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Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar* **L.***)* **as inferred from recoveries of Data Storage Tags**

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Abstract

We released 598 hatchery smolts in a river in Iceland in 2005 and 2006 tagged with DST-tags recording temperature and (depth) continuously. Five salmon returned in 2006 and two in 2007 all spending one year at sea. The complete temperature and depth profiles of the whole ocean migration were measured. The salmon stayed close to the surface most of the time and showed diurnal behavior staying at slightly deeper waters during day. The salmon were at temperature from 6 to 15 ^{o}C with warmer temperatures in the summer. We compared the fish temperature to sea surface temperature (SST) frma an available National Oceanic and Atmospheric Administration (NOAA) database to locate the fish at different times. Utilizing the diurnal behavior of the salmon, we estimated solar noon each day during winter. SST's and diurnal activity was used to estimate daily locations using established Hidden Markov Model (HMM) for fish geo-location. The salmon in the study stayed southwest of Iceland in the Irminger Sea during the first summer months but in the fall they moved towards the Faroes Islands and then back to the Irminger Sea where they

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stayed, until returning to the river. The salmon also took shorter and deeper dives (>100 m) during the latter part of their ocean migration.

Keywords: Atlantic salmon, ocean migration, DST tags, temperature preference, depth habitat.

Introduction

Since the mid-1980s, declines in abundance of Atlantic salmon (*Salmo salar* L.) have been observed both in North American and European stocks (Parrish et al. 1998; Chaput 2012; Mills et al. 2013). The main causes of the decline have been associated with increased marine mortality in the ocean life phase of the species (Friedland et al. 2009a).

Concerns exist that changes in oceanic conditions may be exerting important effects on salmon survival and abundance (Reddin et al. 2011). However, there is insufficient knowledge regarding movement, migration, behavior and survival of Atlantic salmon at sea, and whether consistent, stock-specific foraging areas exist (Friedland et al. 2009b; Chittenden et al. 2013). It is known that Atlantic salmon smolts leave natal rivers in spring (Otero et al. 2014), and that post-smolts are mainly found in the surface layers of the sea (Holm et al. 2006), preferentially selecting temperatures between and 8 to 12°C (Friedland et al. 2000) and salinities > 35psu (Holm et al. 2003). Long migrations to feeding areas (Rikhardsen and Dempson 2011) around Greenland, Faroe Islands and in the Norwegian sea have in the past been associated with mixed-stock fisheries during the salmon's first and second years at sea (Chaput 2012). Once the post-smolts leave the coast, relatively little information is available on their marine feeding habitats. The stock-specific migratory routes and feeding areas may be outcomes of long-term adaptations and more proximate responses to environmental cues such as ocean currents, temperature, salinity, depth and prey availability (Dadswell et al. 2010; Mork et al.2012).

Past information on behavior and life history of salmon at sea has relied mainly on captures from commercial fisheries and research cruises as well as mark-recapture methods (Jensen 1999). In recent years more advanced technologies have come into use such as satellites to collect oceanographic data and the use of fish telemetry, data storage tags (DST) and acoustic tracking (Sturlaugsson 1995; Reddin et al. 2004 Reddin et al. 2006; Reddin et al. 2011; Holm et al. 2004, 2006; Guðjónsson *et al.* 2005; Rikhardsen et al. 2006; Rikhardsen et al. 2007; Davidsen 2013). State space models have also become a powerful tool to estimate fish movements and behavior using such data (Patterson et al. 2008). For example Hidden Markov Models (HMM) have been used to estimate movement of cod in the Baltic sea from tidal patterns (Pedersen et al. 2008) and blue-fin tuna migrations has been estimated from light and sea surface temperature (SST) (Pedersen et al. 2011).

As with most Atlantic salmon stocks, little information is available on migrations, feeding locations and feeding behaviors at sea for stocks emigrating from Iceland's approximately 80 salmon rivers (Ísaksson and Óskarsson 2004). Because it has been illegal since 1932 to catch salmon within Iceland's fishery limits, most of the scant information has been obtained from incidental recoveries of tagged fish in distant, international fisheries such as off Greenland and the Faroe Islands, and from fish caught as by-catch in Icelandic offshore fisheries targeted on marine species (Ísaksson et al. 2002). For effective management and conservation of Iceland's Atlantic salmon in the future, more detailed knowledge is needed on migratory routes and feeding areas of its salmon stocks as it relates to changes in growth and mortality.

The objectives of this study were to utilize available advances in tagging and analytical approaches to obtain specific information on the migratory locations and temperature regimes occupied during the entire life cycle (i.e., from the time the smolts

leave freshwater until return as adults to the river) of a hatchery-reared, Icelandic stock of

Atlantic salmon.

Material and methods

DST tagging, smolt releases and recapture of adults

Smolt releases and recaptures of adults took place in River Kiðafellsá, a small river

in southwestern Iceland (Fig. 1) that also holds small population of wild salmon and sea

trout. Hatchery-reared smolts were produced for the experiment at the Laxeyri fish farm

West Iceland from two-sea-winter fish of the River Rangá stock. In all, 598 tagged smolts

at 1+ age were released in 2005 and 2006. Smolts at the time of tagging averaged 19.0 cm

(±0.89 SD) in length and 78.9 g (±11.3 SD) in weight (Table 1). The DST-micro tags, (2.5

g in weight and 25.4 mm in length) from Star-Oddi (Iceland) used in the study recorded

temperature and pressure (depth) at 1 hour intervals. The smolts were anesthetized using

phenoxylethanol solution. The tags were inserted in the body cavity of smolts, by surgical

procedure (Jepsen et al. 2005), in the period late March to early May prior to smolt release.

The incision was closed with 2 separate stiches of sterile sutures (3/8 needle, USP 2-0,

PGA sterile synthetic absorbable braided polyglycolic acid suture. The smolts were then

injected with antibiotics. Only smolts >60 g were used for implantation of DST tags due to

low survival of smaller smolts in prior experiments done by the authors where DSTs were

implanted in different size groups of smolts. In May smolts were moved to a release pond

excavated in the bank of the river 200 m above the estuary. Ambient flow of water was

through the pond. The ponds were opened on 7th of June in 2005 and 31st of May in 2006

(Table 1) and then the smolts could leave. All DST-tagged smolts were also tagged with

conventional magnetic coded wire tags (Northwest Marine Technology, Shaw Island,

Washington, USA) and the adipose fin clipped for external identification. In 2006 and

2007 all adults returning to the river were captured in a trap situated few meters above the estuary (Fig. 1) and screened for tags from early June to the end of September. Untagged salmon and sea trout were released upstream. A temperature data logger (Tidbit TBI32 -5 + 37) was located in the river near the estuary and recorded water temperatures at 1-hour intervals.

Estimating geolocation from temperature and diurnal vertical behavior

SST estimation

To estimate the time of smolt departure and arrival of adult salmon to Kiðafellsá, we compared daily fluctuations in temperature recorded by the tags with those of a temperature logger in the river (Tidbit TBI32-05+37, Onset, Bourne, Massachusetts, USA). Due to a malfunction of the temperature logger in the spring of 2006, we instead compared the DST tag temperatures in 2006 to air temperatures records from a nearby weather station at Kjalarnes (Icelandic Meteorological Office 2009) where air temperatures at Kjalarnes and water temperatures in Kiðafellsá in 2005 showed high correlation.

As depth data indicated that the salmon at sea spent most of their time at or near the surface, we were able to reliably associate the measured temperature from a DST tag to SST. To get a daily estimate of the SST at a given tag inferred location we first filtered the temperature data to eliminate the effect of depth. We tested daily for negative correlation between temperature and depth and removed the deepest data point until the correlation was not significant (i.e., $P>0.05$). After filtering we took the median for each day as the SST estimate at a given location.

To get the likelihood for the HMM we compared our estimates to daily SST estimates from the American National Center for Atmospheric Research (Reynolds et al. 2007, NOAA (National Oceanic and Atmospheric Administration) OI (optimum interpolation) SST V2 High Resolution Dataset) which has ¼° spatial resolution. We

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assumed the measurements to follow a Gaussian distribution and used the 90% quintile of

the estimated standard error for the whole grid and period as our standard deviation. For

both periods (2005-2006, 2006-2007) it was set to 1/3 °. Likelihood profiles were

visualized in R to restrict further analysis within sensible geographical range to reduce

running time for models.

Longitudinal estimation

The salmon stayed near the surface at nights but dived and stayed at greater depths

during the day. We assume this is related to light and we can therefore get an estimate for

the solar noon and the day length from the middle and length of the dive. A centered form

of a logistic curve has been used to model the diurnal behavior of cod (Hjellvik et al. 2001)

and blue whiting (Johnsen and Godo 2007). Hjellvik et al. (2001) modeled bottom trawl

catches of cod. Since they knew the local time they calculated that beforehand and

centered around 12. They used the function

(1)
$$f_L(t) = \frac{D}{1+\frac{\exp(\beta-12+|t-12|)}{\alpha}}$$

to describe the behavior, where t is the local time, D represents the amplitude, β represents

the time were the fish is at *D/2* and $\alpha+\beta$ indicates the time at which the fish is

approximately at ¾ D $(\frac{1}{(1+e^{-1})}) \approx \frac{3}{4}$. Instead of using the local time they might have used

universal time and added a parameter for the local noon (*N*) changing their function to

(2)
$$f_L(t) = \frac{D}{1+\frac{\exp(\beta-12+|t-N|)}{\alpha}}.$$

We used a similar function

(3)   g(t)= A+(B-A)/(1+exp((β-cos(t*π/12-N))/α))

which is more related to the four parametric logistic function. Here t is the time in the tag (GMT), A represents the depth at day and B the depth at night. N is the local noon in radians and β and α can be interpreted in a similar way as in the previous function. When $\cos\left(t \cdot \frac{\pi}{12} - N\right) = \beta$, $g(t)$ is at $A + \frac{1}{2}(B - A)$, that is halfway between A and B. When $\cos\left(t \cdot \frac{\pi}{12} - N\right) = \alpha + \beta$ the fish is approximately at $+3/4(B - A)$. We chose to use trigonometric function instead of absolute value to have a periodic function and to facilitate convergence in non-linear fitting.

The salmon did not always show diurnal activity. Sometimes they stayed at shallow depths throughout the day and sometimes they dived to greater depths (below 100m) without any obvious correlation with the time of the day (Figs. 2, S1). We developed a filter to extract days with diurnal behavior. For each day (i) we took the next day ($i+1$) and compared three models: I: A generalized additive model (gam) with cyclic cubic spline of the time of day as explanatory variable, II: A gam with cubic spline of the index ($1,\ldots,48$) as explanatory variable and III: An AR1 model. The model with the lowest Akaike information criterion (AIC) was noted. We also did this using day i and $i+2$ and all of these three days ($i,i+1,i+2$). After this we had a total of 7 model selection for each day with different neighboring days ($[i-2, i]$, $[i-1, i]$, $[i, i+1]$, $[i, i+2]$, $[i-2, i-1, i]$, $[i-1, i, i+1]$ and $[i, i+1, i+2]$). If any select model I as the best, day i was kept for further analysis. We used the gam function from the mgcv-package in R (Wood 2011) for the gam-fitting and the gls function from nlme-package for the AR1 model fitting (Pinheiro and Bates 2009). The depth measurements were transformed to log-scale before this filtering step.

To estimate the longitude we fitted the function g above to the filter depth measurements on log-scale in a weekly window centered on 12 pm each day. We used the gnls function from the nlme-package and assumed an AR1 distribution for the errors. To get the estimate of the longitude for each day (d) we transformed our estimate of the dive

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center (N) with the following formula

(4) $(\pi + E_d - N_d) \cdot 180/\pi$

Here E_d is the equation of time for day d (Meeus 1991). The gnls-function also outputs estimates for the standard error of the parameters. We used those estimates in the following HMM step.

HMM-step

To estimate the salmon location, intertwining information from temperature, diving behavior, start and end location (River Kiðafellsá) and maximum swimming speed, we used a HMM (Jonsen et al. 2013) (code available on *http://mwpedersen.dk/tracking.html*).

We ran the model with both time and state (location) as discrete variables. We estimated the location for each day and used the same resolution as for SST-data for the state (1/4 $^{\circ}$). We ran it with two behavioral states. One state was where we allowed the fish to travel up to 11 cells longitudinally and up to 5 cells latitudinally. Since each cell is ¼ $^{\circ}$, this is equivalent to 105 km at 70 $^{\circ}$ latitude and 197 km at 50 $^{\circ}$ latitude for the longitudinal movement and 139 km for the latitudinal movement. In the other behavioral state the fish could travel 4 cells longitudinally and 2 cells latitudinally which is equivalent to 38 km at 70 $^{\circ}$ latitude and 71 km at 50 $^{\circ}$ latitude for the longitudinal movement and 56 km for the latitudinal movement. These distances are close to the maximum estimated migration speed for adult salmon and post-smolts (Thorstad et al. 2011). Based on preliminary modeling and SSTs profiles over the North-Atlantic (Fig. 3) we decided to restrict the model to the geographical area from 50°N to 70°N latitudinally and 50°W to 10°E longitudinally.

Results

Recaptures of tagged salmon

Seven DST-tagged one sea winter salmon were recaptured, five in 2006 and two in 2007, a recapture rate of 1.2 %. One of the salmon recaptures in 2006 was caught by an angler in River Elliðaár (tag 331), 20 km south of R. Kiðafellsá (Fig. 1). Complete data could be retrieved from all the tags except for the one captured in Elliðaár. That tag stopped measuring on January 13, 2006; the data recorded until that date was included in our analysis.

The length and weight of the recaptured salmon were within the typical range of Icelandic grilse in W-Iceland (Table 2). Although three of the salmon were recaptured on the same day in 2006 (Tags 200, 244 and 502, Table 2) their return to the estuary was not coordinated and the time they waited before entering the river varied.

SST profiles

The filtering step removed one measurement each day on average for all the fish. Considerable temporal variability in filtering was evident since dives became deeper as the salmon grew and temperature gradients and ocean stratification is different by season.

The surface temperature measured by our salmon ranged from 6°C to nearly 15°C with warmer temperatures in the summer and cooler during winter. Variability within and between individuals was lowest during late fall and winter (Oct-Jan 2005 and Dec-Feb 2006) but varied substantially in other seasons (Fig. 2).

By comparing the temperature profiles to the NOAA OI SST V2 database certain areas emerged as probable feeding areas. Areas over the Reykjanes ridge, the Irminger Sea and the Norwegian Sea all show high correlation with the salmon temperature profiles (Fig. 3).

Depth

The diurnal vertical behavior was evident, especially during the darkest periods of the year. The salmon stayed near the surface at nights but dived and stayed at greater

depths during the day (Fig. 4).

The salmon showed two types of vertical movement. Diurnal movements were detected where salmon stayed nearer the surface at night and deeper during the day, a behavior more evident in the winter. The salmon also took deeper dives (below 100m) that lasted for shorter time (few hours) without any obvious correlation with the time of the day.

Approximately 80% of the days were retained for longitudinal estimation after the first filtering step with little variation in filtering between individuals. The algorithm used by the gnls-function could not fit our non-linear curve to the data in all cases. This is of no surprise since the diurnal behavior was not always present even after our soft filter. We decided to use only estimates from September through March due to the bad fitting during spring and summer (Fig. S1C). There are small differences between night- and daytime vertical position and limited resolution in the depth measurements especially during the first summer at sea as well as less dependable behavior perhaps due to the long daylight. One individual did only display diurnal behavior during the darkest hour (tag 200) and we only used estimates from December to February for it. A few days were removed by hand before the HMM-step, due to unrealistic estimation of day-length or migration speed and also if the estimate was temporally isolated making the HMM-model dependent on a single value (Table 3, Fig. S1).

In many cases our function described the vertical behavior adequately and reflected the expected day-length very well with few hours spent at greater depths during the darker periods of the year and longer dives during summer (Fig. 4 and S1).

Our estimates of longitude indicate a migration from the areas west of Iceland eastward and back during the mid-winter (Fig. 5). The temperature profiles suggest this might be a likely scenario (Fig. 3).

Feeding areas

Although temperature and longitudinal estimation suggest certain areas being occupied by the salmon we decided to examine the data further by a Hidden Markov Model joining the available information in one framework. The model yielded posterior probabilities for each cell in the grid being occupied by a salmon per day. The results were summarized by looking at the mean posterior probability over time and all the fish for the same year (Figs. 6, S2). The post-smolts spent the first summer west of Iceland over the Icelandic continental shelf and in the Irminger Sea. An eastward migration seems to occur during the winter. They seem to migrate and stay for some time over the ridge between Iceland and Faeroes before migrating back to the Irminger Sea. The two salmon from the latter year underwent this migration a little bit later than the salmon from the first year. We had limited information to estimate this pattern for tag 200 since that individual did not display diurnal behavior at the time of the migration. The HMM output suggests it did not follow the same migratory route. The temperature exposed to that tag is also quite different from the others in the same year (Fig. 2). This might indicate different migration pattern than from the other tagged fishes. For the rest of the year the salmon stayed west and south of Iceland and does not seem to occupy the Norwegian Sea at all although the temperature profiles indicated that as a possibility. The feeding area during the latter spring and summer are by no means narrow and indicate our limited information about the salmon during that time (no longitude) and not as steep temperature gradient during summer as in winter.

There are some differences in the migratory routes between the two years under investigation in this paper (Figs. 3, 6, S2). In the latter year the fish seem to go further south in the fall and winter. The temperature profiles between the years are not so different (Fig. 2) but comparison is difficult as there are differences between individual fishes and

only few fishes to work with.

Discussion

At sea, the temperature range encountered by the salmon in present study was narrow especially during the winter. The fishes stayed at temperatures from 6 to 15 ^{o}C. The warmest temperatures are in the river and at the coast during summer both when fish is entering sea and returning to the coast and the river. In the winter they stay at surface temperature of 6-8 ^{o}C. Temperature of that range is found only in a very limited area in the North Atlantic Ocean, a band that reaches from the Labrador Sea to Iceland and from Iceland to the northeast towards North Norway. This coincides with the findings of the migration of previously spawned salmon (kelts) in Newfoundland (Reddin et al. 2011) and in the Alta River in Norway that were tagged with DST tags (Chittenden et al. 2013). By using the diurnal vertical movement of the fishes in our study the area where the salmon can stay was further narrowed. A clear picture on the area where the fish was staying is revealed both by comparing the surface temperatures of the DST tag and sea surface temperature and the solar noon as revealed in the diurnal activity of the fish. Although we do not use our estimates of longitude during summer in the HMM-step the vertical behavior profiles never suggested noon prior to 12:00 GMT and we therefore can exclude the Norwegian Sea and areas along the Norwegian coast as feeding areas for our salmon from SW-Iceland.

Salmon at sea follow a life history and behavioral strategy aimed at achieving fast growth (Thorstadt et al. 2011). The smolts rapidly move from the river to warm and saline waters as has been showed in Iceland (Gudjonsson et al. 2005) and in Norway (Holm et al. 2000; Holst et al. 2000) as well as in Canada where DST tags where first used on smolts (Reddin et al. 2004; Reddin et al. 2006). Survival rates depend highly on abundant food resources. It is therefore not surprising that the salmon in our study chose areas where

warm and cooler water masses meet and there is abundant food in the sea; west, southwest

and south of Iceland (Green et al. 2003). First the salmon stay at the west coast moving to

the south and along the south coast of Iceland. Then they move back to the Irminger Sea

where they stay during winter until they move back to the river. Beaugrand and Reid

(2012) examined long-term changes in phytoplankton, zooplankton, namely Calanoids,

including *Calanus finmarchicus* and Euphausiids, and salmon in relation to hydro-

meteorological forces in the northeast Atlantic. They found significant linear relationships

and commented on the similarity in their cyclic variability. Climate variations can

influence currents, gyres and sea surface temperature (SST). This is probable explanation

of different migration areas between the two years we had salmon at sea in present study.

Such changes may impact salmon directly through altering migration routes or indirectly

by affecting the distribution and/or quantity of food availability at different levels in the

food chain. Survival rates of salmon during its initial part at sea have been linked to

oceanic condition such as SST (Scarnecchia 1983; Scarnecchia et al. 1989a; Scarnecchia et

al.1989b; Gudjonsson et al. 1995; Antonsson et al. 1996). Survival has also been related to

later stages at sea and to the condition and size of a suitable thermal habitat in winter both

for Canadian stocks and salmon stocks from Scotland and southern Norway (Friedland et

al. 1993; Friedland et al. 1998). Toledano (2006) also found such relationships between

the runs of Icelandic salmon from the west coast of Iceland and SST at certain times and

location as well as to abundance of certain groups of zooplankton in the Irminger Sea

southwest of Iceland, which is in agreement with the migration area shown by the salmon

in present study. Peyronnet (2006) found relationship of salmon run in Irish rivers and

hydro-meteorological factors and zooplankton species, *Calanus finmarchicus i*n the Faroe-

Shetland Channel. Salmon in its second year at sea also show high variability in survival

(Scarnecchia 1984; Jonasson et al. 1994; Gudjonsson et al. 1995; Chaput et al. 2003; Gudbergsson and Gudjonsson 2003).

It has been suggested that, during its marine feeding migration, Atlantic salmon utilizes the North Atlantic Subpolar Gyre (NASpG) to lower energy consumption for movement and provide more accessibility to appropriate food (Dadswell et al. 2010). This is supported in present study. Previous results from tagging programs in the period 1967-1995 yielded a total of 55 marine caught salmon tagged in Iceland (Isaksson et al. 2002). These marine caught salmon suggest that two sea winter Icelandic salmon from the south and west coasts tend to migrate west towards Greenland, and the two sea winter salmon from the north and east coasts of Iceland seem to migrate more into the Iceland Sea and were caught to some degree in the Faroese fishery. Some two sea winter salmon from that area have, however, have been recaptured in West Greenland, and some west coast salmon in the Faroese fishery suggesting that the migration is by no means uni-directional (Isaksson et al. 2002). In present study there are strong indications that indeed salmon migrated into the Faroese waters in the autumn and the back to the Irminger area before winter. The Irminger Sea gyre is a productive area with abundant food for salmon (Greene et al. 2003) and salmon have been caught there earlier (Jensen 1967; Jensen and Lear 1980). It has also been suggested as the feeding area for Icelandic salmon from S- and W-Iceland (Isaksson 1980). With respect to the northern and eastern Icelandic salmon stocks, it can be speculated that they migrate into the Norwegian Sea that is a known feeding area for salmon (Haugland et al. 2006). In the surveys of Jensen and Lear (1980) in the Irminger Sea, tagged fish were recovered both from N-America and Europe. Furthermore, MacKenzie et al. (2011) and Trueman et al. (2012) suggested from studies of isotopes of two salmon populations from the British Isles that one used the area south of Iceland for feeding while another were more likely using the areas in the Norwegian Sea. This

supports the findings of present study that these areas are important for salmon and not only for Icelandic salmon. Furthermore, in mackerel fishery in this area salmon has been caught as by-catch in considerable numbers (Árni Ísaksson Directorate of Fisheries pers. com.).

When approaching the river the salmon seem to stay for some days along the coast or outside the estuary before they migrate into the river as is known from earlier studies (Jonsson et al. 2007, Davidsen 2013)

The fish in our study spent most of the time close to the surface. This manifests that salmon is a pelagic fish in nature and shows similar vertical behavior as many pelagic animals (Ishida et al. 2001; Walker et al. 2007) and has been shown for Atlantic salmon earlier (Reddin et al. 2011; Holm et al. 2006; Chittenden et al. 2013; Lacroix 2013). Diurnal vertical activity could be seen where the fish stayed at more depth during the day. The diel vertical behavior was evident, especially during the darkest periods of the year.

Of particular interest are that all the salmon took deep dives now and then. No dives were taken during the first months of their stay at sea, but the dives became deeper as the fish grew larger and had stayed longer time at sea. These dives only lasted for few hours. This behavior has been seen earlier in Atlantic salmon (Westerberg 1982a; Westerberg 1982b; Sturlaugsson 1995; Holm et. al 2006; Reddin et al. 2011; Lacroix 2013; Chittenden et al. 2013). The dives may be associated with its feeding behavior or avoidance of predators. Westerberg (1982b) suggested that the dives where associated with homing as the salmon took dives to orient itself according to currents. In present study the salmon did not undertake dives for the first months at sea when it was small and when presumably the need to avoid predators is largest. Therefore it is likely that the salmon is chasing prey to deeper water but fast swimming fish are on the salmon menu (Jensen and Lear 1980; Jacobsen and Hansen 2001; Haugland et al. 2006).

The smolts we tagged in this study were reared in a hatchery. Their size at tagging was in the upper limit or larger than known for natural smolts size in Icelandic rivers (Antonsson and Gudjonsson 2002) since natural smolts of normal size could not carry the type of DST tags used. The tagged smolts went to sea within the time frame of the run of natural smolts in that area of Iceland (Antonsson and Gudjonsson 2002; Otero et al. 2014). The returning tagged fish in our study returned within the time of the natural salmon run in R. Kiðafellsá. The size of the returning salmon was also within the range of size distribution of the natural salmon. Production of Atlantic salmon smolts in Iceland is a well known practice as ocean ranching was operated in Iceland for many years (Isaksson 1980). Furthermore, smolts are commonly used for enhancement of the salmon fishery in some Icelandic rivers. River Rangá, South Iceland, with hardly any natural smolt production has been operated by releasing hatchery smolts for many years resulting in thousands of salmon caught every year (Gudbergsson 2014). Smolt production in Iceland is therefore based on long and extensive experience. However, hatchery smolts usually have lower returns than wild smolts, but when the best available rearing practice and release methods are used these differences are small. Returns rates of hatchery smolts show the same fluctuations as catches of wild salmon (Johannsson and Gudjonsson 1996). Therefore, it is likely that hatchery smolts encounter the same environment and show same or similar migratory behavior as wild salmon at sea.

Our study reveals new information on the migratory routes of Atlantic salmon at sea. Never before has the temperature and depth profile of salmon been recorded during its complete life cycle at sea. Analyses where the surface temperature profiles of the tags are compared to available data on SST´s along with location gained from the diurnal activity of the salmon reveal the migratory trajectories of these salmon from the river to the coastal area and to the sea and back again to the river. The salmon is located in areas where

abundant food can be expected and they are staying at temperatures which allow fast growth. These areas and their size, location and quality may change from time to time and therefore affect the survival of the salmon. Such changes are seen in present study as the feeding areas of the salmon in the second year of the study are further south especially in the spring before the salmon return home. This has been emphasized earlier for North American salmon (Friedland et al. 1993; Friedland et al. 2009b) as well as salmon in Europe (Friedland et al. 1998; Friedland et al. 2000; Friedland et al. 2009a). The salmon move to the feeding areas southwest and then south and southeast of the Icelandic coast and back. The salmon are therefore very mobile.

With better knowledge on where and at what conditions salmon is encountering at sea further studies can be undertaken. Then specific areas at certain times can be studied in order to understand the factors that govern different survival rates of salmon at sea and to relate different oceanic factors as well as biological indicators to the survival rates of salmon.

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Tables

Table 1. Release of DST tagged Atlantic salmon smolts in R. Kiðafellsá SW-Iceland 2005 to 2006.

		Releases	
Year	No.	Length cm	Weight
2005	298	19,1±0,94	77,3±11,5
2006	300	18,9±0,82	80,6±10,9
Total	598	19,0±0,89	78,9±11,3

Table 2. Individual returns of DST tagged salmon in R. Kiðafellsá 2006 to 2007.

Tag. Nr	Tag.day	Releases			Recaptures		
		Length cm	Weight g	Rel.date	Date	Length cm	Weight g
200	31.5.2005	19,9	83,5	7.6.2005	17.8.2006	59,0	1811
244	31.5.2005	18,5	70,7	7.6.2005	17.8.2006	64,0	2316
331	31.5.2005	18,5	60,8	7.6.2005	13.8.2006	60,0	270
414	20.5.2005	17,7	59,1	7.6.2005	1.9.2006	61,5	2210
502	20.5.2005	18,7	70,2	7.6.2005	17.8.2006	70,5	3162
1094	9.3.2006	20,2	102,4	31.5.2006	3.8.2007	65,0	2756
1246	9.3.2006	18,7	68,7	31.5.2006	17.8.2007	59,3	1890
Averages		18,9	73,6			63,8	2406

Table 3. Different filtering levels of the longitudinal estimates. The numbers are number of days. First is the number of days each grilse spent at sea (Sea), second the days used for estimation after filtering (Filter), days were we could estimate longitude (Estimate), number of days, within the time-frame (Sept-March) we decided to use (Time-frame) and finally the number of days used in the Hidden-Markov model after few estimates were removed by hand (final).

Tag Nr	Sea	Filter	Estimate	Time-frame	Final
200	406	352	100	19	18
244	421	318	216	124	122
331	219	193	99	62	62
414	446	347	211	130	127
502	408	338	199	118	101
1094	424	344	232	120	116
1246	419	350	252	164	159

Figures

Figure 1. Location of release pond and fish trap in R. Kiðafellsá. Location of the Elliðaár River is show on a smaller map.

Figure 2. Estimation of sea surface temperatures (SSTs) exposed to each fish.

Figure 3. Distribution of the mean likelihood of temperature profiles over year-quarters. The mean likelihood for each cell is calculated and the cumulative distribution is shown.
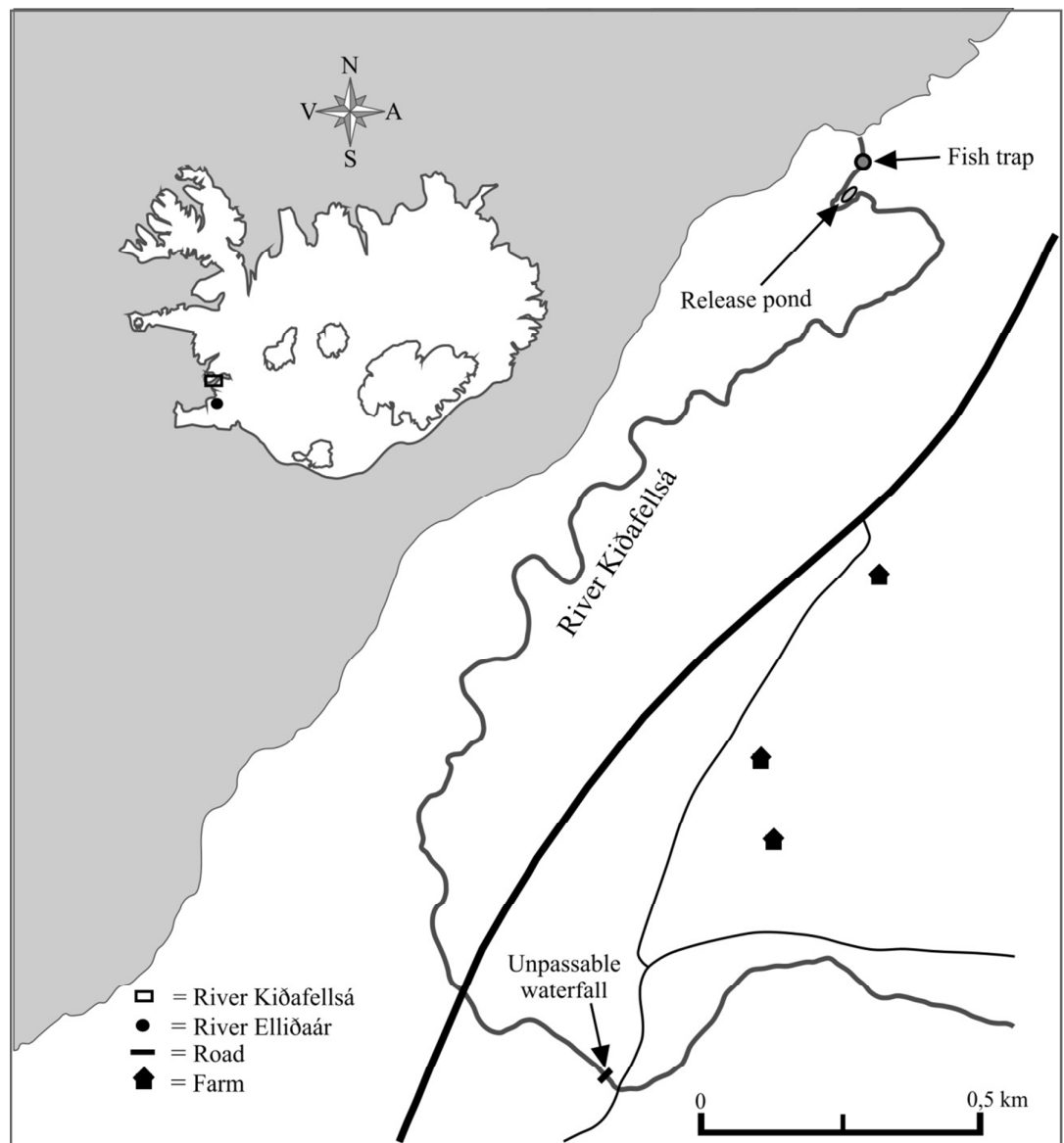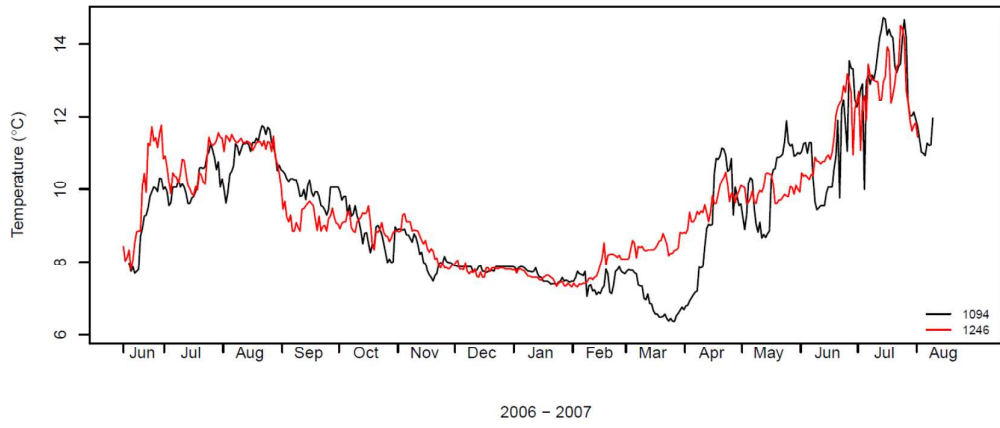
Figure 4. Three examples of weekly diving behavior for tag 1246; cantered on the 31st of August 2006, 26th of December 2006 and 25th of March 2007. On the left are the original measurements with dashed vertical lines indicating midnight (GMT) and the results from the non-linear regression are on the right with the curve and estimation of solar-noon and confidence interval are shown by vertical lines. The estimates for the noon are: A) 13:24, B) 12:51 and C) 14:00. Notice the difference in scale between the left and right panel.

Figure 5. Individual longitudinal estimation after filtering.

Figure 6. Estimated usage distribution for all the fish divided into year-quarters. The fish released in 2005 are on the left and the fish released in 2006 on the right. The mean posterior probability is calculated for each cell and the top 50%, 75% and 95% areas are shown.
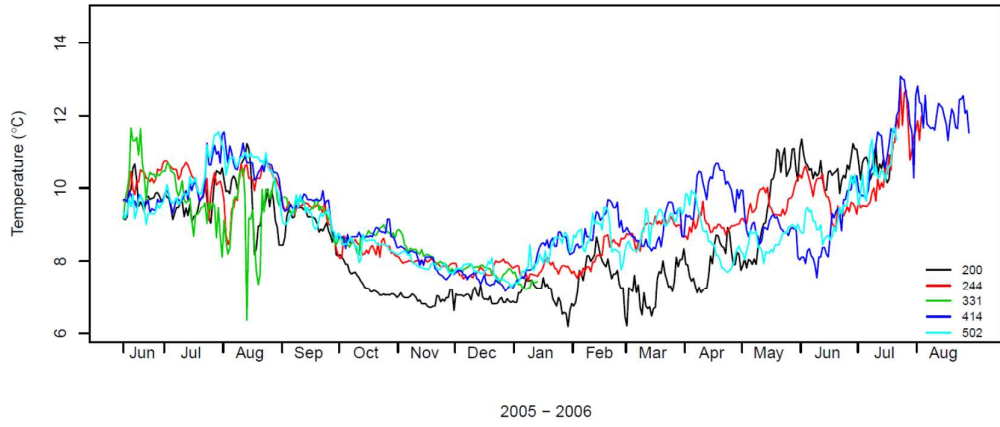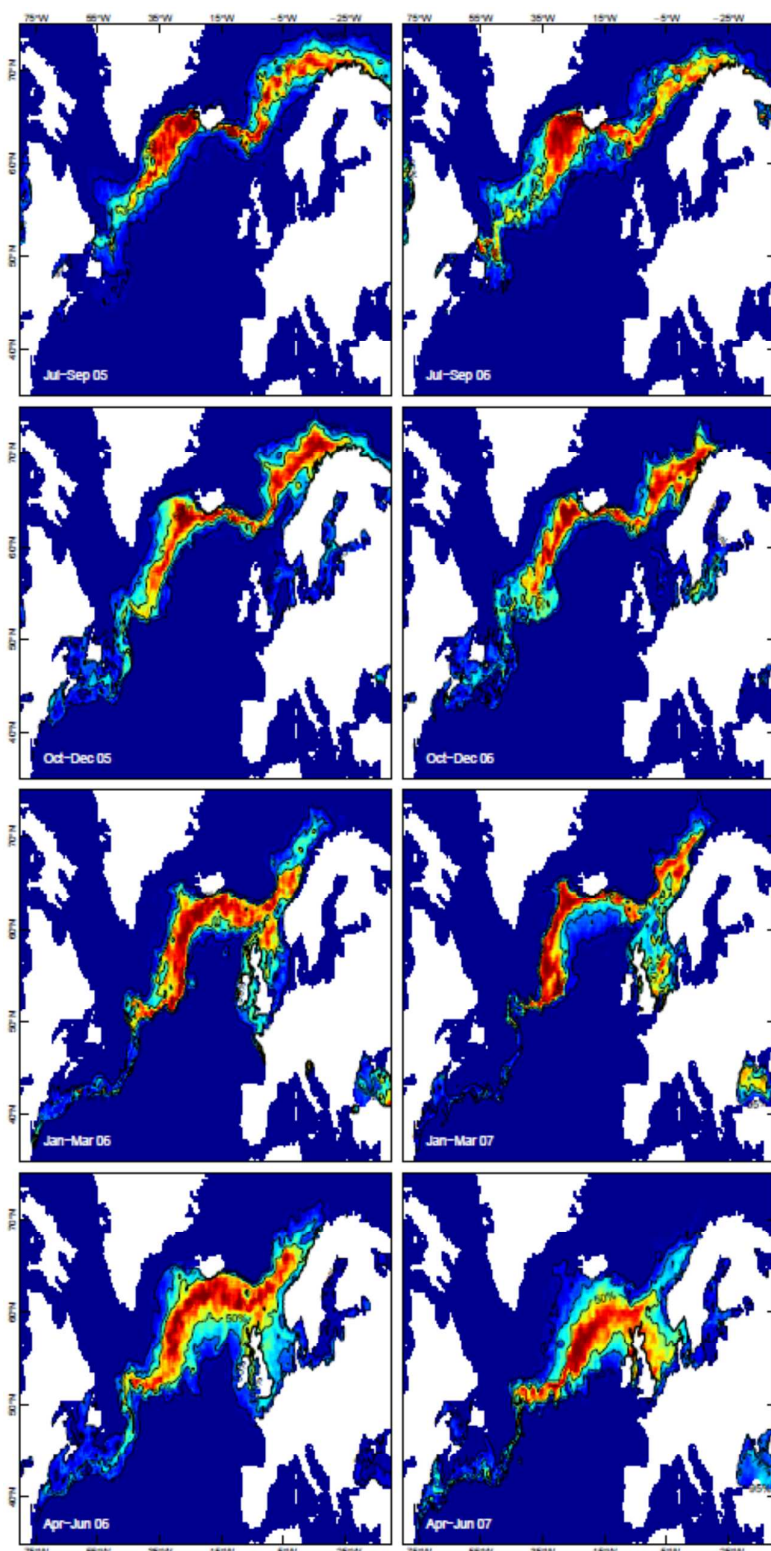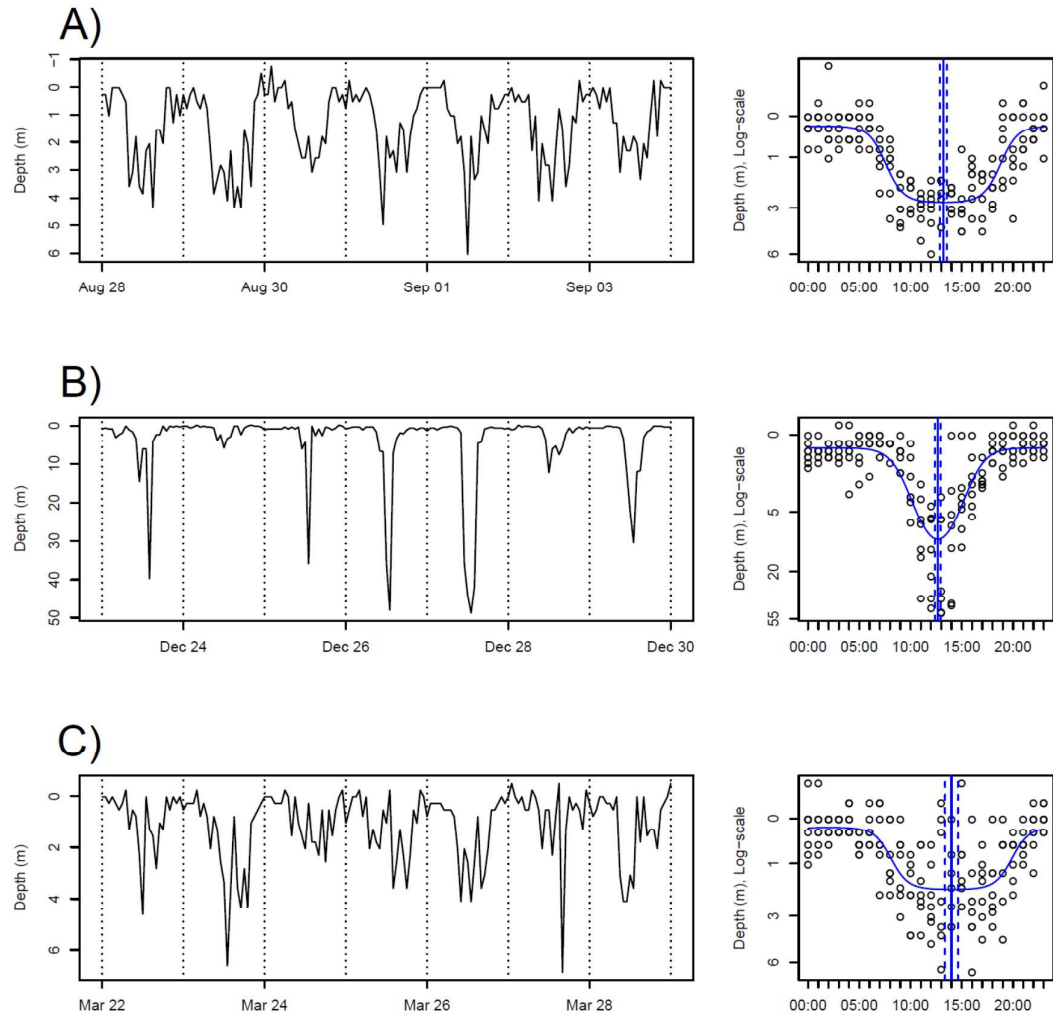
1

1 **Figures**

Figure 1. Location of release ponds and fish trap in R. Kiðafellsá. Location of the Elliðaár
River is show on a smaller map.

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7　　　　Figure 2. Estimation of sea surface temperatures (SSTs) exposed to each fish.
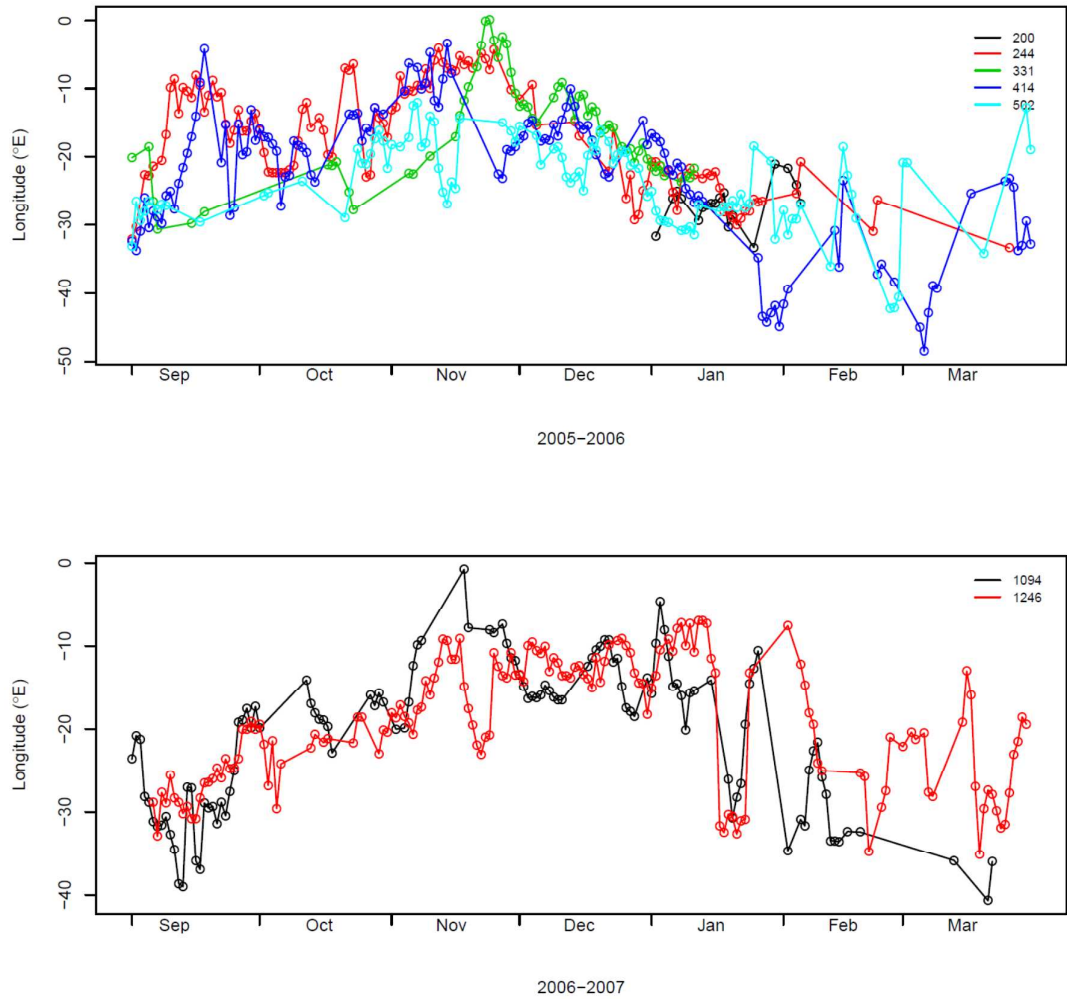
3

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9   Figure 3. Distribution of the mean likelihood of temperature profiles over year-quarters.
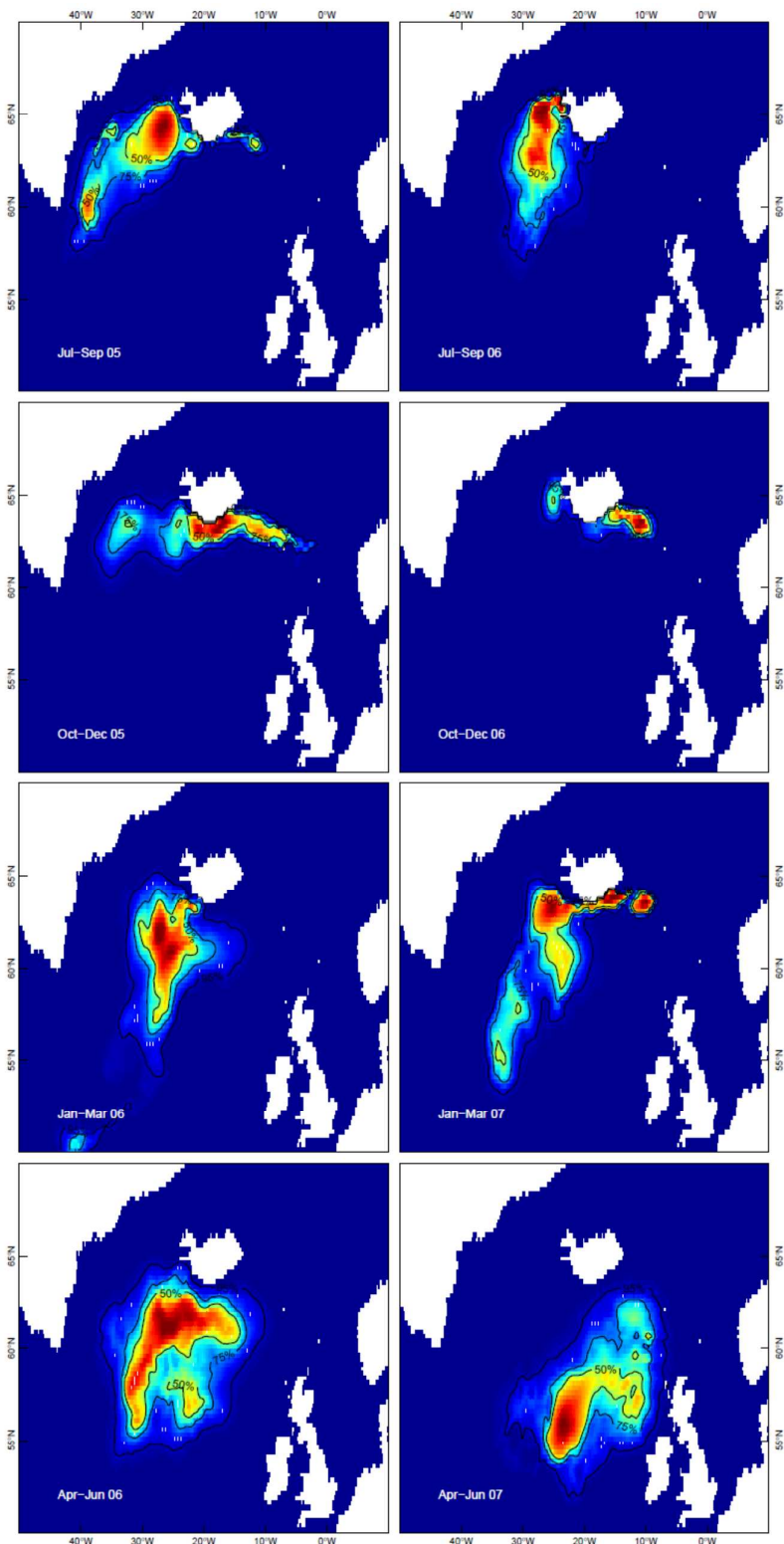10   The mean likelihood for each cell is calculated and the cumulative distribution is shown.

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Figure 4. Three examples of weekly diving behavior for tag 1246; cantered on the 31st of August 2006, 26th of December 2006 and 25th of March 2007. On the left are the original measurements with dashed vertical lines indicating midnight (GMT) and the results from the non-linear regression are on the right with the curve and estimation of solar-noon and confidence interval are shown by vertical lines. The estimates for the noon are: A) 13:24, B) 12:51 and C) 14:00. Notice the difference in scale between the left and right panel.

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19   Figure 5. Individual longitudinal estimation after filtering.

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Figure 6. Estimated usage distribution for all the fish divided into year-quarters. The fish released in 2005 are on the left and the fish released in 2006 on the right. The mean posterior probability is calculated for each cell and the top 50%, 75% and 95% areas are shown.

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## Supplementary material

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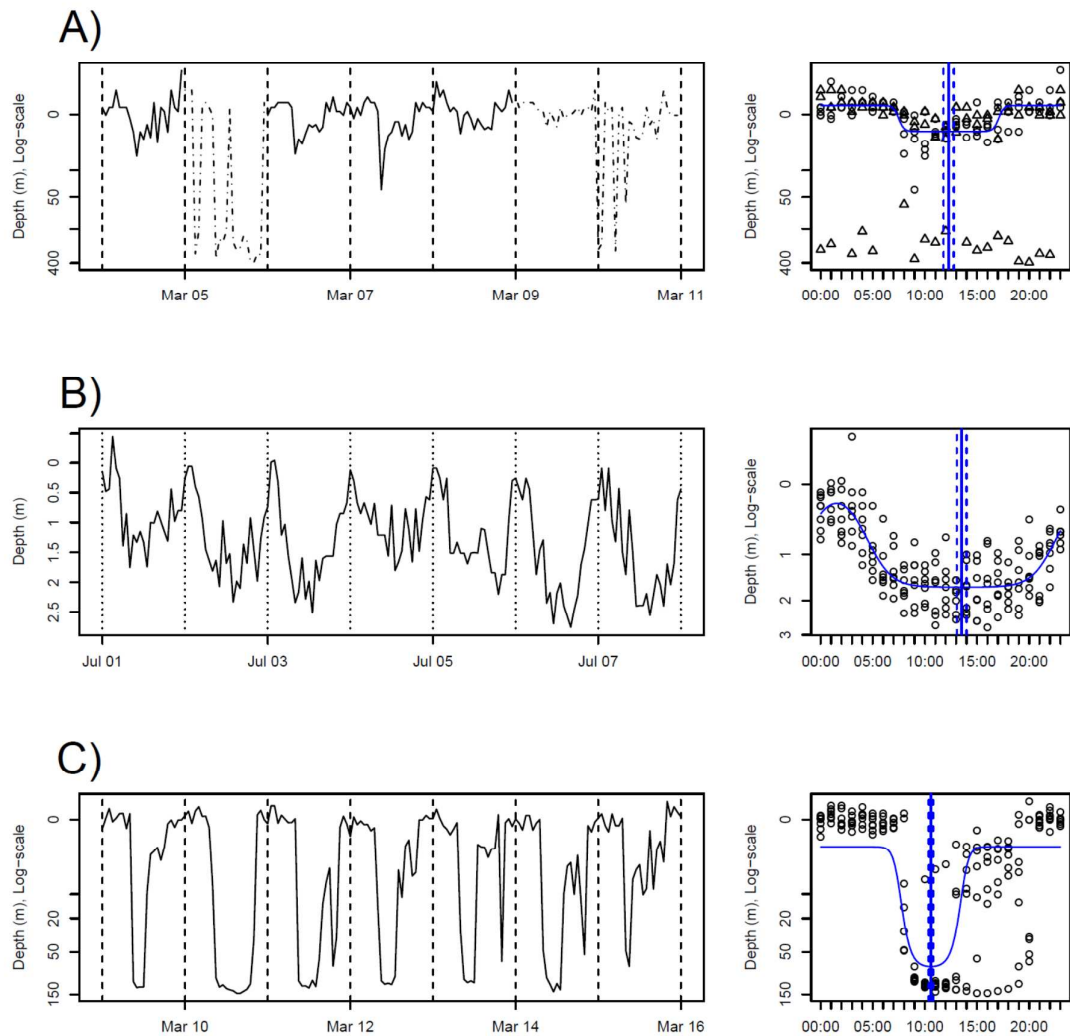
Figure S1. Example of diving behaviors. On the left are the original measurements with
dashed vertical lines indicating midnight (GMT), the dashed depth profile shows days
removed by our filter. The results from the non-linear regression are on the right with the
curve and estimation of solar-noon and confidence interval are shown by vertical lines.
Measurements removed by the filter are shown with triangles. Notice the different scales.
Figure A) is from tag 502 and is an example of the deep dives that do not seem to be light
dependent. The curve was fitted without these measurements. Figure B) is from tag 1094
less than month after it left R. Kiðafellsá. The shape of the curve fits with the long days at
northern latitudes during the summer. Figure C) is also from tag 1094 close to March
equinox but the behavior is not adequately described by our function. The day-length
should be close to 12 hours at this time of year but the non-linear fit indicates about six
hours of sunlight. This is a clear example of a bad fit and is one of the estimates removed
by hand.

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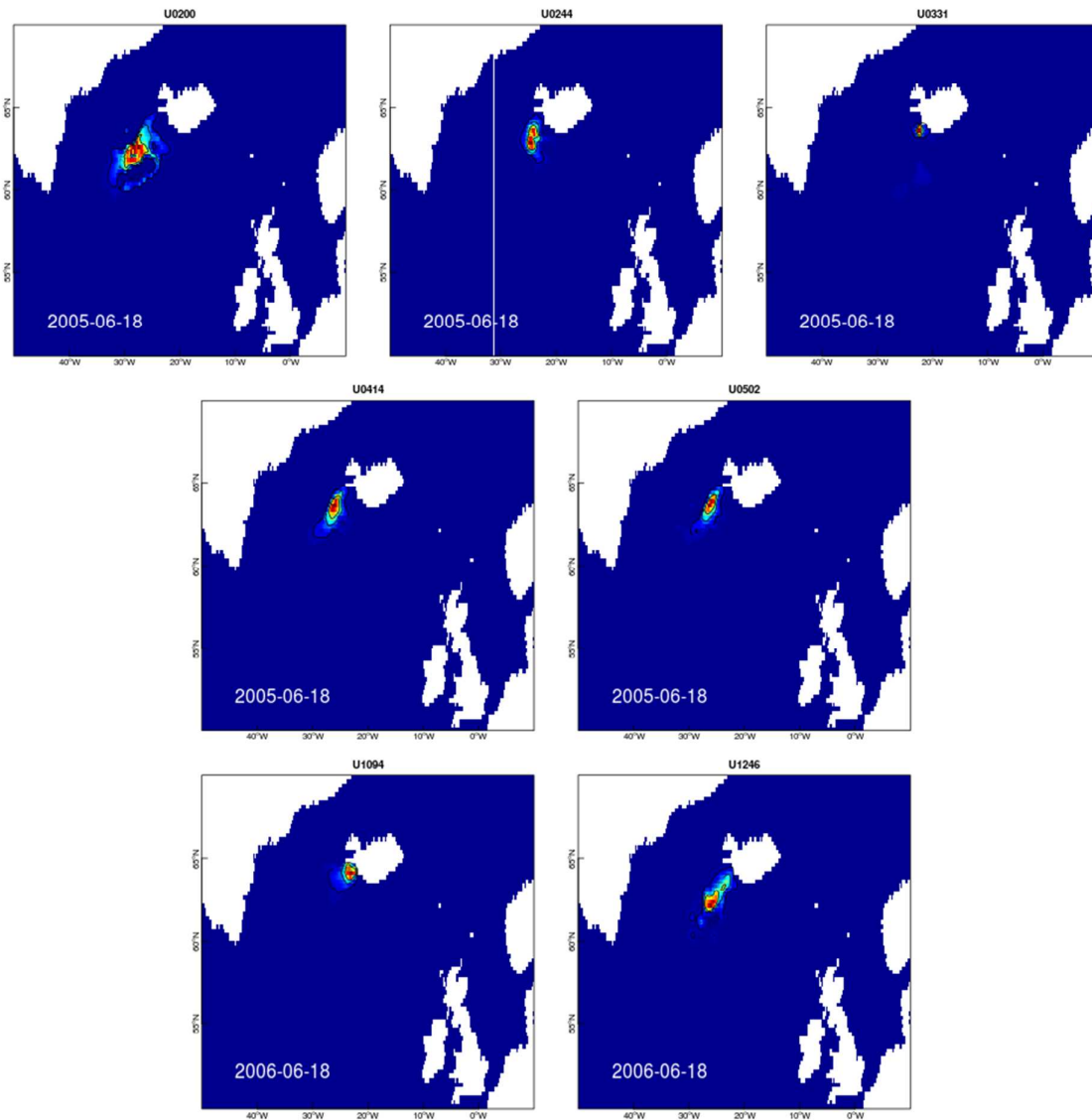
43

44   Figure S2: Individual migration for all tags online. The 50%, 75% and 95% confidence
45   area are shown and more exact spread by color scale.

46   Video in

HMM_result.avi

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