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The Effect of Catch and Release Angling at High Water Temperatures on Behavior and Survival of Atlantic Salmon (*Salmo salar* L.)

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Abstract

Many Atlantic salmon (*Salmo salar* L.) populations have declined during the last decades. A multitude of restrictions on riverine fisheries have been initiated to conserve spawning populations, including increased use of catch and release (C&R) angling. As a result, about half of all Atlantic salmon caught in sport fisheries in the north Atlantic region during the last five years have been released. Previous studies have shown that the majority of the caught and released Atlantic salmon angled at temperatures below 15 °C survived and participated in spawning, while the mortality seemed to increase at higher water temperatures. However, the survival of caught and released Atlantic salmon at water temperatures above 15 °C has so far not been well examined under natural conditions. In this study, I investigated behavior and survival following C&R for wild Atlantic salmon (n = 52) angled on regular sport fishing gear in the River Otra in southern Norway at water temperatures ranging between 16.3-19.7 °C (mean 17.3 °C). The fish were tagged externally with radio transmitters without being anaesthetized and immediately released back into the river to simulate a realistic C&R situation. The results showed that a large proportion survived C&R (92-94%) and that all fish present in the River Otra during the spawning period 3-4 months later were located at known spawning grounds. Downstream movements during the first four days after release were recorded for 74% of the fish, and this was regarded as unusual behavior caused by C&R. The fish spent on average 24 days before commencing their first upstream movement after release and 41 days before they returned to or were located above their release site. The results suggest that C&R at these water temperatures may be a viable management tool as most fish survived and were present on the spawning grounds. However, it is not known if the physiological strain inflicted by C&R and the altered behavior affected reproductive success for caught and released fish compared to non-angled fish.

Sammendrag

I løpet av de siste tiårene har antallet tilbakevandrende laks (*Salmo salar* L.) i mange bestander blitt betydelig redusert. Mange ulike forvaltningstiltak har blitt innført for å bevare bærekraftige gytebestander, inkludert økt bruk av gjenutsetting (fang og slipp) av laks som fanges i sportsfiske. Som en konsekvens har omtrent halvparten av all laks fanget i sportsfiske i det nordatlantiske utbredelsesområdet de siste fem årene blitt gjenutsatt. Tidligere studier har vist at en høy andel av laks fanget og gjenutsatt ved vanntemperaturer lavere enn 15 °C overlever og deltar i gytingen senere på høsten. Dødligheten ser ut til å øke ved høyere vanntemperaturer, men dette har så langt ikke blitt godt undersøkt under naturlige forhold. I denne oppgaven har jeg undersøkt overlevelse og atferd etter gjenutsetting for laks (n = 52) fanget under ordinært sportfiske i Otra i Sør-Norge ved en gjennomsnittlig vanntemperatur på 17.3 °C (16.3-19.7 °C). Fisken ble merket med eksterne radiosendere uten bedøvelse og umiddelbart gjenutsatt for å simulere en realistisk fang og slipp situasjon. Resultatene viste at en stor andel av fisken overlevde (92-94 %) og at overlevende fisk som befant seg i Otra under gytetiden 3-4 måneder senere oppholdt seg på kjente gyteplasser. Uvanlig atferd forårsaket av fang og slipp i form av nedstrøms bevegelser de første fire dagene etter gjenutsetting ble observert for 74 % av fisken. Det tok i gjennomsnitt 24 dager etter gjenutsetting før fisken bevegde seg oppstrøms og 41 dager før de hadde returnert til eller befant seg ovenfor det stedet der de ble gjenutsatt. Resultatene tilsier at gjenutsetting som forvaltningstiltak også ved relativt høye vanntemperaturer kan bidra til å bevare bærekraftige gytebestander ettersom en stor andel av fisken overlevde og sannsynligvis deltok i gytingen. Det er derimot ikke kjent om kvaliteten på gytingen kan ha blitt redusert i forhold til fisk som ikke er fanget og gjenutsatt.

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1. Introduction

Due to anthropogenic impacts both in freshwater and at sea, many populations of wild Atlantic salmon (*Salmo salar* L.) have declined during the last decades (ICES 2013). A multitude of restrictions on riverine fisheries have been developed to maintain sustainable populations (Anon. 2013). Examples of restrictions include fish size limits, bag limits (maximum number of fish caught and killed per day), annual quotas (maximum number of fish caught per year), shortening of the fishing season and increased practice of catch and release (C&R) angling. The latter option refers to the procedure whereby fish are returned back into the same water as they were angled in. The premise is that fish survive and contribute with offspring to their natal population (Tufts *et al.* 2000). C&R is widely used and accepted as an adequate management tool in Atlantic salmon fisheries. In 2012, approximately 173 000 Atlantic salmon were reported released in the north Atlantic region, constituting almost half of all wild Atlantic salmon angled that year (ICES 2013). In Norway, a relatively low proportion (10%) of all Atlantic salmon angled in river fisheries in 2012 were released (Anon. 2013). However, due to voluntary release and increased use of restrictions, C&R has become more common also in Norwegian Atlantic salmon fisheries (ICES 2013).

For C&R to be a management tool, the released fish have to survive until reproduction. C&R may involve multiple stressors, including physical injury (caused by hooking, landing and handling), physiological stress (strenuous exercise and fear response) and oxygen deprivation (air exposure during handling) (Arlinghaus *et al.* 2007). Potential endpoints for C&R may be death (reviewed by Muoneke & Childress 1994; Bartholomew & Bohnsack 2005) or sub-lethal effects such as reduced growth, reduced reproduction success, behavioral impairments and increased susceptibility for diseases (Cooke *et al.* 2012).

Post release survival in fish is influenced by several factors (reviewed by Arlinghaus *et al.* 2007). Deep hooking, characterized by the hook penetrating gills, esophagus or other sensitive tissue beyond the mouth cavity (*e.g.* liver, stomach, eyes), seem to be most important (Pelzman *et al.* 1978; Aalbers *et al.* 2004; Fobert *et al.* 2009). However, angling may also cause considerable physiological disturbances in fish (reviewed by Kieffer *et al.* 2000) due to playing and thus also exhaustion. These physiological disturbances are in some cases severe enough to cause post exercise mortality (*e.g.* Brobbel *et al.* 1996; Wilkie *et al.* 1996; Anderson *et al.* 1998).

Because fish are ectotherms, temperature is important for physiological processes (Brett 1971). Hence, variation in water temperature has distinct impacts such as changes in protein structure (Somero & Hoffman 1996), cellular function (Prosser 1991) and enzyme activity and diffusion rates (Lehninger 1982). Some important physiological challenges at high water temperatures are increased metabolic demand (Hazel 1984), increased susceptibility to some diseases (Ellis 1981) and elevated levels of the stress hormone cortisol (Wendelaar Bonga 1997). In addition, increased water temperature will cause a reduction in the quantity of dissolved oxygen in the water that may result in a greater oxygen debt (McKenzie *et al.* 1996). Consequently, the physiological impact of C&R at water temperatures in the far end and above the thermal optimum for a specific species will be more severe than at lower temperatures (Arlinghaus *et al.* 2007; Gale *et al.* 2011; Olsen *et al.* 2010). Gale *et al.* (2011) found that increased water temperature increased stress levels and mortality rates in 70% of the published studies investigating the effect of C&R in various fish species. The temperature related effects may vary among species due to different thermal tolerances (Cooke & Suski 2005; Arlinghaus *et al.* 2007; Gale *et al.* 2011).

Previous research on survival of Atlantic salmon after C&R show that mortality rates are generally low (0-12%) when water temperatures are below 18 °C (*e.g.* Mäkinen *et al.* 2000; Thorstad *et al.* 2003, 2007). Mortality tends to increase at water temperatures above 17-18 °C (*e.g.* Wilkie *et al.* 1996, 1997; Dempson *et al.* 2002), which is still within the optimal temperature for growth for Atlantic salmon (16-20 °C) (Elliott & Elliott 2010).

The exact mechanisms that may cause elevated mortality in Atlantic salmon 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). Contradicting with these results, 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). Mortalities were only observed at the highest temperatures (30% mortality rate at 23 °C). Further, C&R of Atlantic salmon at 20 °C have been shown to result in an unusual high mortality rate (80%), and the authors suggested that an irregular heart rate during recovery may have caused the mortality (Anderson *et al.* 1998).

Common for the studies referred to above on physiological effects and mortality following exhaustive exercise at high water temperatures is that they were performed in non-natural settings where the fish were confined in tanks, cages or in artificial pools after angling. Keeping fish encaged may in itself be stressful and it could therefore be difficult to separate between effects caused by C&R versus confinement (Gale *et al.* 2011). In addition, implantation of radio transmitters measuring heart rate, manual hooking, extreme exhaustion and other unusual treatments may imply that these studies were not representative for a realistic C&R situation (Dempson *et al.* 2002). The majority of these studies used hatchery reared Atlantic salmon that may rarely have performed anaerobic swimming prior to the study (Booth *et al.* 1995). Thus, it is reasonable to assume that thermal tolerances for fish caught and released under natural circumstances are higher than for fish in a laboratory setup (Whoriskey *et al.* 2000).

Tagging fish with external radio transmitters and releasing them into the same water as they were angled in immediately after angling may reduce the influence of various confounding factors. Telemetry is regarded as one of the most suitable methods to study effects of C&R in fish (Donaldson *et al.* 2008; Gale *et al.* 2011) and several studies on Atlantic salmon have used this approach (*e.g.* Mäkinen *et al.* 2000; Thorstad *et al.* 2003; Jensen *et al.* 2010). Common for these studies are that they have been conducted at water temperatures below 15 °C and they have documented a high survival rate of the fish (94-100%). Most of the studies also showed that C&R at these temperatures had a profound effect on behavior in terms of unusual downstream movements, migration delays, decreased migration distance and erratic movement patterns. However, most fish survived until spawning and were located in known spawning areas during the spawning period (*e.g.* Webb 1998; Thorstad *et al.* 2007; Jensen *et al.* 2010).

The effects of C&R have to my knowledge not been previously examined at water temperatures above 15 °C for Atlantic salmon in a natural setting using telemetry. Such studies are required to fully understand the implications of thermal effects on Atlantic salmon after C&R (*e.g.* Wilkie *et al.* 1996; Thorstad *et al.* 2008a; Gale *et al.* 2011), and to identify the critically high temperatures (Olsen *et al.* 2010).

The aim of this study was to investigate how C&R at high water temperatures affects behavior and survival of wild Atlantic salmon. This was examined by angling Atlantic salmon using ordinary sport fishing gear and tagging them with radio transmitters at water temperatures above 15 °C in the River Otra in southern Norway. Survival and behavior following C&R was examined by tracking the fish manually after release until after the spawning period. Since increased water temperatures enhance the physiological disturbance caused by C&R (as described above), I hypothesized that C&R at water temperatures above 15 °C caused an increased mortality compared to mortality rates recorded after C&R at lower water temperatures in previous studies. Further, I expected an amplified behavioral response with a larger proportion moving downstream and longer delays after release.

2. Materials and methods

2.1 Study area

The study was conducted in the River Otra in southern Norway (58° N 8° E) (Fig. 1). The reason for choosing the River Otra as study area was that it frequently has warm water conditions during the summer with temperatures regularly exceeding 20 °C (Kroglund *et al.* 2008). The river has a catchment area of 3738 km^2, and the mean annual water discharge is 149 m^3 s^{-1} measured 0.7 km below Vigeland waterfall (Fig. 1). The River Otra is regulated for hydropower production with 11 power plants distributed along the river above the Atlantic salmon producing stretch. The Atlantic salmon have access to 16 km of the river up to the Vigeland waterfall power plant, which is the end of the anadromous stretch. The minimum regulated water flow below Vigeland waterfall is 50 m^3 s^{-1} during the summer.

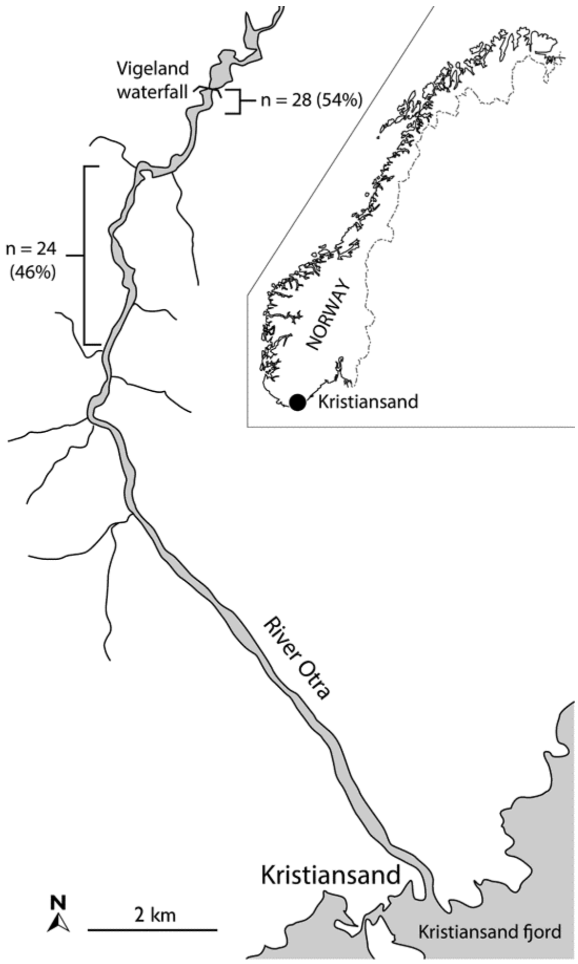

Fig. 1 *The River Otra in Norway. Brackets show where fish were caught, tagged and released. The numbers and percentages show how many fish and the proportion of the total sample that was angled and tagged in the two sections of the river.*

Due to acidification, and industrial and municipal pollution, the original Otra salmon strain went extinct during the 1960s (Hesthagen & Hansen 1991). A reduction in pollutants in the 1990s made it possible for a new Atlantic salmon population to be established (Kroglund *et al.* 2008). The average annual catch in sport fisheries during 2004-2012 was 7 metric tons. The mean individual mass was 2.7 kg. In 2012, 8% (114 individuals) of the total rod catch (1422 individuals) were released when fish released in this study is excluded.

2.2 Tagged fish and angling procedures

A total of 52 Atlantic salmon (mean total length ± SD: 68 ± 9 cm, range 53-90, see Appendix 1 for details) were angled during 9 July-16 August 2012 and tagged with external radio transmitters before being released. The tagged fish consisted of 25 females (mean total length 73 ± 9 cm, range 56-90) and 27 males (mean total length 63 ± 7 cm, range 53-83). Bright color, thin mucus layer and presence of salmon lice (*Lepeophtheirus salmonis*) suggested that 84% of the fish had recently entered the river. The fish were angled in cooperation with five local anglers using sport fishing gear (17 were caught on spoon and 35 on fly). Based on angling location, the fish were divided into two groups; 1) fish caught and released in or close to the pool below Vigeland waterfall at the upper end of the anadromous stretch (n = 28) and 2) fish caught and released over a longer stretch further downstream in the river (n = 24) (Fig. 1). The fish in group 1 were angled on average 0.3 ± 0.1 km (range 0.1-0.6) below Vigeland waterfall and fish in group 2 on average 3.9 ± 1.0 km (range 2.2-5.4) below the waterfall. Fish caught in the upper part of the river were on average larger (group 1/group 2 mean = 74 ± 8/61 ± 5 cm, range 55-90/53-75, Mann-Whitney U test: W = 54, $p < 0.001$) and consisted of a larger proportion of females (group 1: 21 of 28, group 2: 5 of 24, Fisher exact test: $p < 0.001$). Further, the group of fish that were considered to have had a longer freshwater residency based on external characteristics were angled further up in the river than fish considered to have recently entered the river (Mann-Whitney U test: W = 104, $p < 0.03$).

Condition at release was a subjective assessment made by the anglers where factors such as the ability to retain equilibrium, ventilation rate and especially ventilation time at release (time from the fish was placed in the water until it swam off) were important parameters. The assessed condition was reduced into two categories in statistical analyses due to a low sample size in some of the categories (see section 2.6). Fish that were considered to be in good or very good condition at release are termed fish in good condition and fish considered to be in decent or poor condition at release are termed fish in less good condition. Time in air and from hooking to landing was kept to a minimum. Air exposure was restricted to lifting the fish out of the tagging tube before releasing it into the river, lasting no more than a few seconds.

The time from hooking to landing (playing time) was on average 5 ± 1 min (range 3-9). Most of the fish were hooked in the upper or lower jaw (71%, n = 37), while 10% (n = 5) were hooked in the tongue or mouth cavity and 6% (n = 3) in in other places than the mouth region (two in the head area and one in the dorsal muscle). The position of the hook could not be determined for the remaining fish (13%, n = 7) as the hook fell out by itself in the net during landing. Spoons were always equipped with a single treble hook while 31 fish were caught on flies with a treble hook and 4 on flies with a double hook. All hooks were barbed. Fish with distinct bleedings from the gills were killed upon landing (n = 8) instead of being tagged and released as such damages are critical for the fish (reviewed by Bartholomew & Bohnsack 2005). Two fish with minor bleeding in the gill area and ten fish with small bleeding in the hook wound were tagged and released.

2.3 Radio tagging procedures

All fish were landed in a knotless landing net and the hook was removed with a pair of pliers before the fish were transferred to a tagging tube (105 cm long x 21 cm diameter), using a specially designed plastic bag. The tagging tube was filled with water to keep the head and gills submerged during tagging. Radio transmitters (model F2120 from Advanced Telemetry Systems, Minnesota, USA) were attached externally to the fish. This was done by inserting two cannulas through the musculature below the dorsal fin, where steel wires attached to the radio transmitter were inserted and twisted on the opposite side before being cut off, leaving a 2-3 cm stub. The fish were not anesthetized during tagging to simulate a realistic angling situation. The head of the fish was covered with a wet towel to keep it calm. Handling time from the fish was netted until release was on average 3 ± 0.5 min (range 2-5). The described methodology and sample size in this study were approved by NARA (the Norwegian Animal Research Authority).

The transmitters were rectangular with outline dimensions 21 x 52 x 11 mm weighing 16 g in air and transmitted signals on radio frequency 142 MHz with 40 ppm (pulses per minute). Thorstad & Økland (2000) found no effect of radio transmitters attached in the same manner with similar dimensions on swimming performance of adult farmed Atlantic salmon (range total length 44-59 cm). Some of the transmitters (n = 10) were equipped with an activity sensor that produced additional pulses when the fish were moving. To further aid in detecting mortality, the ppm of these transmitters increased from 40 to 80 if the fish did not move within eight hours. Fish caught in the upper end of the anadromous stretch had restricted upriver movement possibilities, and as upstream movements were used to assess survival (see below), activity transmitters were primarily used on fish tagged in the pool below the Vigeland waterfall. Limited previous experience and uncertainty about functionality and tracking properties was the reason for not tagging all the fish with activity transmitters. Guaranteed battery lifetime was 144 days for transmitters with sensors and 195 days for transmitters without. Each transmitter had signals on a unique radio frequency to be able to recognize different individuals.

2.4 Tracking of radio tagged fish and survival assessment

The migratory behavior after release was monitored by manual tracking. A car equipped with a whip antenna (142 MHz, Laird Technologies, Missouri, USA) on the roof was used to search for radio tagged fish in the river. When the fish was located, a more accurate position was obtained by cross-bearing using a 4-element yagi antenna (142 MHz, Laird Technologies, Missouri, USA) and adjusting the gain of the receiver (model R2100, Advanced Telemetry Systems, Minnesota, USA). The accuracy of the manual positioning varied depending on the characteristics of the river such as depth, width and substrate at the site. The location for each tagged fish was determined daily for four days after release and thereafter once every week until the end of the fishing season (15 September 2012). Tracking continued once every second week until December 2012. Additional tracking of individuals of which survival was uncertain were performed in January 2013. Each tagged fish was on average tracked 16 ± 6 times (range 1-26).

Mortality caused by C&R is often divided into three categories; immediate (dead before release), short term (~ 24-72 h) and long term (> 72 h) (Pollock & Pine 2007). Assessment of mortality was based on the assumption that a surviving fish at varying intervals would change its position in the river, while the radio transmitter attached to a decaying corpse will eventually detach and get lodged between rocks on the bottom of the river and cease to move. Obviously, only surviving fish have the ability to move upstream. Hence, mortality was assumed if a fish showed no upstream movements and remained stationary in the same position until the end of the tracking period. One or several upstream movements after the first two days following C&R were set as criteria for determining short term survival.

Movements up or downstream the river between 14 October and 14 January was interpreted as signs of continued survival until spawning. Fish that left the River Otra (n = 5) and moved to other rivers were only tracked once after they left. Hence, we were unable to determine if these fish were alive during spawning as multiple positions are needed to detect movement. The peak spawning in the River Otra is considered to take place early in November (pers. comm. S. Philips, J. Mosby and E. Odderstøl). Positions of the fish acquired 11 November were used to represent the positions of the fish in the spawning period. The water temperature at this date was 5.5 °C. A mapping of spawning grounds in the River Otra (Kroglund *et al.* 2008), local knowledge (pers. comm. S. Philips, J. Mosby and E. Odderstøl) and personal observations of suitable spawning substrate were used to determine if the fish were located at spawning grounds or not.

2.5 Environmental data

Water temperature during catch and release for the fish in this study was on average 17.3 ± 0.7 °C (range 16.3-19.7) (Fig. 2). The water temperature was measured immediately after the fish was tagged with a digital thermometer (model 9841, Taylor, Illinois, USA). In addition, a submerged data logger (HOBO Pendant Temperature/Light Data Logger 64K-UA-002-64, Onset, Massachusetts, USA) positioned 5.5 km downstream of the Vigeland waterfall

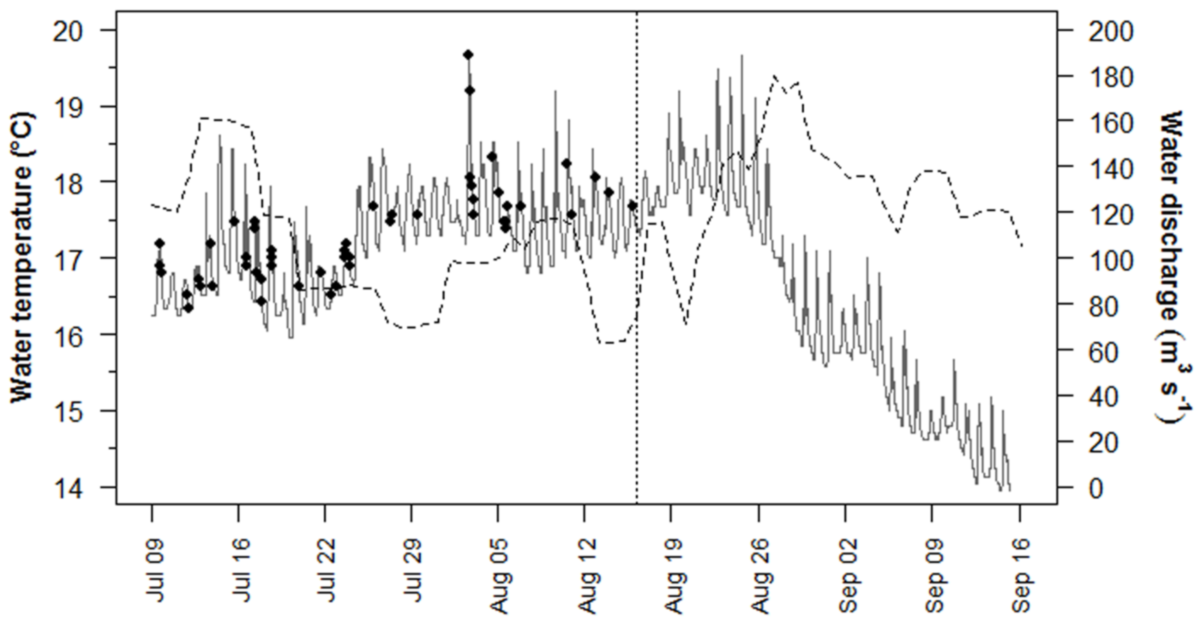

Fig. 2 *Water temperature (solid line) and discharge (dotted line) in the River Otra from start of the tagging period until the end of the fishing season (9 July-15 September 2012). Black dots show the date and temperature at release for individual fish. The vertical dotted line indicates the end of the tagging period (16 August).Temperature data was measured by a data logger 5.5 km downstream of the Vigeland waterfall. Water discharge was measured 0.7 km downstream of the Vigeland waterfall.*

measured the temperature continuously each hour from the start of the tagging period until the end of the fishing season (9 July-15 September 2012). The data from the data logger was used in the further analyses as it measured temperature more precisely than the handheld thermometer. Water temperature after 15 September and pH and water discharge values for the entire study period was measured 0.7 km below Vigeland waterfall and provided by Agder Energi Kraftforvaltning.

Daily water temperature during the first 16 days of the tagging period (9 July-24 July) was on average 16.8 ± 0.5 °C (range 16.0-18.6). The temperature increased slightly in the end of June and was on average 17.6 ± 0.4 °C (range 16.8-19.7) for the remaining tagging period (25 July-16 August). The temperature remained high throughout August before declining in September. A maximum water temperature of 19.7 °C was recorded 3 August.

Water discharge was higher in the first part of the tagging period (mean water discharge 138 $m^3\ s^{-1}$, 9 July-20 July) than in the remaining two thirds of the tagging period (mean water discharge 89 $m^3\ s^{-1}$, 21 July-16 August) (Fig. 2.). Daily change in water discharge was on average 6.5 $m^3\ s^{-1}$, but daily fluctuations of more than 10 $m^3\ s^{-1}$ associated with adjustments related to hydropower occurred at nine occasions during the tagging period (range 12-40 $m^3\ s^{-1}$).

Water temperature and discharge at release were not significantly different between the group of fish caught in or close to the pool below Vigeland waterfall and the group caught further down the river (Mann-Whitney U tests, water temperature: $W = 289$, $p = 0.39$, water discharge: $W = 403$ $p = 0.22$). Water pH remained stable at a mean of 6.1 ± 0.1 (range 6-6.4) throughout the study period.

2.6 Data analysis

The most important response variables in this study were whether the fish moved downstream or not during the first four days after release, the length of the farthest downstream movement during the first four days after release, condition at release, ventilation time and playing time. The data was analyzed using parametric statistics (two-way and one-way ANOVA, linear regression and t-tests) when assumptions of normality, equal variance and independence of the residuals were met. In addition to visual inspection of diagnostic plots, Shapiro-Wilk tests were used to test for normality and Bartlett`s tests and Breusch-Pagan tests for equal variance. Log transformation was used in an attempt to normalize the variables if the assumption of normality was violated. Non-parametric statistics (Mann-Whitney U tests, Kruskal-Wallis tests and Fisher`s exact tests) were used if any parametric assumptions were violated. Both mean (± SD) and median is provided in descriptive analyses of highly skewed distributions. All statistical tests have a total sample size of 52 unless another figure is specified.

The number of categories was reduced in statistical analyses of some variables compared to the finer categorization that was used when the data was collected. This applied for variables with either a low sample size ($n \leq 4$) in a specific category or if the number of categories could be reduced without losing biological relevance. This was done to improve statistical power and enable the use of statistical analyzes. Variables in which the number of categories was reduced include hook location, condition at release, bleeding and bait type (see Appendix 2 for details).

The positions of the fish were plotted in Arcmap 10 (ESRI Inc., New York, USA) where distances between positions along the center line of the river were measured and extracted. All statistical analyses were done using the statistical software package R v3.0.0 (The R Project for Statistical Computing 2013).

3. Results

3.1 Mortalities after C&R

In total, four fish (8%) died possible due to C&R. Three (6%) of these were short-term mortalities. Two of them (angled at 18.2 °C and 17.1 °C) were found dead in the river six and seven days after release. One was released in apparently good condition without any bleeding or injuries, while the second suffered a small bleeding in the gill area. Both moved downstream (1.4 and 0.2 km) during the first day after release, and remained stationary before they were found floating in the river with bloated bodies covered by a thick layer of fungus. The fungus layer indicated that they had died shortly after release. The third fish (angled at 16.6 °C) probably also suffered mortality shortly after C&R as it dropped downstream (0.5 km) during the first week after release and thereafter remained stationary until the end of the tracking period. This fish had an old damage to its caudal fin and was in generally poor condition. One additional fish (2%) suffered mortality after long term and was found dead 23 days after release 0.5 km upstream from where it was tracked the same day. The upstream movement and physical appearance when found suggested that it had recently died.

Other mortalities that were assumed to be unrelated to C&R included three fish that were recaptured and killed by anglers (23, 25 and 30 days after C&R) and one fish that was foul hooked and killed by an angler (two days after C&R). In addition, one fish was hooked in the steel wire keeping the transmitter attached (one day after C&R), and the transmitter was torn off while the fish was played. The two fish that were foul hooked or lost the transmitter in the first couple of days after C&R were reported to be in good condition by the anglers as indicated by the fighting resistance and observation of the one that was landed. Additional two fish survived being caught and released by anglers a second time (16 and 6 days after the initial C&R), giving an overall recapture rate of 11.5% (6 of 52, the one hooked in the steel wire attachment is not included).

3.2 Condition at release and playing time

At release, 67% (n = 35) of the fish were considered to be in good or very good condition, 31% (n = 16) in decent and 2% (n = 1) in poor condition. Almost half of the fish (44%, n = 23) swam off immediately. The average ventilation time was 9 ± 26 seconds (median 5, range 0-90). There was no difference in water temperature during C&R between fish considered to be in good and less good condition at release (Mann-Whitney U test: W = 360, p = 0.23). There was no relationship between ventilation time and water temperature at release (Spearman's rank-order correlation: r_s = -0.20, p = 0.15). However, fish considered to be in less good condition were ventilated longer (mean 19 ± 21 seconds, range 0-60) than those in good condition (mean 5 ± 11 seconds, range 0-90, Mann-Whitney U test: W = 104, p < 0.001). A larger proportion of the fish considered to be in less good condition than fish in good condition were bleeding at the hook wound (8 of 17 and 5 of 35, respectively, Fisher`s exact test: p = 0.02). The fish that were bleeding also had a longer ventilation time (mean 19 ± 25 seconds, range 0-90, n = 13) than those that did not (mean 6 ± 11 seconds, range 0-60, n = 39, Mann-Whitney U test: W = 343 p = 0.05).

Fish size, playing time and handling time did not differ between fish considered to be in good condition and fish in less good condition at release (Mann-Whitney U tests: W range 235-329, all p-values ≥ 0.21). Further, the proportion of fish considered to be in good condition or less good condition did not differ between the sexes, fish hooked in potentially harmful versus less harmful locations, fish caught on spoon versus flies, or between freshly run fish versus fish with a longer freshwater residency (Fisher`s exact tests: all p-values ≥ 0.13). There was no relationship between ventilation time and fish size, playing time or handling time (Spearman's rank-order correlations: r_s range 0.05-0.13, all p-values ≥ 0.35). Ventilation time did not differ between the sexes, fish hooked in potentially harmful versus less harmful locations, fish caught on spoon versus flies, or between freshly run fish versus fish with a longer freshwater residency (Mann-Whitney U tests: W range 184-381, all p-values ≥ 0.19).

The time from the fish was hooked until it was landed increased with increasing fish size (linear regression: r^2 = 0.12, p = 0.02). There was no relationship between playing time and water temperature (Spearman's rank-order correlation: r_s = -0.04, p = 0.77). Further, there was no difference in playing time between anglers (Kruskal-Wallis test: H = 6.1, p = 0.19) and playing time did not differ between the sexes, fish hooked in potentially harmful versus less harmful locations, fish caught on spoon versus flies, or between freshly run fish versus fish with a longer freshwater residency (Mann-Whitney U tests: W range 153-353, all p-values ≥ 0.27). Three fish were removed from the analysis because playing time was influenced by problems finding a suitable landing site along the river.

3.3 Behavior after C&R

Behavior after C&R varied among individuals and differed based on where the fish were caught and released (see Appendix 3 for individual behavior plots). However, a general movement pattern after release was apparent and could be divided into three phases: (1) a downstream movement, followed by (2) a stationary period, before (3) upstream movement towards or beyond the site where the fish was angled (Fig. 3).

During the first day after release, 59% (n = 29) of the fish moved downstream (on average 0.7 ± 0.7 km, median 0.5, range 0.1-3.1), 37% (n = 18) remained stationary within 50 m of the release site and 4% (n = 2) moved upstream (on average 0.1 ± 0.05 km, range 0.1-0.2) when the fish that died shortly after C&R (n = 3) are not accounted for. Four days after release, 74% (n = 35) of the fish had been recorded downstream of the release site, and the farthest position was on average 1.3 ± 2.0 km (median 0.6, range 0.1-11.0 km) downstream of the release site when the fish that were foul hooked (n = 2) or died shortly after C&R (n = 3) were not

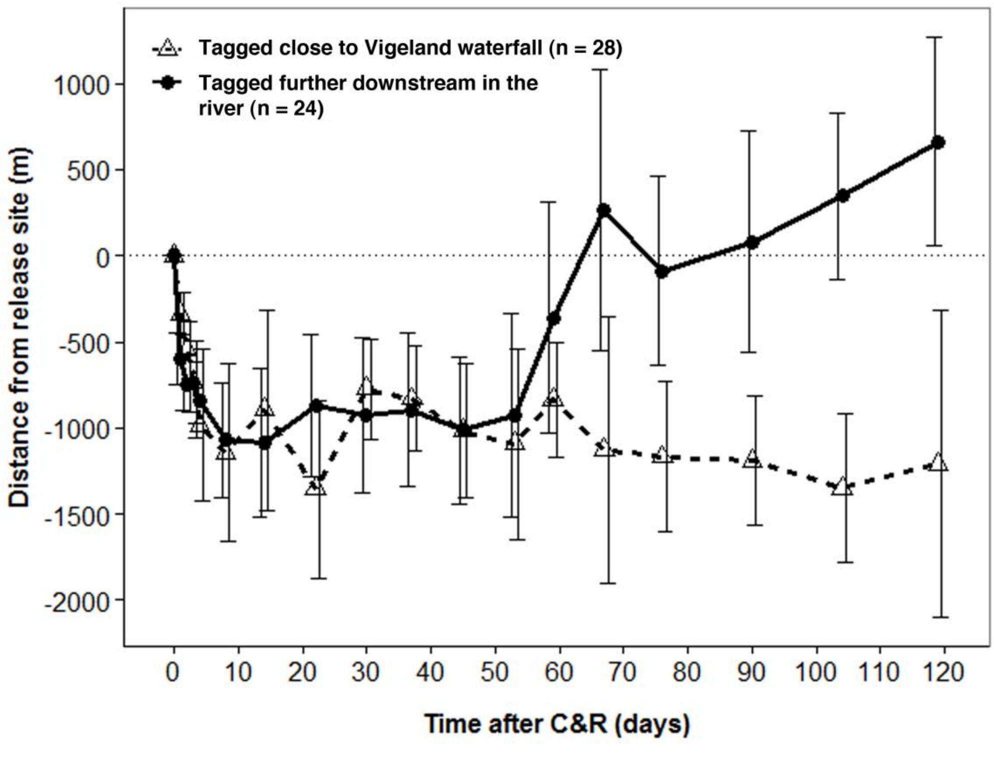

Fig. 3 *Movement after release for radio tagged Atlantic salmon in the River Otra. The release site is set as zero. A positive distance from the release site is upstream and negative distance downstream. Positions are given as average distance from the release site ± 1 SE against average number of days days after C&R for the group of fish tagged at the upper end of the anadromous stretch close to Vigeland waterfall (blue triangles) and for the group tagged further downstream (red dots).*

accounted for. Of the total summed movements for all fish after four days, 94% was downstream, with 49% and 68% of the downstream movements occurring during the first and two first days after release, respectively. The total distance moved was on average 1.0 ± 1.8 km (median 0.5, range 0-11km) for individual fish four days after release.

Fish that stayed stationary or moved upstream during the first four days after release was on average larger (one way ANOVA: $F = 3.8$, $p = 0.06$, *i.e.*, near significant), consisted of more females (Fisher`s exact test: $p = 0.01$) and was caught further up in the river than those that moved downstream (Mann-Whitney U test: $W = 302$, $p = 0.02$). Accordingly, the downstream movement was shorter for females than for males (Mann-Whitney U test: $W = 413$, $p = 0.05$). However, there was no relationship between the length of the downstream movement and fish size (Spearman's rank-order correlation: $r_s = 0.21$, $p = 0.14$), and the length of the movement did not differ between fish caught in the upper versus lower parts of the river (Mann-Whitney U test: $W = 229$, $p = 0.11$). Although the propensity to remain stationary or move downstream after release did not differ between newly ascended fish and those with a longer freshwater residency (Fisher`s exact test: $p = 0.69$), newly ascended fish moved further downstream when moving (Mann-Whitney U test: $W = 97$, $p = 0.03$). There was no relationship between the length of the downstream movement and water temperature, playing time, handling time, ventilation time or water discharge at release (Spearman's rank-order correlations: $0.21 \geq r_s \geq -0.20$, all p-values ≥ 0.12). Further, the length of the downstream movement did not differ between fish considered to be in good condition versus less good condition at release, fish hooked in potentially harmful versus less harmful locations, fish caught on spoon versus flies, or between fish with bleedings versus without (Mann-Whitney U tests: W range 125-336, all p-values ≥ 0.15). Fish that were foul hooked ($n = 2$) or died shortly after release ($n = 3$) were removed from the analyses.

The fish spent on average 24 ± 29 days (median 12, range 1-153) before commencing their first movement upstream after release. Those moving downstream during the first four days after release were recorded near (within 100 m) or upstream of the release site on average 41 ± 38 days (median 35, range 3-153) after release. The length of the delay did not differ between the group of fish caught close to Vigeland waterfall and those caught further downstream in the river (first movement upstream: Mann-Whitney U test: $W = 252$, $p = 0.79$, return to release site: Mann-Whitney U test: $W = 45$, $p = 0.79$). The proportion of fish that did not return to their release site did not differ between the group of fish caught close to

Vigeland waterfall and those caught further down the river (5 of 22 and 6 of 21 respectively, Fisher`s exact test: $p = 1$).

Four fish left the River Otra and were later found (within 28 October-6 November) in neighboring rivers and creeks (see position during spawning in Appendix 1). Another fish that was released in very good condition also seemed to leave the river 11 days after C&R but was not found in other rivers. It is unlikely that it was recaptured and killed without being reported as there was a high reward for reporting recaptures (160 USD) and good collaboration with the anglers in the river. These five fish stayed in the River Otra for an average of 51 ± 34 days (range 11-89) days after C&R before leaving.

3.4 Positions during spawning

All the fish that did not die after C&R and that were present in the river until spawning ($n = 38$) were located at known spawning grounds (Fig. 4). The fish that were caught and released in the upper end of the anadromous stretch were on average positioned 1.5 ± 1.8 km downstream of their release site during spawning ($n = 19$, range 5.2 downstream to 0.2 upstream). Thirteen fish (69%) were located below, five (26%) close to (within 200 m) and one fish (5%) above their respective release sites. The fish in the group that was caught and released further downstream in the river were on average positioned slightly upstream ($n = 19$, mean 0.5 ± 1.9 km, range 3.2 downstream to 4.2 upstream), but not significantly different from their release sites (one sample t-test: $t = 1.3$, $p = 0.21$), during spawning. Seven (37%) fish were located below, two (10%) close to and ten fish (53%) above their release sites.

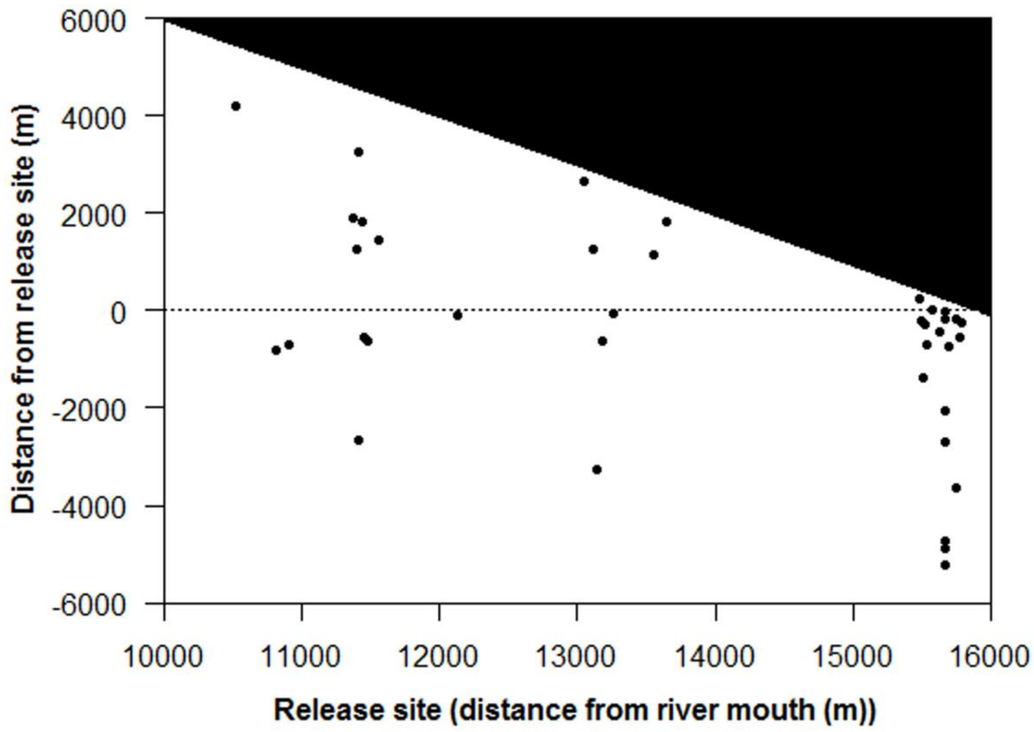

Fig. 4 *Positions during spawning (11 November 2012) for radio tagged fish in the River Otra (n = 38). The positions are given as distance from the release site, where the release site is set as zero for each fish. A positive distance from the release site is upstream and negative distance downstream. The diagonal line show the distance to Vigeland waterfall from any given release site. The shaded area represents the river above Vigeland waterfall which is inaccessible for Atlantic salmon.*

4. Discussion

4.1 Mortality after C&R

Three out of 52 tagged fish (6%) in the River Otra died shortly after release most likely due to impacts from being captured and released. A fourth fish died three weeks after release, perhaps also due to the C&R. Thus the mortality associated with C&R in the current study was estimated to be 6-8%. As some fish normally die during their spawning migration (Baisez *et al.* 2011), it is difficult to separate between natural mortality and mortality caused by C&R without a control group. However, C&R mediated mortalities usually occur within the first 24 hours after release (Muoneke & Childress 1994). Thus, the short time span between angling and time of death for three of the fish make it plausible that C&R caused these short-term mortalities. Long-term mortality after C&R may be linked with immune suppression and disease development (Gale *et al.* 2011), but the cause of death for the fourth fish that might have died due to C&R is uncertain.

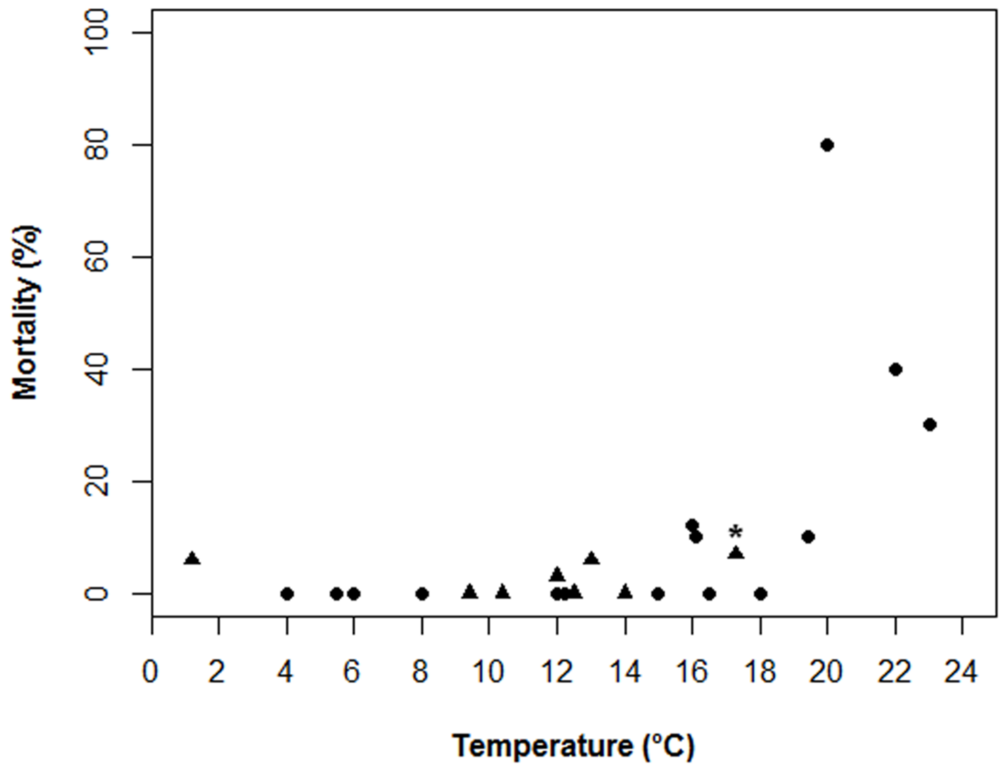

Fig. 5 *Mortality rates after C&R in different studies related to water temperature for Atlantic salmon (Tufts et al. 1991; Davidson et al. 1994; Booth et al. 1995; Brobbel et al. 1996; Wilkie et al. 1996, 1997; Anderson et al. 1998; Gowans et al. 1999; Mäkinen et al. 2000; Dempson et al. 2002; Kieffer et al. 2002; Thorstad et al. 2003, 2007; Halttunen et al. 2010; Jensen et al. 2010). Triangles represent studies with radio tagged fish and dots laboratory-based studies. An asterisk indicates the result from the present study.*

The high water temperatures in this study did not largely elevate the mortality rate after C&R compared to previous studies at lower water temperatures (*e.g.* Brobbel *et al.* 1996; Dempson *et al. 2*002; Thorstad *et al.* 2007). In addition, the mortality observed in this study may be explained by other factors than water temperature as one of the fish that died were released with physical damages and another with minor bleeding in the gill area, which could have reduced their likelihood to survive because such bleedings often result in death in fish (Bartholemew & Bohnsack 2005). The mortality rate is consistent with previous C&R studies at similar water temperatures where Atlantic salmon were confined in pens or in cages in the river after angling (*e.g.* Tufts *et al.* 1991; Brobbel *et al.* 1996; Dempson *et al.* 2002, see Fig. 5). A second order polynomial made by Dempson *et al.* (2002) fitted to results from published C&R studies performed under non-natural conditions predicts a mortality of 8% at the average water temperature that fish were caught and released at in this study.

The use of experienced anglers could have contributed to limit the mortality in this study as the fish were handled carefully and playing time was not unnecessary extended. The handling of fish in normal sport fisheries may be less optimal and thus result in higher mortality rate than found in this study. On the other hand, additional handling time and stress due to the tagging procedure could have negatively affected the probability of survival. Further, the small size of the fish included in this study may actually have limited the mortality as small Atlantic salmon are rarely played to full exhaustion (Dempson *et al.* 2002) while larger fish require a longer time to land (this study; Thorstad *et al.* 2003). Thorstad *et al.* (2003) found that playing time increased with fish size, and that increased playing time elevated the physiological disturbance in Atlantic salmon following C&R. Contrary, other studies have found that the physiological disturbance post-angling is greater for grilse than for MSW-salmon (Booth *et al.* 1995; Tufts *et al.* 2000). The impact of fish size on mortality following C&R is in general poorly understood and has not been well examined for Atlantic salmon (Kieffer *et al.* 2000; Gingerich & Suski 2012).

4.2 Condition at release and playing time

Two thirds of the fish were classified as being in good condition at release, which is less than what is reported in studies at colder water conditions (80-100%, Appendix 4). Comparing this parameter between studies should be done with care as condition of a fish at release is a subjective measure. Ventilation time is a more objective parameter as it can be measured and may be a better measure for comparison among studies. While the condition of the fish in the River Otra was considered to be poorer than reported by Thorstad *et al.* (2003), ventilation time in the latter study was longer than in this study. However, ventilation time correlated with condition at release within studies (this study; Thorstad *et al.* 2003) implying that the subjective assessment reflected the actual state of the fish at release. In addition, subjectively assessing the state of a fish allows for observing reflex impairments which could be a direct sign of stress and mortality outcomes (Davis 2010). These include impaired orientation, fin erection and operculum and mouth clamping or gaping, which give a better impression of the overall state of the fish than when using ventilation time solely.

There was no relationship between increased water temperatures and condition at release in this study. In contrast, Anderson *et al.* (1998) found that Atlantic salmon angled at 16.5 °C and 20 °C were docile and unable to maintain equilibrium after release, while fish angled at 8 °C were in better condition. Increased water temperatures result in a reduced aerobic scope for fish (Farrell *et al.* 2008) and we, therefore, expected playing time to decrease in warmer water conditions. The lack of a relationship between these variables and water temperature in this study could be related to the narrow water temperature range (~ 2 °C).

4.3 Behaviour after C&R

Significant immediate downstream movements after release and delays in the upriver migration were recorded for caught and released salmon in the River Otra. These results are in accordance with previous C&R studies on Atlantic salmon where most report delays and immediate downstream movements after release (*e.g.* Mäkinen *et al.* 2000; Thorstad *et al.* 2007; Jensen *et al.* 2010). The natural riverine migration of Atlantic salmon takes place in three distinct phases; (1) direct, or stepwise upstream migration with resting periods lasting on average 5-9 days, (2) a short search phase with down and upstream movements in close proximity of the position held at spawning, and (3) a long holding phase with none or little movement prior to spawning (Økland *et al.* 2001; Finstad *et al.* 2005; reviewed in Thorstad *et al.* 2008b). Downstream movements are rarely observed in the upriver migration phase and are usually only associated with the short search phase (Økland *et al.* 2001; Finstad *et al.* 2005). Delays lasting longer than 5-9 days and downstream movements after C&R are therefore considered to be a negative behavioral response to C&R. The downstream movements immediately after release may be a result of exhaustion, a flight response or both (Thorstad *et al.* 2003; Jensen *et al.* 2010).

A central question is if the increased water temperatures in this study resulted in a greater negative behavioral response in terms of more pronounced downstream migration and longer delays following C&R. The proportion of fish that moved downstream after release in the River Otra resembles C&R studies at temperatures below 15 °C where 8-46% of the Atlantic salmon moved downstream within one day and 30-100% within 7-10 days after release (Appendix 4). Further, the delay in studies at colder water conditions range between 14-34 days (Appendix 4), which does not differ from the delay observed in this study. The results from studies at colder water temperatures vary as different environmental parameters, river morphologies, and handling procedures may influence behavior after release (Jensen *et al.* 2010) and because different tracking schemes affect how the behavioral data is presented. To conclude, the behavioral response to C&R was not noticeably different at high water temperatures in the River Otra compared to what is reported at colder water conditions.

It is not necessarily given that the propensity to move downstream after release should increase at water temperatures in the upper end of the optimal temperature range. Wilkie *et al.* (1997) found that that the post exercise physiological disturbances in Atlantic salmon were more rapidly corrected in warmer water (18 °C) than at colder water (12 °C), but that extremely high temperatures (23 °C) resulted in mortalities. If the downstream movement is primarily an escape response, a higher proportion could move downstream after release at water temperatures close to the optimal temperature range as the fish may be in a better condition to escape. Similarly, C&R at unfavorable high water temperatures could potentially result in a smaller proportion moving downstream after release if the fish is in a poor condition.

Large females caught and released in the upper end of the anadromous stretch of the river were more inclined to remain stationary and had shorter downstream movements after release than smaller fish caught further downstream. The physiological disturbance post-angling may be greater for grilse than for MSW-salmon (Booth *et al.* 1995; Tufts *et al.* 2000). Thus, the smaller fish may have been more exhausted and as a consequence moved further downstream. Further, fish with a longer freshwater residency had less extensive downstream movements than newly ascended fish. Being caught in the upper end of the anadromous stretch at the end of their migration is probably an important explanatory factor as these fish may have reached their intended spawning grounds and could have started to establish territories. Hence, the motivation to remain where they were released may have been stronger than for migrating fish. To my knowledge there are no studies on behavioral differences between the sexes for migrating Atlantic salmon that could explain why more females remained more stationary after release. The correlation between size, sex, tagging location and migratory phase in this study makes it difficult to separate between their effects on behavior after C&R.

It is not known why five of the tagged fish left the River Otra after release. Behavioral responses to C&R usually occur during the first few days after release (*e.g.* Mäkinen *et al.* 2000; Thorstad *et al.* 2003). Thus, having stayed in the river for an average of 51 days before leaving, there may be other reasons that the fish left the river than being caught and released. Most Atlantic salmon return to spawn in the river where they were hatched (Harden Jones 1968; Stasko *et al.* 1973). However, a small proportion (3-6%) spawns in other rivers than their natal river (Stabell 1984; Jonsson *et al.* 2003). Recent tagging of returning Atlantic salmon in the Trondheimsfjord showed that 29% of the fish 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), confirming that migration between rivers may occur unrelated to catch and release. Little is known about migration of Atlantic salmon between rivers prior to the spawning period.

4.4 Spawning

All surviving fish that were present in the River Otra were located at known spawning grounds during the spawning period. This is consistent with previous C&R studies at lower water temperatures where most Atlantic salmon have been shown to survive until spawning (90-100%) and to be present on spawning grounds (Appendix 4). The methodology used in this study cannot be used for confirming actual participation in spawning, and presence at spawning ground does therefore not necessarily mean that the fish spawned as normal. Positive population effects following C&R have, however, been documented indirectly by increased number of spawning redds (Thorstad *et al.* 2003) and by higher densities of juvenile fish (Whoriskey *et al.* 2000). In addition, Atlantic salmon caught and released in similar water temperatures as in this study have directly by genetic analysis been shown to play an important role in the population reproductive output and to have the same probability of spawning as non-angled salmon (Richard *et al.* 2013). Hence, being alive and present on the spawning grounds indicate that the caught and released fish in this study contributed to the spawning.

A higher proportion of the caught and released fish (53%) stayed below their release site during spawning in the River Otra than in previous studies (40%, 24%, 30%, Thorstad *et al.* 2003; 2007; Jensen *et al.* 2010, respectively). The fact that half of all the tagged fish in this study were caught and released close to the end of the anadroumous stretch probably contributed to this as most of these fish had ended their upstream migration without possibilities to move further upstream. The upper part of the pool below Vigeland waterfall is not suitable for spawning, leaving fish that is caught here with no other choice than to move downstream. It is difficult to determine if the fish caught and released further down the river that spawned downstream of their release site had their upriver migration aborted by C&R. How the altered behavior caused by C&R affect the reproductive success is unknown (Thorstad *et al.* 2003).

Physiological disturbances caused by C&R could potentially reduce the spawning quality as stress has been shown to have deleterious effects on fish reproduction (Pickering *et al.* 1987; Wendelaar Bonga 1997; Tveiten *et al.* 2010). While angling of Atlantic salmon just prior to spawning at low water temperatures (5-6 °C) showed no effects on gamete viability or hatching success in Atlantic salmon (Davidson *et al.* 1994; Booth *et al.* 1995), Richard *et al.* (2013) found that offspring production was negatively correlated with increasing water temperatures for large Atlantic salmon caught and released earlier in the fishing season at warmer water conditions (mean 16 °C, range 10.5-19.1). Thus, the reproductive success of the fish in the present study may have been reduced compared to non-angled fish.

4.5 Conclusions

A large proportion of the fish (92-94%) survived C&R at the highest water temperatures so far recorded in published C&R-studies of free swimming Atlantic salmon in nature (mean 17.3 °C, range 16.3 - 19.7 °C). Thus, C&R at these water temperatures did not increase the mortality compared to previous C&R studies at colder water temperatures. C&R had profound effects on behavior, consistent with the behavior observed for caught and released Atlantic salmon at colder water conditions. However, the results indicate that C&R at these higher water temperatures may be a viable management tool as most fish survived until spawning and were present at known spawning grounds. C&R angling seems to always involve a certain level of mortality, and the results from this study and previous C&R studies utilizing telemetry suggest the loss percentage is 5-10% for Atlantic salmon caught and released below 18 °C. These losses should be accounted for by management authorities in rivers where C&R is practiced and catch statistics is used to evaluate the status of spawning stocks.

Further studies at higher water temperatures are needed as water temperatures frequently exceed the water temperatures recorded in this study in many rivers where C&R of Atlantic salmon is practiced. Preferably, these studies should be performed at water temperatures overlapping with the temperatures in this study due to a low sample size of caught and released fish at the highest temperatures. In addition, further studies should include multiple populations as they may be adapted to different water temperatures and thus have different thermal tolerances (Cooke & Suski 2005).

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Appendix

Appendix 1 Details for all caught, radio tagged and released Atlantic salmon in the River Otra in 2012. Fish number refers to plot number in Appendix 3. Fish body length is given as total length. C&R location 1 is close to Vigeland waterfall and 2 is further down in the river (see methods). Ventilation time is the time from the fish was placed in the water after tagging until it swam off. Recaptured indicate if the fish was recaptured by other anglers or not. Furthest position downstream during the first four days after release and position during spawning is given in relation to the release site (*i.e.* as distance from release site, with negative distances downstream and positive upstream). Sensors show whether the transmitter was equipped with activity and mortality sensors or not. Asterisks indicate mortalities that may have been caused by C&R.

Fish #	Sex	Fish body length (cm)	C&R location	Bait	Time from hooking until landing (min)	Ventilation time (min)	Water temperature at release (°C)	Survival	Recaptured	Furthest position downstream, 4 days (m)	Position during spawning (m)	Sensors
1	Male	55	1	Spoon	6	0.2	16.8	Yes	Yes	-206	4197	No
2	Male	60	1	Fly	4	1.5	17.2	Yes	No	-1030	1431	No
3	Female	57	1	Spoon	5	0.2	16.9	No	Yes	-47	-	No
4	Female	76	2	Fly	3	0.4	16.3	Yes	No	-11012	River Søgne	No
5	Female	79	2	Fly	4	0.3	16.5	Yes	No	145	-4752	No
6*	Male	65	1	Spoon	9	0.0	16.6	No	No	-387	-	No
7	Male	65	1	Spoon	9	0.6	16.7	Yes	No	-2748	Creek Kjos	No
8	Female	80	2	Fly	5	0.0	16.6	Yes	No	-589	-174	No
9	Female	78	2	Fly	5	0.4	17.2	Yes	No	-577	-6	No
10	Male	74	2	Fly	5	0.0	17.5	No	Yes	-814	-	No
11*	Male	75	1	Spoon	8	0.0	17.0	No	No	-1940	-	No
12	Male	60	1	Spoon	5	0.0	17.0	Yes	No	-3448	-636	No
13	Female	57	1	Fly	5	0.1	17.5	Yes	No	-600	-545	No
14	Male	59	1	Spoon	5	0.0	17.5	Yes	No	-504	1814	No
15	Male	65	1	Spoon	9	0.4	16.8	Yes	No	-3747	-2667	No
16	Male	55	2	Fly	3	0.1	16.7	Yes	No	-1328	River Tovdal	No

Appendix 1 (Continued)

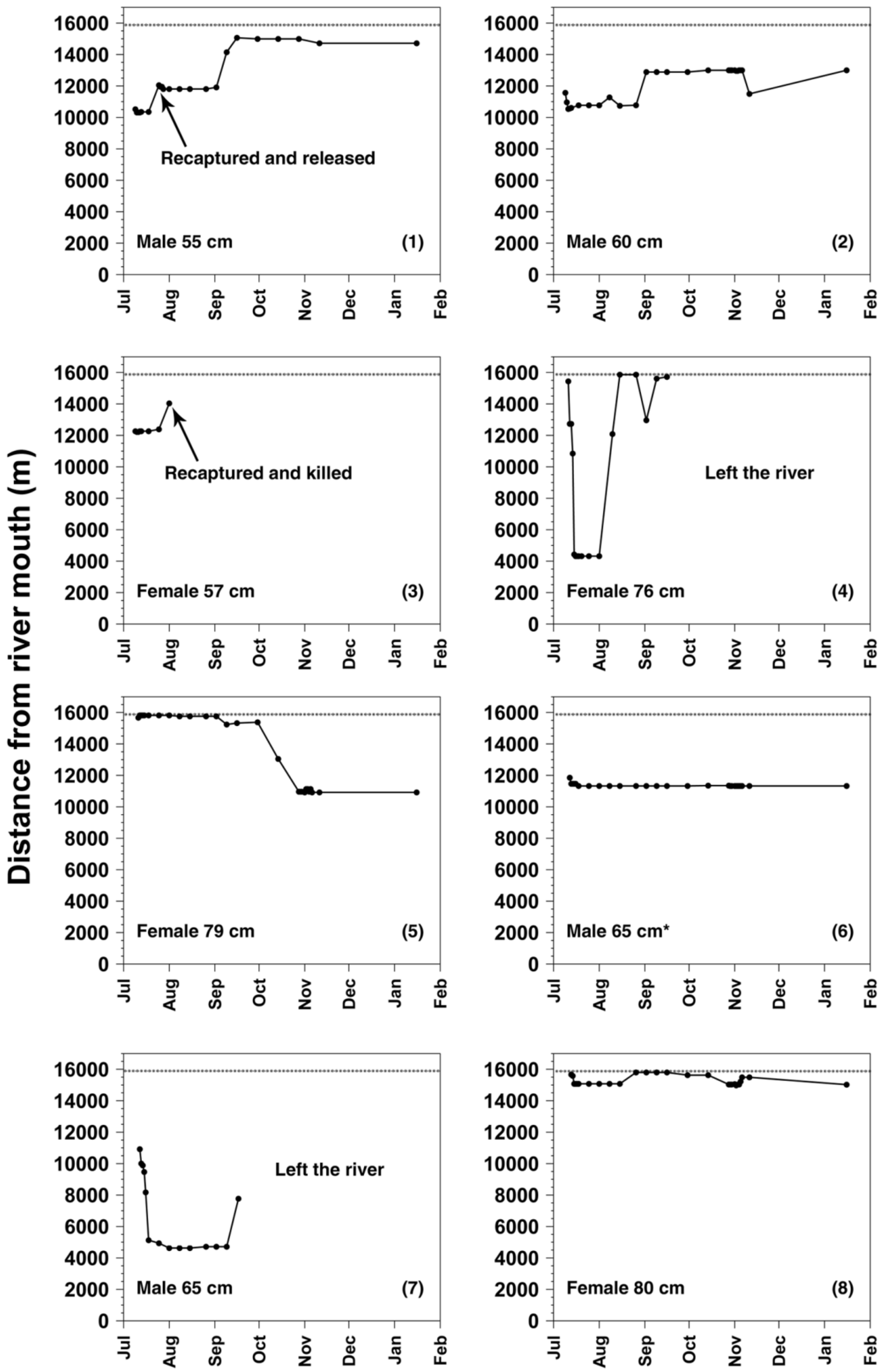
Fish #	Sex	Fish body length (cm)	C&R location	Bait	Time from hooking until landing (min)	Ventilation time (min)	Water temperature at release (°C)	Survival	Recaptured	Furthest position downstream, 4 days (m)	Position during spawning (m)	Sensors
17	Female	75	2	Fly	6	0.6	16.4	Yes	No	-	-691	No
18	Male	70	1	Fly	7	0.1	16.9	Yes	No	-161	3272	No
19	Male	57	1	Spoon	4	0.0	17.1	Yes	No	-644	1263	No
20	Female	63	1	Spoon	5	0.1	17.1	Yes	No	-204	1918	No
21	Female	71	2	Fly	5	0.2	16.6	Yes	No	-364	-433	No
22	Male	60	1	Spoon	4	0.0	16.8	Yes	Yes	-1140	-698	No
23	Female	63	1	Spoon	3	0.0	16.5	Yes	No	-825	1811	No
24	Male	60	1	Fly	3	0.2	16.6	Yes	No	-203	-81	No
25	Female	62	2	Fly	3	0.0	17.1	No	Foul hooked	-	-	No
26*	Female	75	2	Fly	5	0.2	17.1	No	No	-1356	-	No
27	Female	75	2	Fly	6	0.0	17.2	Yes	No	-1170	-4896	No
28	Female	90	2	Fly	6	0.0	17.0	Yes	No	-	228	No
29	Male	60	1	Spoon	5	0.1	17.0	Yes	No	-1306	-633	No
30	Male	58	1	Fly	4	0.0	17.7	Yes	No	-520	-808	No
31	Female	76	2	Fly	4	0.1	17.5	Yes	No	-	-2051	Yes
32	Female	81	2	Spoon	4	0.0	17.6	No	Foul hooked	-	-	Yes
33	Female	75	2	Fly	5	0.2	17.6	Yes	No	-	0	Yes
34	Male	58	1	Fly	5	0.1	17.6	Yes	No	-826	1142	No
35	Male	62	1	Fly	4	0.0	19.7	Yes	No	-204	-3247	Yes
36	Male	58	1	Fly	4	0.0	19.2	Yes	No	-165	1242	No
37	Male	59	1	Fly	4	0.0	18.0	Yes	No	-1300	2641	No
38	Male	70	2	Fly	4	0.0	18.0	Yes	No	-116	-231	Yes
39	Female	80	2	Fly	5	0.0	17.8	Yes	No	-	-533	Yes
40	Male	73	2	Fly	5	0.0	17.6	Yes	No	-	-3651	Yes

Appendix 1 (Continued)

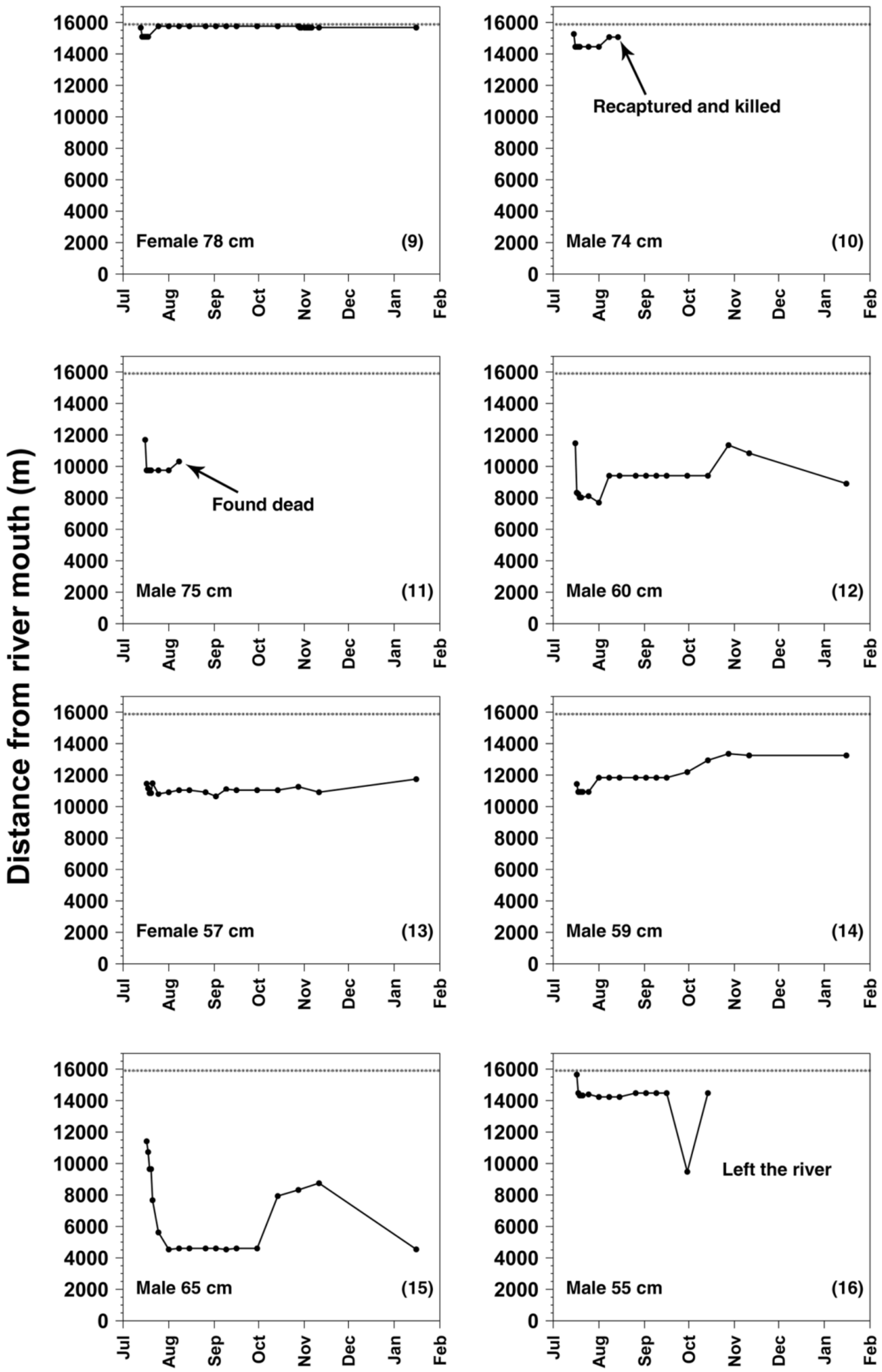
Fish #	Sex	Fish body length (cm)	C&R location	Bait	Time from hooking until landing (min)	Ventilation time (min)	Water temperature at release (°C)	Survival	Recaptured	Furthest position downstream, 4 days (m)	Position during spawning (m)	Sensors
41	Female	56	1	Fly	4	0.0	18.3	Yes	No	-	-	No
42	Female	75	2	Spoon	4	0.0	17.9	Yes	No	-406	-172	Yes
43	Female	90	2	Spoon	5	0.1	17.5	Yes	No	-	River Audna	Yes
44	Female	65	2	Fly	4	1.0	17.5	Yes	No	-1424	-2715	Yes
45	Female	65	2	Fly	5	0.0	17.5	Yes	No	-	-1386	No
46	Male	63	2	Spoon	4	0.3	17.7	Yes	No	-4435	-730	No
47	Male	53	1	Fly	4	0.3	17.7	Yes	No	-	-60	No
48*	Female	76	2	Fly	5	0.1	18.2	No	No	-217	-	Yes
49	Male	67	2	Fly	5	0.1	17.6	Yes	No	-142	-277	No
50	Male	83	2	Fly	5	0.2	18.0	Yes	No	-125	-5235	No
51	Female	74	2	Fly	6	0.3	17.9	No	Yes	-1724	-	No
52	Female	73	2	Fly	7	0.1	17.7	Yes	No	-132	-195	No

Appendix 2 Overview over the categories that were used to describe hook location, fish condition at release, bleeding and bait type when the data was collected and the reduced categories that were used in statistical analyses.

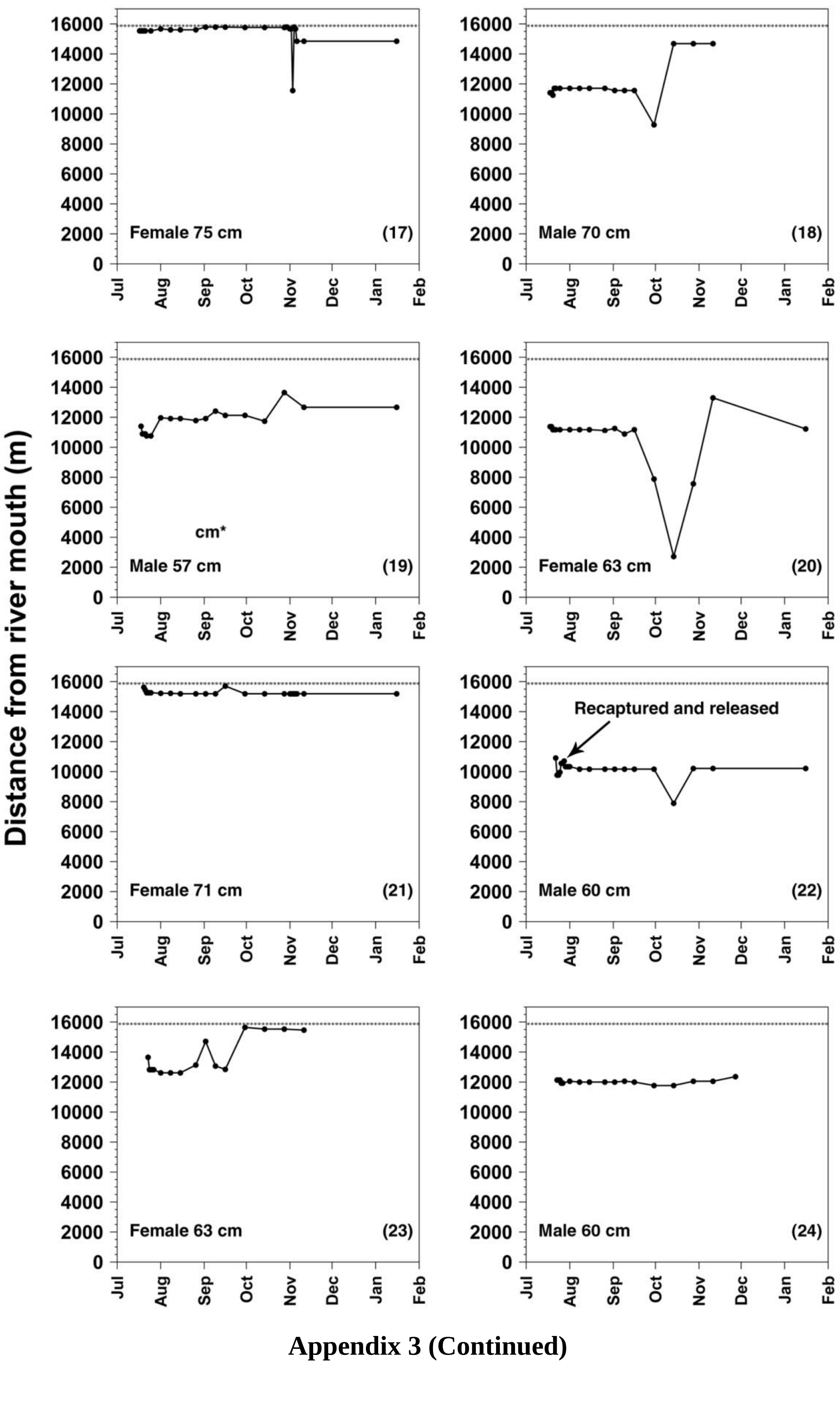
	Variable			
	Hook location	**Condition**	**Bleeding**	**Bait type**
Original categories	Upper jaw	Very good	Gills	Spoon
	Lower jaw	Good	Mouth	Fly
	Corner of the mouth	Decent	None	Fly and bobber
	Mouth cavity	Poor		
	Esophagus			
	Gills			
	Tounge			
	Other			
Reduced categories	Potentially harmful	Good/very good	Yes	Spoon
	Not harmful	Decent/poor	No	Fly



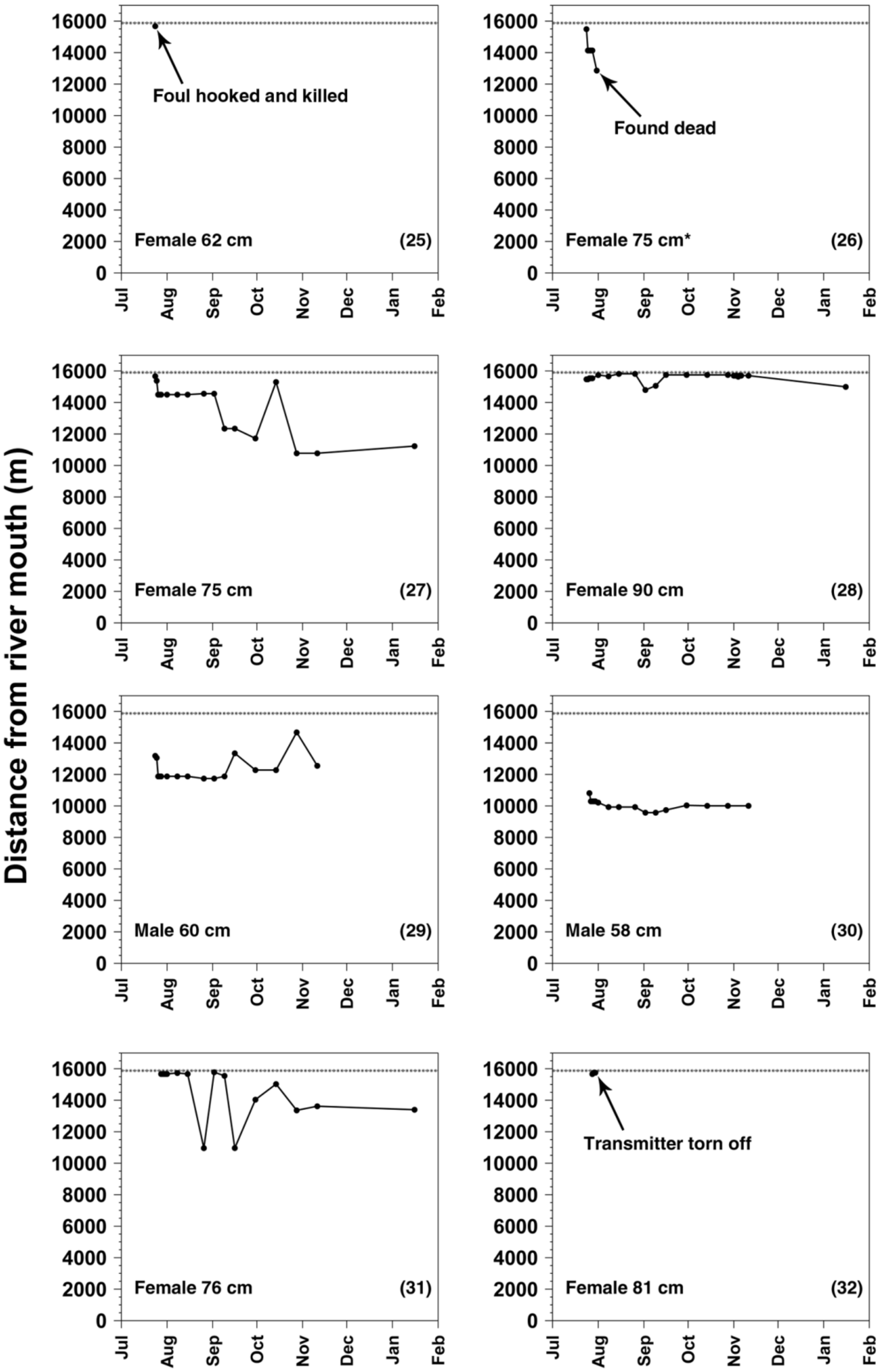
Appendix 3 Migration after C&R for individual radio tagged Atlantic salmon (9 July 2012-16 January 2013) in the River Otra. Positions are given as a distance from the river mouth (zero on the y-axis) where the first position is the C&R-site. The end of the anadromous stretch is indicated by a dotted horizontal line. Plot numbers refer to fish number in Appendix 1 and asterisks identify mortalities that may have been caused by C&R. Text and arrows in some of the plots indicate specific information for some individuals.



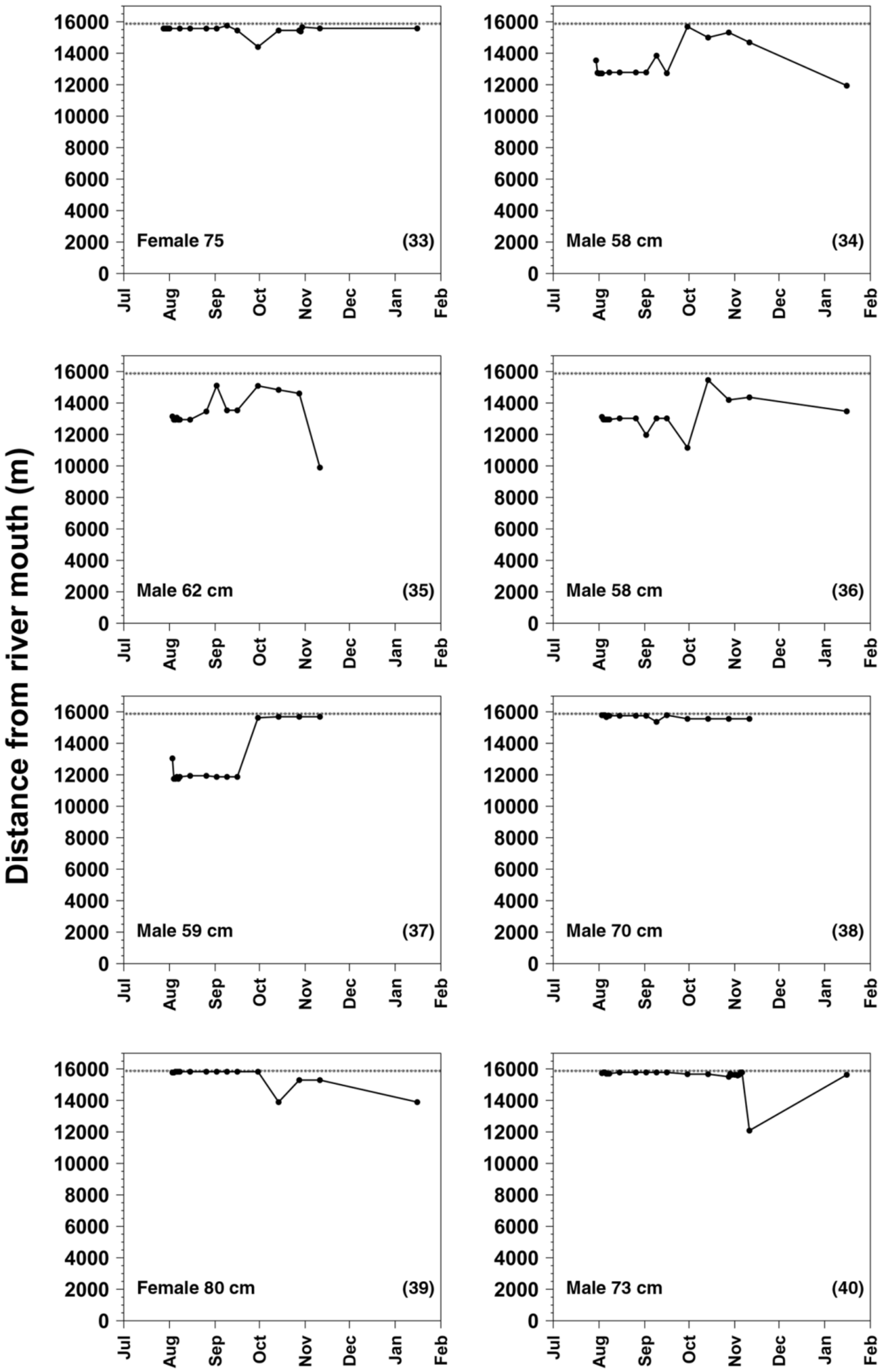
Appendix 3 (Continued)



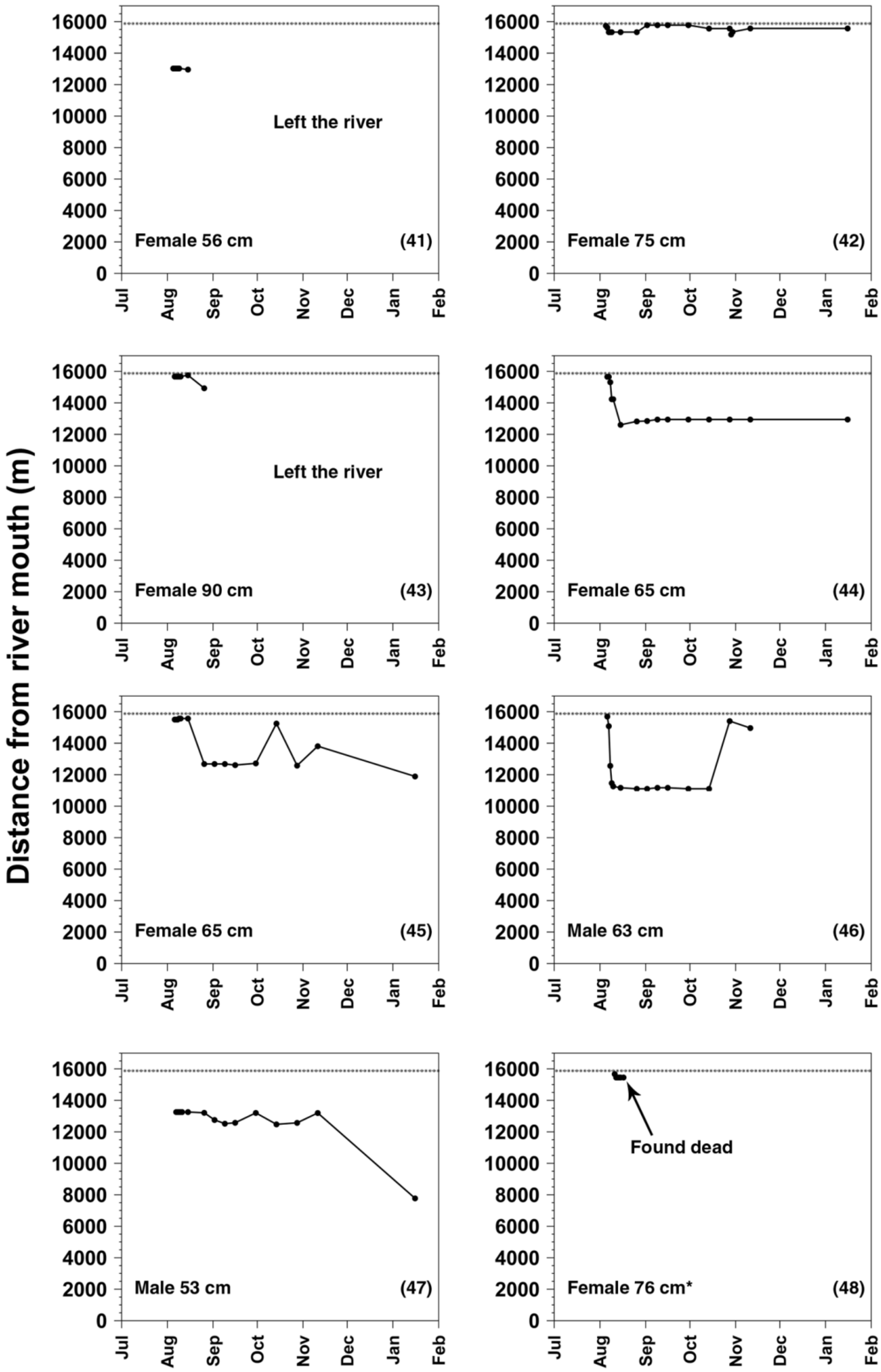
Appendix 3 (Continued)



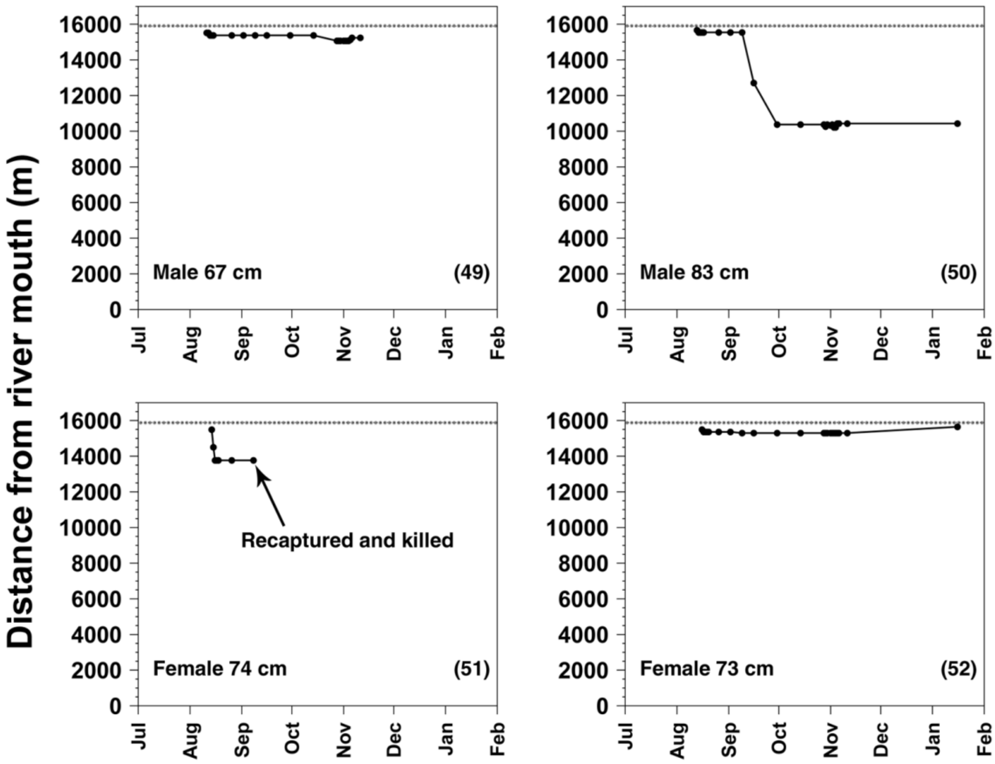
Appendix 3 (Continued)



Appendix 3 (Continued)



Appendix 3 (Continued)



Appendix 3 (Continued)

Appendix 4 Summary of key findings in C&R studies on free swimming Atlantic salmon in nature. Survival is the proportion of fish that survived being caught and released. Survival until spawning is the proportions of caught and released fish that survived C&R and were still alive and located at known spawning grounds during the spawning period. Downstream movement is given as proportion of the fish that moved downstream after release. Condition at release is given as the proportion of the fish considered to be in good or very good condition at release. Migration phase indicates which phase that the caught and released salmon were in at capture, where 1 is the upstream migration phase, 2 is the search phase and 3 is the holding phase (see discussion for further explanations).

Study	Number of tagged fish	Water temperature (°C)	Survival	Survival until spawning	Downstream movement	Delay (days)	Condition at release	Migration phase
Webb (1998)	25	Not given	95%	100%	8% (1 day)	14-24*	Not given	Mainly 1
Gowans *et al*. (1999)	39	10.4 °C	100%	Not given	46% (1 day)	Yes	Not given	Not given
Mäkinen *et al*. (2000)	5	9.4 ± 1.0 °C	100%	100%	100% (9 days)	28* (max)	100%	1
Mäkinen *et al*. (2000)**	19	9.4 ± 1.0 °C	84%	42%	100% (9 days)	28* (max)	100%	1
Thorstad *et al*. (2003)	30	10-14.5 °C	97%	100%	83% (7 days)	Not given	90%	Mainly 2,3
Thorstad *et al*. (2007)	18	12-14 °C	94%	100%	31% (1 day)	34***	100%	1
Thorstad *et al*. (2007)	14	10-15 °C	100%	93%	Not given	Not given	Not given	Mainly 2,3
Jensen *et al*. (2010)	10	< 14 °C	100%	90%	30% (10 days)	Yes	80%	1,2,3
Halttunen *et al*. (2010)	73	1.2 °C	96%	Not given	Not given	Yes	Not given	Kelts
This study	52	17.3 ± 0.7 °C	92-94%	100%	59% (1 day)/ 74% (4 days)	24*/41****	67%	1,2,3

*Number of days before first upstream movement. **Gill-net caught fish. ***Number of days before the fish was located 1 km upstream of the tagging site.
**** Number of days before the fish was located close to or above the tagging site