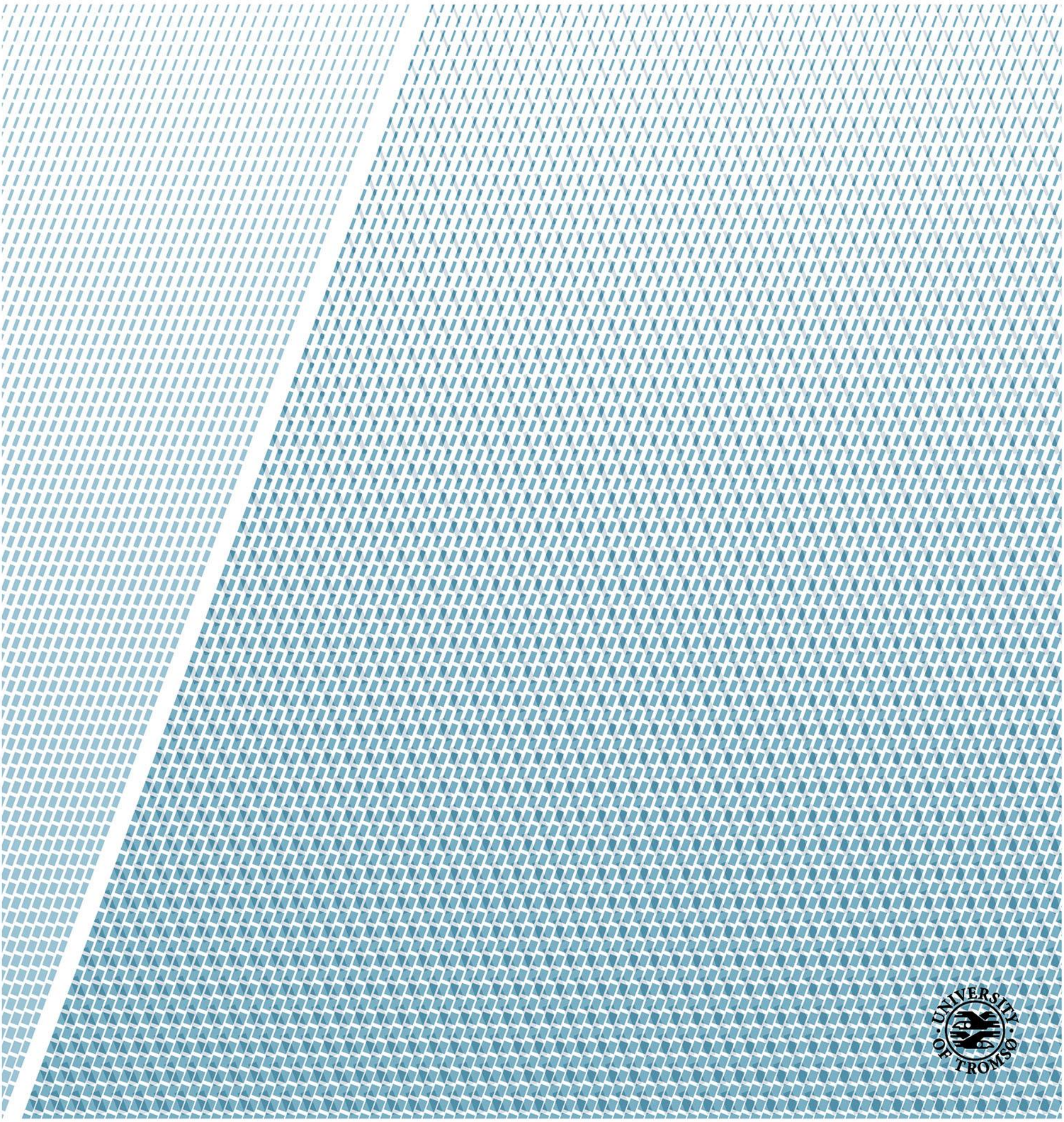
UiT
THE ARCTIC
UNIVERSITY
OF NORWAY

Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

Depth use of adult Atlantic salmon during the first and last phase of the marine migration

Mari Kjellman

BIO-3950 Master Thesis in Arctic and Marine Biology, May 2015



Acknowledgements

This thesis is part of the Salmotrack project. The project has been made possible due to great help and support from Alta Laksefiskeri Interessentskap (ALI). The experimental procedures were approved by the Norwegian National Animal Research Authority.

I thank my supervisor, Audun Rikardsen, for letting me take part in this project. Great thanks also goes to my two other supervisors, Eva B. Thorstad and John Fredrik Strøm. Eva for always being enthusiastic, supportive and available, and John for never saying no when I needed help. I also wish to thank Richard Hedger for valuable help with R. Further, Karin Strand Johannessen, Cesilie Bye and Jens Olav Østerdal are thanked for doing the laboratory analyses of the stomach samples. Thanks to my parents, for always supporting me and believing in me. To Eirik and Anne Cathrine: thank you for all the good and bad days at the office, for all the laughs and all the coffees. Last, but not least, thanks to Martin for being both positive and understanding through the whole process.

Tromsø, May 2015
Mari Kjellman

Abstract

The Atlantic salmon has declined in numbers over the last decades. Given the species' anadromous nature, management is a challenge, and information is lacking, especially from the marine migratory phase. Information about repeat spawners and their migratory behaviour may be of major importance in management questions, as these individuals have been found to contribute significantly to spawning populations. The aims of this study were to analyse depth use during the first and last phase of the marine migration and to investigate if the Atlantic salmon forage during the return migration. During the years 2008-2014, 630 post-spawned Atlantic salmon were tagged with depth-recording data storage tags in the river Alta. Of these, 41 salmon were recaptured. Usable data were retrieved from 29 salmon during outward migration and from 20 salmon during return migration. In addition, stomachs were collected from 939 returning salmon in the Alta fjord. The salmon spent most of the time in the upper five meters of the water column in the fjord and outer coast both during outward and inward migration. Number of depth recordings at 0-5 m decreased with time from seawater entry during outward migration from 96% during the first 24h after seawater entry, to 75% at the fourteenth day. During the inward migration, the proportion of recordings at this depth interval was smaller in the outer coast areas (50%) than in the inner and outer fjord (88 and 91% respectively). Diving intensity increased with time and distance from the estuary, both during outward and inward migration, and so did the proportion of diving salmon and the overall maximum diving depths. Large individual variations in depth use was observed, and the deepest recorded dives were 337m during outward migration and 97m deep during inward migration. The stomach analyses showed that a large proportion (59%) of the returning salmon had empty stomachs. A proportion of the salmon (14%) also had only small fractions of stomach contents. All feeding salmon had fed exclusively on fish, including herring, capelin and sand eel, but the contents were often highly digested, suggesting that the food intake had occurred some time ago. This suggests that other explanations than feeding have to be considered for diving behaviour during inward migration. The proximity to surface and diving behaviour observed in both outward migrating and inward migrating salmon is likely a combination of factors like orientation, predator avoidance, control of body temperature, or other unknown factors.

Table of Contents

1 **Introduction**

The Atlantic salmon (*Salmo salar*) is a species of great economic and recreational value. Management of the species is a challenge, given that it is anadromous and divides its time between freshwater systems and marine habitats and may spend several years in the ocean performing long migrations (Rikardsen et al. 2008, Dadswell et al. 2010). Atlantic salmon has been widely studied in freshwater systems, whereas the marine migratory phase is the least studied part of the life cycle (Thorstad et al. 2011). The Atlantic salmon differs from Pacific salmon species (*Oncorhynchus* spp.) in that it is iteroparous, which means it can spawn repeatedly (Klemetsen et al. 2003). Post-spawned Atlantic salmon reenter the sea between spawnings, and post-spawning survival may be high both in rivers and during the initial marine phase in estuaries and fjords (Halttunen et al. 2009, Hedger et al. 2009, Reddin et al. 2011). Halttunen (2011) found that the return rates of previous spawners were substantial (39% of females and 19% of males), but post-spawning survival and occurrence of multiple spawners vary among populations (Crespi and Teo 2002). Repeat spawners may contribute significantly to the spawning population of Atlantic salmon stocks (Niemelä et al. 2006, Halttunen 2011), and knowledge about repeat spawners may therefore be of major importance for management of Atlantic salmon populations, especially considering the population declines observed over the last decades (ICES 2014).

During the initial marine migratory phase, post-spawners generally stay close to the surface, but may perform occasional dives to various depths, according to tagging studies from Newfoundland and Northern Norway (Hubley et al. 2008, Halttunen et al. 2009, Hedger et al. 2009). Halttunen et al. (2009) reported most post-spawners to move fast through the Alta Fjord, while other studies have found large shares of the post spawners to linger in estuaries and coastal habitats with frequent changes in directions before entering the open ocean (Hubley et al. 2008, Hedger et al. 2009). The homing migration of Atlantic salmon appears to be divided into two parts: the first navigation from the feeding areas towards coastal areas, and a second, more precise navigation in coastal areas close to the home river (Hansen et al. 1993). During the near coastal migration towards the natal river, adult Atlantic salmon from Northern Scotland were highly oriented to the surface, with regular vertical movements, but with large individual variation (Godfrey et al. 2015). Homing adult salmon in the Alta fjord were also recorded at mean depths close to the surface, with a few deeper dives (Davidsen et al. 2013). The swimming depth decreased as the salmon moved closer to the estuary. It is believed that the migration of kelts and repeat spawners resembles the migration of post-smolt and first time spawners (Dadswell et al. 2010). In a study of homing Pacific salmon, Wada and Ueno (1999) suggested three hypotheses for explaining diving behaviour; feeding, search for olfaction cues, and control of body temperature. Reddin et al. (2004) added a fourth hypothesis that proposed predator avoidance as another possible explanation for diving.

Research of marine diet and feeding behaviour of the Atlantic salmon have been largely concentrated on post-smolts and pre-adults in the initial marine phase and at known feeding grounds in the open ocean (Levings et al. 1994, Rikardsen et al. 2004, Rikardsen and Dempson 2011). Due to the precise homing behaviour showed by returning Atlantic salmon, one may expect that their main priority in near coastal areas is navigation. To my knowledge, no feeding studies have been conducted on returning Atlantic salmon, leaving it an open question whether returning salmon forage during their homing migration.

Most of the existing information from the ocean phase originates from conventional mark- and recapture studies and scale analysis. These methods fail to provide detailed information from the period between mark and recapture. During recent years, the development of new tagging technology has made it possible to collect detailed information on the marine migration and behaviour of the Atlantic salmon. Direct tracking methods like radio and acoustic transmitters have been widely used in fish research (e.g. Ovidio and Philippart 2002, Chittenden et al. 2011, Davidsen et al. 2013), but have limitations due to the fact that the fish have to be either followed by manual trackers or recorded by automatic listening stations (Reddin et al. 2004, Thorstad et al. 2013). The development of data storage tags (DSTs), has made it possible to collect data with a high temporal solution over longer time intervals and distances (Reddin et al. 2004, Rikardsen et al. 2007), as these tags do not depend on signal transmission to receivers like radio and acoustic tags. DSTs record data, e.g. on depth and temperature, at preset time intervals and it has been stated that DSTs are among the most cost-effective methods available for studying the marine migration of Atlantic salmon (Reddin et al. 2006, Rikardsen et al. 2007).

In this study, the depth use of Atlantic salmon post-spawners during the first and last phase of the marine migration was examined by the use of data storage tags. The aims were to 1) record and analyse the individual depth use in inner and outer parts of the fjord and outer coastal areas with data storage tags, and 2) use stomach samples to investigate if the Atlantic salmon forage during the last part of the return migration, and discuss if food intake may be related to the vertical migration pattern.

2 Methods

2.1 Study area

The river Alta (70°N 23°E) is a sub-arctic river in the county of Finnmark, Northern Norway. It is 160 km long, of which the lower 46 km is accessible for anadromous salmon (Ugedal et al. 2008). The river empties into the Alta fjord, which is a large fjord with a maximum depth of 488 m and a width of 15 km at its widest (Figure 1). Due to large outflow of water from the Alta river, the surface layers of the fjord largely consists of brackish water in summer (Davidsen et al. 2013). A wide range of marine fish species is found in the fjord, and in addition the fjord contains many anadromous populations of salmonids, due to the inflow of several rivers. The fjord has been given status as a "National salmon fjord". This grants the salmon stock special protection to secure future diversity (Anon 2007), but still fish farming is a major industry, dominated by Atlantic salmon and rainbow trout (*Oncorhynchus mykiss*).

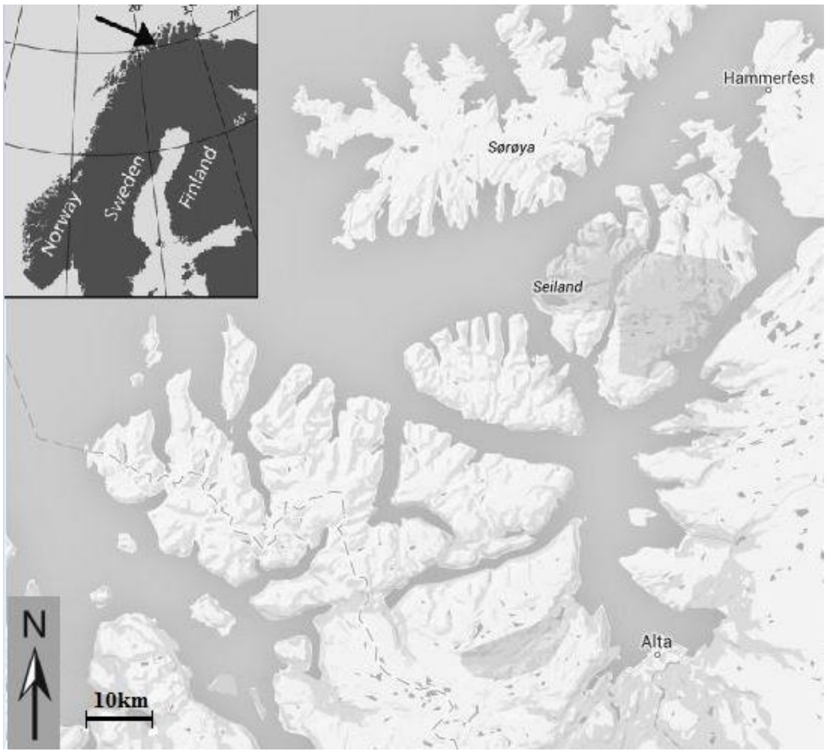


Figure 1. Map showing the Alta fjord and the surrounding coastal areas.

2.2 Fieldwork

The fieldwork was conducted over the years 2008-2014. Kelts were captured and tagged each year just after the ice break-up in May. The total number of fish tagged was 630 (mean fork length = 92.7cm, range = 56.6-118.5cm. Mean weight = 6.1kg, range = 1.4-13.0kg). Female kelts were preferred for tagging, because they are known to have a higher survival than males (Halttunen 2011) (tagged females = 604, tagged males = 26).

The fish were captured in the river Alta using fishing rods. The bait was two-hooked lures where the barbs had been removed to cause as little harm as possible to the fish during capture. The fish was brought to shore as quickly as possible after taking the bait, and placed in a cage in the river until tagging. In total, 509 salmon were tagged with Data Storage Tags (hereafter called DSTs) (DSTmilli: 13mm x 39.4mm, 9.2g in air and DST centi: 15mm x 46mm, 19g in air, Star Oddi, Reykjavik, Iceland) recording pressure (depth) and temperature. Further, 121 salmon were tagged with geolocation tags (hereafter called GEOTs) (LAT2810L 13mm x 44 mm, 13.0g in air, Lotek Wireless Inc., Ontario, Canada), recording internal and external temperatures, pressure (depth) and light. Recording intervals ranged from 30sec to 30min (Table 1). Due to battery capacity, tags have been programmed to start recording at 4h intervals after 15 months. Both DSTs and GEOTs are tags that save and store recorded information, and have to be retrieved to download the data.

Table 1. Overview of number of tagged Atlantic salmon (N) per year, and depth recording intervals of the tags used.

Year	Tag Type	N	Recording interval (depth)
2008	DST	54	30min
2009	DST	60	30min
2010	DST	94	30min
2011	DST	67	30min
2012	DST	73	10min
2013	DST	80	5min
2013	GEO	60	30sec
2014	DST	81	5min
2014	GEO	61	30sec

2.3 Tagging procedure

The fish was anesthetized in an aqueous solution of 2-phenoxy ethanol (EC No 204-589-7, Sigma Chemical Co., St Louis, Missouri, USA, 0.5ml L^1). Thereafter, it was placed in a tagging tube containing fresh water. A lateral cut (~2-2.5cm long) was made through the fish's body wall. The tag was placed inside the body cavity. Using a hypodermic needle, the light sensitive antenna (applies to GEOTs), or an internal anchor tag (Floy tag and Mfg., Inc., Seattle, Washington, USA) (applies to DSTs), was exited through the body wall. The incision was closed using 2-3 stiches made with absorbable surgical suture (2.0, Ethicon Endo-Surgery Europe, Norderstedt, Germany). For the fish tagged with GEOTs, the antenna was secured exteriorly by a single stich of non-absorbable suture (3.0, Ethicon Endo-Surgery Europe, Norderstedt, Germany). In addition to the internal GEOT, these fish also had an external Carlin tag deployed below the dorsal fin. A Carlin tag is a small plastic tag carrying an identification number. The Carlin tag was deployed by pushing two hypodermic needles through the fish's back below the dorsal fin and securing the tag with an attachment wire on the opposite side of the dorsum. This double tagging (Carlin tag for GEOT salmon, internal anchor tag for DST salmon) was done to secure identification at recapture, as these tags carried information that the fish was internally tagged, in addition to identification number and contact information. In addition to tagging, the fish's length and weight were recorded. Scale samples and a sample of the adipose fin were taken for possible later investigations, but were not used in this thesis. After finishing the handling and tagging procedure (~6 min), the fish was released directly into the river. This applies to all fish except the fish tagged in 2009, which were transported to the fjord and released directly into seawater.

Local people were informed about the tagging project, and anglers were asked to release fish with fresh surgery wounds in the abdomen and report the catch. Recapture of returning fish was dependent on fishers, and a 1000NOK reward was given for each returned tag to ensure reports of recaptured tags. Recaptures of tagged fish were done by anglers in the river and bag net fishers in the fjords and at the outer coast. Hence, fish were either recaptured within a few weeks after tagging as kelts during their outward migration, or recaptured as returning salmon after the ocean migration. There were no recaptures from the ocean migration phase, which was expected, because there is no targeted fishery for salmon in the ocean.

2.4 Stomach samples

Stomach samples were collected from 939 returning salmon in the Alta fjord during fishing seasons in June-August 2008-2010. The sampling was done by local bag net fishers in the outer and inner parts of the fjord. The fishers measured fish body weight and fork length, and collected scale samples, livers, gills, gonads and stomachs.

Further investigation of the samples was done in laboratories at the University of Tromsø. Each stomach was opened and studied for grade of filling in percent, with 0% representing an empty stomach and 100% representing a completely filled stomach. All stomachs with content were further investigated to decide diet composition if possible. The proportional composition of prey types was calculated and expressed as prey abundance for individual salmon, by calculating the weight of each prey type as percentage of the total weight of the stomach content. The result for each prey type is given as the mean of percentages for all individuals. In addition, the content of each stomach was given a digestion rating ranging from 1-5 (Table 2).

Table 2. Explanation of the different digestion values used to rate the contents in salmon stomachs.

Digestion rating value	Explanation
1	Undigested
2	Partly digested (some skin digested, head mostly intact)
3	Skin and flesh mostly disappeared (head partly digested)
4	Vertebrae with flesh remainders
5	Almost completely digested (soup-like substance)

2.5 Data analyses and statistics

Data from the retrieved tags were downloaded using the specialized computer programs SeaStar and TagTalk (for DSTs and GEOTs respectively). Timing of seawater entry for individual salmon was decided based on temperature patterns in the data. Analyses of the depth data and diet samples were done using R (R core team 2014). Significance level was set to $p < 0.05$.

Dives were defined as any movement passing from shallower depths to below 10 m.

To investigate depth use, percentage depth use at different depth intervals was calculated for each salmon, based on number of recordings. The mean percentage composition for all salmon was calculated to investigate depth use in different zones and in different days. This was done as a standardization because of different recording intervals in the tags. To investigate diving intensity, a relative number was calculated for each salmon (number of dives in a 24 h period/number of measurements in 24 h) to be able to compare diving behaviour in fish with tags of different recording intervals. To investigate for differences in diving intensity and maximum depths in different days and different zones, exact two sample permutation tests were run.

2.5.1 Outward migration

Halttunen et al. (2009) found that 52% of tagged kelts migrated through the inner 30 km of the Alta fjord within 24h during their outward migration, whereas the remaining 48% spent a longer time (up to 138 h). Considering these results, depth data from the first 24h after the salmon was leaving the river and entering the fjord were included in the analyses. This was done to maximize the likelihood that the analysed data were from the period when the salmon were still inside the fjord system. In addition, day 3, day 7 and day 14 after seawater entry were extracted from the data to compare depth use and diving behaviour at different stages in the marine migration. Considering findings from other studies, one could expect the salmon to be in the inner or outer fjord system at day 3, in the coastal zone at day 7, and in the open waters at day 14 (Hubley et al. 2008, Halttunen et al. 2009).

2.5.2 Inward migration

For analyses of the depth data from the Atlantic salmon's return migration, the study area was divided into three zones: inner fjord, outer fjord, and coast, according to where they were recaptured (Figure 2). Data from the last 24 h period before recapture were analysed.

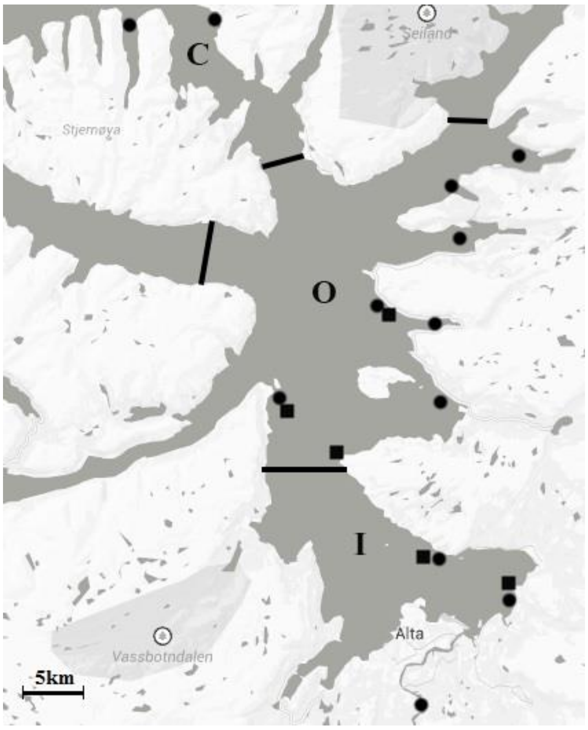


Figure 2. Map of the Alta fjord showing the different zones used in analyses of inward migration (I = inner fjord, O = outer fjord, C = coast). Recapture locations for all salmon included in the study are also indicated (● = returning salmon, ■ = outward migrating kelts). Some individuals were also recaptured outside the map area, and were included in the coastal zone.

3 Results

3.1 Recaptures

During 2008-2014, tags were retrieved from 41 recaptured Atlantic salmon (33 DSTs, 8 GEOTs). Of these, 32 were recaptured during their migration back to the river, while nine were recaptured during their outward migration as kelts (Table 3). Of the 32 returning salmon, 27 were recaptured in the sea, while five were recaptured in the river (Figure 2). Data were successfully downloaded from all retrieved DSTs. Of the eight recaptured GEOTs, data were successfully downloaded from six tags. All four salmon with GEOTs recaptured as kelts were captured immediately after seawater entry, and it was not possible to extract useable data from these short marine periods. The same were the case for two salmon with DSTs, from 2010 and 2011, respectively. Thus, these six kelts were not included in the analyses. Due to limited memory capacity in the DSTs from 2008/2009, logging had stopped prior to fjord entry for all six returning salmon recaptured in 2009, and depth data from the inwards fjord migration were not available for these fish. Four fish with DSTs were recaptured after the tags had started to record at 4h intervals. Data from these four fish during their inward migration were therefore excluded, due to limited data. The three returning salmon recaptured in 2010, had been transported from the river and released directly into seawater. Data from the outward migration of these fish were excluded to avoid using results from possibly altered behaviour. Based on this, the analyses and results are based on data from 29 salmon during outward migration from the river towards the ocean, and from 20 salmon during return migration from the ocean towards the river (Table 3).

Table 3. Overview of recaptures of Atlantic salmon during outward migration (kelts) and inward migration (returning salmon) for fish tagged in 2008-2015. The table includes an overview of number of fish with usable data. "Usable data out" represents data from outward migration. "Usable data in" represents data from inward migration.

TAGGING	KELTS		RETURNING SALMON		
YEAR	Recaptured	Usable data	Recaptured	Usable data out	Usable data in
2008	0	0	6	6	0
2009	0	0	3	0	3
2010	2	1	7	7	7
2011	2	1	6	6	3
2012	0	0	2	1	1
2013	1	0	8	6	6
2014	4	1	-	-	-
Total	9	3	32	26	20

3.2 Outward migration

The proportion of recordings close to the surface was larger during the fist 24h after entering the sea than later during the marine migration (Figure 3). The salmon had on average 96% (range 77-100%) of the recordings in the upper five meters during the first 24 h after seawater entry. The average number of recordings at these shallow depths decreased from day 1, through day 3 (81%, range 23-100%) and day 7 (84%, range 46-100%), to an average of 75% (range 11-100%) during day 14 of the marine migration (Figure 3). The variations in individual depth use were smallest at day 1. During the later days some individuals were recorded only in the upper five meters (eight individuals at day 3, five individuals at day 7, six individuals at day 14), while others had an extensive proportion of depth recordings at greater depths. Eleven, nine and sixteen individuals had more than 10% (range 10-81%) of the recordings at depths greater than 20m at day 3, day 7 and day 14, respectively (Appendix 1). One extreme individual had 48% of the recordings at day 14 at depths greater than 200m (Appendix 1, ID12263). Individuals showed diving behaviour to a varying extent, and a large individual variation in diving intensity was observed (Appendix 1). The proportion of salmon that performed dives increased from 45% during day 1, to 65% at day 3, 69% at day 7, and 77% at day 14. Similarly, the diving intensity increased with time at sea (Figure 4). The diving intensity was significantly larger at all the later days compared to day 1 (Day 3, $p = 0.001$. Day 7, $p = 0.003$. Day 14, $p < 0.001$). The largest number of dives recorded during a 24 h period was 35 dives at day 7 from a tag with 10 min recording interval (Appendix 1, ID6672).

The maximum diving depths increased with time after seawater entry (Figure 5). The deepest dive was recorded at 337m during day 14 in a tag with 30 min recording interval. Mean maximum depth at day 1, day 3, day 7 and day 14 was 14m (range 2.6-46m), 40m (range 1.9-182m), 48m (range 3.3 -142m) and 109m (range 2.3-337m), respectively. The maximum diving depths at day 1 were significantly different from all the other days (day 3, $p = 0.002$, day 7 and day 14, $p < 0.001$). The same applies to the maximum diving depths recorded at day 14, which was significantly different from the maximum diving depths at day 3 ($p = 0.006$) and day 7 (0.02) in addition to day 1. No significant difference was found between the maximum diving depths at day 3 and day 7 ($p = 0.50$).

The variation in diving intensity among individuals was smaller during day 1 than the variation during the other days (Figure 4). Similarly, the variation in the maximum depth recordings among individuals increased from day 1 to day 14 (Figure 5).

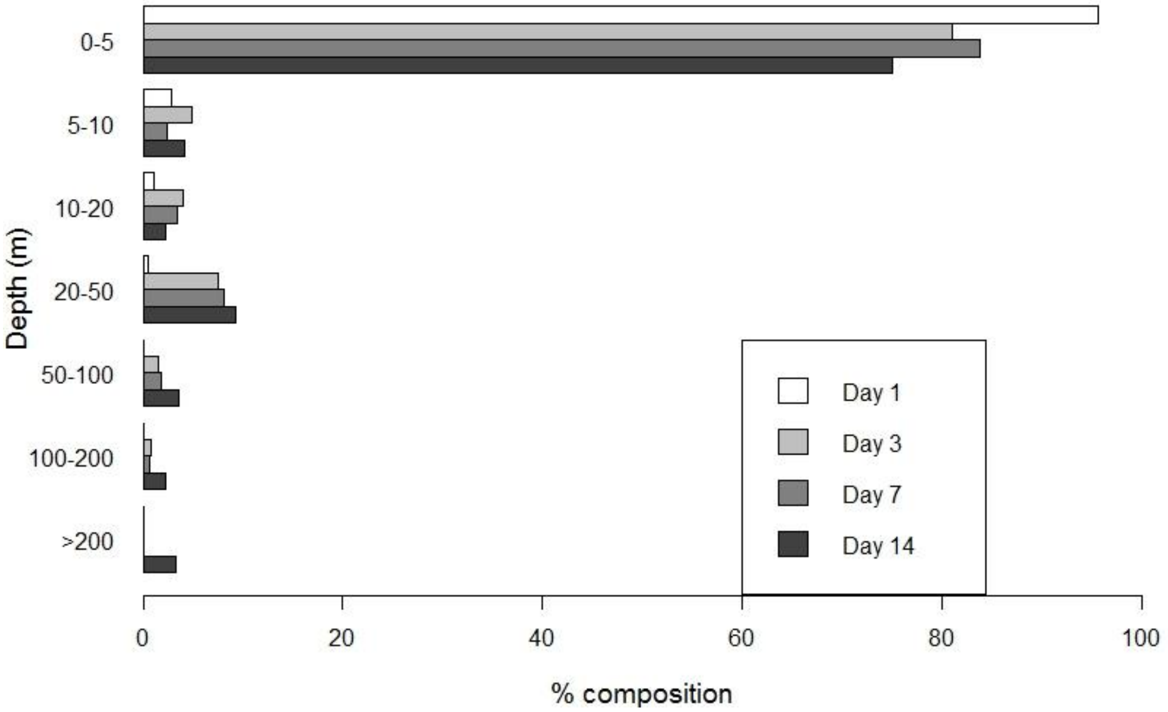


Figure 3. Percentage depth use for outward migrating salmon during day 1 (n = 29), day 3 (n = 26), day 7 (n = 26) and day 14 (n = 26) after seawater entry. The % composition is calculated as the mean percentage composition of depth recordings for all salmon.

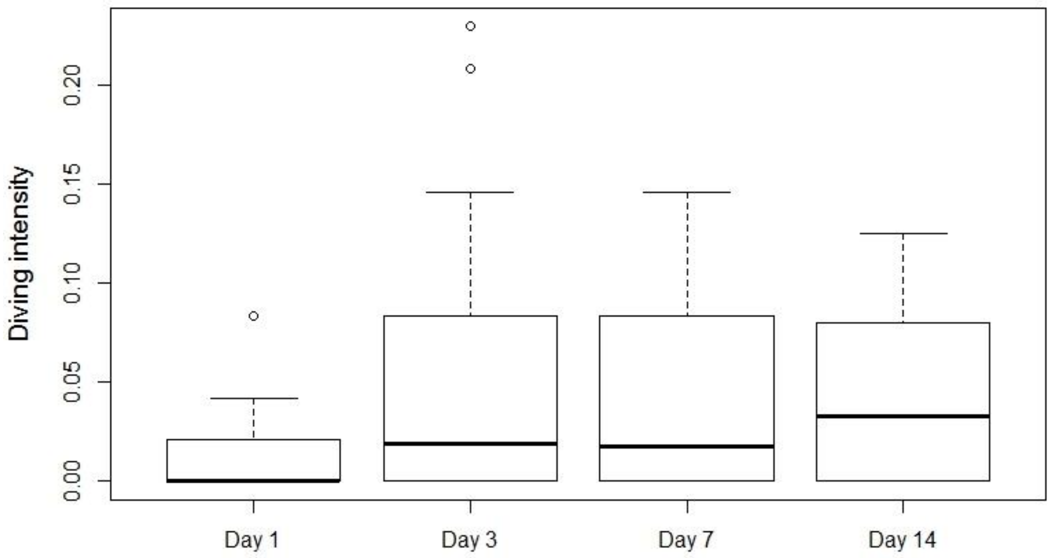


Figure 4. Diving intensity (number of dives divided by number of observations), for outward migrating salmon at different times after seawater entry. The black lines represent median values, the boxes show the interquartile ranges, and the whiskers show the 5th and 95th percentiles. Open circles indicate outliers.

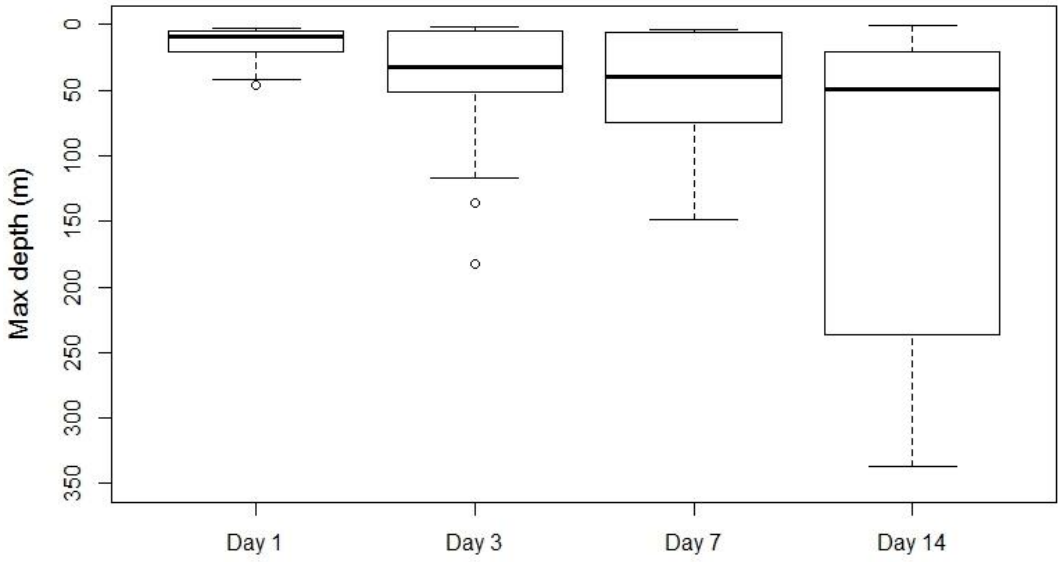


Figure 5. Maximum depth recorded for outward migrating salmon at different times after seawater entry. The black lines represent median values, the boxes show the interquartile ranges, and the whiskers show the 5th and 95th percentiles. Open circles indicate outliers.

3.3 Inward migration

The inward migrating salmon recaptured in the coastal zone had a smaller proportion of recordings in the upper 5 m during the last 24 h before recapture than salmon recaptured in the outer and inner fjord zones (Figure 6). The proportion of recordings in the upper five meters increased from an average of 50% (range 0-85%) in the coastal zone, to 88% (range 49-99%) and 91% (range 85-94%) in the outer and inner fjord zones. The salmon recaptured in the coastal zone had also spent a considerable part of their time, 29% of the recordings, at depths from five to ten meters, compared to only 7% in both the outer and inner fjord zone. In addition, five individuals in the coastal zone had more than 10% (range 10-27%) of the recordings at depths greater than 20m, whereas no individuals in the outer and inner fjord zones had such extensive proportions of depth recordings at depths greater than 20m. No individuals were recorded only in the upper five meters of the water column in any of the zones. As observed for the outward migrating salmon, there was individual variation in diving behaviour (Appendix 2). A difference was observed between the coastal zone and the outer and inner fjord zones, showing that the diving intensity generally was higher in the coastal zone (Figure 7). The overall proportion of salmon that performed dives decreased from 89% in the coastal zone, to 38% in the outer fjord zone and 66% in the inner fjord zone. The differences in diving intensity was only significant between the coastal zone and the outer fjord zone ($p = 0.01$).

The deepest dive was 97 m deep, recorded in the coastal zone by a 30 min interval tag. The mean maximum depths in the different zones were 43m in the coastal zone (range 7.6-97m), 20m in the outer fjord zone (range 7.2-90m) and 18m in the inner fjord zone (range 7.7-35m) (Figure 8). These maximum diving depths were not significantly different between any of the zones ($p > 0.05$). The highest number of dives observed in one individual salmon was 24, recorded in the coastal zone by a 5 min interval tag (Appendix 2, ID6688).

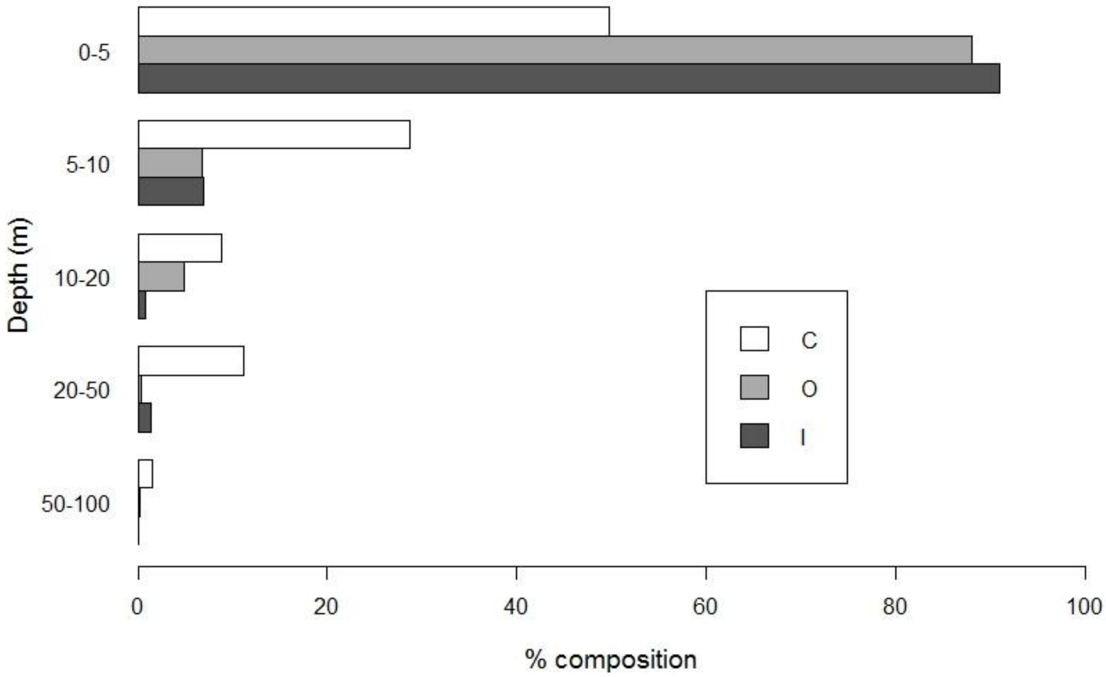


Figure 6. Percentage depth use in the 24 last hours before recapture for inward migrating salmon recaptured in the coastal zone (C) and the outer (O) and inner (I) fjord zones. The % composition is calculated as the mean percentage composition of depth recordings for all salmon.

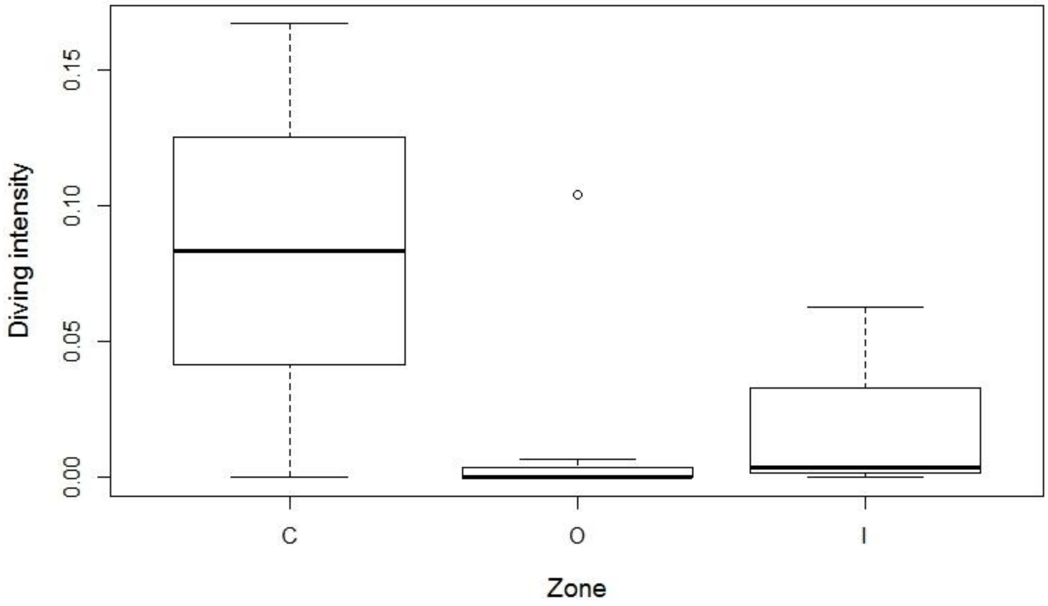


Figure 7. Diving intensity in the 24 last hours before recapture (given as number of dives divided by number of observations), for inward migrating salmon recaptured in the coastal zone (C) and outer (O) and inner (I) fjord zones. The black lines represent median values, the boxes show the interquartile ranges, and the whiskers show the 5th and 95th percentiles. Open circles indicate outliers.

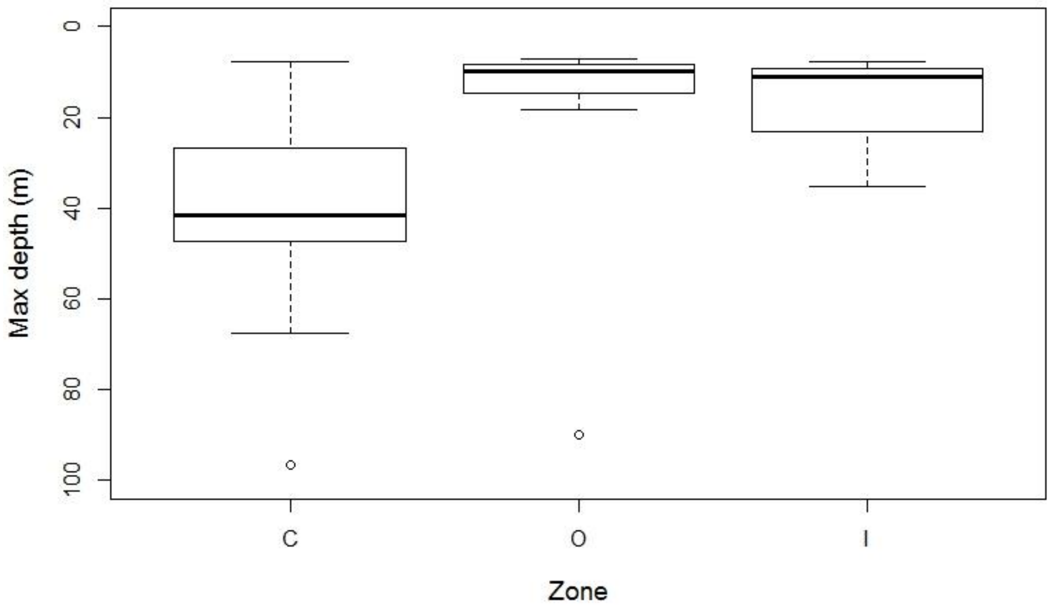


Figure 8. Maximum depth in the 24 last hours before recapture, recorded for salmon recaptured in the coastal zone (C) and outer (O) and inner (I) fjord zones. The black lines represent median values, the boxes show the interquartile ranges, and the whiskers show the 5th and 95th percentiles. Open circles indicate outliers.

3.4 Feeding

Out of 939 salmon analysed for stomach content, 553 (59%) had empty stomachs, while 386 (41%) had some stomach content. Out of the 386 salmon with stomach content, 126 salmon (14% of the total sample) had only small amounts of content (0.1-10% grade of filling) (Figure 9). Hence, only 260 salmon (28% of the total sample) had a larger stomach content than 10% grade of filling.

No traces of other food items than fish was identified in the stomach contents. A large part (mean 57%) of the fish in the salmon stomachs was so highly digested that it was not possible to identify at species level. The rest of the contents were dominated by herring (*Clupea harengus*) (mean 37%), while the last parts were identified as capelin (*Mallotus villosus*) (mean 4%) and sand eel (*Ammodytes sp.*) (mean 2%). In almost all individual stomachs, only one prey species was identified, and there were only six stomachs where two different prey species were identified. Most of the stomachs (81%) were given a digestion value 3 or 4 (3 =

52%, 4 = 29%), while 15% were given digestion value 1 or 2 (1 = 2%, 2 = 13%). Only 4% of the stomach contents were given a digestion value of 5 (Figure 11).

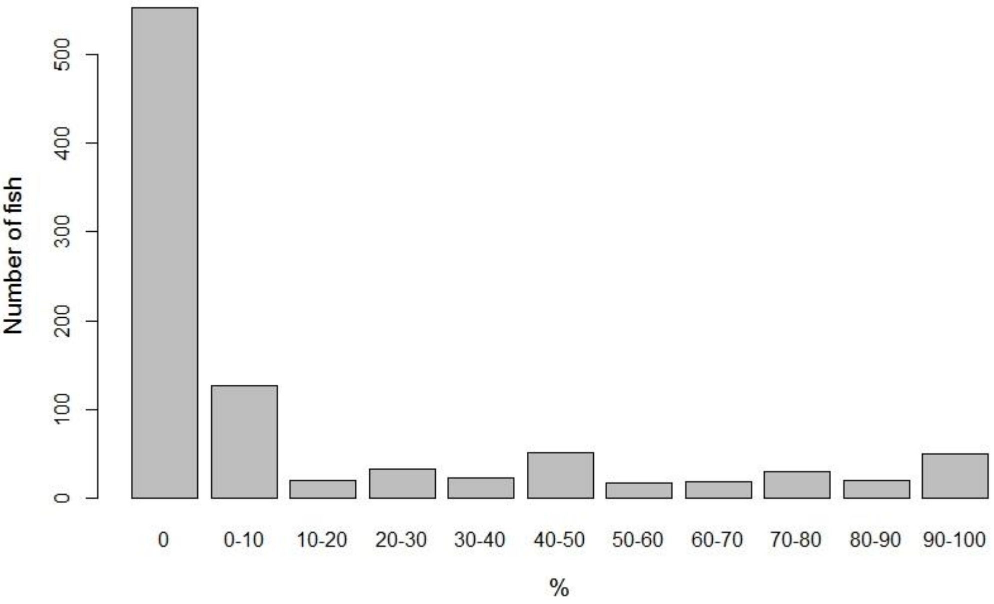


Figure 9. Number of fish with different percentages of stomach filling (n = 939). A percentage value of 0 represents a completely empty stomach, while a percentage value of 100 represents a completely filled stomach.

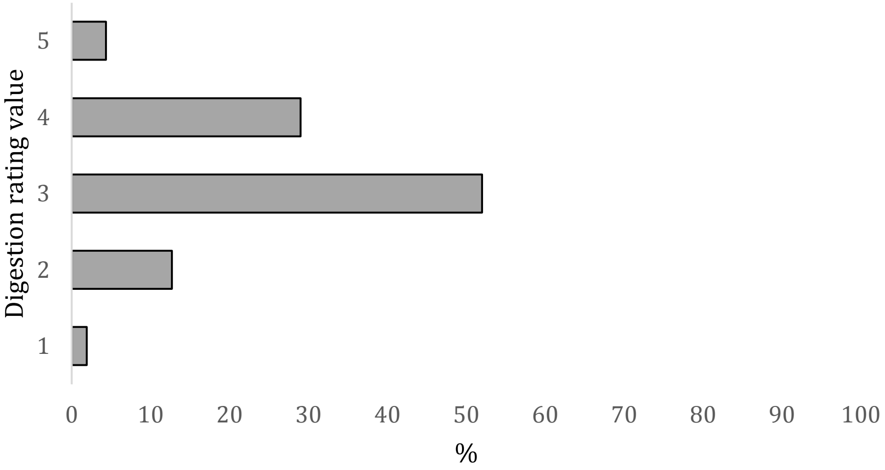


Figure 11. Percentage distribution of the digestion rate values given for stomachs sampled from returning Atlantic salmon. Only salmon with stomach content are included (n = 386). Digestion value 1 represents undigested content, while digestion value 5 represents almost completely digested content.

4 Discussion

This study focused on migration behaviour of Atlantic salmon in the fjord phase just after entering seawater as post-spawners, and during return migration. The results showed that the salmon spent more time in the upper five meters of the water column than at greater depths in inner parts of the marine system. This was the case for both the first and last phase of the marine migration. Dives were also shallower and less frequent in the inner parts of the marine system than compared to outer coastal areas. Both Hubley et al. (2008) and Halttunen et al. (2009) reported that the Atlantic salmon post-spawners spent more than 90% of the time at near-surface depths during outward migration. This was also found in the present study, where an average of 96 % of the recordings were in the upper five meters of the water column during the first 24 h after seawater entry. In salmon studied during outward migration in an estuary in Canada, only four single dives were detected (Hubley et al. 2008), while in the Alta fjord individual dives up to 83 m depth was reported in the outer parts of the fjord (Halttunen et al. 2009). The diving behaviour during the first 24 h in this study varied among individuals. Whereas 55% of the salmon did not perform any dives, defined as recordings passing a depth of 10m, one individual performed 31 dives during the initial 24 h. This salmon was applied with a geolocation tag recording depth every 30sec, and when data from this tag was filtered to 30 min intervals, 30 of the 31 dives were lost (own unpublished result). This result therefore shows the importance of fine-scale data when conducting depth studies. It also indicates that some of the individuals in this study could have performed more dives than those recorded by the tags, given the different recording intervals. The few dives observed by Hubley et al. (2008) were not particularly deep (up to 15 m), but reported to be approaching the depths at receiver locations, and thus the salmon were expected to have been diving to or near the bottom. Some of the individuals in the present study performed dives down to maximum 46m during the first day after seawater entry. However, the Alta fjord is relatively deep, meaning that unless the salmon strayed in the estuary for a significant time period, or migrated very close to the shoreline, it is not likely that the observed dives were to or near the bottom.

Proportions of recordings in the upper five meters during outward migration decreased from the first day after seawater entry to the third, seventh and fourteenth day of the marine migration. Depth use varied more among individuals during day three, seven and fourteen than during the first day after seawater entry, when the majority of individuals had more than 90% of the recordings in the upper five meters. The most extreme individual had only 11% of the recordings in the upper five meters during the fourteenth day. At the same time, there were individuals that had 100% of the recordings in the upper five meters at all days. These individual differences corresponds to the findings in homing Atlantic salmon by Godfrey et al. (2015), who found considerable variation among individuals. Diving intensity and the proportion of individuals performing dives also increased significantly from the first day after seawater entry to later in the migration. This could be expected, as other studies have found diving behaviour to increase as the salmon leave the estuary and fjord system and encounter open waters (Reddin et al. 2011).

During inward migration, the depth use in the coastal zone differed considerably from that in the outer and inner fjord zones. In the latter two, the salmon spent much more time in the upper five meters. Also the diving frequency was higher in the coastal zone. Reddin et al. (2011) reported the diving behaviour to decrease as the salmon returned to the estuary and river during their homing migration. Homing salmon in the Alta fjord were also found to swim closer to the surface as they approached the estuary (Davidsen et al. 2013), and thus, the present results concur with these findings. However, some individuals were observed to perform dives to various depths only hours prior to river entry. Godfrey et al. (2015) suggested two different depth patterns for homing salmon, one group being more surface-oriented and one inhabiting deeper waters. This did not seem be the case for the inward migrating salmon in this study. Although individual variation in diving behaviour was observed, the individual proportions of recordings at different depth intervals did not vary as much as seen during the outward migration, suggesting a more standardized behaviour during the homing migration. Individuals recaptured in both the coastal zone and in the outer and inner fjord zones performed dives to some extent. The highest diving intensity was seen in the coastal zone, where the salmon also were found to spend an extensive proportion of their time at 5-10 m.

Hypotheses that can explain diving behaviour are feeding, search for olfaction cues, control of body temperature and predator avoidance (Wada and Ueno 1999, Reddin et al. 2004). The stomach samples analysed in this thesis showed that a large proportion (59%) of salmon had completely empty stomachs when captured in the outer and inner parts of the Alta fjord. In addition, a large proportion of the salmon with stomach content had only small fragments of stomach content, and/or the stomach contents were highly digested, suggesting that some time had gone by since the last intake of food items. This means that other possible explanations for the observed diving behaviour than feeding must be taken into account for the homing salmon. Due to the poor condition of most post-spawned salmon (Jonsson et al. 1997) and results from studies of Atlantic salmon post-smolts (Hvidsten et al. 2009, Rikardsen and Dempson 2011) it is likely that the outward migrating post-spawners will start feeding as soon as possible after entering seawater, to regain their condition. Thus, the frequent dives observed in some individuals shortly after seawater entry, may be related to prey search and feeding. No stomach samples were collected from the initial marine phase in this study, and to my knowledge, no studies have been focusing on feeding behaviour of post-spawned Atlantic salmon during the first days of the marine migration.

Analyses of stomach contents showed that all feeding salmon had fed exclusively on different fish species, i.e. no traces were found of other food items like crustaceans, squids and amphipods. Pre-adult salmon in the open oceans of the Northwest Atlantic have been found to feed heavily on marine fish species and to some extent crustaceans (Lear 1972, Neilson and Gillis 1979), while in the Northeast Atlantic pelagic crustaceans have been found to be more important than in the Northwest Atlantic studies (e.g. Hansen and Pethon 1985). Newer studies using other methods like stable isotope analyses, corroborate these earlier findings, suggesting differences in marine feeding across populations and life stages (Dempson et al. 2010, Dixon et al. 2012). Atlantic salmon post-smolt are known as opportunistic feeders (Rikardsen et al. 2004), and the above-mentioned studies from the Northwest and Northeast Atlantic suggest that the opportunistic feeding behaviour continues throughout different life stages at sea. However, as stated by Rikardsen and Dempson (2011), many of the studies on feeding were conducted several decades ago, and may not reflect the current situation. Nevertheless, MacKenzie et al. (2012) concluded that salmon from UK rivers fed opportunistic as adults at sea, but showed a larger specialization towards higher trophic levels as they grew larger. The stomach samples analysed in the present study were taken from salmon captured in the fjord, assumingly just prior to river entry. The results are new compared to previous studies, and although there may be geographical differences, they suggest that a large share of the salmon does not feed at all during the final part of the homing migration, whereas the ones that did seemed to be highly specialized. In only six of the feeding individuals, more than one fish species were identified in the stomach, corresponding to findings by Hansen and Pethon (1985), who also found that most salmon had eaten only one species. This indicates that even though the Atlantic salmon can feed on a variety of prey items, individuals may specialize to some extent in their consumption of prey.

It is known that olfaction cues are important in migration for the Atlantic salmon (Hasler 1966), and especially during homing migration back to the natal river (Døving et al. 1985). As stated by Hansen et al. (1993), the homing migration seems to be divided in two parts, the first part with navigation from feeding areas towards the coast, and a second, more precise navigation towards the river. The results from the homing salmon in this study showed a tendency that the salmon dived more frequently and deeper into the water column in the coastal zone than in the fjord. This may correspond to the two phases of homing migration, and the deeper and more frequent dives observed in the coastal zone may be related to scanning of the water column for olfaction cues. The salmon spent more time close to the surface in the outer and inner fjord zones as they approached the river, than in the coastal zone. Similar findings have previously been related to the brackish water layer in the upper part of the water column, as the salmon could be expected to use this to locate and recognize the river (Quinn 1990, Davidsen et al. 2013). A few dives were also observed in the outer and inner fjord zones, and according to previous studies (Westerberg 1982, Døving et al. 1985) these could also be related to search for olfaction cues. Thus, much of the behaviour of the inward migrating salmon, both diving and the great use of the upper five meters, could be a result of navigation towards the river. Search for olfaction cues during the outward migration has been less discussed than for homing migration, and it is difficult to know the importance of these cues in navigation towards the open ocean. Nevertheless, Halttunen et al. (2009) observed a higher frequency of dives as kelts progressed further out the fjord, and concluded that this could be related to orientation.

Due to the large size of the salmon used in the study, predator avoidance is not likely to have been the reason for the observed dives, neither during outward nor inward migration. The fish would have been too large for predation by seabirds and other marine fish species. Although seals are known to feed on Atlantic salmon (Hammill and Stenson 2000, Carter et al. 2001), it is not expected that the abundance of seals in the Alta fjord was great enough during the study period to have caused the observed diving behaviour.

As the temperature recordings from the tags were not analysed for this thesis, it is difficult to know if diving could be related to control of body temperature. Wada and Ueno (1999) found that chum salmon often performed dives when water temperatures were higher. However, they often stayed in warmer water at night, suggesting that this hypothesis for diving behaviour may not be the most plausible one for the observed behaviour in this study. Overall, the diving behaviour observed in both outward migrating and inward migrating salmon in this study, is most likely to be caused by a combination of the described factors, or together with other unknown factors.

The high degree of surface-orientation seen in the post-spawned salmon resemble that of post-smolts during the initial phase of their marine migration (Reddin et al. 2006, Davidsen et al. 2008). However, the post-spawners had a higher frequency of dives, and to much greater depths than the post-smolts. Post-smolts have been found to spend most time at 1-3m depth with occasional dives down to 6.5m (Davidsen et al. 2008). The initial marine phase of post-smolts is known as a critical phase and a possible biological bottleneck (Thorstad et al. 2012). Davidsen et al. (2008) interpreted their results on depth use as a possible trade-off between avoidance of avian and marine predators (attacking from above and below, respectively), in combination with navigation, prey search and avoidance of osmoregulatory problems. The differences observed between post-spawners and post-smolts may likely be linked to differences in predation pressure. The physiological stress experienced by post-smolts in relation to salt water tolerance could possibly be greater than that experienced by the much larger post-spawners. This could lead to the post-smolts choosing more surface-near swimming depths if brackish water layers are present. However, no such acclimation period have been identified (Moore et al. 1998), and smolts also seem to adapt to salt water while still in freshwater (Hoar 1988).

Commercial fisheries for returning salmon in the Alta fjord are mainly conducted with bag nets and bend nets in may-august (Halttunen et al. 2009), resulting in risk of being captured for both outward migrating post-spawners and salmon returning to the river. The nets are placed close to the surface, and the salmons’ swimming depths are therefore an important factor for the possibility of being caught. Both outward and inward migrating salmon in this study were surface oriented. This indicates that the salmon are in danger of being caught in the surface-near bag nets, and indeed, 36 of 41 recaptured salmon in this study were caught in bag nets or bend nets in the sea. However, this is a small share of the total number of tagged fish (630). The tagged fish that were not recaptured could be expected to have died during outward migration or during the open ocean phase. A number of fish would also be expected to have survived and returned to the river as multiple spawners, as the proportion of repeat spawners that survive and return from the sea have been found to be high for Atlantic salmon from the river Alta (39% of females, 19% of males, Halttunen 2011). Studies in Alta of both outward and inward migrating Atlantic salmon tagged with acoustic transmitters have reported the proportion of tagged fish caught in fisheries to be surprisingly small, considering the overlapping of the migration and the fishing season (Halttunen et al. 2009, Davidsen et al. 2013). The proportion of salmon caught in the study of homing salmon (Davidsen et al. 2013), were larger (6.8%) than the proportion of salmon caught in the study of outward migrating post spawners (1%, Halttunen et al. 2009) The total reported recapture rate in the present study was 6.5%, corresponding to the findings by Davidsen et al. (2013). However, this has to be considered a minimum, as tags could have been lost, or recaptures not reported.

The tagging methods used in this study are much used and well-studied (Cooke et al. 2011). Surgical implantation of tags have advantages compared to external attachment, as it does not affect the streamlined shape of the fish (Thorstad et al. 2013) or affect swimming performance in the way that externally attached tags may do (Thorstad et al. 2001). In addition, external attachment of tags can increase the risk of being caught in nets (Rikardsen and Thorstad 2006). Disadvantages with surgical implantation are among others the risks of tag expulsion and/or infections (Thorstad et al. 2013). However, the surgery was performed by experienced taggers to ensure the best possible procedure. Non-absorbable sutures were chosen to secure sufficient healing of the wounds. In addition, several of the tagged fish took the bait a second time after going through handling and surgery, and visual observations of the wounds showed no signs of infection or other problems (own unpublished results). In every tagging study, there is a risk of altered behaviour due to handling and tagging (Bridger and Booth 2003). The salmon in this study were captured and tagged in the river, and all salmon stayed a considerable time in the river (minimum 3 weeks) before entering seawater. During these weeks, we would expect the fish to have recovered from capture and handling and adjusted to the tag. Thus, the behaviour recorded by the tags during outward migration is assumed natural and not largely altered by the tag.

In conclusion, the results show that there was large variation in depth use among individuals. In general, the Atlantic salmon were observed to be highly surface-oriented. There were similarities between outward and inward migration, with a gradual change in depth use between coastal areas and fjord areas. Many individuals performed frequent and deep dives, both close to the river and further out in the marine system. This behaviour may be related to a combination of factors, like navigation, predator avoidance, control of body temperature, prey search or other unknown factors. Results from the stomach analyses suggest that a large proportion of the Atlantic salmon did not feed during the last phase of the homing migration, indicating that other factors may be the reason for the observed diving behaviour. Although the Atlantic salmon is among the most studied fish species in the world, knowledge is still lacking, especially about marine migrations and about multiple spawners. The electronic tags now available may provide more detailed information on migratory behaviour, as demonstrated by the high-resolution tags used in this study. In combination with detailed feeding studies of both post-spawners in the initial marine phase and returning salmon, this may be essential information for management considering the continuous population declines observed over the last decades.

5 References

Anon. 2007. Om vern av villaksen og ferdigstilling av nasjonale laksevassdrag og laksefjorder St.prp. nr. 32: 1-143. Det kongelige miljøverndepartement.

Bridger, C. J., and R. K. Booth. 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Reviews in Fisheries Science 11:13–34.

Carter, T. J., G. J. Pierce, J. R. G. Hislop, J. A. Houseman, and P. R. Boyle. 2001. Predation by seals on salmonids in two Scottish estuaries. Fisheries Management and Ecology 8:207–225.

Chittenden, C. M., A. H. Rikardsen, O. T. Skilbrei, J. G. Davidsen, E. Halttunen, J. Skardhamar, and R. S. McKinley. 2011. An effective method for the recapture of escaped farmed salmon. Aquaculture Environment Interactions 1:215–224.

Cooke, S. J., C. M. Woodley, M. B. Eppard, R. S. Brown, and J. L. Nielsen. 2011. Advancing the surgical implantation of electronic tags in fish: A gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. Reviews in Fish Biology and Fisheries 21:127–151.

Crespi, B. J., and R. Teo. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. Evolution 56:1008–1020.

Dadswell, M. J., A. D. Spares, J. M. Reader, and M. J. W. Stokesbury. 2010. The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the “Merry-Go-Round” hypothesis. Journal of fish biology 77:435–467.

Davidsen, J. G., N. Plantalech Manel-la, F. Økland, O. H. Diserud, E. B. Thorstad, B. Finstad, R. Sivertsgård, R. S. McKinley, and a. H. Rikardsen. 2008. Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. Journal of Fish Biology 73:1065–1074.

Davidsen, J. G., A. H. Rikardsen, E. B. Thorstad, E. Halttunen, H. Mitamura, K. Præbel, J. Skarðhamar, and T. F. Næsje. 2013. Homing behaviour of Atlantic salmon (*Salmo salar*) during final phase of marine migration and river entry. Canadian Journal of Fisheries and Aquatic Sciences 802:794–802.

Dempson, J. B., V. A. Braithwaite, D. Doherty, and M. Power. 2010. Stable isotope analysis of marine feeding signatures of Atlantic salmon in the North Atlantic. ICES Journal of Marine Science 67:52–61.

Dixon, H. J., M. Power, J. B. Dempson, T. F. Sheehan, and G. Chaput. 2012. Characterizing the trophic position and shift in Atlantic salmon (*Salmo salar*) from freshwater to marine life-cycle phases using stable isotopes. ICES Journal of Marine Science 69:1646–1655.

Døving, K. B., H. Westerberg, and J. P. B. 1985. Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. Canadian Journal of Fisheries and Aquatic Sciences 42:1658–1667.

Godfrey, J. D., D. C. Stewart, S. J. Middlemas, and J. D. Armstrong. 2015. Depth use and migratory behaviour of homing Atlantic salmon (*Salmo salar*) in Scottish coastal waters. ICES Journal of Marine Science 72:568–575.

Halttunen, E. 2011. Staying Alive - The survival and importance of Atlantic salmon post-spawners. Ph.D. thesis. University of Tromsø, Tromsø Norway.

Halttunen, E., A. H. Rikardsen, J. G. Davidsen, E. B. Thorstad, and J. B. Dempson. 2009. Survival, migration speed and swimming depth of Atlantic salmon kelts during sea entry and fjord migration. Pages 35–49 *in* J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, and J. Sibert, editors. Tagging and Tracking of Marine Animals with Electronic Devices, Reviews: Methods and Technologies in Fish Biology and Fisheries 9. Springer Netherlands, Dordrecht.

Hammill, M. O., and G. B. Stenson. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fishery Science 26:1–23.

Hansen, L. P., N. Jonsson, and B. Jonsson. 1993. Oceanic migration in homing Atlantic salmon. Animal Behaviour 45:927–941.

Hansen, L. P., and P. Pethon. 1985. The food of Atlantic salmon, *Salmo salar* L., caught by long-line in northern Norwegian waters. Journal of Fish Biology 26:553–562.

Hasler, A. D. 1966. Underwater guideposts: Homing of salmon. Madison, WI: University of Wisconsin Press.

Hedger, R., D. Hatin, J. Dodson, F. Martin, D. Fournier, F. Caron, and F. Whoriskey. 2009. Migration and swimming depth of Atlantic salmon kelts *Salmo salar* in coastal zone and marine habitats. Marine Ecology Progress Series 392:179–192.

Hoar, W. S. 1988. The physiology of smolting salmonids. Pages 275–343 *in* W. S. Hoar and D. J. Randall, editors. Fish Physiology, Vol. XIB. New York: Academic Press.

Hubley, P. B., P. G. Amiro, A. J. F. Gibson, G. L. Lacroix, and A. M. Redden. 2008. Survival and behaviour of migrating Atlantic salmon (*Salmo salar* L.) kelts in river, estuarine, and coastal habitat. ICES Journal of Marine Science 65:1626–1634.

Hvidsten, N. A., A. J. Jensen, A. H. Rikardsen, B. Finstad, J. Aure, S. Stefansson, P. Fiske, and B. O. Johnsen. 2009. Influence of sea temperature and initial marine feeding on survival of Atlantic salmon *Salmo salar* post-smolts from the Rivers Orkla and Hals, Norway. Journal of Fish Biology 74:1532–48.

ICES. 2014. Report of the Working Group on North Atlantic Salmon (WGNAS).ICES CM 2014/ACOM:09. International Council for the Exploration of the Sea, Copenhagen, Denmark.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. Journal of Animal Ecology 66:425–436.

Klemetsen, A., P.-A. Amundsen, J. Dempson, B. Jonsson, N. Jonsson, M. O'Connel, and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L ., brown trout *Salmo trutta* L . and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12:1–59.

Lear, W. H. 1972. Food and feeding of Atlantic salmon in coastal waters and over oceanic depths. International Comission for the Northwest Atlantic Fisheries Research Bulletin 9:27–39.

Levings, C. D., N. A. Hvidsten, and B. O. Johnsen. 1994. Feeding of Atlantic salmon (*Salmo salar* L.) postsmolts in a fjord in central Norway. Canadian Journal of Zoology 72:834–839.

MacKenzie, K. M., C. N. Trueman, M. R. Palmer, A. Moore, A. T. Ibbotson, W. R. C. Beaumont, and I. C. Davidson. 2012. Stable isotopes reveal age-dependent trophic level and spatial segregation during adult marine feeding in populations of salmon. ICES Journal of Marine Science 69:1637–1645.

Moore, A., S. Ives, T. A. Mead, and L. Talks. 1998. The migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts in the River Test and Southampton Water, southern England. Hydrobiologia 371/372:295–304.

Neilson, J. D., and D. J. Gillis. 1979. A note on the stomach contents of adult Atlantic salmon (*Salmo salar*, Linnaeus) from Port Burwell , Northwest Territories. Canadian Journal of Fisheries and Aquatic Sciences 57:1502–1503.

Niemelä, E., J. Erkinaro, M. Julkunen, E. Hassinen, M. Länsman, and S. Brørs. 2006. Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. Journal of Fish Biology 68:1222–1240.

Ovidio, M., and J.-C. Philippart. 2002. The impact of small physical obstacles on upstream movements of six species of fish. Hydrobiologia 483:55–69.

Quinn, T. P. 1990. Current controversies in the study of salmon homing. Ethology Ecology and Evolution 2:49–63.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reddin, D. G., P. Downton, I. A. Fleming, L. P. Hansen, and A. Mahon. 2011. Behavioural ecology at sea of Atlantic salmon (*Salmo salar* L.) kelts from a Newfoundland (Canada) river. Fisheries Oceanography 20:174–191.

Reddin, D. G., P. Downton, and K. D. Friedland. 2006. Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (*Salmo salar* L.) during their early marine life. Fishery Bulletin 3:415–427.

Reddin, D. G., K. D. Friedland, P. Downton, J. B. Dempson, and C. C. Mullins. 2004. Thermal habitat experienced by Atlantic salmon (*Salmo salar* L.) kelts in coastal Newfoundland waters. Fisheries Oceanography 13:24–35.

Rikardsen, A. H., and J. B. Dempson. 2011. Dietary life-support: The food and feeding of Atlantic salmon at sea. Pages 115–143 *in* Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal, editors. Atlantic Salmon Ecology. First Edit. Blackwell Publishing Ltd.

Rikardsen, A. H., O. H. Diserud, J. M. Elliott, J. B. Dempson, J. Sturlaugsson, and A. J. Jensen. 2007. The marine temperature and depth preferences of Arctic charr (*Salvelinus alpinus*) and sea trout (*Salmo trutta*), as recorded by data storage tags. Fisheries Oceanography 16:436–447.

Rikardsen, A. H., L. P. Hansen, A. J. Jensen, T. Vollen, and B. Finstad. 2008. Do Norwegian Atlantic salmon feed in the northern Barents Sea? Tag recoveries from 70 to 78° N. Journal of Fish Biology 72:1792–1798.

Rikardsen, A. H., M. Haugland, P. A. Bjørn, B. Finstad, R. Knudsen, J. B. Dempson, J. C. Holst, N. A. Hvidsten, and M. Holm. 2004. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. Journal of Fish Biology 64:1655–1679.

Rikardsen, A. H., and E. B. Thorstad. 2006. External attachment of data storage tags increases probability of being recaptured in nets compared to internal tagging. Journal of Fish Biology 68:963–968.

Thorstad, E. B., A. H. Rikardsen, A. Alp, and F. Økland. 2013. The use of electronic tags in fish research – an overview of fish telemetry methods. Turkish Journal of Fisheries and Aquatic Sciences 13:881–896.

Thorstad, E. B., F. Whoriskey, A. H. Rikardsen, and K. Aarestrup. 2011. Aquatic nomads: The life and migrations of the Atlantic salmon. Pages 1–32 *in* Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal, editors. Atlantic Salmon Ecology. First Edit. Blackwell Publishing Ltd.

Thorstad, E. B., F. Whoriskey, I. Uglem, A. Moore, A. H. Rikardsen, and B. Finstad. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. Journal of Fish Biology 81:500–542.

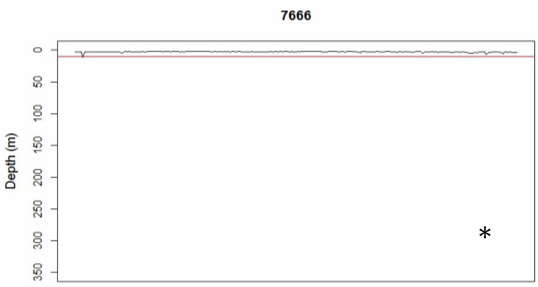
Thorstad, E. B., F. Økland, and T. G. Heggberget. 2001. Are long term negative effects from external tags underestimated? Fouling of an externally attached telemetry transmitter. Journal of Fish Biology 59:1092–1094.

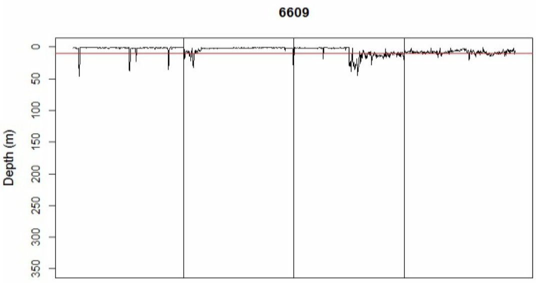
Ugedal, O., T. F. Næsje, E. B. Thorstad, T. Forseth, L. M. Saksgård, and T. G. Heggberget. 2008. Twenty years of hydropower regulation in the River Alta: long-term changes in abundance of juvenile and adult Atlantic salmon. Hydrobiologia 609:9–23.

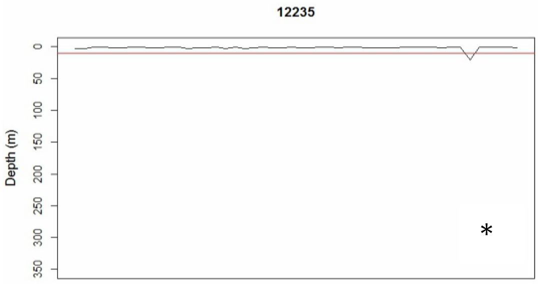
Wada, K., and Y. Ueno. 1999. Homing behavior of chum salmon determined by an archival tag. North Pacific Anadromous Fish Comission Doc. 425:29pp.

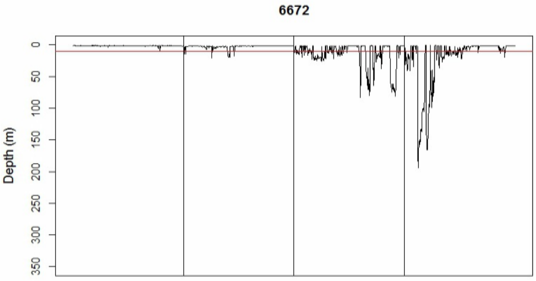
Westerberg, H. 1982. Ultrasonic tracking of Atlantic salmon (*Salmo salar*) - II. Swimming depth and temperature stratification. Report of the Institute of Freshwater Research Drottningholm 60:102–120.

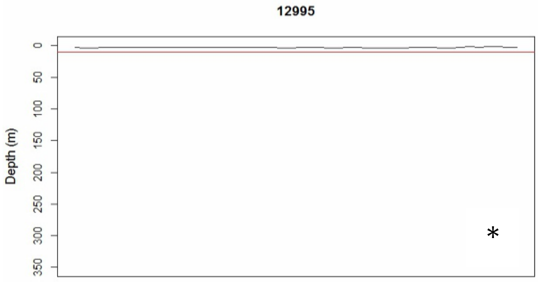
6 Appendix

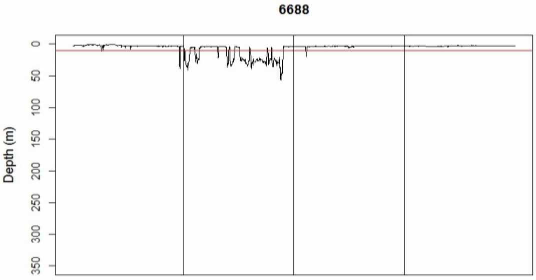

7666
Depth (m)
0
50
100
150
200
250
300
350
*

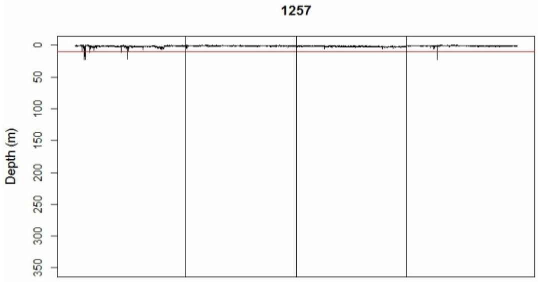

6609
Depth (m)
0
50
100
150
200
250
300
350

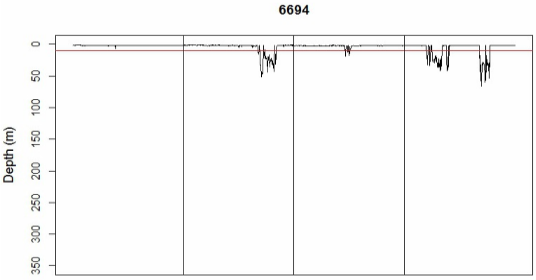

12235
Depth (m)
0
50
100
150
200
250
300
350
*

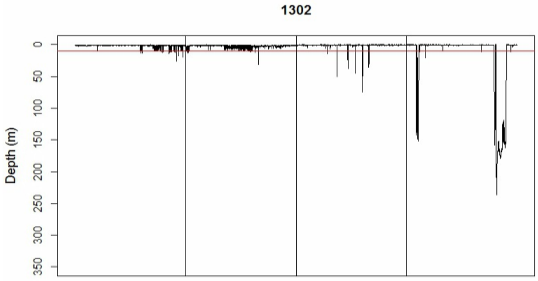

6672
Depth (m)
0
50
100
150
200
250
300
350

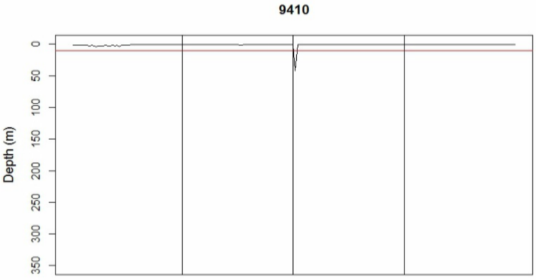

12995
Depth (m)
0
50
100
150
200
250
300
350
*

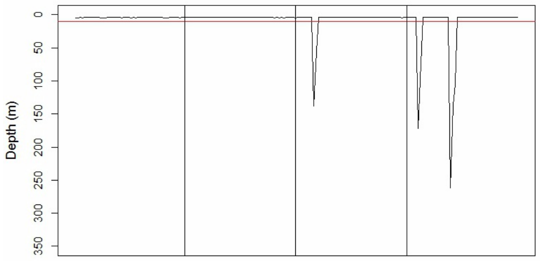

6688
Depth (m)
0
50
100
150
200
250
300
350


1257
Depth (m)
0
50
100
150
200
250
300
350

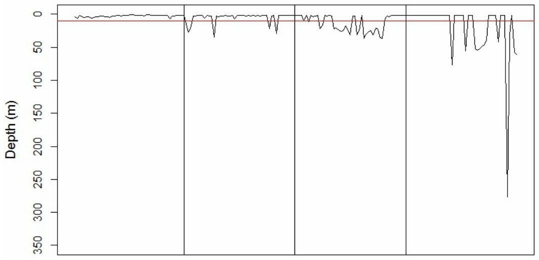

6694
Depth (m)
0
50
100
150
200
250
300
350


1302
Depth (m)
0
50
100
150
200
250
300
350

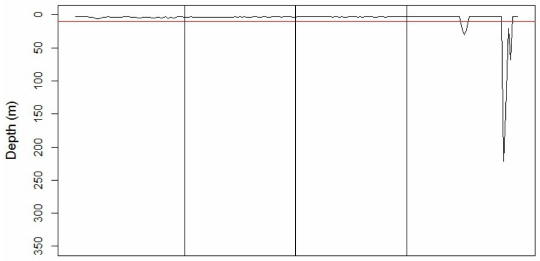

9410
Depth (m)
0
50
100
150
200
250
300
350



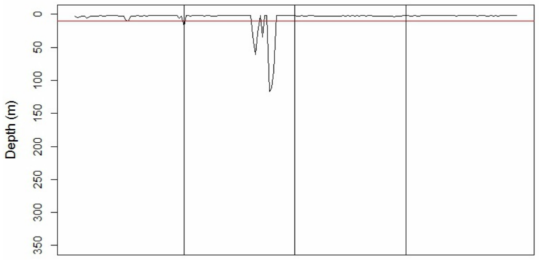
9415



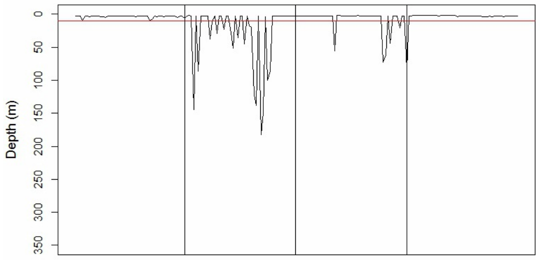
12100



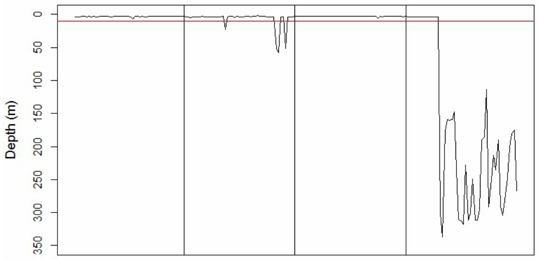
9424



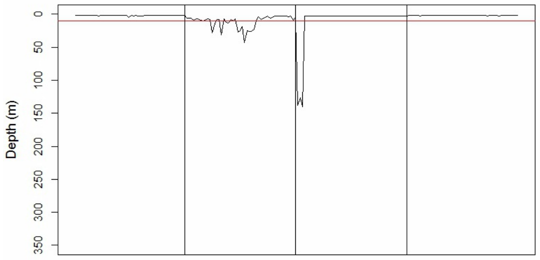
12243



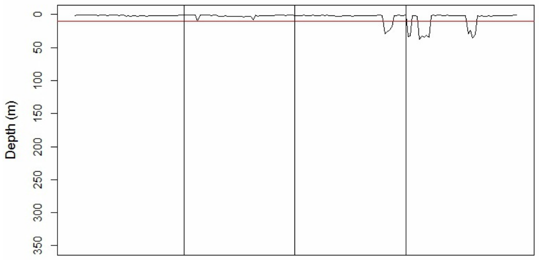
9431



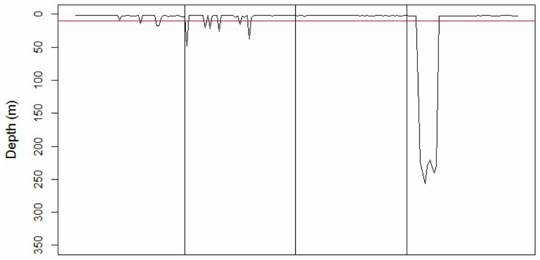
12263



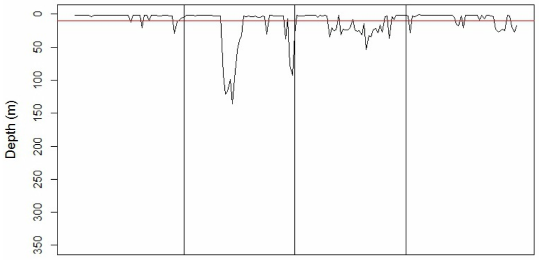
9440



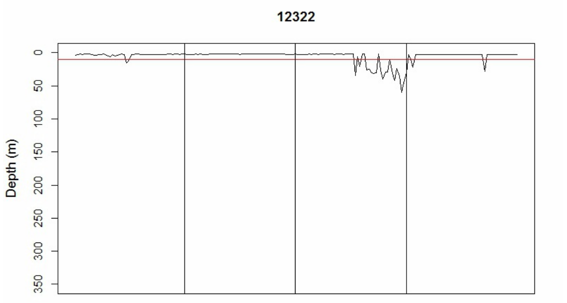
12276

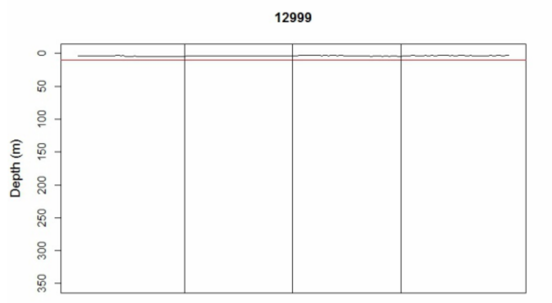


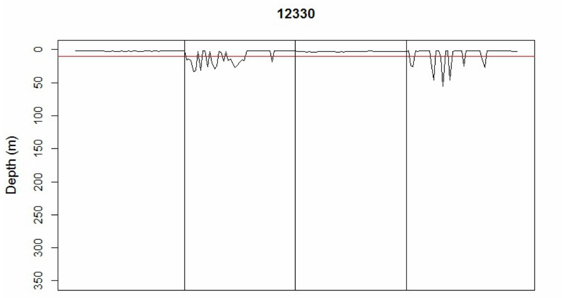
9441

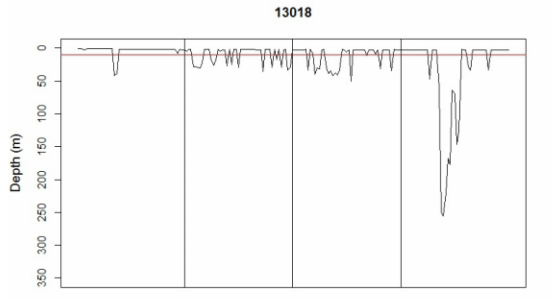


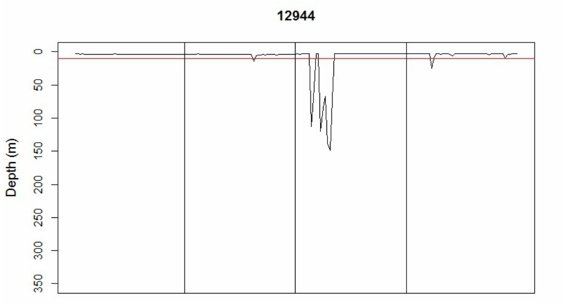
12286

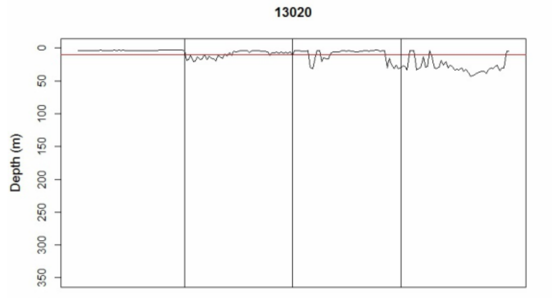


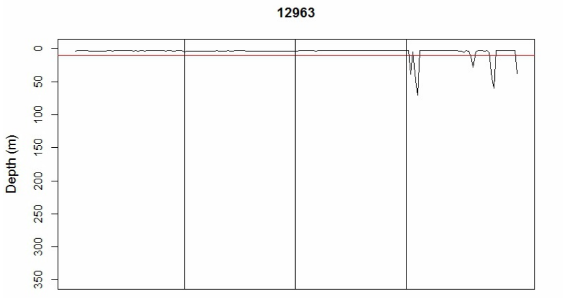


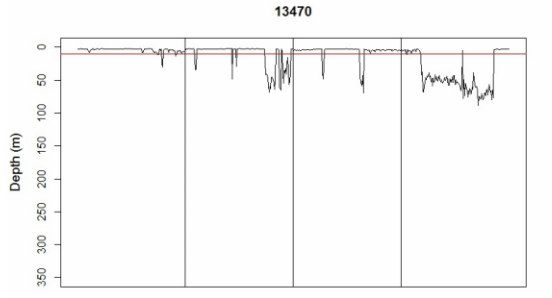


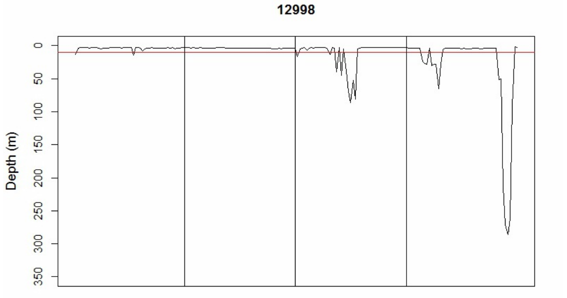




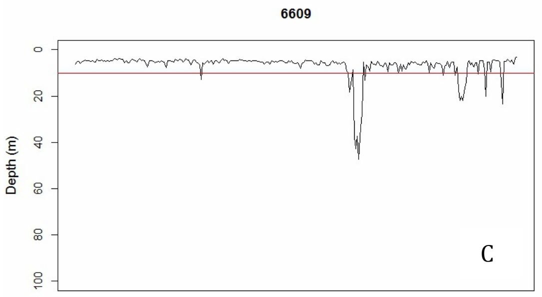


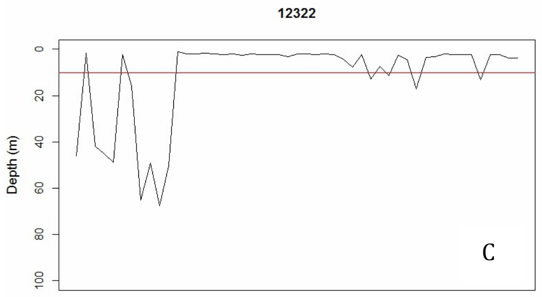


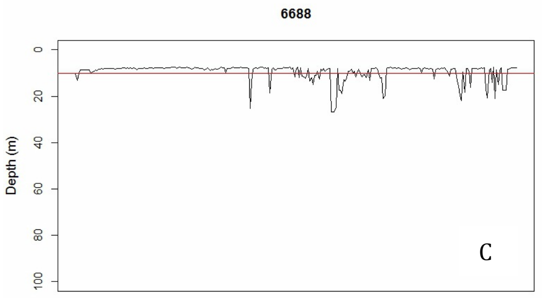


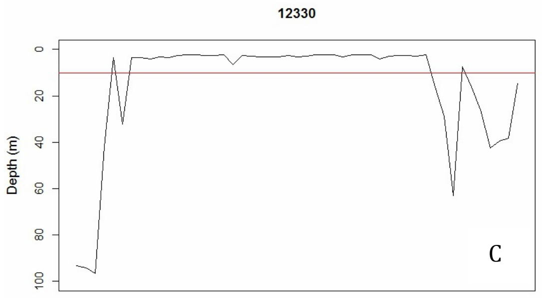


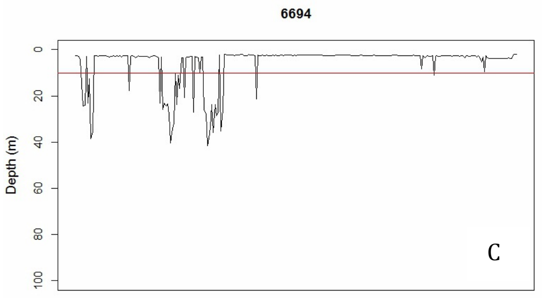
Appendix 1. Individual depth use of post-spawned Atlantic salmon at day 1, day 3, day 7 and day 14 after seawater entry (n = 29). The different days are separated by vertical lines. A red line is drawn at depth = 10m, and passing this depth is defined as a dive. Individual fish marked with * were recaptured as kelts, and these depth graphs therefore include only the initial 24h after seawater entry.

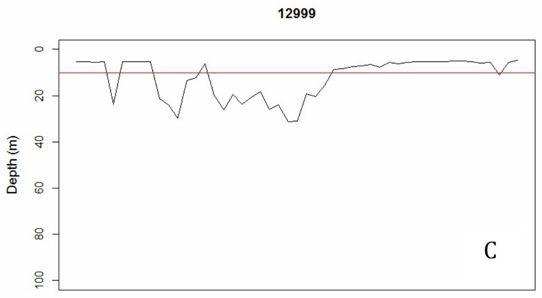

6609
Depth (m)
0
20
40
60
80
100
C

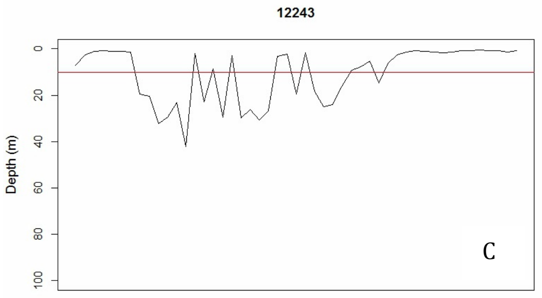

12322
Depth (m)
0
20
40
60
80
100
C

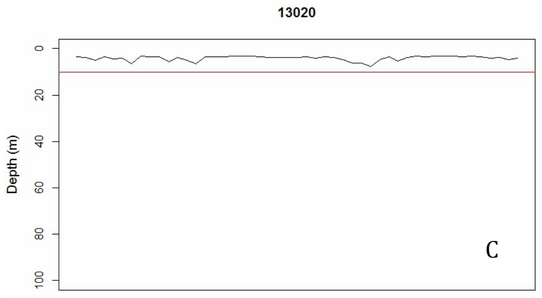

6688
Depth (m)
0
20
40
60
80
100
C

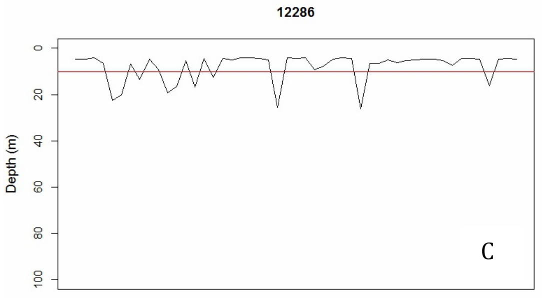

12330
Depth (m)
0
20
40
60
80
100
C

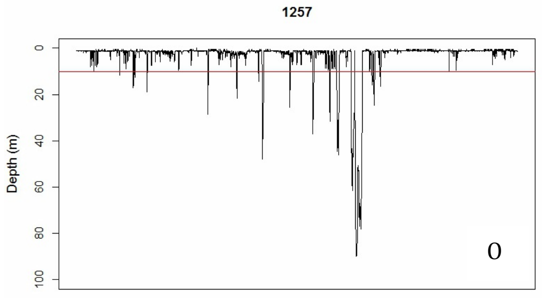

6694
Depth (m)
0
20
40
60
80
100
C

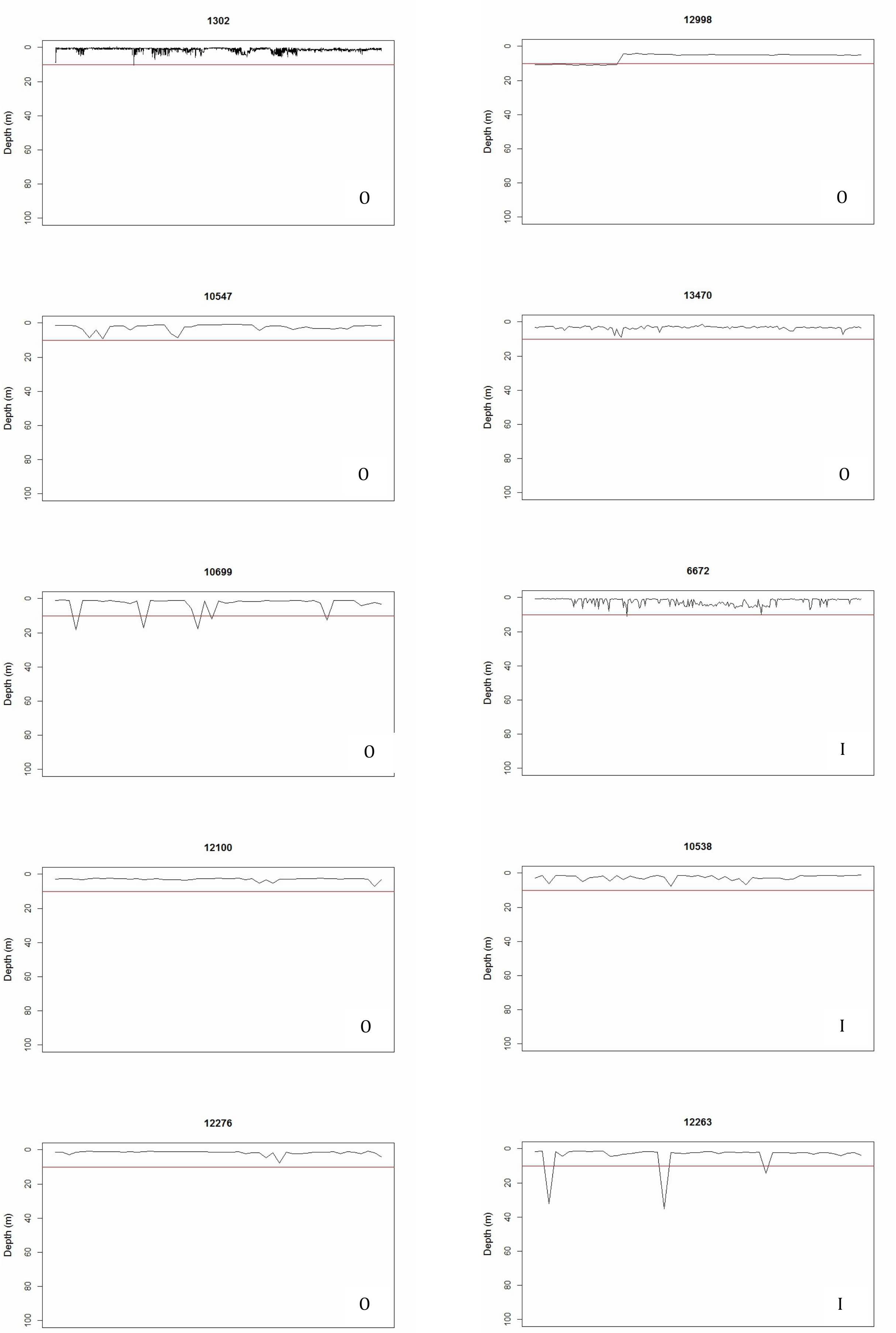

12999
Depth (m)
0
20
40
60
80
100
C


12243
Depth (m)
0
20
40
60
80
100
C


13020
Depth (m)
0
20
40
60
80
100
C


12286
Depth (m)
0
20
40
60
80
100
C


1257
Depth (m)
0
20
40
60
80
100
O



Appendix 2. Individual depth use the last 24 h before recapture for inward migrating Atlantic salmon. The zone is given in the lower right corner for each individual. C = coastal zone, O = outer fjord zone, I = inner fjord zone. A red line is drawn at depth = 10m, and passing this depth is defined as a dive.