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

Torgeir B. Havn[1], Ingebrigt Uglem[1], Øyvind Solem[1], Steven J. Cooke[2], Frederick G. Whoriskey[3] & Eva B. Thorstad[1]

[1]Norwegian Institute for Nature Research, Høgskoleringen 9, NO-7034 Trondheim, Norway

[2]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6, Canada

[3]Ocean Tracking Network, Dalhousie University, 1355 Oxford St., Halifax, NS B3H 4R2, Canada.

Corresponding author and address: Torgeir B. Havn, Norwegian Institute for Nature Research, Høgskoleringen 9, NO-7034 Trondheim, Norway. Email: torgeir.havn@nina.no. Tel.: +47 92620787

Havn, Torgeir Børresen; Uglem, Ingebrigt; Solem, Øyvind; Cooke, Steven J.; Whoriskey, Frederick G.; Thorstad, Eva Bonsak. The effect of catch-and-release angling at high water temperatures on behaviour and survival of Atlantic salmon Salmo salar during spawning migration. *Journal of Fish Biology* 2015 ;Volum 87.(2) s. 342-359 DOI: 10.1111/jfb.12722

ABSTRACT

In this study, behaviour and survival following catch-and-release (C&R) angling was investigated in wild *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. *S. salar* were tagged externally with radio transmitters and immediately released back into the river to simulate a realistic C&R situation. The majority of the *S. salar* (91%) survived C&R. Most *S. salar* that were present in the River Otra during the spawning period 3 to 4 months later were located at known spawning grounds. Downstream movements (median farthest position: 0.5 km, range: 0.1-11.0 km) during the first 4 days after release were recorded for 72% of the *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 practiced. Refinement of “best practices” for catch-and-release may help to reduce mortality, particularly at warmer temperatures.

Keywords: Biotelemetry; Fisheries management; Radio telemetry; Recreational Fishing; *Salmo salar*.

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). Catch-and-release for *S. salar* has been routinely practiced since 1984 in some areas of Canada and USA, and since about 1990 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 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. However, angling of *S. salar* may cause considerable physiological disturbances due to stress and exhaustion (reviewed by Kieffer *et al*., 2000), which at a later time may lead to mortality (*e.g.* 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 impact 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 (*e.g.*, 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). However, Wilkie *et al*. (1997) 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), seeming 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/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 (*e.g.*, Booth *et al*., 1995; Brobbel *et al*., 1996; Wilkie *et al*., 1996), extreme exhaustion (*e.g.*, 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 (*e.g.*, 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 impacts 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 (*e.g.*, 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). However, 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 impact on the potential for reproduction (*e.g.*, Webb, 1998; Thorstad *et al*., 2007; Jensen *et al*., 2010).

Impacts 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 (Baisez *et al*., 2011; Lund *et al*., 2002). 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 our understanding of thermal effects on *S. salar* after C&R (*e.g.*, Thorstad *et al*., 2008a; 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. Since 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 to the 0-6% mortality at lower water temperatures in earlier studies (see references above) 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 hydro power production, and the guaranteed minimum water flow in the part of the river accessible for *S. salar* is 50 $m^3 s^{-1}$ 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 metric tons (about 2,637 *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. However, scale readings of a selection of the sport fishery catch in 2011-2013 showed that 4% of the *S. salar* were farm escapees.

TAGGED *S. SALAR* AND ANGLING PROCEDURES

A total of 75 *S. salar* (mean L_T ± S.D.: 67 ± 9 cm, range: 50-90 cm) were angled during 9 July-16 August in 2012 (*n* = 52) and 2013 (*n* = 23) and tagged with external radio transmitters before being released. These were 43 females (L_T ± S.D.: 70 ± 10 cm, range: 50-90 cm) and 32 males (L_T ± S.D.: 64 ± 8 cm, range: 51-83 cm), 28 of which were caught on spoons and 47 by fly fishing. The *S. salar* were angled in cooperation with five highly experienced local anglers that 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* were in the net. Both the use of pliers and dip-netting while the *S. salar* is 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 x 21 cm diameter) filled with water to keep the head and gills submerged during tagging. The *S. salar* were examined for bleeding and damages, 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") color, a thin mucus layer and the presence of salmon lice *Lepeophtheirus salmonis* Krøyer. 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 less than 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. *S. 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 most likely would release such individuals.

The *S. salar* were tagged with external radio transmitters without being anesthetized (transmitter model F2120 from Advanced Telemetry Systems, Minnesota, USA, www.atstrack.com) as described in Økland *et al*. (2001). Anesthesia 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 anesthetics would have confounded the experiment and potentially contributed to abhorrent behaviour. The transmitters were rectangular with dimensions of 21 x 52 x 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 per minute 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 the *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.

S. salar caught in the upper end of the anadromous stretch had constrained upriver movement possibilities compared to 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 distance ± S.D. of 0.3 ± 0.1 km (range: 0.1-0.6 km) below the waterfall and *S. salar* in group 2 at a mean distance ± S.D. of 4.0 ± 0.9 km (range: 2.2-5.4 km) below the waterfall.

TRACKING AND SURVIVAL ASSESSMENT

S. salar behaviour after release was monitored by manual tracking (receiver model R2100, Advanced Telemetry Systems, Minnesota, USA). Since the river is located close to roads, a car equipped with a roof whip antenna (142 MHz, Laird Technologies, Missouri, USA, www.lairdtech.com) was used to search for tagged *S. salar*. When a *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, Missouri, USA). 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 on average ± S.D. located 15 ± 6 times (range: 1-26 times). *S. 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-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 the end of the tracking period. The transmitters with activity sensors used on 10 *S. salar* tagged in the pool below Vigeland waterfall (see above) also aided in determining whether these particular individuals were dead or alive.

Positions of the *S. salar* acquired 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, SWECO, unpublished data), local knowledge, and personal observations of suitable spawning substrate were used to determine if the *S. salar* were located at spawning grounds or not.

ENVIRONMENTAL DATA

Water temperature during C&R was on average (± S.D.) 17.3 ± 0.7 °C (range: 16.3-19.7 °C) in 2012 and 20.0 ± 0.5 °C (range: 19.4-21.1 °C) in 2013 (Fig. 2). The water temperature in the river peaked at 19.7 °C on 3 August in 2012 and at 21.5 °C on 31 July in 2013 (HOBO Pendant Temperature/Light Data Logger 64K-UA-002-64, Onset, Massachusetts, USA, www.onsetcomp.com, located 5 km downstream of the Vigeland waterfall). Water discharge at the time of *S. salar* release was on average (± 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 (± S.D.) of 6.1 ± 0.1 (range: 6.0-6.4) in 2012 and 6.1 ± 0.1 (range: 5.7-6.4) in 2013.

DATA ANALYSIS

Non-parametric statistics (Mann-Whitney U tests and Fisher`s Exact tests) were used to analyze 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 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, vs. resident in the river for an extended period based on loss of silver coloration), 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 non-significant parameters until a minimal adequate model was found. The fit of each reduced model was compared with the previous model by ANOVA chi-square tests. A p-value ≤ 0.05 was used to reject a reduced model and select the preceding model.

A generalized linear model 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 log 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.

S. 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. However, the *S. salar* that were recaptured were included in the descriptive analysis of the behaviour that occurred one day after release as these individuals survived until the next day after release. All statistical analyses were conducted using R v3.0.0 (The R Project for Statistical Computing 2013).

RESULTS

MORTALITIES AFTER C&R

In total for both study years, seven (9%) out of 75 tagged *S. salar* died after C&R (four *S. salar*, 8%, in 2012 and three *S. salar*, 13%, in 2013, Table I). Six of these *S. salar* died shortly after release (~ 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 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 16-18 °C was 7% (three of 46), for *S. salar* captured between 18-20 °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). Further, the proportion of *S. salar* that were caught on a fly versus a spoon, were bleeding versus not bleeding, were hooked in potentially harmful versus less harmful locations, or were caught in 2012 versus 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 the angler 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 (one 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 after release, 72% (n = 48) of the *S. salar* had been recorded downstream of the release site (Table II). The median farthest 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 67% occurred during the first and two first days after release, respectively. 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 chi-square tests with preceding models, all P-values > 0.05, the minimal adequate model versus intercept-only model, $X^2 = 4.6$, 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 to 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 chi-square tests with preceding models, all P-values > 0.05, exclusion of water temperature, $X^2 = 3.6$, 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). However, relatively low proportions of the total variation 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 for the first time recorded 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, n in 2012/2013 = 35/13, return to release site: Mann-Whitney U test, W = 81, P > 0.05, n in 2012/2013 = 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-11 November in neighboring 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. However, six of the seven *S. salar* that died did so shortly after release (~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 (*e.g*., 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 (*e.g.*, 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. However, Booth *et al*. (1995) found that the physiological post-angling disturbance was greater for grilse (*S. salar* returning to spawn for the first time after one year at sea) than for much larger multi-sea-winter *S. salar*.

In the current 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 anesthesia 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 representable 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 *(e.g.,* 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 "unfavorable conditions" (Thorstad *et al*., 2008b).

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 to newly ascended *S. salar* is speculative. However, the fact that the *S. salar* that moved away from the capture site almost exclusively moved downstream may suggest that the observed behaviour is not exclusively an escape response since 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, see 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 (summarized by 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 (*e.g.*, 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, NINA, 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 (*e.g.*, Webb, 1998; Mäkinen *et al*., 2000; Thorstad *et al*., 2007). However, the methodology used in this study 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 fishes reproduction (Wendelaar Bonga, 1997), *e.g.* lower survival rates for progeny of stressed rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) compared to unstressed control fish (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 to the control animals (Tufts *et al*., 2000; Richard *et al*., 2014; Lennox *et al*., in press). The relatively high proportion (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 the present study as well. *S. 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 demonstrated to impact 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. However, 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 adaptions to different thermal conditions also involve different tolerance levels to C&R-stressors (as shown for Pacific salmon; Donaldson *et al*., 2010), are required to determine more precise impacts 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 fish 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 impact 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).

ACKNOWLEDGEMENTS

The study was financed by the Research Council of Norway, contract number 216416/O10, and by the County Governors of Vest-Agder and Aust-Agder. We thank J. Mosby, S. Philip, E. Odderstøl and I. Odderstøl whose extensive help in capturing, tagging and tracking the *S. salar* have been essential for our success. We also thank H. Endresen for facilitating the fieldwork, anglers and people at the Otra House for kind cooperation, and O. Diserud for help with statistical analyses. Cooke is supported by NSERC and the Canada Research Chairs Program and Cooke and Whoriskey are supported by Dalhousie University's Ocean Tracking Network.

References

Anderson, W. G., Booth, R., Beddow, T. A., McKinley, S., Finstad, B., Økland, F. & Scruton, D. (1998). Remote monitoring of heart rate as a measure of recovery in angled Atlantic salmon, *Salmo salar* (L.). *Hydrobiologia* **371/372**, 233-240.

Arlinghaus, R., Cooke, S. J., Lyman, J., Policansky, D., Shwab, A., Suski, C., Sutton, S. G. & Thorstad, E. B. (2007). Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science* **15**, 75-167.

Baisez, A., Bach, J-M., Leon, C., Parouty, T., Terrade, R., Hoffmann, M. & Laffaille, P. (2011). Migration delays and mortality of adult Atlantic salmon *Salmo salar* en route to spawning grounds on the River Allier, France. *Endangered Species Research* **15**, 265-270.

Bartholomew, A. & Bohnsack, J. A. (2005). A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* **15**, 129-154.

Bendock, T. & Alexandersdottir, M. (1993). Hooking mortality of Chinook salmon released in the Kenai River, Alaska. *North American Journal of Fisheries Management* **13**, 540-549.

Bernard, D. R., Hasbrouck, J. J. & Fleischman, S. J. (1999). Handling-induced delay and downstream movement of adult Chinook salmon in rivers. *Fisheries Research* **44**, 37-46.

Booth, R. K., Kieffer, J. D., Davison, K., Bielak, A. T. & Tufts, B. L. (1995). Effects of late-season catch and release angling on anaerobic metabolism, acid-base status, survival, and gamete viability in wild Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 283-290.

Brett, J. R. (1971). Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist* **11**, 99-113.

Brobbel, M. A., Wilkie, M. P., Davidson, K., Kieffer, J. D., Bielak, A. T. & Tufts, B.L. (1996). Physiological effects of catch and release angling in Atlantic salmon (*Salmo salar*) at different stages of freshwater migration. *Canadian Technical Report of Fisheries and Aquatic Sciences* **53**, 2036-2043.

Caissie, D. (2006). The thermal regime of rivers: a review. *Freshwater Biology* **51**, 1389-1406.

Campbell, P. M., Pottinger, T. G. & Sumpter, J. P. (1992). Stress reduces the quality of gametes produced by rainbow trout. *Biology of Reproduction* **47**, 1040-1050.

Carragher, J. F., Sumpter, J. P., Pottinger, T. G. & Pickering, A. D. (1989). The deleterious effects of cortisol implantation on reproductive function in two species of trout, *Salmo trutta* L. and *Salmo gairdneri* Richardson. *General and Comparative Endocrinology* **76**, 310-321.

Cooke, S. J. & Suski, C. D. (2005). Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? *Biodiversity and Conservation* **14**, 1195-1209.

Cooke, S. J. & Schramm, H. L. (2007). Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology* **14**, 73-79.

Davidson, K., Hayward, J., Hambrook, M., Bielak, A. T. & Sheasgreen, J. (1994). The effects of late-season angling on gamete viability and early fry survival in Atlantic salmon. *Canadian Technical Report of Fisheries and Aquatic Sciences* **1982**, 1-12.

Dempson, B., Furey, G. & Bloom, M. (2002). Effects of catch and release angling on Atlantic salmon, *Salmo salar* L., of the Conne River, Newfoundland. *Fisheries Management and Ecology* **9**, 139-147.

Donaldson, M. R., Arlinghaus, R., Hanson, K. C. & Cooke, S. J. (2008). Enhancing catch-and-release science with biotelemetry. *Fish and Fisheries* **9**, 79-105.

Donaldson, M. R., Hruska, K. A., Hinch, S. G., Patterson, D. A., Farrell, A. P., Shrimpton, J. M., Miller-Saunders, K. M., Robichaud, D., Hanson, K. C., English, K. K. & Cooke, S. J. (2010). Physiological condition differentially affects the behaviour and survival of two populations of sockeye salmon during their freshwater spawning migration. *Physiological and Biochemical Zoology* **83**, 446-458.

Donaldson, M. R., Raby, G. D., Nguyen, V. N., Hinch, S. G., Patterson, D. A., Farrell, A. P., Rudd, M., Thompson, L. A., O'Connor, C. M., Colotelo, A. H., McConnachie, S. H., Cook, K. V., Robichaud, D., English, K. K. & Cooke, S. J. (2013). Evaluation of a simple technique for recovering Pacific salmon from capture stress: integrating comparative physiology, biotelemetry, and social science to solve a conservation problem. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 90-100.

Einum, S. & Nislow, K. H. (2005). Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. *Oecologia* **143**, 203-210.

Elliott, J. M. & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology* **77**, 1793-1817.

Finstad, A. G., Økland, F., Thorstad, E. B. & Heggberget, T. G. (2005). Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology* **67**, 919-930.

Gale, M. K., Hinch, S. G. & Donaldson, M. R. (2011). The role of temperature in the capture and release of fish. *Fish and Fisheries* **14**, 1-33.

Gargan, P.G., Stafford, T., Økland, F. & Thorstad, E.B. (2015). Survival of wild Atlantic salmon (*Salmo salar*) after catch and release angling in three Irish rivers. *Fisheries Research* **161**, 252-260.

Gowans, A. R. D, Armstrong, J. D. & Priede, I. G. (1999). Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology* **54**, 713-726.

Halttunen, E., Rikardsen, A. H., Thorstad, E. B., Næsje, T. F., Jensen, J. L. A. & Aas, Ø. (2010). Impact of catch-and-release practices on behaviour and mortality of Atlantic salmon (*Salmo salar* L.) kelts. *Fisheries Research* **105**, 141-147.

Heggberget, T. G., Lunda, R. A., Ryman, N. & Ståhl, G. (1986). Growth and genetic variation of Atlantic salmon (*Salmo salar*) from different sections of the River Alta, North Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1828-1835.

Heggberget, T. G., Hansen, L. P. & Næsje, T. F. (1988). Within-river spawning migration of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 1691-1698.

Jensen, J. L. A., Halttunen, E., Thorstad, E. B., Næsje, T. F. & Rikardsen, A. H. (2010). Does catch-and-release angling alter the migratory behaviour of Atlantic salmon? *Fisheries Research* **106**, 550-554.

Jonsson, B. & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology* **75**, 2381-2447.

Kieffer, J. D. (2000). Limits to exhaustive exercise in fish. *Comparative Biochemistry and Physiology Part A* **126**, 161-179.

Kieffer, J. D., Rossiter, A. M., Kieffer, C. A., Davidson, K. & Tufts, B. L. (2002). Physiology and survival of Atlantic salmon following exhaustive exercise in hard and softer water: Implications for the catch-and-release sport fishery. *North American Journal of Fisheries Management* **22**, 132-144.

Lennox, R. J., Uglem, I., Thorstad, E. B., Cooke, S. J., Næsje, T. F., Whoriskey, F. G., Havn, T. B., Ulvan, E. & Solem, Ø. (in press). Does catch-and-release angling alter the behavior and fate of adult Atlantic salmon *Salmo salar* during upriver migration? *Transactions of the American Fisheries Society*.

Lund, S.G, Caissie, D., Cunjak, R.A., Vijayan, M.M. & Tufts, B.L. (2002). The effects of environmental heat stress on heat-shock mRNA and protein expression in Miramichi Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 1553-1562.

Mäkinen, T. S., Niemelä, E., Moen, K. & Lindström, R. (2000). Behaviour of gill-net and rod-captured Atlantic salmon (*Salmo salar* L.) during upstream migration and following radio tagging. *Fisheries Research* **45**, 117-127.

Muoneke, M. I. & Childress, W. M. (1994). Hooking mortality: a review for recreational fisheries. *Reviews in Fisheries Science* **2**, 123-156.

Nielsen, J.L., Ruggerone, G.T. & Zimmerman, C.R. (2013). Adaptive strategies and life history characteristics in a warming climate: Salmon in the Arctic? *Environmental Biology of Fishes* **96**, 1187-1226.

Økland, F., Erkinaro, J., Niemelä, E., Fiske, P., McKinley, R. S. & Thorstad, E. B. (2001). Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. *Journal of Fish Biology* **59,** 862-874.

Pickering, A. D, Pottinger, T. G, Carragher, J. & Sumpter, J. P. (1987). The effects of acute and chronic stress on the levels of reproductive hormones in the plasma of mature male brown trout, *Salmo trutta* L. *General and Comparative Endocrinology* **68**, 249-259.

Portz. D. E., Woodley, C. M. & Cech Jr., J. J. (2006). Stress-associated impacts of short-term holding on fishes. *Reviews in Fish Biology and Fisheries* **16**, 125-170.

Richard, A., Dionne, M., Wang, J. & Bernatchez, L. (2013). Does catch and release affect the mating system and individual reproductive success of wild Atlantic salmon (*Salmo salar* L.)? *Molecular Ecology* **22**, 187-200.

Richard, A., Bernatchez, L. Valiquette, E. & Dionne, M. (2014). Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **71**, 1730-1739.

Robinson, K. A., Hinch, S. G., Gale, M. K., Clark, T. D., Wilson, S. M., Donaldson, M. R., Farrell, A. P., Cooke, S. J. & Patterson, D. A. (2013) Effects of post-capture ventilation assistance and elevated water temperature on sockeye salmon in a simulated capture-and-release experiment. *Conservation Physiology* **1**, 1-10. doi: 10.1093/conphys/cot015.

Thorstad, E. B., Økland, F. & Finstad, B. (2000). Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. *Journal of Fish Biology* **57**, 531-535.

Thorstad, E. B., Næsje, T. F., Fiske, P. & Finstad, B. (2003). Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. *Fisheries Research* **60**, 293-307.

Thorstad, E. B., Forseth, T., Aasestad, I., Økland, F. & Johnsen, B. O. (2005). In situ avoidance response of adult Atlantic salmon to waste from the wood pulp industry. *Water, Air and Soil Pollution* **165**, 187-194.

Thorstad, E. B., Næsje, T. F. & Leinan, I. (2007). Long-term effects of catch-and-release angling on Atlantic salmon during different stages of return migration. *Fisheries Research* **85**, 330-334.

Thorstad, E. B., Næsje, T. F., Mawle, G. W. & Policansky, D. (2008a). The Atlantic salmon C&R story. In *Global Challenges in Recreational Fisheries* (Aas, Ø., ed), pp. 219-222. West Sussex: Blackwell Publishing.

Thorstad, E. B., Økland, F., Aarestrup, K. & Heggberget, T. G. (2008b). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish biology and Fisheries* **18**, 345-371.

Tufts, B. L., Yang, Y., Tufts, K. & Boutilier, R. G. (1991). Exhaustive exercise in "wild" Atlantic salmon (*Salmo salar*): Acid-base regulation and blood gas transport. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 868-874.

Tufts, B. L., Davidson, K. & Bielak, A. T. (2000). Biological implications of "catch and release" angling of Atlantic salmon. In *Managing wild Atlantic salmon* (Whoriskey, F. G. & Whelan, K. E., eds), pp. 195-225. St. Andrews, New Brunswick: Atlantic Salmon Federation.

Webb, J. H. (1998). Catch and release: the survival and behavior of Atlantic salmon angled and returned to the Aberdeenshire Dee, in spring and early summer. *Scottish Fisheries Research Report* **62**, 1-15.

Wendelaar Bonga, S. E. (1997). The stress response in fish. *Physiological Reviews* **77**, 591-625.

Whoriskey, F. G., Prusov, S. & Crabbe, S. (2000). Evaluation of the effects of catch-and-release angling on the Atlantic salmon (*Salmo salar*) of the Ponoi River, Kola Peninsula, Russian Federation. *Ecology of Freshwater Fish* **9**, 118-125.

Wilkie, M. P., Davidson, K., Brobbel, M. A., Kieffer, J. D., Booth, R. K. & Bielak, A. T. (1996). Physiology and survival of wild Atlantic salmon following angling in warm summer waters. *Transactions of the American Fisheries Society* **125**, 572-580.

Wilkie, M. P., Brobbel, M. A., Davidson, K., Forsyth, L. & Tufts, B. L. (1997). Influences of temperature upon the postexercise physiology of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 503-511.

Electronic References

ICES. (2014). Report of the Working Group on North Atlantic Salmon (WGNAS), 19-28 March 2014, Copenhagen, Denmark. ICES CM 2014/ACOM:09, 1-433. Available at http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2014/WGNAS/wgnas_2014.pdf

Kroglund, K., Høgberget, R., Hindar, K., Østborg, G. & Balstad, T. (2008). Laks og vannkvalitet i Otra, 1990-2006. *NIVA Rapport* **5531-2008**, 1-72. Available at http://www.nina.no/archive/nina/PppBasePdf/rapport/2008/326.pdf

Olsen, R. E., Næsje, T. F., Poppe, T., Sneddon, L. & Webb, J. (2010). Risk assessment of catch and release. Opinion of the panel on animal health and welfare of the Norwegian Scientific Committee for Food Safety. *Norwegian Scientific Committee for Food Safety*, doc.nr 09/804, 1-79. Available at http://www.vkm.no/dav/e49f60ea8f.pdf

Tables

Table I Total number of caught, tagged and released *Salmo salar* in the two study years and the mortalities after C&R.

Year	Average water temperature ± SD 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

Table II Median position for the *S. salar* that moved downstream during the first 4 days after 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 were recorded after release. Returned to release site (%) is the cumulative proportion 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
	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
2012	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
	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
2013	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	0	8	15	15	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 *S. salar* that moved downstream within 4 days after C&R.

	Estimate ± SE	T	P
Intercept (newly ascended)	10.59 ± 2.17	4.88	< 0.001
Water temperature	-0.22 ± 0.12	-1.84	0.07
Longer freshwater residency[1]	-1.00 ± 0.40	-2.51	< 0.05

Estimates are given on the log scale.

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

Figure captions

Fig. 1

The River Otra in Norway. The anadromous stretch ends at Vigeland waterfall. Brackets show where fish were caught, tagged and released. The numbers and percentages show how many *Salmo 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.

Fig. 2 Water temperature in 2012 (solid line) and 2013 (dotted line) in the River Otra from 9 July-15 September both years. Date and temperature at release are shown for individual *S. salar* (dots for *S. salar* caught and released in 2012, triangles in 2013). Arrows identify *S. salar* that died after C&R, while fish without arrows survived C&R.

Fig. 3 Mortality rates after C&R in different studies related to water temperature for *S. 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. Triangles represent studies with radio tagged *S. salar* released back into the river environment, and dots studies which were laboratory-based or where the *S. salar* were confined in cages in the river after C&R.