effect with 7 levels
Migration day of year	DOY	Control & experimental; experimental-only	Day of year that individual was observed migrating to sea	Continuous explanatory variable
Length at PIT-tagging	L_{Ftag}	Control & experimental	Fork length (mm) of individual at time of PIT-tagging in Sept the previous year	Continuous explanatory variable
Water temperature at detection–capture	T_{cap}	Control & experimental; experimental-only	Water temperature reading in 15 min period closest to time of individual detection or capture	Continuous explanatory variable
Day or night sampling period	Period	Control & experimental; experimental-only	Whether the smolt was observed migrating in the day or night	Categorical explanatory variable with 2 levels
Winter (Dec–Mar) flow anomaly	Wntflow	Control & experimental; experimental-only	Difference in mean daily winter (Dec–Mar) flow for each year and the mean daily winter flow for all years	Continuous explanatory variable
Winter (Dec–Mar) temperature anomaly	Wnttemp	Control & experimental; experimental-only	Difference in mean daily winter (Dec–Mar) temperature for each year and the mean daily winter temperature for all years	Continuous explanatory variable
RST capture	Capture	Control & experimental	Whether the smolt was captured in the RST (0 = no, 1 = yes)	Categorical explanatory variable with two levels
Number of smolts in RST	Ntrap	Experimental-only	Number of smolts caught in each 30 min trap check	Continuous explanatory variable
Length at RST capture	L_{Frst}	Experimental-only	Fork length (mm) of individual at time of capture in the RST	Continuous explanatory variable
Autumn to spring tag count ratio	Pautumn	Control & experimental; experimental-only	Number of PIT-tags detected in autumn as a proportion of those detected in spring	Continuous explanatory variable

Note. RST = rotary screw trap; L_F = fork length.

TABLE 4 Comparison of detected adult *Salmo salar* return rates from control and experimental group smolts. Includes all smolts detected at East Stoke during rotary screw-trap operation period each year (age 1+ smolts only in parentheses)

Smolt run	Sea age	Experimental			Control		
		Smolts	Returns	Return rate	Smolts	Returns	Return rate
2006	All	325 (320)	9	2.77 (2.81)%	969 (940)	27 (26)	2.79 (2.77)%
2006	1SW	325 (320)	5	1.54 (1.56)%	969 (940)	22 (21)	2.27 (2.23)%
2006	MSW	325 (320)	4	1.23 (1.25)%	969 (940)	5	0.52 (0.53)%
2007	All	604 (586)	8	1.32 (1.37)%	693 (678)	23	3.32 (3.39)%
2007	1SW	604 (586)	5	0.83 (0.85)%	693 (678)	21	3.03 (3.10)%
2007	MSW	604 (586)	3	0.50 (0.51)%	693 (678)	2	0.29 (0.30)%
2008	All	402 (394)	1	0.25 (0.25)%	718 (695)	2	0.28 (0.29)%
2008	1SW	402 (394)	1	0.25 (0.25)%	718 (695)	2	0.28 (0.29)%
2008	MSW	402 (394)	0	0.00 (0.00)%	718 (695)	0	0.00 (0.00)%
2009	All	447 (439)	13 (11)	2.91 (2.51)%	621 (613)	20	3.22 (3.26)%
2009	1SW	447 (439)	6 (5)	1.34 (1.14)%	621 (613)	11	1.77 (1.79)%
2009	MSW	447 (439)	7 (6)	1.57 (1.37)%	621 (613)	9	1.45 (1.47)%
2010	All	363 (359)	12	3.31 (3.34)%	557 (544)	18	3.23 (3.31)%
2010	1SW	363 (359)	8	2.20 (2.23)%	557 (544)	13	2.33 (2.39)%
2010	MSW	363 (359)	4	1.10 (1.11)%	557 (544)	5	0.90 (0.92)%
2011	All	247 (226)	4	1.62 (1.77)%	476 (457)	13 (12)	2.73 (2.63)%
2011	1SW	247 (226)	2	0.81 (0.89)%	476 (457)	6 (5)	1.26 (1.09)%
2011	MSW	247 (226)	2	0.81 (0.89)%	476 (457)	7	1.47 (1.53)%
2012	All	244 (224)	4	1.64 (1.79)%	210 (196)	11	5.24 (5.61)%
2012	1SW	244 (224)	2	0.82 (0.89)%	210 (196)	7	3.33 (3.57)%
2012	MSW	244 (224)	2	0.82 (0.89)%	210 (196)	4	1.90 (2.04)%
All	Total	2,632 (2548)	51 (49)	1.94% (1.92)%	4,244 (4123)	114 (112)	2.69% (2.72)%

Note. 1SW = One sea-winter, *i.e.* adults that spent one winter at sea before returning to freshwater; MSW = multi sea-winter, *i.e.* adults that spent multiple (> 1) winters at sea before returning to freshwater.

thermistors. Thermistors were periodically tested and found to be within 1°C of a calibrated mercury thermometer. Where equipment failure interrupted data collection, data collected nearby in the River Frome by the Freshwater Biological Association (J Davy-Bowker, pers. comm.) were used. Readings were taken at 15 min intervals then averaged to hourly means. River discharge was measured at the same location as river temperature, sourced from U.K. Environment Agency. Readings were available at 15 min intervals.

The ecological drivers for autumn migrations of *S. salar* parr are unknown (Riley *et al*., 2008), although a number of mechanisms have been proposed including the requirement for juveniles to migrate to more suitable freshwater habitats where environmental conditions experienced are poor for over-wintering (Riddell & Leggett 1981; Huntingford *et al*., 1992). Therefore, the number of PIT-tagged parr detected migrating downstream the previous autumn and early winter divided by the number of PIT-tagged spring smolts detected, was included as a variable in the analysis, for each year, as a possible biological indicator of in-river environmental conditions.

2.6 | Data processing

The information collected was converted into 12 variables (Table 3), but as there were additional variables for the experimental group smolts, statistical analysis was carried out on two data sets. One compared control and experimental group smolts (hereafter control &

experimental), the other, the subset of the data for experimental group smolts only (hereafter experimental-only).

2.7 | Statistical analysis

Before model fitting, all continuous covariates were examined for outliers (Supporting Information Figure S1) and categorical covariates were examined for balanced sample sizes. Since the large majority of smolts were age 1+ (6671), all older smolts (204 aged 2+ and 1 aged 3 + smolts) were removed from further analysis because there were frequently < 5 individuals per group when stratified by categorical covariate. One record was dropped from modelling as it had an outlying temperature value (Supporting Information Figure S1). Furthermore, continuous covariates were examined for collinearity (Supporting Information Figure S2), which resulted in the exclusion of smolt mass (collinear with smolt length), with smolt length retained as it was considered the more generic and reliable measurement in field conditions. To compare the experimental and control groups, plots of detection dates were inspected and mean parr and smolt L_F assessed using plots and linear models. A table of annual summary statistics of the continuous covariates on their unstandardized scale is presented in Table S1. All continuous covariates were standardized by subtracting their mean and dividing them by the S.D.; this made it easier to compare the effects between covariates.
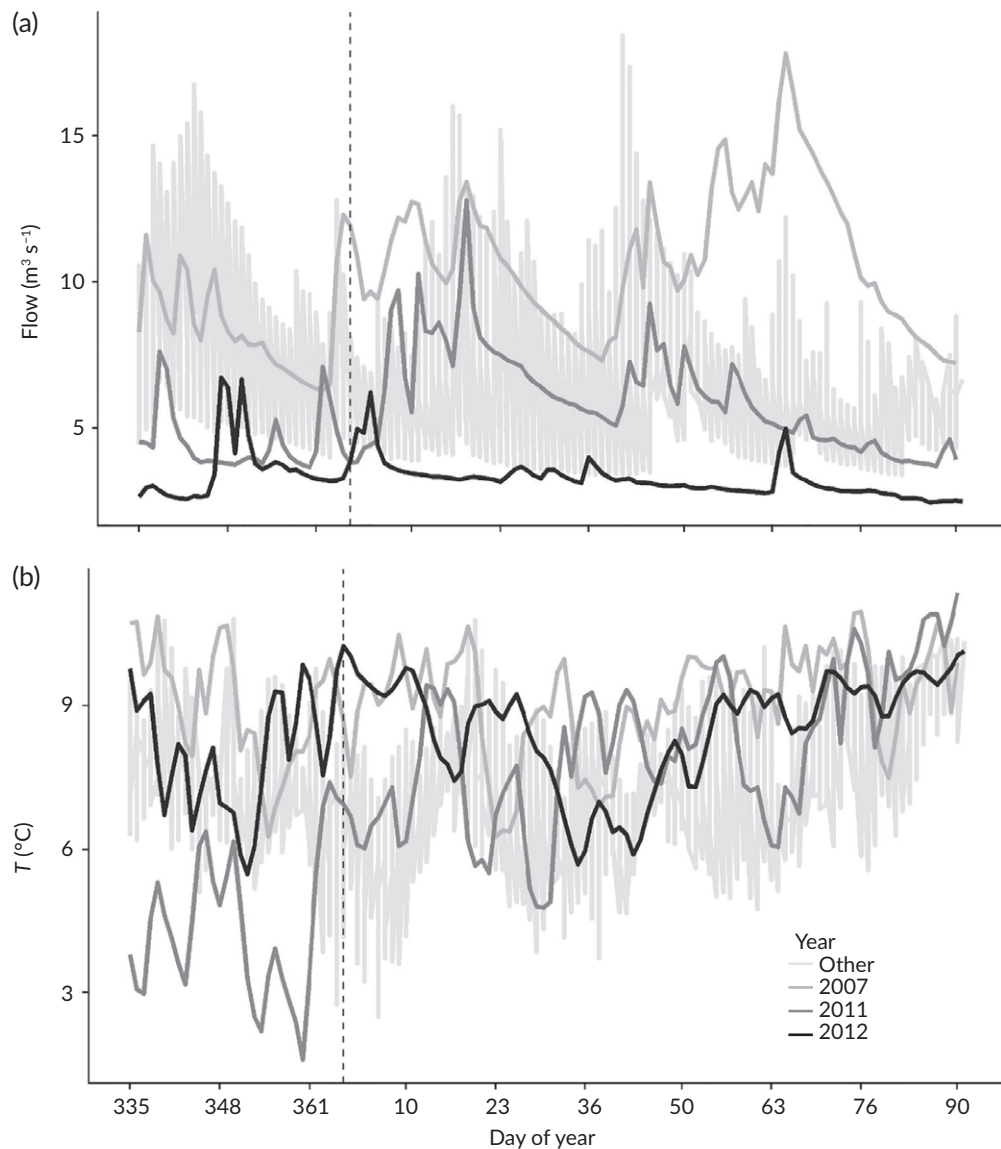
FIGURE 2 Mean daily (a) water flow and (b) water temperature (T) during winter (December–March) in each year, highlighting years 2007, 2011 and 2012

2.7.1 | Analysis of detected adult return rates

To assess the probability of detected adult returns, a binomial generalized linear mixed model (GLMM) with a logit link was fitted with adult return as the response variable and smolt year as a random intercept, *i.e.* treating smolt years as samples from a longer period. For the control & experimental analysis, explanatory variables were day or night-sampling period and RST capture, with linear terms for migration day of year, length at PIT-tagging L_{Ftag}, water temperature at capture (T_{cap}), winter (December–March) flow anomaly and winter (December–March) temperature anomaly (Table 3). For the

TABLE 5 Table of model performance statistics for the models comparing detected adult *Salmo salar* return rates from control and experimental group smolts

Model	logLik	d.f.	AIC	δAIC	Marginal R^2	Conditional R^2
m5	−742.199	7	1,498.399		0.042	0.142
m4	−740.620	9	1,499.239	0.841	0.046	0.144
m3	−738.861	11	1,499.723	1.324	0.053	0.151
m6	−745.199	5	1,500.398	1.999	0.017	0.122
m7	−747.338	3	1,500.676	2.277	0.010	0.113
m2	−738.463	13	1,502.926	4.527	0.058	0.148
m1	−738.309	15	1,506.618	8.219	0.059	0.146
m0	−738.060	17	1,510.120	11.721	0.061	0.145

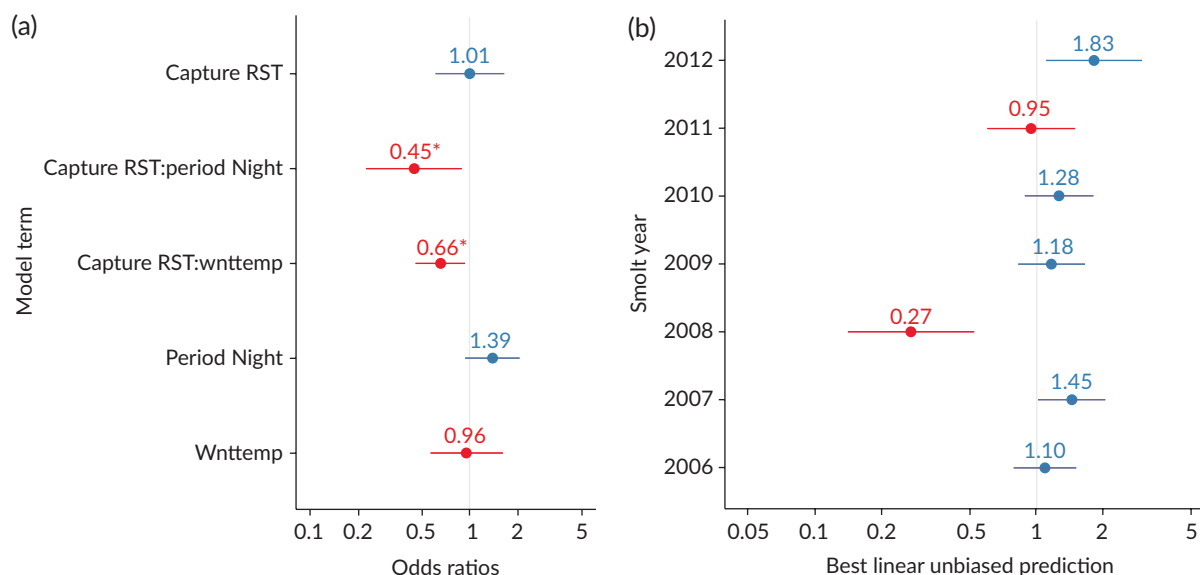*Note.* AIC = Akaike information criteria; logLik = log likelihood.

FIGURE 3 Caterpillar plots showing the mean ($\pm$95% C.I.) (a) fixed and (b) random coefficient estimates for the most parsimonious models comparing detected adult *Salmo salar* return rates from control and experimental group smolts. ━●━, negative estimates; ━●━, positive estimates; *p < 0.05; RST, rotary screw trap; wnttemp, winter water temperature anomaly

experimental-only analysis, the explanatory variables were the same except they omitted RST capture and L_{Ftag} and included additional linear terms for number of smolts in RST and length at RST capture (L_{Frst}; Table 3). For both data sets, an appropriate saturated model was fitted and then simplified using single term deletion to explore models with combinations of the covariates, which were further compared using AIC and goodness-of-fit statistics. In the case of the control & experimental analysis, interactions with the factor for RST capture were included to assess any differences of the effect of the other covariates between the two groups. Estimated coefficients and their marginal effects were plotted for the most parsimonious model for each analysis.

3 | RESULTS

3.1 | Smolt run timing and size

The run-timing of the experimental group was similar to the control group detected by the PIT-tag antenna systems (Supporting Information Figure S3). However, there was a large annual variation in the percentage of smolts detected and captured migrating past East Stoke during the day during the period of RST operation (Supporting Information Table S2). The years 2007 and 2012 were atypical with the highest and lowest values (for groups combined: 2007 = 65.6%; 2012 = 8.8%, daytime 1+ smolts).

The L_{Ftag} were similar for experimental and control group smolts migrating during both day and night (control-experimental effect $F_{1,6,661} = 0.06$, $p > 0.05$; day–night effect $F_{1,6,661} = 0.02$, $p > 0.05$; Supporting Information Table S3 and Figure S4) supporting the a priori expectation that the experimental group would be a representative sample of the smolt run.

The mean L_{Frst} at capture of the experimental group smolts caught during the day was 3.3 mm longer (95% C.I. = 2.5 to 4.3 mm)

than those caught at night ($F_{1,2,540} = 57.6$, $p < 0.001$; Supporting Information Table S4 and Figure S5).

3.2 | Detected adults return rates

The number of returning adults detected and associated return rates, for one-sea winter (1SW) & multi-sea winter (MSW) adult salmon, by smolt year, for the experimental and control groups are summarized in Table 4.

For the smolt years of 2006, 2008, 2009 and 2010 the overall detected return rates were similar for the experimental and control groups, whether considering all smolts or age 1+ smolts only. However, for the 2007, 2011 and 2012 smolt years, overall detected return rates were lower for the experimental group among both all smolts and age 1+ smolts only. Lower detected return rates for the experimental group were apparent for 1SW adult salmon for all smolt years and for MSW adults in 2011 and 2012.

These patterns motivated a model fitting exercise to better understand whether there was an effect of capture and CW-tagging on age 1+ smolts and what could be driving any possible effect. Although examining each year separately was motivating, it was preferable to treat the years as samples from a longer period (*i.e.*, as random effects) and investigate potential explanatory variables that had to be summarized at an annual scale, such as winter (December–March) flow and temperature anomalies, with particular emphasis on years 2007, 2011 and 2012 (Figure 2).

3.2.1 | Control & experimental analysis

Exploration of GLMM models with different combinations of variables yielded a single most parsimonious model; model m5 (Table 5). This model suggested that day or night sampling period and winter (December–March) temperature anomaly significantly affected the probability of detected adult return when considered in interaction with RST capture (Figure 3 and Table 6). Therefore, capture and CW-tagging

TABLE 6 Model parameter estimates (±s.e.) statistics for comparing detected adult *Salmo salar* return rates from control and experimental group smolts

| Variable	Model							
	m0	m1	m2	m3	m4	m5	m6	m7
Intercept	-3.879*** (±0.282)	-3.865*** (±0.282)	-3.843*** (±0.281)	-3.820*** (±0.287)	-3.809*** (±0.285)	-3.837*** (±0.287)	-3.848*** (±0.289)	-3.658*** (±0.259)
Capture	-0.020 (±0.278)	-0.073 (±0.267)	-0.076 (±0.265)	-0.056 (±0.261)	-0.048 (±0.260)	0.009 (±0.253)	-0.008 (±0.255)	-0.387* (±0.174)
Fork length (L_F)	0.128 (±0.098)	0.128 (±0.098)	0.126 (±0.098)	0.131 (±0.098)				
Day of year (DOY)	-0.166 (±0.108)	-0.146 (±0.097)	-0.150 (±0.096)	-0.142 (±0.095)	-0.154 (±0.095)			
Water temperature at capture (T_{cap})	0.049 (±0.127)							
Period (±night)	0.280 (±0.214)	0.254 (±0.208)	0.252 (±0.208)	0.262 (±0.207)	0.253 (±0.207)	0.333 (±0.200)	0.327 (±0.200)	
Winter flow anomaly (wntflow)	-0.173 (±0.263)	-0.162 (±0.262)	-0.207 (±0.254)					
Winter temperature anomaly (wnttemp)	0.086 (±0.278)	0.088 (±0.280)	0.050 (±0.277)	-0.042 (±0.266)	-0.045 (±0.265)	-0.040 (±0.267)		
Autumn to spring tag count ratio (pautumn)	0.130 (±0.249)	0.139 (±0.250)						
Capture × L_F	0.068 (±0.175)	0.066 (±0.175)	0.069 (±0.174)	0.061 (±0.174)				
Capture × DOY	0.320 (±0.199)	0.288 (±0.193)	0.292 (±0.189)	0.284 (±0.189)	0.270 (±0.188)			
Capture × tempc	-0.142 (±0.201)							
Capture × period (±night)	-0.734 (±0.403)	-0.637 (±0.377)	-0.635 (±0.376)	-0.677 (±0.366)	-0.673 (±0.365)	-0.798* (±0.354)	-0.690 (±0.353)	
Capture × wntflow	0.122 (±0.211)	0.110 (±0.212)	0.115 (±0.208)					
Capture × wnttemp	-0.434* (±0.215)	-0.442* (±0.217)	-0.437* (±0.211)	-0.379* (±0.184)	-0.383* (±0.184)	-0.418* (±0.180)		
Capture × pautumn	-0.017 (±0.200)	-0.025 (±0.197)						
Variance (±c.1 year)	0.326	0.332	0.345	0.379	0.375	0.383	0.393	0.384

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.
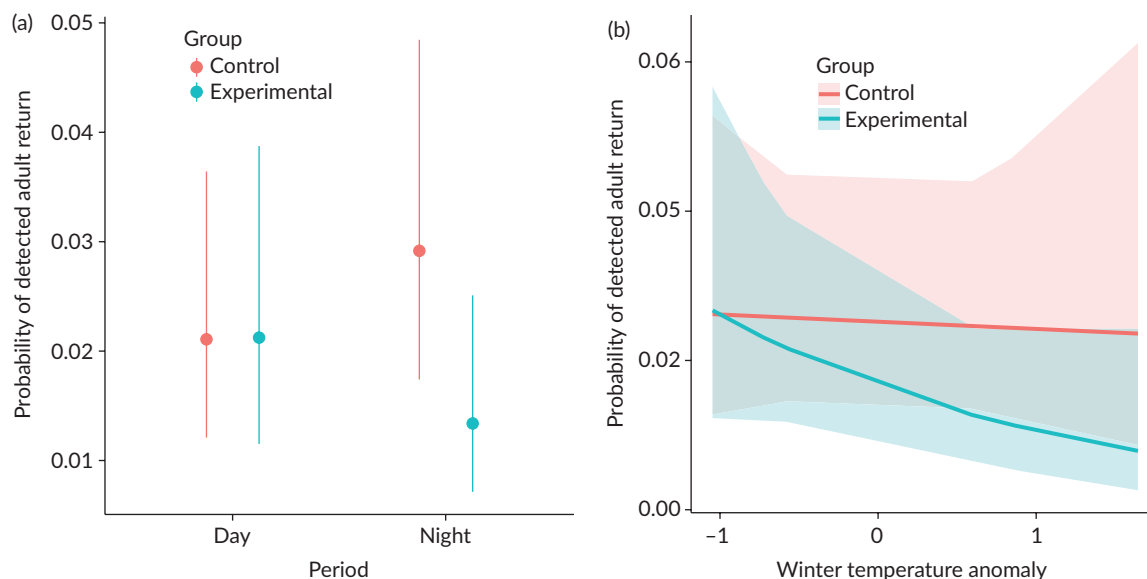
FIGURE 4 Marginal effect of (a) period (mean ± 95% C.I.) and (b) winter temperature anomaly on the probability of detected adult *Salmo salar* return from control and experimental group smolts

only affected return rates under certain conditions. The effect of day or night sampling period was negative such that smolts in the experimental group captured and CW-tagged at night had a lower probability of detected adult return compared with control smolts detected during the same period (Figure 4(a)). Similarly, the effect of winter (December–March) temperature anomaly on the probability on detected adult return was negative for captured and CW-tagged smolts (Figure 4(b)). Interestingly, models that retained L_{Ftag} and, to a lesser extent, T_{cap} explained more variation in the probability of detected adult return but were more complicated, albeit not substantially (*i.e.*, their difference in AIC, δAIC, from m5 was < 2; Table 5).

Visual inspection of the distribution of random effect estimates suggested one of the years was unduly influencing the other estimates; the random effect estimate of year 2008 was large and negative compared with other years (Supporting Information Figure S6). Consequently, the analysis was repeated excluding 2008, which on further investigation, negated the need for a random effect of smolt year; repeating the model selection process above with binomial GLM identified the most parsimonious model as the GLM equivalent of the GLMM model 5 and the parameter estimates were similar (not shown).

TABLE 7 Table of model performance statistics for the models considered only for the experimental group

Model	logLik	d.f.	AIC	δAIC	R^2
m6	−237.616	3	481.231		0.019
m5	−236.750	4	481.500	0.269	0.022
m7	−238.884	2	481.768	0.537	0.013
m4	−236.531	5	483.061	1.830	0.023
m3	−236.374	6	484.748	3.517	0.024
m8	−242.137	1	486.273	5.042	0.000
m2	−236.305	7	486.609	5.378	0.024
m1	−236.292	8	488.583	7.352	0.024
m0	−236.291	9	490.582	9.351	0.024

Note. AIC = Akaike information criteria; logLik = Log likelihood.

3.2.2 | Experimental-only analysis

Preliminary investigations suggested that the smolt-year random effect was not required (all random year estimates were close to 0) and binomial GLM was appropriate. Repeating the same procedure as for the control and experimental analysis did not yield a single most parsimonious model (Table 7 and Supporting Information Table S5). Rather, it suggested that the model that had a negative effect of winter (December–March) temperature anomaly and a positive effect of L_{Frst} on probability of detected adult return, could not be distinguished from a simpler (and therefore preferred) model that retained only the winter (December–March) temperature anomaly effect (Figure 5(a), (b)). It is interesting to note that a model retaining day or night sampling period explained more variance than the more parsimonious models at the cost of some extra complexity.

4 | DISCUSSION

Under certain circumstances the capture and CW-tagging of wild *S. salar* smolts had a negative effect on the rates of detected adult returns. Capture and CW-tagging following mild winter river temperature anomalies and during the night, decreased the probability of adult return for smolts in the experimental group compared with the control group. Moreover, there was a marginal positive effect of length at PIT-tagging as parr. Similarly, for the experimental group, the capture and CW-tagging of smolts following mild winters decreased their probability of return as adults compared with those smolts caught and CW-tagged following more typical winter temperatures. Smolt length and being caught and CW-tagged at night both had a marginal effect (positive and negative, respectively) on individual probability of return as adult.

Mild winters will modify parr metabolic rate (Fry, 1971; Enders & Boisclair, 2016), growth (Elliott & Hurley, 1997), and the physiological and morphological changes associated with smoltification (McCormick *et al.*, 1998), which could affect migration timing and smolt length or condition. Consequently, one might also expect the covariates representing smolt-run timing (day of year) and smolt length (experimental
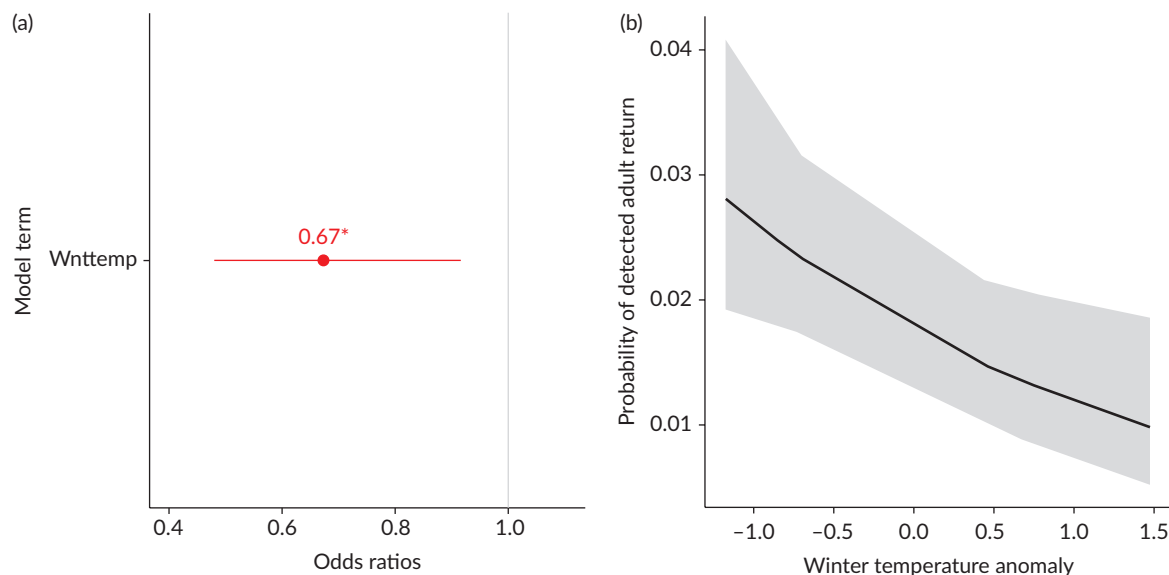
(a)

(b)

FIGURE 5   (a). Caterpillar plot showing the fixed coefficient estimates (mean $\pm$ 95% c.i.) for the most parsimonious model only for the experimental group smolts. *p < 0.05 (b) mean ($\pm$95% c.i.) marginal effect of winter temperature anomaly on the probability of detected adult *S. salar* return for experimental-only individuals

smolts only) to affect probability of adult return. This, however, was not clear from the results: day of year had no apparent effect (for run-timing distribution see Supporting Information Figure S3 and for means see Supporting Information Table S1), whereas the effect of smolt length was marginal. There was also no clear correlation between mean smolt length and mild-winter anomaly, with experimental smolts aged 1+ in 2007 recorded as the second longest following the mildest winter, while smolts aged 1+ in 2006 were recorded as the longest following the coolest winter (Supporting Information Table S4 and Figure S5).

Smolts that are ready to migrate earlier following mild winters (cumulative temperature effect; Zydlewski *et al*., 2005) could subsequently lose condition and physiological smolt characteristics (McCormick *et al*., 1997), or become stressed, while they await the environmental cues required to initiate downstream migration in the spring, making them more susceptible to the effect of capture and tagging. Such multiple-stressors can interact to the detriment of smolt survival (Barton *et al*., 1986) and even when not directly lethal could, through physiological effects, increase susceptibility to predation.

Mild winters could affect predator (or alternative prey) abundance or activity the following spring, all of which could have a direct effect on smolt predation rates. There are no data on these variables, so this cannot be tested.

Migration theory states that migratory behavioural strategies should be optimised to maximise fitness (Berthold, 2001; Hedenstrom, 2008). Ibbotson *et al*. (2006) reported that the migration patterns of *S. salar* smolts on the River Frome were related to water temperature, such that migration rates during the day were significantly lower than those at night when daily mean river temperatures were below 12°C. However, when the mean daily river temperature exceeded 12°C there was no significant difference between the hourly rates of migration during the day and night. In the current investigation, differences in detected adult return rates between control and experimental groups (calculated as control minus experimental adult return rate) were large and positive in 2 years (2007 & 2012) corresponding with the largest and smallest

percentage of smolts migrating during daylight hours (Supporting Information Figure S7 and Table S2). Smolts moving in an atypical pattern could conceivably be relatively successful at reaching the marine environment by either avoiding typical predator hunting periods or by moving in schools that satiate or confuse any active predators. However, disruption to migration under these circumstances could also cause individuals to disproportionately lose any migratory advantage.

Nocturnal *S. salar* smolt migration and fry dispersal, is generally accepted to be a predator avoidance tactic (Crozier & Kennedy, 2002; Fraser *et al*., 1993; Riley *et al*., 2002; Riley & Moore, 2000; Solomon, 1978). There is some evidence to support this for smolts in the current investigation (Figure 3(a)). However, smolts that were captured and CW-tagged at night had a lower probability of return as adults compared with smolts in the control group (Figure 4(a)). It could be that subsequent migratory behaviour (Riley *et al*., 2007) or physiology (N. Lower, W. D. Riley, T. Ellis, & A. Moore, unpubl. data) of tagged smolts released at night is different to those released during the day and this might affect their ability to avoid predators. Riley *et al*. (2014) proposed that the migratory patterns observed on the River Frome suggest those migrating during the night are moving independently (alone), whereas those detected migrating during the day often move in groups (schooling). Predator attacks can be concentrated around crepuscular periods (Major, 1977; Parrish, 1992), including those from piscivorous birds and fish, that are common on the River Frome (Beaumont *et al*., 2005; Cook & Bergersen, 1988; Emery, 1973; Kennedy & Greer, 1988; Riley *et al*., 2011). Predation risk might therefore be high during crepuscular periods and smolt migratory suppression observed at these times (Ibbotson *et al*., 2006) could also be a predator avoidance strategy, with the speed of school dispersal and reformation at dusk and dawn playing a key role in smolt vulnerability to predation (Pitcher & Turner, 1986; Riley *et al*., 2014; Ryer & Olla, 1998; Suzuki *et al*., 2007). Smolts caught, CW-tagged and released in batches during the day are in ready-made schools that may afford protection from visual predators, in a similar manner to smolts in the

control group. Whereas lone migrating smolts caught, CW-tagged and released at night may be less able to mitigate predatory threats from nocturnal predators. Surprisingly, in the current investigation, there was no effect on return probability of number of smolts captured in the RST and processed in any given 30 min period. Whereas one might expect a high number to have negative care implications to the standard CW-tagging process and positive survival implications in terms of optimum migratory conditions and opportunities for schooling and predator satiation.

Predation is probably the most important source of mortality as smolts leave freshwater (Hansen *et al.*, 2003) and smaller smolts might experience higher losses as they will be vulnerable to a broader range of predators. Smolt mortality at sea is also thought to be growth mediated (Friedland *et al.*, 1996, 2009). There is extensive evidence for size being an important factor determining the marine survival of hatchery-reared *S. salar* smolts (Lundqvist *et al.*, 1994; Kallio-Nyberg *et al.*, 2004). However, the role of smolt size in influencing survival for wild *S. salar* stocks has been less well studied and evidence remains equivocal (Gregory *et al.*, 2018).

Ibbotson *et al.* (2011) recorded the size of smolts as they passed East Stoke on the River Frome using video equipment. In all years, the mean size of nocturnal migrating smolts was significantly lower than the mean size of diurnal migrating smolts. They proposed that nocturnal migration is an adaptive behaviour that small *S. salar* smolts employ to avoid predation by daylight-feeding visual predators. In the current investigation, experimental group smolts caught and CW-tagged during the day were also significantly longer than those caught at night. Taken together with the observation that smolts that were larger at CW-tagging have a marginally higher probability of adult return, the results suggest that the effect of capture and CW-tagging might also be mediated by smolt length, which merits further investigation, perhaps using state–space models that also account for imperfect adult detection (Gregory *et al.*, 2018).

Although some of the findings of the current investigation are supported by previous studies on the River Frome and other rivers, others are not. It would, therefore, be misleading to assume that they offer the only explanation for the observed patterns in the probability of adult return. Therefore, we simply recommend caution when capturing and tagging smolts particularly following mild winters and when releasing smolts during the night. As always, the results are constrained to the covariates that were examined and it is feasible that important covariates were omitted, or that certain covariates captured effects other than those they were designed to measure.

The efficiency of the PIT-antenna system to detect returning adults could also have played a role. Not all PIT-tagged adults were detected (therefore, survival rates were higher than the detected adult return rates). Detection probabilities are unknown but between 2011 and 2015, the PIT-antenna systems at East Stoke detected 56% (59 of 105) of fish detected by a second PIT-antenna system installed at Bindon Mill (3 km upstream of East Stoke). Systematic differences in detection between the control and experimental group seem unlikely unless driven by an additional variable, while random differences in detection may have strengthened or weakened the effects found.

On balance, we believe it was smolt vulnerability to predation following release that was the most likely explanation for the observed differences in detected return rate between the control and experimental groups, and smolts in the experimental group CW-tagged during the day and at night. Fishery managers and researchers should remain cognisant that mild-winter river-temperature anomalies are likely to occur with an increased frequency in the future due to climate change, could be more pronounced in lowland rivers, and at the southern geographical range for *S. salar* such as the River Frome. They should be mindful, therefore, of the possible implications on adult return rates of trapping and tagging smolts following such conditions.

Nevertheless, the results of this study are reassuring in the context of ongoing investigations to derive and report marine return rates for *S. salar* in support of national and international stock assessments (ICES, 2017). The larger differences in return rates between CW-tagged and control groups reported by Crozier & Kennedy (2002) may reflect site-specific issues related to predation (e.g., the presence of a large cormorant *Phalacrocorax carbo* breeding colony near the mouth of the River Bush), local topography (the River Bush discharges to the sea over a beach), or other methodological differences. The results of the present study suggest that marking fish with CW tags remains a reliable and informative method for deriving information on marine return rates of *S. salar*. As such, return-rate data are likely to be particularly useful in indicating trends over time rather than single year-on-year changes. This highlights the need for managers to recognize the importance of long-term monitoring programmes of *S. salar* juveniles and emigrant smolts as indicators of change and for assessing biological responses to environmental variables (Russell *et al.*, 2012). While logistical constraints may restrict wider application in many cases, it should further be recognised that hands-off facilities, such as those on the River Frome, where out-migrating smolts and returning adults can be monitored and enumerated remotely, are likely to represent the optimum approach for evaluating marine return rates. Further development of such facilities would be of value.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.