The effect of catch-and-release angling at high water temperatures on behaviour and survival of Atlantic salmon *Salmo salar* during spawning migration

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In this study, behaviour and survival following catch-and-release (C&R) angling was investigated in wild Atlantic salmon *Salmo salar* ($n = 75$) angled on sport fishing gear in the River Otra in southern Norway at water temperatures of 16·3–21·1° C. *Salmo salar* were tagged externally with radio transmitters and immediately released back into the river to simulate a realistic C&R situation. The majority of *S. salar* (91%) survived C&R. Most *S. salar* that were present in the River Otra during the spawning period 3–4 months later were located at known spawning grounds. Downstream movements (median furthest position: 0·5 km, range: 0·1–11·0 km) during the first 4 days after release were recorded for 72% of *S. salar*, presumably stress-induced fallback associated with C&R. Individuals that fell back spent a median of 15 days before commencing their first upstream movement after release, and 34 days before they returned to or were located above their release site. Mortality appeared to be somewhat elevated at the higher end of the temperature range (14% at 18–21° C), although sample sizes were low. In conclusion, C&R at water temperatures up to 18° C had small behavioural consequences and was associated with low mortality (7%). Nevertheless, low levels of mortality occur due to C&R angling and these losses should be accounted for by management authorities in rivers where C&R is practised. Refinement of best practices for C&R may help to reduce mortality, particularly at warmer temperatures.

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Key words: biotelemetry; fisheries management; radio-telemetry; recreational fishing.

INTRODUCTION

Many populations of the anadromous Atlantic salmon *Salmo salar* L. 1758 have declined during the last decades (ICES, 2014). Various restrictions on riverine fisheries have been introduced to attempt to maintain sustainable populations, including an increased use of catch-and-release (C&R) angling (ICES, 2014). C&R for *S. salar* has been routinely practised since 1984 in some areas of Canada and U.S.A., and since about 1990, it has also been widely used and accepted as a management tool in many European countries. The proportion of caught and released *S. salar* range from

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15% of the total catch in Norway to as high as 80% in Scotland, reflecting compliance with various management regulations and conservation-oriented behaviours among anglers (ICES, 2014). In 2013, 174 000 *S. salar* were reported caught and released in the North Atlantic region (North America and Europe combined), constituting almost half of all wild *S. salar* angled in the countries included in ICES statistics (ICES, 2014).

For C&R to be a successful management tool, released fishes have to survive and reproduce successfully (Cooke & Schramm, 2007). Where survival to reproduction is high in caught and released fishes, recreational angling can, in theory, be conducted without reducing spawning stocks, and thereby preserve the economic and social benefits of recreational fisheries. Angling of *S. salar*, however, may cause considerable physiological disturbances due to stress and exhaustion (Kieffer, 2000), which at a later time may lead to mortality (Brobbel *et al.*, 1996; Wilkie *et al.*, 1996; Anderson *et al.*, 1998). Because fishes are ectotherms, temperature is an important regulating factor of physiological processes (Brett, 1971), and the effect of C&R at high water temperatures above the thermal optimum may be more severe than at lower temperatures (Arlinghaus *et al.*, 2007; Gale *et al.*, 2011). Indeed, Gale *et al.* (2011) found that stress levels and mortality rates increased with increasing water temperature in 70% of the published studies that investigated the effects of C&R.

Mortality rates of *S. salar* after C&R are generally between 0 and 12% at water temperatures below 18° C (Brobbel *et al.*, 1996; Dempson *et al.*, 2002; Thorstad *et al.*, 2007) but tend to increase at water temperatures above 17–18° C (Wilkie *et al.*, 1996, 1997; Anderson *et al.*, 1998). This is somewhat surprising as the optimal thermal range for *S. salar* is reported to fall in the range of 16–20° C (Elliott & Elliott, 2010). The exact mechanisms that cause elevated mortality in *S. salar* following C&R at high water temperatures are not known (Wilkie *et al.*, 1997). Extreme biochemical alterations, including elevated levels of white muscle acidosis at increasing temperatures, have been proposed to be important determinants of mortality (Brobbel *et al.*, 1996; Wilkie *et al.*, 1996). Wilkie *et al.* (1997), however, found that peak lactate levels remained the same in different temperature regimes (12, 18 and 23° C) and that lactate catabolism was faster at high temperatures (18 and 23° C), seemingly discounting acidosis as a direct cause. Mortalities were only observed at the highest temperatures (30% mortality rate at 23° C; Wilkie *et al.*, 1997). Anderson *et al.* (1998) suggested that an irregular heart rate during recovery, perhaps indicating cardiac collapse, may have caused the unusually high mortality rate (80%) that was observed for *S. salar* caught-and-released at 20° C.

All studies on *S. salar* regarding the effects of C&R at water temperatures above 15° C have been performed under experimental conditions, *i.e.* in tanks in the laboratory, or in cages and artificial pools in a river after angling (Thorstad *et al.*, 2007; Gale *et al.*, 2011). Because artificial confinement in itself may be stressful (Portz *et al.*, 2006), it is difficult to separate effects on survival caused by C&R from those due to being kept in captivity (Donaldson *et al.*, 2008; Gale *et al.*, 2011). Moreover, the use of hatchery-reared *S. salar* (Wilkie *et al.*, 1997; Anderson *et al.*, 1998), surgical implantation of radio transmitters measuring heart rate (Anderson *et al.*, 1998), manual hooking (Booth *et al.*, 1995; Brobbel *et al.*, 1996; Wilkie *et al.*, 1996), extreme exhaustion (Tufts *et al.*, 1991; Booth *et al.*, 1995; Wilkie *et al.*, 1996) and other unusual treatments may imply that these studies were not representative of normal C&R performed by anglers in rivers (Whoriskey *et al.*, 2000; Dempson *et al.*, 2002).

Monitoring the behaviour and survival of free-swimming fishes in their natural environment is advocated as one of the best approaches for evaluating the effects of C&R given that it provides ecological realisms (Donaldson *et al.*, 2008) making results directly applicable to the resource managers. This type of *in situ* monitoring can be achieved by applying various biotelemetry techniques, for instance by tagging released fishes with a radio transmitter and by subsequently tracking their movements to assess potential changes in behaviour and survival following C&R (Donaldson *et al.*, 2008). Hitherto, such studies on *S. salar* have been carried out at water temperatures below 15° C only (Webb, 1998; Gowans *et al.*, 1999; Mäkinen *et al.*, 2000; Thorstad *et al.*, 2003, 2007; Halttunen *et al.*, 2010; Jensen *et al.*, 2010). Although the mortality after C&R was consistently low in these studies (0–6%), C&R frequently affected individual *S. salar* behaviour, resulting in rapid downstream movements (*i.e.* fallback), migration delays and erratic movement patterns (Mäkinen *et al.*, 2000; Thorstad *et al.*, 2003, 2007). As the normal movement pattern during the riverine migration phase of *S. salar* involves a direct or stepwise upstream movement to the spawning areas, rapid downstream movements are regarded as being atypical (Økland *et al.*, 2001; Finstad *et al.*, 2005). Despite observed downstream movements for a relatively high proportion of the experimental *S. salar* in these studies, most individuals were subsequently located in known spawning areas during the spawning period and C&R was therefore assumed to have no major negative effect on the potential for reproduction (Webb, 1998; Thorstad *et al.*, 2007; Jensen *et al.*, 2010).

Effects of C&R for *S. salar* have not been systematically examined in rivers using biotelemetry methods at water temperatures above 15° C, despite temperatures >15° C occurring frequently throughout the distributional range of this species. In some cases, water temperatures in *S. salar* rivers can exceed 25° C in the summer (Lund *et al.*, 2002; Baisez *et al.*, 2011). In the future, higher temperatures may also be anticipated due to climate change effects (Caissie, 2006; Jonsson & Jonsson, 2009; Nielsen *et al.*, 2013). Thus, studies at high temperatures are required to extend the understanding of thermal effects on *S. salar* after C&R (Thorstad *et al.*, 2008*a*; Gale *et al.*, 2011), and to identify the critically high temperatures above which C&R mortality is so high that it is ineffective as a management tool (Olsen *et al.*, 2010).

The aim of this study was to generate realistic mortality estimates and to assess behavioural effects for caught and released *S. salar* at water temperatures above 15° C. This was done by tagging recreationally angled *S. salar* with external radio transmitters at water temperatures between 16 and 21° C in the River Otra in southern Norway in 2012 and 2013. Survival and behaviour following C&R was examined by tracking the *S. salar* after release and throughout the spawning period. As increased water temperatures most likely would magnify the physiological disturbance caused by C&R, an increased mortality following C&R at water temperatures above 15° C compared with the 0–6% mortality at lower water temperatures in earlier studies was expected.

MATERIALS AND METHODS

STUDY AREA

The study was conducted in the River Otra in southern Norway (58° N; 8° E, catchment area of 3738 km^2; Fig. 1). Mean annual water discharge 15 km upstream from the river mouth is 149 m^3 s^{-1}. The river is regulated for hydropower production, and the guaranteed minimum
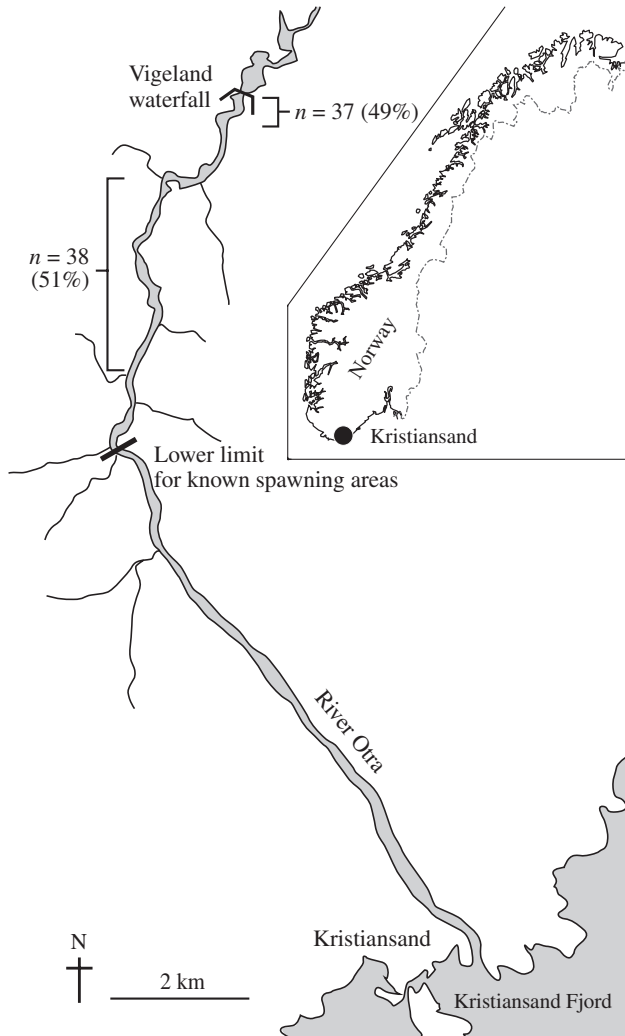
FIG. 1. The River Otra in Norway. The anadromous stretch ends at Vigeland waterfall. The brackets show where *Salmo salar* were caught, tagged and released. The numbers and percentages show how many *S. salar* and the proportion of the total sample that was angled and tagged in the two sections of the river. The lower limit for known spawning areas of *S. salar* (Kroglund *et al.*, 2008) is shown on the map.

water flow in the part of the river accessible for *S. salar* is 50 m³ s⁻¹ during summer. *Salmo salar* have access to 16 km of the river, which is free of migration obstacles, before they encounter their limit at the Vigeland waterfall (Fig. 1). The average annual rod catch during 2004–2013 was 6·7 t (about 2637 *S. salar*; the mean individual mass was 2·7 kg). In 2013, 10% of the total rod catch was released. Most of the *S. salar* in the river result from natural reproduction in the wild, and there is no hatchery supplementation. Scale readings of a selection of the sport fishery catch in 2011–2013, however, showed that 4% of the *S. salar* were farm escapees.

TAGGED *SALMO SALAR* AND ANGLING PROCEDURES

A total of 75 *S. salar* (mean ± S.D. total length, L_T, 67 ± 9 cm, range: 50–90 cm) were angled from 9 July to 16 August in 2012 ($n = 52$) and 2013 ($n = 23$) and tagged with external radio transmitters before being released. There were 43 females (70 ± 10 cm, range: 50–90 cm) and 32 males (64 ± 8 cm, range: 51–83 cm), 28 of which were caught on spoons and 47 by fly fishing. *Salmo salar* were angled in cooperation with five highly experienced local anglers who were instructed to play the *S. salar* as they normally would. All *S. salar* were landed in the presence of a member of the research team by dip-netting while the *S. salar* were in the water using a knotless landing net. The hook was removed with a pair of pliers while the *S. salar* was in the net. Both the use of pliers and dip-netting while *S. salar* are in the water are methods which are recommended by the Norwegian Scientific Committee for Food Safety (Olsen *et al.*, 2010) and commonly used by Norwegian anglers. Immediately after landing, the *S. salar* was transferred from the landing net to a tube with closed ends (105 cm long × 21 cm diameter) filled with water to keep the head and gills submerged during tagging. The *S. salar* was examined for bleeding and damage, L_T was measured and sex was determined based on secondary sexual characteristics (head shape and presence of a kype). It was estimated that 84% of the *S. salar* had recently entered the river based on their silver (bright) colour, a thin mucous layer and the presence of salmon lice *Lepeophtheirus salmonis*. After tagging, the *S. salar* were held with a loose grip in the river until they recovered and were able to swim freely away. Air exposure was restricted to short periods during dip-netting after capture, transfer from the net to the tagging tube and while lifting the *S. salar* out of the tagging tube for release. The total air exposure period from the combined three actions was typically <20 s.

The mean ± S.D. time (to the nearest whole minute) from hooking to landing (playing time) was 5 ± 2 min (range: 3–11 min). Most of the *S. salar* were hooked in the upper or lower jaw (71%, $n = 53$), while 12% ($n = 9$) were hooked in the tongue or mouth cavity and 4% ($n = 3$) in other locations (two in the head area and one in the dorsal muscle). The hook position could not be determined for 13% of the *S. salar* ($n = 10$) because the hook fell out in the landing net. Individuals hooked in the tongue or mouth cavity were defined as being hooked in harmful locations as deep hooking has been shown to increase mortality (Bartholomew & Bohnsack, 2005; Gargan *et al.*, 2015). Spoons were always equipped with a single treble hook. By contrast, 43 *S. salar* were caught on flies with a treble hook and four on flies with a double hook. All hooks were barbed. *Salmo salar* bleeding from the gills upon landing ($n = 8$) were not used in the experiments as such injuries are known to significantly reduce the survival probability (Bartholomew & Bohnsack, 2005) and such individuals are normally killed rather than being released by anglers. Three *S. salar* showing minor bleeding in the gill area and 11 *S. salar* with minor bleeding in the hook wound were tagged and released, because anglers normally would release such individuals.

The *S. salar* were tagged with external radio transmitters without being anaesthetized (transmitter model F2120 from Advanced Telemetry Systems; www.atstrack.com) as described in the study of Økland *et al.* (2001). Anaesthesia was not necessary, given that the *S. salar* were held in water for all procedures and given that the entire tagging process was so rapid. Moreover, use of anaesthetics would have confounded the experiment and potentially contributed to aberrant behaviour. The transmitters were rectangular with dimensions of 21 mm × 52 mm × 11 mm (mass: 16 g in air). Thorstad *et al.* (2000) found no effect of radio transmitters with similar dimensions attached in the same manner as in this study on swimming performance of farmed *S. salar*. Ten transmitters were equipped with an activity sensor that produced additional pulses when the *S. salar* were moving. The pulse rate of these transmitters also increased from 40 to 80 pulses min^{-1} if the *S. salar* did not move within 8 h. The manufacturer's guaranteed transmitter lifetime was 144 and 195 days respectively, for transmitters with and without sensors. The mean ± S.D. handling time from the moment when an *S. salar* was netted until release was 3 ± 0·5 min (range: 2–5 min). All experimental procedures were approved by the Norwegian Animal Research Authority.

Salmo salar caught in the upper end of the anadromous stretch had constrained upriver movement possibilities compared with those captured further downstream, and the behaviour after C&R may therefore differ between these groups. The *S. salar* were therefore divided into two groups based on angling location for the analyses of behaviour after C&R: (1) *S. salar* caught and released in or close to the pool below the Vigeland waterfall at the upper end of the anadromous

stretch ($n = 37$) and (2) *S. salar* caught and released over a river stretch further downstream ($n = 38$; Fig. 1). The *S. salar* in group 1 were angled at a mean $\pm$ s.d. distance of $0\cdot3 \pm 0\cdot1$ km (range: $0\cdot1 - 0\cdot6$ km) below the waterfall and *S. salar* in group 2 at a mean $\pm$ s.d. distance of $4\cdot0 \pm 0\cdot9$ km (range: $2\cdot2 - 5\cdot4$ km) below the waterfall.

TRACKING AND SURVIVAL ASSESSMENT

Salmo salar behaviour after release was monitored by manual tracking (receiver model R2100, Advanced Telemetry Systems). As the river is located close to roads, a car equipped with a roof whip antenna (142 MHz, Laird Technologies; www.lairdtech.com) was used to search for tagged *S. salar*. When an *S. salar* was located, a more accurate position was obtained by using a four-element yagi antenna to obtain cross-bearings (142 MHz, Laird Technologies). The locations of each *S. salar* were determined once every day for 4 days after release and thereafter once every week until the end of the fishing season (15 September in both study years). Tracking continued once every second week until January the year after tagging. Each tagged *S. salar* was located 15 ± 6 times (mean $\pm$ s.d.; range: $1 - 26$ times). *Salmo salar* that left the River Otra ($n = 11$) and moved to other rivers were only tracked once after they left. These individuals were searched for during tracking surveys (between 28 October and 11 November) that covered most rivers and creeks in the area between River Lygna, Lyngdal (73 km west of Otra) and River Nidelva, Arendal (60 km east of Otra).

Assessment of survival after C&R was based on the assumption that a surviving *S. salar* at varying intervals would change its position in the river, while mortality was assumed if the *S. salar* showed no upstream movements and the signal from its tag was recorded from the same position through to the end of the tracking period. The transmitters with activity sensors used on 10 *S. salar* tagged in the pool below Vigeland waterfall also aided in determining whether these particular individuals were dead or alive.

Positions of the *S. salar* acquired between 11 November 2012 and 1 December 2013 were used to indicate the positions of the *S. salar* in the spawning period. Maps of the known spawning grounds in the River Otra (Kroglund *et al.*, 2008; M. Finne, H. Gregersen, H. Kaasa, Ø. P. Hveding, A. Poléo, unpubl. data), local knowledge and personal observations of suitable spawning substrata were used to determine if the *S. salar* were located at spawning grounds or not.

ENVIRONMENTAL DATA

Mean $\pm$ s.d. water temperature during C&R was $17\cdot3 \pm 0\cdot7°$ C (range: $16\cdot3 - 19\cdot7°$ C) in 2012 and $20\cdot0 \pm 0\cdot5°$ C (range: $19\cdot4 - 21\cdot1°$ C) in 2013 (Fig. 2). The water temperature in the river peaked at $19\cdot7°$ C on 3 August in 2012 and at $21\cdot5°$ C on 31 July in 2013 (HOBO Pendant Temperature/Light Data Logger 64 K-UA-002-64; www.onsetcomp.com; located 5 km downstream of the Vigeland waterfall). Water discharge at the time of *S. salar* release was mean $\pm$ s.d. 111 ± 29 m^3 s^{-1} (range: $63 - 161$ m^3 s^{-1}) in 2012 and 96 ± 27 m^3 s^{-1} (range: $60 - 131$ m^3 s^{-1}) in 2013. Water pH during the study period remained stable at a mean $\pm$ s.d. of $6\cdot1 \pm 0\cdot1$ (range: $6\cdot0 - 6\cdot4$) in 2012 and $6\cdot1 \pm 0\cdot1$ (range: $5\cdot7 - 6\cdot4$) in 2013.

DATA ANALYSIS

Non-parametric statistics (Mann–Whitney-*U* tests and Fisher's exact tests) were used to analyse differences between *S. salar* that died and those that survived, because the parameters in most cases were not normally distributed and the number of dead *S. salar* was low.

A generalized linear model (GLM) with binomial error structure and a logit link function was used to test for effects on whether the *S. salar* moved downstream or not within 4 days after C&R (no = 0, yes = 1). Predictor variables included in the model were water temperature and water discharge at release, L_T, playing time, study year, sex, hooking location (harmful or less harmful location), C&R site (below Vigeland waterfall or further downstream), migration status (newly entered the river from the sea *v.* resident in the river for an extended period based on loss of silver colouration), bleeding (yes or no) and angling gear (fly or spoon). A maximal model without interactions was fitted and then simplified by backwards stepwise deletion of
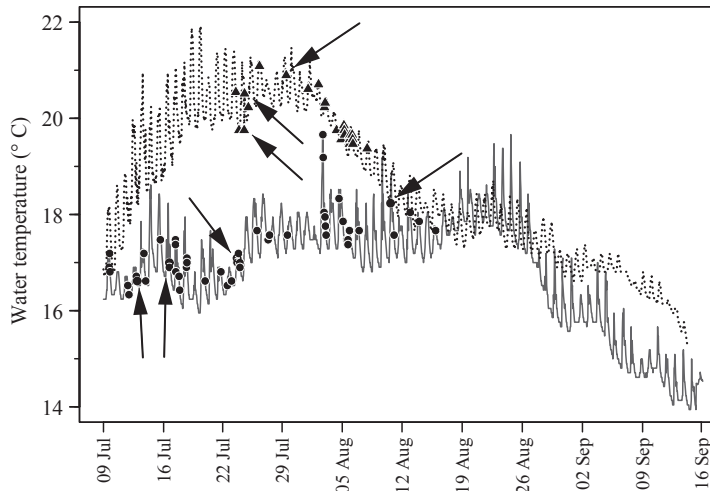
FIG. 2. Water temperature in 2012 (——) and 2013 (.....) in the River Otra from 9 July to 15 September in both years. Date and temperature at release are shown for individual *Salmo salar* (●, *S. salar* caught and released in 2012; ▲, *S. salar* caught and released in 2013). ——→, *S. salar* that died after catch and release (C&R), while fish without ——→ survived C&R.

non-significant parameters until a minimal adequate model was found. The fit of each reduced model was compared with the previous model by ANOVA χ^2 tests. A *P*-value of ≤0·05 was used to reject a reduced model and select the preceding model.

A GLM with Gaussian error structure was used to test for the effects of predictor variables on the distance of the downstream movement for the *S. salar* moving downstream within 4 days after C&R. The distance was ln transformed in order to meet the assumption of normality. This model contained the same predictor variables as described in the binomial regression and the same model selection procedure was used. A probability (*P*) of ≤0·05 was used as a critical level for rejection of the null hypothesis for all analyses.

Salmo salar that were recaptured within 4 days after C&R (*n* = 2) or died shortly after C&R (*n* = 6) were excluded from the descriptive and statistical analysis of behaviour. The *S. salar* that were recaptured, however, were included in the descriptive analysis of the behaviour that occurred 1 day after release as these individuals survived until the next day after release. All statistical analyses were conducted using R 3.0.0 (The R Project for Statistical Computing; www.r-project.org).

RESULTS

MORTALITIES AFTER C&R

Seven (9%) out of 75 tagged *S. salar* died after C&R, four (8%) in 2012 and three *S. salar*, (13%) in 2013 (Table I). Six of these *S. salar* died shortly after release (*c*. 1 day). Carcasses of four of the six were found in the river downstream of the capture site 5–6 days after release, and as they were covered with fungus it is likely that they had died shortly after release. The remaining two of the six were not found dead in the river but were believed to have died shortly after release because they moved rapidly downstream and thereafter their tags were continuously located at the same spot until the end of the tracking period 5–6 months later. The seventh *S. salar* was found dead

TABLE I. Total number of caught, tagged and released *Salmo salar* in the two study years and the mortalities after catch and release (C&R)

Year	Mean ± s.d. water temperature during C&R (° C)	Number of tagged *S. salar*	Number of dead *S. salar* after C&R	Mortality (%)
2012	17·3 ± 0·7	52	4	8
2013	20·0 ± 0·5	23	3	13
Both years	18·2 ± 1·4	75	7	9

23 days after release 0·5 km upstream from the location where it was tracked previously the same day. The previous upstream movement and physical appearance when it was found suggested that it had recently died. At release, four of the seven dead *S. salar* were in apparently good condition without any bleeding or injuries. One *S. salar* exhibited a small amount of bleeding in the gill area, one had a long healed wound to its caudal fin, while one needed an unusually long time (3 min) to recover prior to release. For both years combined, the mortality after C&R for *S. salar* captured at water temperatures between 16 and 18° C was 7% (three of 46), for *S. salar* captured between 18 and 20° C it was 10% (two of 20) and for *S. salar* captured >20° C it was 22% (two of nine).

There was no difference in water temperature at time of capture between *S. salar* that died after C&R ($n = 7$, mean ± s.d.: 18·6 ± 1·8° C, range: 16·6–20·9° C) and survivors ($n = 68$, mean ± s.d.: 18·1 ± 1·3° C, range: 16·3–21·1° C, Mann–Whitney U-test, $W = 276$, $P > 0·05$). There was no difference in *S. salar* L_T, playing time or handling time between the dead *S. salar* and survivors (Mann–Whitney U-tests, W range: 240–272, all P-values > 0·05). Furthermore, the proportion of *S. salar* that were caught on a fly *v.* a spoon, were bleeding *v.* not bleeding, were hooked in potentially harmful *v.* less harmful locations or were caught in 2012 *v.* 2013 did not differ between dead *S. salar* and survivors (Fisher's exact tests, all P-values >0·05).

Some of the *S. salar* that survived after C&R were later recaptured by anglers. Five were caught and killed by anglers 2–37 days after being tagged and released. Two additional individuals survived being caught and released by anglers a second time (16 and 6 days after the first release), giving an overall recapture rate of 9% (seven of 75). One *S. salar* was hooked in the steel wire keeping the transmitter attached (1 day after release), and the transmitter was torn off while the *S. salar* was played. This individual was not landed and its subsequent fate is unknown.

BEHAVIOUR AFTER C&R

During the first day after release, 57% ($n = 39$) of the *S. salar* moved a median distance of 0·5 km downstream from the release site (mean ± s.d.: 0·7 ± 0·7 km, range: 0·1–3·1 km), 36% ($n = 25$) remained stationary close to the release site and 7% ($n = 5$) moved a median distance of 0·1 km upstream (mean ± s.d.: 0·1 ± 0·3 km, range: 0·1–1·2 km). Within 4 days of release, 72% ($n = 48$) of the *S. salar* had been recorded downstream of the release site (Table II). The median furthest position downstream during this period was 0·5 km (mean ± s.d.: 1·1 ± 1·7 km, range: 0·1–11·0 km). Of the total number of movements for all *S. salar* after 4 days, 84% was downstream, of which 48 and 19% occurred during the first and second day after release, respectively.

TABLE II. Median position for the *Salmo salar* that moved downstream during the first 4 days after catch and release (C&R) (*n* = 48) in the two study years. The release site is set as zero, and a positive distance from the release site is upstream and negative distance downstream. Moved upstream (%) gives the cumulative proportion of *S. salar* of which at least one upstream movement was recorded after release. Returned to release site (%) is the cumulative percentage of *S. salar* that were recorded close to or upstream from the release site.

									Days after C&R							
	1	2	3	4	5–11	12–18	19–25	26–34	35–41	42–47	48–54	55–68	69–82	83–96	97–110	111–124
2012 Number of tracked *S. salar*	35	35	35	35	32	32	35	33	31	30	23	32	30	30	26	13
Median position (m)	−504	−589	−600	−589	−649	−584	−589	−433	−433	−508	−433	−200	−368	−188	−186	−71
Interquartile range (m)	695	1030	1112	1113	1068	1074	1213	1052	1403	1303	1763	1603	2523	2539	2106	2359
Moved upstream (%)	–	0	14	23	37	49	60	74	74	83	86	89	91	94	94	100
Returned to release site (%)	–	0	3	9	11	23	26	31	37	40	43	49	51	51	54	60
2013 Number of tracked *S. salar*	13	13	13	13	12	13	9	13	–	11	–	11	11	9	9	9
Median position (m)	−321	−400	−394	−400	−358	−321	−441	−324	–	−424	–	−697	−522	−433	−232	−136
Interquartile range (m)	294	144	262	382	270	346	1861	686	–	868	–	1259	2539	3687	4659	4354
Moved upstream (%)	–	0	15	31	46	61	69	92	–	92	–	92	100	100	100	100
Returned to release site (%)	–	0	8	15	15	23	23	31	–	31	–	31	38	46	54	54

TABLE III. Parameter estimates from a general linear model explaining variation in the length of the downstream movement for *Salmo salar* that moved downstream within 4 days after catch and release (C&R). Estimates are given on a ln scale

	Estimate ± s.e.	t	P
Intercept (newly ascended)	10·59 ± 2·17	4·88	<0·001
Water temperature	−0·22 ± 0·12	−1·84	<0·05
Longer freshwater residency*	−1·00 ± 0·40	−2·51	<0·05

*Intercept of *S. salar* with a longer freshwater residency relative to newly ascended *S. salar*.

The median total distance moved was 0·5 km (mean ± s.d.: 0·9 ± 1·5 km, range: 0·0–11·0 km) for individual *S. salar* during the first 4 days after release.

L_T was the only variable that influenced whether *S. salar* moved downstream or not during the first 4 days after C&R as this was the single variable left in the minimal adequate model (binomial regression, ANOVA χ^2 tests with preceding models, all P-values > 0·05, the minimal adequate model *v.* intercept-only model, $\chi^2 = 4·6$, d.f. = 1, $P < 0·05$). According to the model, the probability for moving downstream after C&R was twice as high for the smallest *S. salar* caught and released in this study (50 cm, 88% probability) compared with the largest *S. salar* (90 cm, 40% probability, binomial regression, $y = 5·13 ± 2·09$ s.e. + (−0·06 ± 0·03 s.e.) L_T, $P < 0·05$, estimates are given on the logit scale).

When testing for effects on the distance of the downstream movement during the first 4 days after C&R, both water temperature and migration status were retained in the final model (GLM, ANOVA χ^2 tests with preceding models, all P-values > 0·05, exclusion of water temperature, $\chi^2 = 3·6$, d.f. = 1, $P = 0·07$, *i.e.* near significant). The length of the movement decreased with increasing water temperatures at release, and newly ascended *S. salar* moved further downstream than those with a longer freshwater residency (Table III). Relatively low proportions of the total variation, however, was explained by these variables (adjusted $r^2 = 0·20$).

The median time until an upstream movement was recorded for the *S. salar* that moved downstream during the first 4 days after C&R was 15 days (mean ± s.d.: 26 ± 28 days, range: 1–153 days, $n = 48$). Of the *S. salar* that initially moved downstream, 28 (58%) were recorded for the first time at or upstream of their original release site a median of 34 days after C&R (mean ± s.d.: 43 ± 38 days, range: 3–153 days, $n = 28$). The remaining 20 *S. salar* (42%) never again moved as far upstream as their initial release site during the study period. The length of the delay did not differ between the years (first movement upstream: Mann–Whitney *U*-test, $W = 184$, $P > 0·05$, in 2012/2013 $n = 35/13$, return to release site: Mann–Whitney *U*-test, $W = 81$, $P > 0·05$, in 2012, 2013 $n = 21, 7$). Likewise, the proportion of *S. salar* that did not return to their release site did not differ between the years (14 of 35 in 2012 and six of 13 in 2013, Fisher's exact test, $P > 0·05$).

Eleven *S. salar* (15%) left the River Otra prior to the spawning period, after staying in the river for a median of 49 days (range: 11–89 days) after C&R. Eight were later found during tracking surveys between 28 October and 11 November in neighbouring rivers and creeks known for having wild *S. salar* populations. The median approximate distance these individuals had to cover from the river mouth of the River Otra to the river mouth of the rivers where they were located was 14 km (range: 6–56 km).

POSITIONS DURING SPAWNING

All except one of the *S. salar* that were alive and present in the river until spawning were located in known spawning areas (50 of 51, 98%) (Fig. 1; for further details on spawning areas, see Kroglund *et al.*, 2008). The median positions during the spawning period for *S. salar* that were caught and released in the upper end of the anadromous stretch were 0·4 km downstream of their release sites ($n = 23$, mean ± s.d.: 1·3 ± 1·7 km, range: 5·2 km downstream to 0·2 km upstream). Fifteen *S. salar* (65%) were located below and eight *S. salar* (35%) close to (within 250 m) their respective release sites. The *S. salar* that were caught and released further downstream in the river were on average positioned slightly, but not significantly, upstream of their release sites at spawning time ($n = 28$, mean ± s.d.: 0·4 ± 2·4 km, range: 5·9 km downstream to 4·2 km upstream, paired *t*-test, $t = 0·8$, d.f. = 27, $P > 0·05$). Eleven (39%) *S. salar* were located below, three (11%) close to and 14 *S. salar* (50%) above their release sites.

DISCUSSION

The mortality after C&R in this study was 9% at water temperatures above 16° C (mean 18·2° C, range: 16–21° C). This must be regarded as a maximum mortality caused by C&R because without a control group it is difficult to determine if any of the mortalities were caused by other reasons than C&R. Six of the seven *S. salar* that died, however, did so shortly after release (*c*. 1 day), making it plausible that these mortalities were caused by C&R. C&R-mediated mortalities usually occur within the first 24 h after release (Muoneke & Childress, 1994). For the last individual that died more than 3 weeks after C&R, it cannot be excluded that it died due to long-term effects of C&R, although other mortality reasons are also plausible. Mortalities caused by C&R could emerge several days after release (Donaldson *et al.*, 2013; Robinson *et al.*, 2013) and may be linked with immune suppression and disease development (Muoneke & Childress, 1994; Arlinghaus *et al.*, 2007).

The mortality recorded after C&R in this study is slightly higher than that reported in similar studies at lower water temperatures (Webb, 1998; Thorstad *et al.*, 2007; Jensen *et al.*, 2010; Fig. 3). The mortality at the highest water temperatures in this study (mean 20° C in 2013, 13% mortality) is in the same range as that observed by Dempson *et al.* (2002) in Newfoundland, where *S. salar* were held in cages in a river after angling (9·5% mortality at 19° C). In contrast, Anderson *et al.* (1998) reported a very high mortality rate (80%) at 20° C; however, the sample size was low (five *S. salar*) and the mortality could have been elevated due to additional stress caused by surgical implantation of large internal transmitters measuring heart rate.

The size of the *S. salar* has also been hypothesized to be related to mortality after C&R angling as larger *S. salar* are stronger making it difficult for anglers to land them before they are exhausted, and due to their longer play times they suffer increased physiological disturbance (Thorstad *et al.*, 2003). By contrast, smaller *S. salar* are rarely played to full exhaustion (Dempson *et al.*, 2002). Although the results did not indicate that the mortalities were associated with *S. salar* size, the generally small size of the *S. salar* in this river may have contributed an overall high survival. Booth *et al.* (1995), however, found that the physiological post-angling disturbance was greater for grilse (*S. salar* returning to spawn for the first time after 1 year at sea) than for much larger multi-sea-winter *S. salar*.
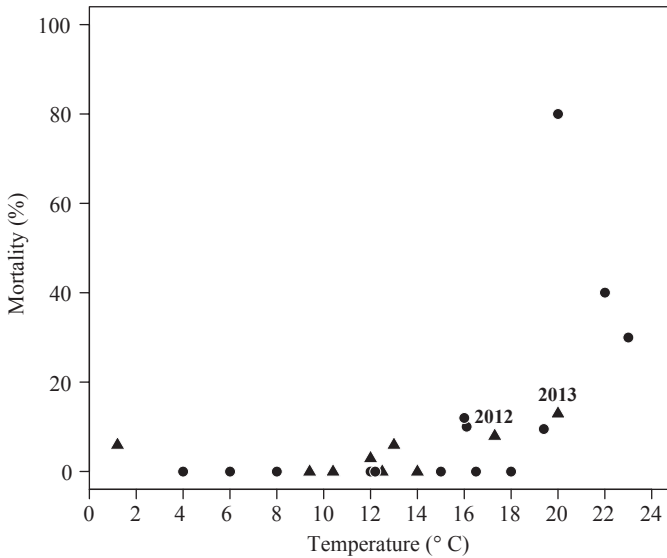
FIG. 3. Mortality rates after catch and release (C&R) in different studies related to water temperature for *Salmo salar* (Tufts *et al.*, 1991; Davidson *et al.*, 1994; Booth *et al.*, 1995; Brobbel *et al.*, 1996; Wilkie *et al.*, 1996, 1997; Anderson *et al.*, 1998; Gowans *et al.*, 1999; Mäkinen *et al.*, 2000; Dempson *et al.*, 2002; Kieffer *et al.*, 2002; Thorstad *et al.*, 2003, 2007; Halttunen *et al.*, 2010; Jensen *et al.*, 2010), including results from both years in this study. The values for temperature are given as the average temperature in studies where this is provided. If the temperature or mortality is provided as a range, they are presented here as the central value. ▲, studies with radio-tagged *S. salar* released back into the river environment; ●, studies that were laboratory-based or where the *S. salar* were confined in cages in the river after C&R.

In this study, the *S. salar* were caught and handled by experienced anglers in the presence of trained scientific personnel and it is reasonable to assume that the playing time was shorter and that the *S. salar* were handled more carefully than would have occurred with less experienced anglers in the regular recreational fisheries. Therefore, the survival of the C&R-angled *S. salar* in this study may be higher than what would be the case if the *S. salar* had been caught by less skilled anglers. On the other hand, although tagging was rapid and conducted in water without anaesthesia in an attempt to minimize tagging-related effects as per Donaldson *et al.* (2008), additional handling time and stress due to the tagging procedure could have negatively affected the probability of survival. Thus, the overall stress subjected on experimental animals in this study was probably similar to that of *S. salar* released by the average angler, and the mortality estimates presented here should therefore be representative for the regular recreational fisheries.

The results indicated that caught and released *S. salar* showed atypical migration behaviour following release, with a rapid downstream movement post-release and delayed return upstream migration. These findings are similar to results from previous studies on *S. salar* at water temperatures below 15° C (Mäkinen *et al.*, 2000; Thorstad *et al.*, 2007; Jensen *et al.*, 2010). In addition, the proportion of Otra *S. salar* that moved downstream after release and the time it took before their upstream migration was resumed were also similar to what was observed in the studies referred to above. Downstream movements and delays lasting longer than a few days are rarely observed

in the upriver migration phase of wild *S. salar* (Økland *et al.*, 2001; Finstad *et al.*, 2005). The reasons for altered movement and migration patterns after C&R for *S. salar* are not known but it has been suggested that downstream movements and delays may result from a slow physical recovery after C&R-mediated stress, a loss of orientation from the capture process or downstream movements could simply be an avoidance response in order to escape areas that are perceived to have unfavourable conditions (Thorstad *et al.*, 2008*b*).

The causality behind this study's findings that the extent of downstream movements decreased with both increasing temperatures and increasing *S. salar* size and that *S. salar* with a longer freshwater residency moved shorter distances downstream after C&R compared with newly ascended *S. salar* is speculative. The fact that the *S. salar* which moved away from the capture site almost exclusively moved downstream may suggest that the observed behaviour is not exclusively an escape response as a more random movement direction would have been anticipated if the *S. salar* were solely escaping (as shown for *S. salar* avoiding an accidental release of waste from the wood pulp industry; Thorstad *et al.*, 2005). Unusual downstream movements have also been observed for caught and released Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) (Bendock & Alexandersdottir, 1993), and handling in general of this species (*e.g.* gillnetting or trapping) has been shown to result in downstream movements and delays after release in several studies (Bernard *et al.*, 1999). Bernard *et al.* (1999) found no evidence that size, sex or when the individuals were released influenced the migratory behaviour of gillnetted *O. tshawytscha*.

Eleven of the tagged *S. salar* left the River Otra after staying in the river for a median time period of 49 days after C&R. Behavioural responses caused by C&R usually occur within the first few days after release (Mäkinen *et al.*, 2000; Thorstad *et al.*, 2003), and it is plausible and perhaps probable that the observed out-migration was caused by other factors than C&R angling. Recent tagging of returning *S. salar* in the Trondheimsfjord showed that 29% of the *S. salar* that initially entered the River Nidelva left and were later located in other rivers draining into the same fjord during the spawning period (E. M. Ulvan, pers. comm.). Hence, the observed out-migration may actually reflect a normal situation in some rivers and may reflect initial mistakes on the part of *S. salar* attempting to home to natal rivers.

The high proportion of *S. salar* present on known spawning grounds during the spawning period is consistent with results from previous C&R studies at lower water temperatures where most *S. salar* survived until spawning (90–100%) and were present on spawning grounds (Webb, 1998; Mäkinen *et al.*, 2000; Thorstad *et al.*, 2007). The methodology used in this study, however, cannot confirm actual participation in spawning or if the performance of experimental *S. salar* on the spawning grounds was optimal. Positive population-level effects from using C&R as a management measure have been documented in other rivers such as increased number of spawning redds (Thorstad *et al.*, 2003) and by higher densities of juvenile *S. salar* (Whoriskey *et al.*, 2000). In addition, genetic analyses have shown that *S. salar* caught and released in Quebec at similar water temperatures as occurred in this study contributed significantly to population reproductive output and had the same probability of spawning as non-angled *S. salar* (Richard *et al.*, 2013). Hence, it is reasonable to suggest that the caught and released *S. salar* in this study were able to reproduce successfully.

Nevertheless, physiological disturbances caused by C&R could potentially reduce the spawning quality as stress can have deleterious effects on fish reproduction

(Wendelaar Bonga, 1997), *e.g.* lower survival rates for progeny of stressed rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) compared with unstressed control *O. mykiss* (Campbell *et al.*, 1992) and reduced gonad size and lowered levels of sex steroids in stressed brown trout *Salmo trutta* L. 1758 (Pickering *et al.*, 1987; Carragher *et al.*, 1989). While angling of *S. salar* just prior to spawning at low water temperatures (5–6° C) has been shown not to affect gamete viability or hatching success (Davidson *et al.*, 1994; Booth *et al.*, 1995), Richard *et al.* (2013) found that offspring production was negatively correlated with water temperatures at the time of release for *S. salar* that had been caught and released at 10–19° C. Further, studies incorporating both angled *S. salar* and control groups have shown that C&R may decrease the total migration distance of the angled compared with the control animals (Tufts *et al.*, 2000; Richard *et al.*, 2014; Lennox *et al.*, 2015). The relatively high percentage (42%) of *S. salar* that did not return to or migrate further upstream of their release site suggests that C&R may have reduced the migration distance for the *S. salar* in this study as well. *Salmo salar* return to spawn in the same area where they spent their pre-smolt period (Heggberget *et al.*, 1986, 1988), and failing to reach the intended area could potentially result in sublethal fitness consequences. The spatial arrangement of spawning redds has been shown to affect density-dependent survival for juvenile *S. salar* on very small spatial scales (10–100 s of metres), with survival decreasing at higher densities of redds, probably due to juvenile competition (territoriality) and a cost (metabolic or predation) of dispersal (Einum & Nislow, 2005). Hence, C&R could potentially result in an increased local density-dependent mortality of juveniles in some areas due to the suppression of movements of spawning adults which could concentrate them in subset of the available breeding habitat.

In conclusion, 91% of the *S. salar* in this study survived C&R at water temperatures above 15° C (mean 18·2° C, range: 16·3–21·1° C). A significant proportion of the caught and released *S. salar* did, however, show atypical behaviour after release with rapid downstream movements and delayed upstream migration. As most *S. salar* survived until spawning and were present at known spawning grounds, the results indicated that C&R at water temperatures up to at least 18° C is a viable management tool, assuming that the observed atypical behaviour and possible physiological disturbances caused by C&R did not have major negative reproductive effects. As hypothesized, the mortality of caught and released *S. salar* appeared to be slightly elevated at the higher end of the temperature range (18–21° C), although the sample sizes and consequent statistical power to detect differences were relatively low. Further studies, regarding how the atypical behaviour after release may affect individual reproduction and to determine if local adaptations to different thermal conditions also involve different tolerance levels to C&R-stressors (as shown for Pacific salmon *Oncorhynchus* spp.; Donaldson *et al.*, 2010), are required to determine more precise effects of C&R angling.

The results in this and previous studies show that C&R angling has the potential to result in mortalities, either in terms of seriously harmed fishes being culled without being released or through mortalities after release. These losses should be accounted for by management authorities in rivers where C&R angling is pursued. It is likely that the negative effect of C&R angling may be minimized through continued refinement and application of best practices for C&R (Cooke & Suski, 2005), particularly at higher water temperatures when small differences in fish handling are more likely to influence the outcome of the C&R event (Arlinghaus *et al.*, 2007).

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