UiT

THE ARCTIC
UNIVERSITY
OF NORWAY

Faculty of Biosciences, Fisheries and Economics,

Department of Arctic and Marine Biology

Development of diving capacity and behaviour in harp seal (*Pagophilus groenlandicus*) weanlings from the Greenland Sea Stock

—

Aleksander Malde

BIO-3950 Master`s thesis in Biology - May 2019

UiT
THE ARCTIC
UNIVERSITY
OF NORWAY

Faculty of Biosciences, Fisheries and Economics,

Department of Arctic and Marine Biology

Development of diving capacity and behaviour in harp seal (*Pagophilus groenlandicus*) weanlings from the Greenland Sea Stock

—

Aleksander Malde

BIO-3950 Master`s thesis in Biology

May 2019

Supervisors

Lars P. Folkow, UiT – The Arctic University of Norway

Erling S. Nordøy, UiT - The Arctic University of Norway

Martin Biuw, Institute of Marine Research

Preface

Five years of study has come to an end, and I am so relieved to finish this thesis, and move on to new challenges.

Firstly, I wish to thank my supervisor Prof. Lars P. Folkow for the opportunity to work with this project and for all the guiding, support and supervision.

Secondly, I wish to thank my two co-supervisors: Prof. Erling S. Nordøy for all the feedback and insightful inputs and Senior Scientist Martin Biuw for all the help, and feedback regarding data treatment in R, and for the help developing and coding the duration model in R.

I also wish to thank Senior Scientist Aqqalu Rosing-Asvid at the Greenland Institute of Natural Resources for letting me use the harp seal data in this study.

Additionally, I wish to thank the crew of RV Helmer Hanssen for enabling me to have this data and making the cruise to the West Ice a wonderful experience.

Lastly, I wish to thank my family and friends for supporting me trough this experience. And a special thank goes out to my wife Ingeborg for her patience and thorough support.

Tromsø, May 2019,

Aleksander Malde

Abstract

This study represents one of the first studies that has explored the spatial and temporal differences in diving behaviour of weaned harp seal pups (*Pagophilus groenlandicus*) from the Greenland Sea stock. The study is also the first to map the weaned harp seal pups from the Greenland Sea population. In April 2017, newly weaned harp seal pups (n=26) from the Greenland Sea stock were tagged with satellite linked dive recorders. The dives and the movement of the pups were recorded and were then relayed. After release, the pups quickly began to dive and reached a diving performance of 4.27 (SD = 0.61) minutes after just 29.44 (SD = 22.00) days. This quick increase of diving performance is probably the result of dive training, increasing the myoglobin stores due to hypoxia and activity. Later in the study, the diving performance stabilised at about ~6 minutes, this is more due to external factors. The pups mostly dived shallow, but one seal had a dive to the depth of 600 meters. The harp seal pups followed the pack-ice north-east into the Barents Sea over the winter and comes back to the Greenland Sea in the end of April 2018, corresponding to the moulting. They mostly followed the distribution of the adults from the Greenland Sea stock, but most pups did not go into the Denmark Strait before the whelping period in the end of March. Foraging focal areas were by the ice-edge in the Northern Barents Sea, Svalbard Bank and around Bjørnøya.

III

Table of contents

1 Introduction:

1.1 Study area

In the arctic there are a lot of seasonal environmental differences, temperature fluctuates between the summer and winter and high latitude causes a large variation in day length between the summer and the winter. The Greenland Sea is one of these seas and is located on the east side of Greenland. The Greenland Sea is ice covered for large proportion of the year and maintain this sea ice longer in the summer than other arctic seas (Defant, 1961; Smith et al., 1985). This is because the Greenland Sea is dominated by the East Greenland Current, which transports sea ice out from the Arctic Ocean (Smith et al., 1985; Smedsrud et al., 2017). The Greenland Sea current keeps the Greenland Sea cold (<2°C) the whole year, whilst the neighbouring Norwegian Sea is much warmer (4°C - 6°C) (Smith et al., 1985).

The Barents Sea is another one of the seas located in the arctic. It is a shallow sea with an average depth of ~230 meters (Loeng, 1991). The Barents Sea is divided into two different parts, the southern part characterised by warm (4°C - 6 °C) Atlantic Ocean water, and the Arctic part, which is in the north side of the Barents Sea and is characterised by cold waters (< 0°C) and is seasonally ice covered (Loeng, 1991). The dividing waters between these areas is called the "Polar Front". On average the Barents Sea produces around 110 g C m^{-2} yr^{-1} (Sakshaug & Slagstad, 1992), which is quite normal for continental seas which have bioproductivity numbers around 100 g C m^{-2} yr^{-1} (Sakshaug, 1997). Here the most productive areas are in the south and west part of the Barents Sea. Here south of the polar front in the productivity is highest in the area that surround Bjørnøya and the Svalbard Bank where productivity comes up to 125 – 200 g C m^{-2} yr^{-1} (Sakshaug, 1997; Sakshaug & Slagstad, 1992). North of the "Polar Front" productivity numbers is usually less than 70 g C m^{-2} yr^{-1} (Sakshaug, 1997; Sakshaug & Slagstad, 1992). Main production in this area happens in a 50 – 60 km wide band by the ice edge and follows this northward during the summer (Sakshaug & Holm-Hansen, 1984; Sakshaug & Slagstad, 1992). These dynamics makes it possible for grazers and predators to follow this band of high productivity northwards or to seek the "hot-spots" around Bjørnøya and the Svalbard Bank. This belt of high productivity by the ice edge, not only occurs in the Barents Sea, but also occurs by the ice edge in the Greenland Sea and Norwegian Sea (Sakshaug & Holm-Hansen, 1984; Smith et al., 1985).

1.2 The harp seal

Harp seals (*Pagophilus groenlandicus*) are one of the species of seals that inhabit the northern waters of the Atlantic Ocean. Harp seals are the most abundant seal species in the

North Atlantic Ocean numbering approximately 9.4 million in total (ICES, 2008, 2014 2016; Laidre et al., 2015). Being this abundant the Harp Seal is an important ecological species occupying the pelagic realm in the North-East Atlantic Ocean (Nordøy, et al., 2008). Harp seals live in several populations in the North Atlantic: The North west and in the North East. The breeding populations in the North West Atlantic are in the Gulf of Saint Lawrence and outside the coast of Newfoundland (Nansen, 1924; Sergeant, 1991). The North West Atlantic populations number approximately 7.4 million (ICES, 2014; Laidre et al., 2015). In the North Eastern Atlantic Ocean there are two more breeding populations: The White Sea/Barents Sea population with whelping grounds in the White Sea (Nansen,1924; Nordøy et al., 2008), and the Greenland Sea population with whelping grounds on the drift ice between Greenland and Jan Mayen (Nansen, 1924; Folkow et al., 2004). The eastern populations number ~1 400 000 and ~650 000 for the Barents Sea and the Greenland Sea populations respectively (ICES, 2016).

The harp seal is a medium sized pinniped species. Males reach lengths of 1.6 to 1.9 meters and the female is a bit smaller and they weigh 135 kg and 120 kg in the winter, for males and females, respectively (Blix, 2005). They weigh ~100kg after moult in summer (Nansen, 1924; Sergeant, 1991). Both sexes mature at around 5-7 years of age (ICES, 2008, 2016; Sergeant, 1991). Pelages of adult animals are characterised by a grey background and large dark 'harp' on the back, the head is also usually dark (Blix, 2005; Nansen, 1924). Younger animals do not have a "harp" and are randomly spotted (Blix, 2005).

1.2.1 Life history
Harp seals are a pack ice associated species. Their scientific name (*Pagophilus groenlandicus*) means "ice lover from Greenland". They congregate on the pack ice in the whelping areas to pup, breed and moult (Nansen 1924). After the whelping and moulting period, they return out to sea to feed and restore their blubber reserves.

Harp seal pups are born in the end of February to the end of March. This birthdate is dependent on which population the animals belong to, with the White Sea population being born in the end of February and in the start of March, and the western populations being born in the start of March and lastly the Greenland Sea population in the end of March (Nansen, 1924; Khuzin, 1967, as cited in Sergeant, 1991). They are born well developed (precocial) with a thick lanugo pelage and a layer of blubber (Nansen, 1924). Nursing lasts 12 to 15 days (Kovacs & Lavigne, 1985) and they are abandoned shortly after being weaned. This short duration of the nursing period is second only to the hooded seal (*Cystophora cristata*) were

the nursing period is only 3 – 5 days (Bowen et al. 1985). In the nursing period harp seal pups gain 2.5 kg per day, most of this is deposited as blubber (1.9 kg/day), and the rest is deposited as lean body mass (Stewart & Lavigne, 1980). When the pups are born they are covered in a 3-4 cm long white lanugo fur which is shed after ~15 days of birth (Nansen, 1924; Stewart & Lavigne, 1980).
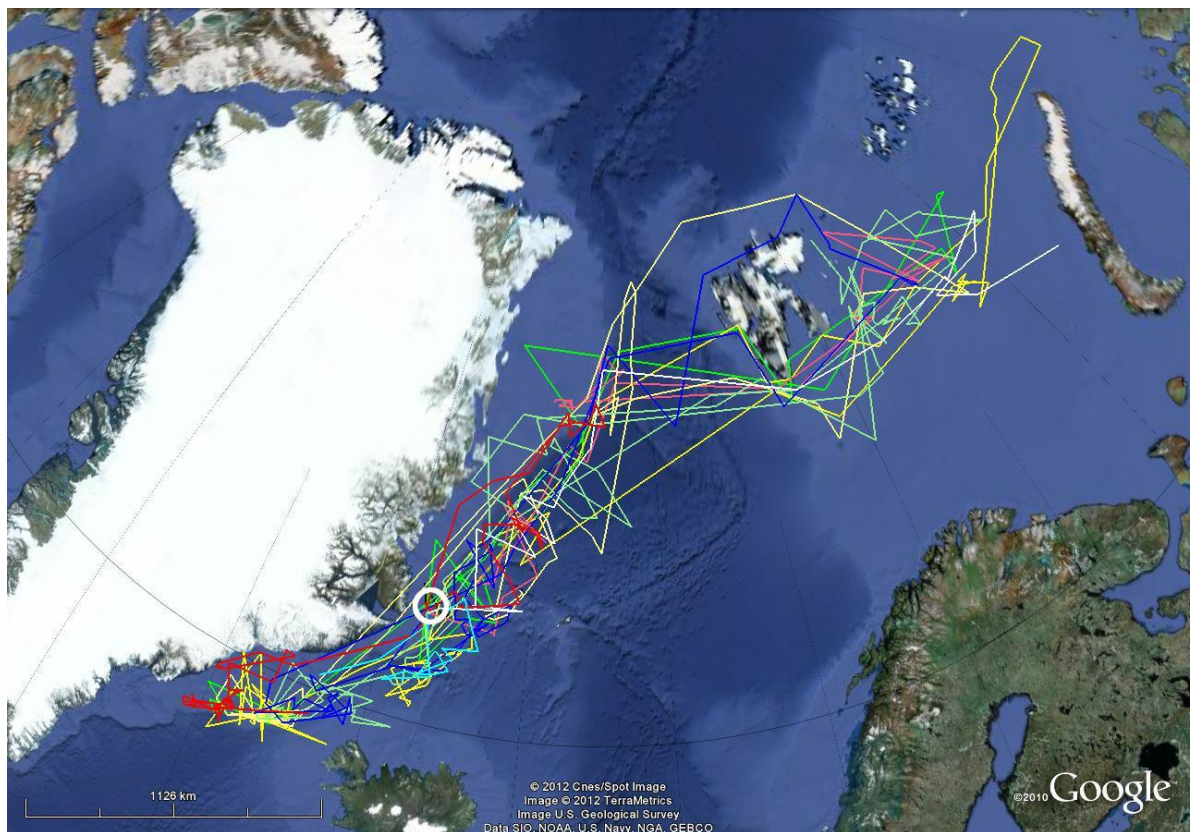
Harp seal pups are divided into arbitrary easy recognisable age categories and are based on pelage colour and condition, general appearance and movement. First, "newborn" pups are characterised by awkward movements and the presence of a wet placenta nearby, this is typical for pups younger than 24 hours. Pups get their lanugo fur stained by the amniotic fluid and stay this way a few days after birth, pups in this stage are called "yellowcoats". When the staining fades after ~3 days after birth they are referred to as "thin whitecoats". Pups rapidly gain weight over the next days and are referred to as "fat whitecoats". After about 10 days after birth the new fur starts to grow in and can be seen trough the lanugo fur, at this stage the pups are called "greycoats". Soon after, at the age of ~15 days, pups begin to shed the lanugo fur these are called "ragged-jackets", because they shed their lanugo fur in patches (Nansen, 1924). Lastly 18-30 days after birth the pups are completely shed, and they are called "beaters" (Stewart & Lavigne, 1980). "Beaters" are characterised by a pelage with dark spots on a lighter background. This background colour is darker on the back and lighter on the stomach (Nansen, 1924). Pups are called "beaters" for the rest of their first year of life.

After the pups are weaned, they lie on the pack ice and finish their moult into the "beater" phase. Pups normally stay fasting on the ice for around 2 weeks before they start feeding (Sergeant, 1991). The pups can with ease fast for 6 weeks and grow when food becomes available (Worthy & Lavigne, 1983). They start diving quite early after they weaned and use the fasting period to train foraging and swimming abilities (Worthy & Lavigne, 1983).

Moulting occurs on the pack ice in the same general area as the whelping, this starts in the end of April and in the beginning of May, immatures and males moult first, and the females join them later (Sergeant, 1991). The animals then complete their moult within one month (Nansen, 1924). In the period between the whelping and moulting, the animals stay mostly in the pack ice with low diving activity, probably opportunistically hunting prey that live close to the pack ice (Folkow et al., 2004).

Harp seals are a migratory species and is known to migrate over vast distances. Known distribution of the Harp Seals in the Greenland Sea stock, as described in Folkow, et al. (2004), and can be seen in **Fig. 1.** The seals in Folkow et al. (2004) were tagged in the moulting period in May (See the white circle in **Fig. 1**). After the moulting the animals migrate and follow the pack-ice edge northwards towards the Barents Sea. They stay in the Barents Sea over the summer and autumn and return to the Denmark Strait in the winter (Folkow et al., 2004). In the end of March, they return to the whelping grounds in the Greenland Sea (See the white circle in **Fig. 1**). Although distribution of the adult animals is relatively well known, little is known of the distribution of pups of the year. According to Nansen (1924) the pups follows the pack ice and hunts crustaceans in the waters close to the pack ice. Rasmussen and Øritsland (1964) did a mark-recapture experiment in the Greenland Sea, that did show that the pups drifted with the pack-ice southwards, but did not pass the south end of Greenland, indicating that they then began following the ice northwards again.

Figure 1: Overall movements of 10 adult harp seals from the Greenland Sea stock. The seals were tagged in the white circle in 29-31 May 1999 with satellite linked dive recorders (SLDRs) (Blix et al., 2013 (adapted from Folkow and colleagues, 2004)).

4

1.3 Telemetry

Catching or studying seals in the open ocean is very challenging and costly, therefore it is much easier to catch them when they are congregated within a certain area, for example in the whelping period or moulting period. For long the diving depth of seals was determined by seals which became entangled in fishing equipment, for instance, two harp seals became entangled on 190 meters and 280 meters depth, respectively, in the early 20th century (Nansen, 1924). Later, Kooyman (1965), transformed the field when he made the depth-time recorder, which he deployed on Weddell seals (*Leptonychotes weddellii*). The challenge with these early depth-time recorders is that the animals had to be recaptured to receive the data.

The research field was transformed yet again when the satellite-linked transmitters became available. Satellite-linked transmitters have been used the last three decades (Tanaka, 1987; McConnell et al., 1992). This has made it possible to follow the location and dives in real time, and the tags does not have to be recovered to receive data from them. This has made it possible to deploy satellite-linked transmitters on animals which return to a specific site (e.g. beach) where they can be recaptured.

The early versions of these satellite transmitters used the transmitter system called CLS Argos and is located on the NOAA-satellites (National Oceanic and Atmospheric Agency) (Argos, 2016), and this is still used to this day. Many newer tags use GPS (Global positioning system), which gives locations very precisely, but is rather costly (Sea Mammal Research Unit, n.d. a). Near shore deployments can use GSM (normal mobile phone coverage), as this can transmit more date due to a higher bandwidth (Sea Mammal Research Unit, n.d. b).

1.4 Diving

To survive as a marine mammal, harp seals must dive. Marine mammals have several adaptations to be able to dive. They store oxygen in the muscles, on myoglobin, and in the blood, on haemoglobin. Total body oxygen stores (Burns et al., 2007) and aerobic diving limit (ADL). Long diving specialists like the Hooded seal, which can dive down to over 1000 meters and durations up to 70 minutes (Folkow, 2001). The harp seal is a more moderate species like the harp seal.

One way to measure diving capacity is the aerobic diving limit (ADL). ADL is measured experimentally to the maximum length of a dive that do not elevate lactate over resting levels (Kooyman et al., 1980). For adult female Weddell seals weighing 450 kg the ADL is between

20 and 25 minutes (Kooyman et al., 1980). ADL for juvenile Weddell seals were 10 minutes and 13 minutes for the 140 kg and 200 kg juveniles, respectively (Kooyman et al., 1983). Juveniles exceeded their ADL more regularly than the adults did, and this means that the juveniles need a lot more time in the surface to recover from the dives, and process the lactic acid (Kooyman et al., 1983). These experimental free-range measured ADL measurements are unfortunately not applicable for most seals as most other seals live in open water, therefore an estimation of ADL based on total oxygen stores (TO_2) can be calculated. Calculated ADL (cADL) (Costa et al., 2001) is calculated for a range of pinnipeds, and luckily it is calculated for the harp seal, both adult female harp seals with a cADL of 12.1 minutes and pups at 4.3 minutes, respectively (Burns et al., 2007). Most dives of a diving animal are within the ADL, this is to keep the proportion of resting at the surface at a minimum to maximise the foraging time. Most diving mammals does not exceed their ADL more than 5% of the dives (Kooyman et al., 1980). Some benthic feeding species may have a higher proportion of dives above ADL as the payoff of long recovery times in the surface is worth the prey they are caching (Costa et al., 2001). Using this knowledge, it is possible to approximate the ADL by using computer models based on the diving duration. One of these models is the quantile model (asymptotic exponential-rise model) to estimate ADL (Bradshaw et al., 2007). They used 97.5 percentile to estimate the ADL.

Diving behaviour of adult harp seals is well studied and shows that they are adept divers. In the Barents Sea most dives were shallower than 200 meters being around the mean bottom depth of the Barents Sea (Folkow et al., 2004; Nordøy et al., 2008). They are known to dive down to over 500 meters depth with records of 510 meter (Nordøy et al., 2008) and 568 meters depth (Folkow et al., 2004). Little is known about the diving behaviour of the harp seal pups.

1.5 Aim of the study

This project represents the first study to investigate the development of diving performance, behaviour and distribution of weaned harp seal pups and how they cope with the transition to a mainly aquatic/diving lifestyle during their first months of life. The main aim of this study was to explore the development of diving performance of the seal weanlings throughout their first months of life. A secondary goal was to explore how, where and when they migrate and what part the water column they use, and if they use structures in the ocean, such as shelf breaks or the ice edge, as focal areas of diving and feeding.
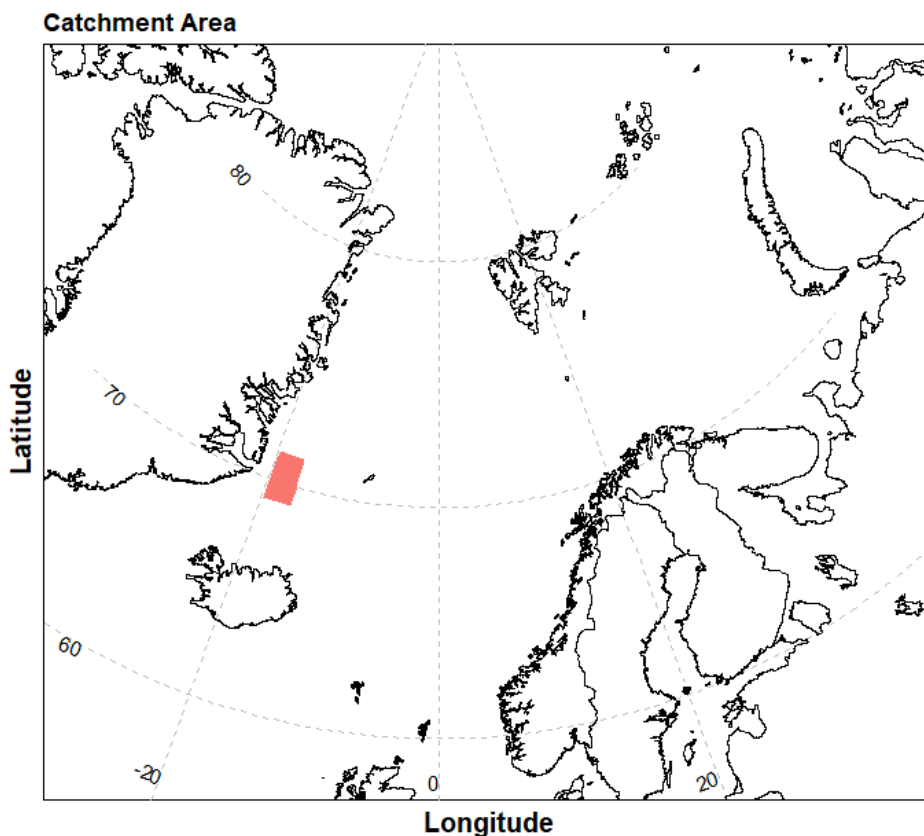
2 Materials and methods:

2.1 Collecting:

Weaned harp seal pups (n=26) were caught off the dense pack ice on a cruise to the Greenland Sea in early April of 2017. Collection of the animals were granted by the The Ministry of Fisheries, Hunting and Agriculture, In Greenland (Verbal note from Det Danske Utenrigsministeriet referanse JTHAV J.nr.2017-1054). Funding was provided by "Råstofstyrelsen" Denmark/Greenland and Greenland Institute of Natural Resources (GINR): 2016-2017. Funding of project entitled "Tagging of harp seal pups in the Greenland Sea" (US $ 330.000.). Project leader: Dr. Aqqalu Rosing-Asvid, GINR, Nuuk, Greenland.

The seals were caught on the dense pack ice and drift ice in the area outside Ittoqqortoormiit (formerly known as Scoresbysund), within the coordinates 69°10' N to 71°14' N, and 16°35'W to 19°45'W (**Fig. 2**).

Figure 2: *Area where the animals were caught. The red rectangle indicates the catchment area.*

When the ship came into whelping patches, animals with pelage in the "ragged-jacked" and "grey-coats" phase (Stewards & Lavigne, 1980) were selected. This is when the lanugo is replaced with juvenile hairs and is either seen through the lanugo, "grey-coats", or the lanugo

has begun falling off, "ragged-jacked". When the lanugo is fully lost the pups are called "beaters" and were at least ~18 days old. Pups were approached by the ship, and a person with a burlap sack was lifted onto the ice floe with the help of a crane with a cage. The pup was then caught by hand, and the burlap sack put around the animal to keep it calm.

When the pups were caught, some morphometrics were done. The length, girth and weight were taken. Further morphometrics were done on the release (**Table 1**).

Table 1: Animal information. *With Animal ID (n=26), Sex, Mass (kg) at the release date, Latitude and Longitude of release location, Tag Date (same as release date), End Date (Last transmission from the tag), and Longevity of the tag in days. All animals are present (n=26), with both SMRU animals (n=16) indicated by the ID "L***" or "M***", and SPLASH animals (n=10), indicated by ID "W***".*

Animal ID	Sex	Mass (kg)	Latitude	Longitude	Tag Date (dd.mm.yyyy)	End Date (dd.mm.yyyy)	Longevity (days)
L516	Male	23.9	69.31360713	-18.55945908	14.04.2017	11.05.2017	27
L519	Male	30.5	69.31341235	-18.55416828	14.04.2017	11.07.2017	88
L520	Male	26.5	69.32076418	-18.51438263	14.04.2017	10.05.2017	26
L517	Male	21.6	69.31341235	-18.55416828	14.04.2017	14.04.2017	0
L484	Female	23.6	69.31360713	-18.55945908	14.04.2017	14.06.2017	61
L521	Male	31.5	69.32076418	-18.51438263	14.04.2017	08.06.2017	55
M491	Male	23.9	69.5230047	-18.95047753	12.04.2017	11.05.2017	29
M490	Female	31.1	69.23853222	-18.43616428	13.04.2017	03.06.2017	51
M487	Male	28.4	69.2088525	-18.35827882	13.04.2017	05.06.2017	53
M492	Male	30.2	69.32275983	-18.51203607	14.04.2017	18.06.2017	65
M489	Male	30.2	69.26044178	-18.56271858	13.04.2017	11.07.2017	89
M488	Male	31.2	69.3220252	-18.51399933	14.04.2017	18.07.2017	95
M486	Male	31.4	69.25995388	-18.56445018	13.04.2017	14.05.2017	31
M483	Male	26.4	69.2055355	-18.35988327	13.04.2017	14.05.2017	31
M485	Female	27.6	69.23967595	-18.43426608	13.04.2017	19.07.2017	97
M518	Male	25.3	69.47647373	-18.81766762	12.04.2017	16.06.2017	65
W708	Female	29.2	69.26044178	-18.56271858	13.04.2017	10.05.2018	392
W709	Male	28.6	69.25995388	-18.56445018	13.04.2017	22.08.2017	131
W710	Female	34.5	69.23967595	-18.43426608	13.04.2017	27.04.2018	379
W711	Female	30	69.5222516	-18.92458222	12.04.2017	05.01.2018	268
W712	Female	31.2	69.32275983	-18.51203607	14.04.2017	18.09.2017	157
W713	Female	26.4	69.3220252	-18.51399933	14.04.2017	16.08.2017	124
W714	Female	24.3	69.23853222	-18.43616428	13.04.2017	17.05.2018	399
W715	Female	31.3	69.47655213	-18.81764365	12.04.2017	21.04.2018	374
W716	Male	33.6	69.2088525	-18.35827882	13.04.2017	25.04.2018	377
W717	Female	29.1	69.2055355	-18.35988327	13.04.2017	20.02.2018	313

To make sure the juvenile fur was long enough for the transmitters to adhere to (it should be over 5mm) the pups was stored onboard in pens on the deck. Pens were ~1*2m², and the pups did have some fresh snow supplied to them, as a source of water. Food was not offered to the animals as they do not usually eat in this period. Pups can fast for up to 6 weeks post weaning with no adverse effects (Worthy & Lavigne, 1983).

2.2 Tagging:

Tagging of the animals was granted by the Norwegian Food Safety Authority (Mattilsynet, FOTS11546). As the seal pups were collected in the "ragged-jacked-phase", there was some waiting until the lanugo fell off and the underneath hair was long enough to fasten the tags (>5 mm). This amount of hair was needed to get a secure fit.

The tagging was done as described in Fedak et al (1983), with a few modifications to the original procedure. The seal pups were restrained to a plywood board with belts, with a burlap bag over the head, to keep the animal calm during the procedure. The whole procedure did not take more than 5 minutes in total. Then the tag location (back of the neck) was thoroughly washed with acetone to remove any oils from the fur. Fast setting superglue (Loctite® 422, Henkel AG & Company, KGaA, Düsseldorf, Germany) was applied to the back of the tag with a scuffed surface, and the tag was then placed on the cleaned patch of fur on the upper back. When the glue was set, after approx. 30 seconds, the seal was unstrapped and brought into a holding pen, where it was until a suitable ice floe for release was found.

When a suitable ice floe was found the seals were then released on the ice-flow. There was one sealing vessel ("Havsel") in the area in the start April in 2017, therefore most of the animals were also marked with orange spray paint to not get harvested. Some animals were photographed when freed (**Fig. 3 and cover photo**).

2.2.1 Tags

The satellite tags that were used was of two types and of three models. We used 16 SMRU Low Profile SRDL units(Sea Mammal Research Unit Low Profile Satellite Relay Data Logger) (Sea Mammal Research Unit, University of St Andrews, St Andrews, UK), measuring 102 mm×72 mm×24 mm and weighing 305 g in air (Hereafter referred to as SMRU-Tags). Moreover, we used two models from Wildlife Computers (Wildlife Computers Inc., Redmond, WA, USA) with 7 SPLASH10-F-296, measuring 86 mm×85 mm×29 mm and weighing 192 g in air and 3 SPLASH10-F-297, measuring 86 mm×55 mm×26 mm and weighing 130 g in air (These are hereafter collectively referred to as SPLASH-Tags). The back of the tags was scuffed up with a sandpaper to provide good adherence for the glue.

Fig. 3: *Two of the released tagged harp seal pups in the "ragged-jacked" phase, note the location of the tags on the upper back. The pup in the front (Animal ID = W715) has the SPLASH10-F-296 tag. The pup in the back (Animal ID = M518) has the SMRU low-profile-SRDL. (Photo: A. Malde)*

2.2.2 Functional properties

Both the SMRU-tags and the SPLASH-tags use the Argos system to relay data back to shore. Relaying data over the Argos system has a transmission limitation, the maximum data that can be sent in one transmission is 32-bytes (248 bit) (Argos, 2016). This means that the tag cannot send everything it records from the environment, but the tag can send a compressed version of the data which can be used for analysis. SMRU-tags and SPLASH-tags have different ways to compress and relay the data.

The SMRU-tags used in this study include a depth sensor (with a resolution of 5m at 2000m, and a depth rating at 500 m) and defines a dive if the tag is deeper than 1.5 m and for 8 seconds on the descend, and if the tag is at a depth shallower than 1.5 m on the ascent the dive ends (Sea Mammal Research Unit, n.d.a). These tags send both single dives and summaries. The single dives give a lot of detailed information like dive profile and accelerometers, which was not used in this study. These tags also take temperature at different parts of the dive, this was also not explored in this study. After each recorded dive the maximum depth and the duration is stored and transmitted.

Both tag models of the SPLASH variety send back the same data format and was therefore considered the same with regards to data (SPLASH10-F TAG PRODUCT SHEET, n.d.). The SPLASH-tags used in this study define a dive if the tag is wet, i.e. when the tags wet/dry sensor gets dry the dive is over (Depth sensor range, 0 - 2000 m and resolution of 0.5m). The

data was sent back as summaries and in predetermined bins. There is binned data for depth (The bins can look like this, bin1 = <1m, bin2 = 1-5 m, bin3 = 5-10m, etc.), dive duration, time at depth (proportion of time spent at different depth) and haul out. Data binning allow the SPLASH-tags to send back large amounts of dives in a very compact format, but this was on the expense of the temporal resolution the SMRU-tags have. SPLASH-tags do take some absolute values, like maximum depth within a period. Unfortunately, the SPLASH-tags did not save the maximum diving duration data as absolute values.

2.3 Data treatment:

The software "R" (R Core Team, 2018) was used for all data treatment. R version 3.5.1 (2018-07-02) (R Foundation for Statistical Computing, Vienna, Austria). Not all the 26 animals could be used for all aspects of this study as one of the animals stopped transmission the same day as released (**Table 1**, L517), and another animal did for some unknown reason have enough locations recorded but had however sufficient amount of diving data (**Table 1**, W708).
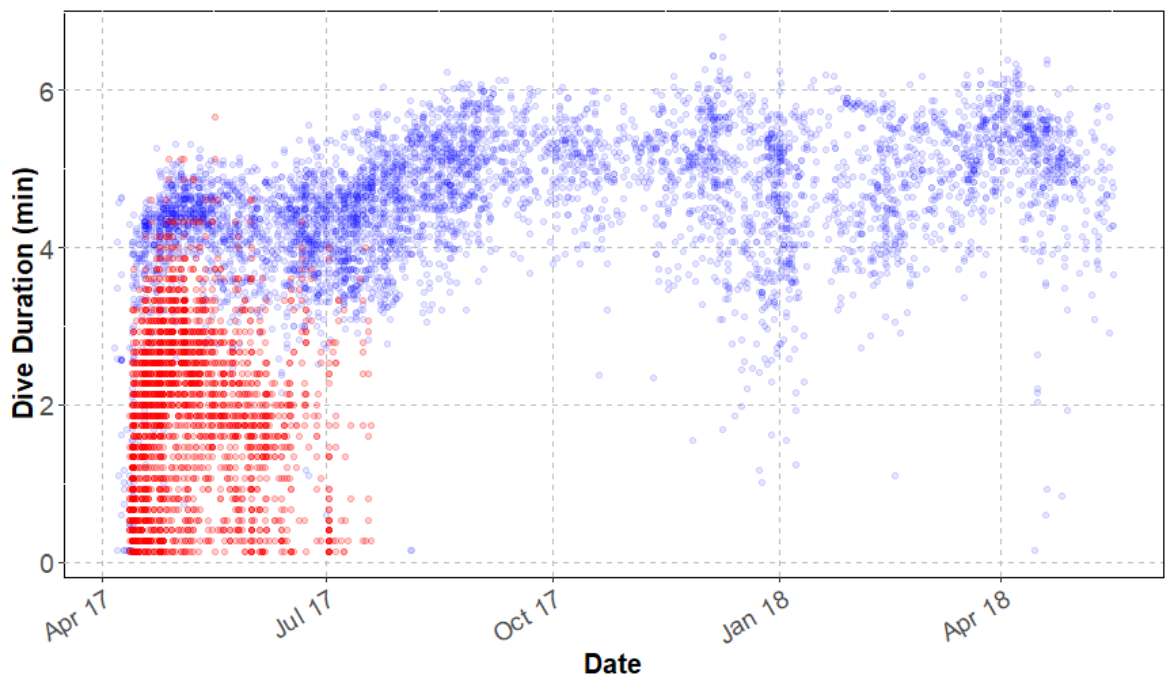
2.3.1 Location data

Both SMRU and SPLASH-tags sends back location data based on the Argos system of location estimation. This system estimates the position of the tag by doppler shift, and the more transmissions the satellite captures the better the location estimate becomes (Argos, 2016). The location estimates get a score by Argos after how accurate the estimation is, this score is called a location class (LC) (Argos, 2016). A LC 3 is the most accurate with error radius of < 250 m, a LC 2 means the error is 250m< <500m, a LC 1 means the error is 500m< -< 1500m, and lastly a LC 0 means the error is >1500 m. LC A and B are not given error estimates by Argos. LC Z is classified as an invalid location by Argos (Argos, 2016). Vincent and colleagues (2002) tested these LCs experimentally on seals and found that they mostly were correct as Argos lists them now, but LC A locations were of a similar error to that of LC 1, and much better than LC 0.

The SPLASH-tags used in this study, also were equipped with Fastloc® GPS, which is a way of obtaining position trough GPS relaying this back via the Argos system (Argos, 2016; SPLASH10-F TAG PRODUCT SHEET, n.d.). This location data for the SPLASH-tags was not explored in this study, as the Argos positioning system was deemed adequate and comparable.

To get a good presentation of the path the animals took, the location data had to be filtered. The filter function 'sdafilter' in the package "argosfilter" (Freitas, 2012) in R was used. This filter uses the algorithm described in Freitas et al. (2008), and then removes all the locations that has LC Z (classified as invalid locations by Argos (Argos, 2016)). Lastly the filter removes all the locations which have unrealistic swimming speeds (>2m/s) using the algorithm described in McConnell and colleagues (1992), unless they are closer than 5 km to the previous location.

2.3.2 SPLASH duration model:

Due to the challenge that the SPLASH-tags did not measure the absolute duration of dives, we developed a model that tried to estimate the likely maximum dive duration across the range of observed depths. This was based on the SMRU data, for which depth and duration data exists. To find this upper edge, we fitted a quantile regression model (Koenker & Bassett, 1978), using the 95% quantile. The median of this model was the most reliable estimate. The SPLASH duration model can be seen in **Fig. 4** where it was plotted over the real diving data from the SMRU-tags.
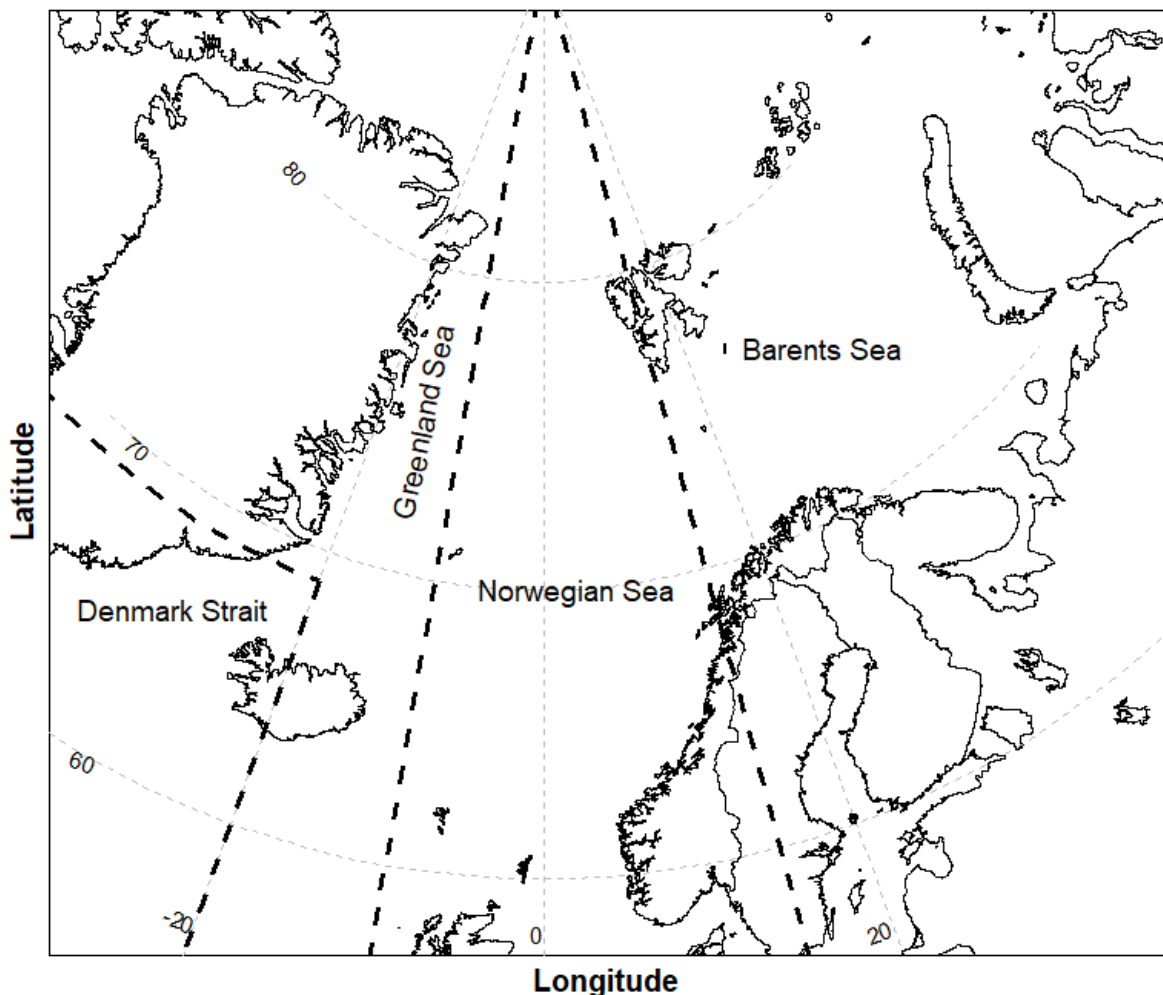

Figure 4: Predicted dive duration of seals equipped with SPLASH-tags, based on the quantile regression model developed on SMRU depth and duration data. SMRU depth data is in red, and the predicted duration of the SPLASH animals in blue.

2.4 Area differentiation.

The study area was divided into 4 main areas, based on the characteristics in the different areas (**Fig. 5**). The first; Denmark Strait, is defined as south of 69°N and west of 20°W, this area is characterised by a shelf sea of approx. 500 meters depth, with a trough of 1000 meters of depth. The second area was the Greenland Sea which is defined as west of 10°W, except of the Denmark Strait. The Greenland Sea is, at least mostly in the northern part (north of 70°N), a shelf sea with approx. 500 meters of depth. Thirdly, the Norwegian Sea was defined as east of 10°W and west of 15°E. The Norwegian sea is mostly very deep and do reach over 3000 meters in some areas, but in this definition some of the shelf sea around Svalbard, which is shallow, is included. Finally, the Barents Sea was defined as east of 15°E, and incorporates the Barents Sea shelf, which is shallow at approx. 230 meters depth.

Figure 5: The different subareas within the study area. Black dashed lines reflect the different subareas within the study area; Denmark Strait (Latitude under 69 and Longitude under -20), Greenland Sea (Longitude under -10 except Denmark Strait), Norwegian Sea (Longitude between -10 and 15) and Barents Sea (Longitude over 15). Many of the figures further on in this thesis has a colour coding for the different areas; with organge being the Denmark Strait; green being the Greenlad Sea; blue being the Norwegian Sea; and lastly red being the Barents Sea.
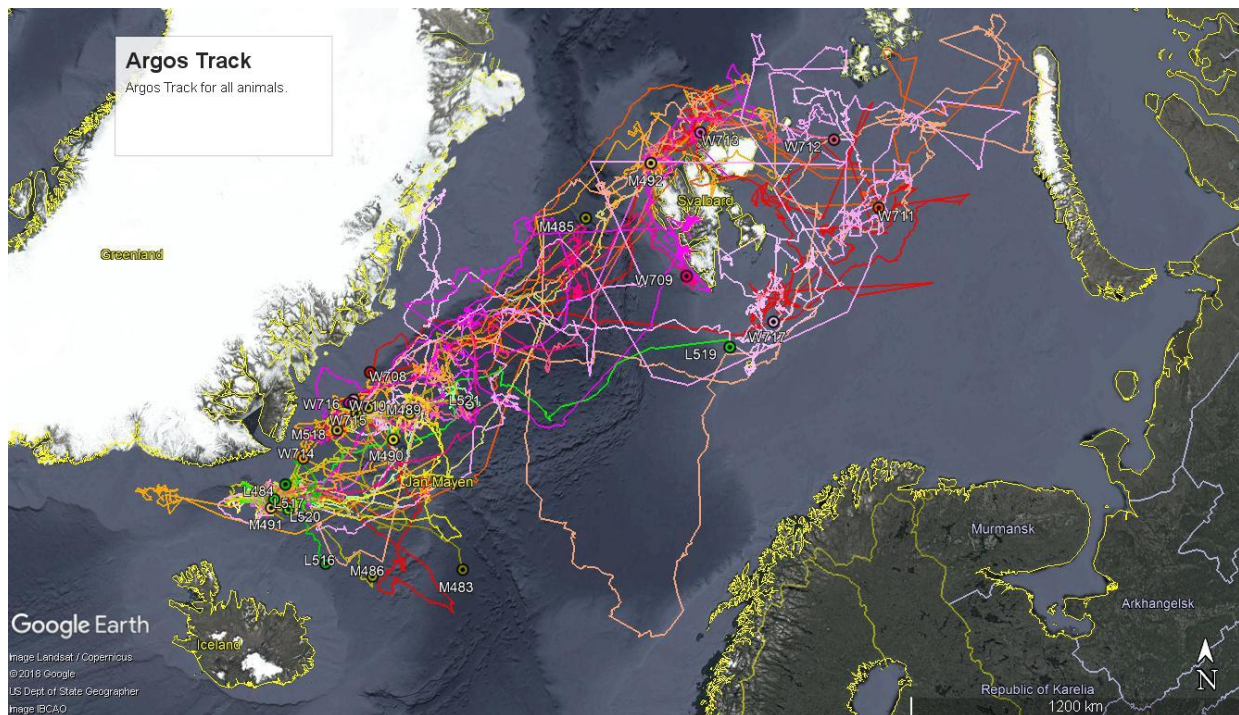
13

2.4 Figures:

All figures were also made in "R" (R Foundation for Statistical Computing, Vienna, Austria), using RStudio® (RStudio®, Boston, MA, USA). The package "tidyverse" (Wickham, 2017) was used in the plotting of the figures. Google Earth Pro version: 7.3.2.5776 (©2019 Google Inc. CA, USA) was also used in the creation of **Fig. 6**.

3 Results:

3.1 Distribution

After the seals were released at 13th April 2017 (±1 day), see figure 9 in the Appendix. **Fig. 6** shows the whole path of each animal, the different colours indicate different animals, see **Table 1** for longevity for each tag. Here we can see that there is some radiation in the Greenland Sea. When the pups were in the Norwegian Sea they were mostly going north-west or south-east following the ice-edge. The pups that reached the Barents Sea they mostly were in the Northern Barents Sea probably feeding at the ice-edge. There were also a lot of activity around Svalbard, especially on the west and north side. Some single individuals went on longer radiations, like the pup (peach- colour on **Fig. 6**) that went on a roundtrip down to Lofoten off the coast of Norway, another (light purple – colour on **Fig. 6**) went into the coast of East Greenland. Yet another (Orange-colour on **Fig. 6**) stayed for some time in the Denmark Strait.
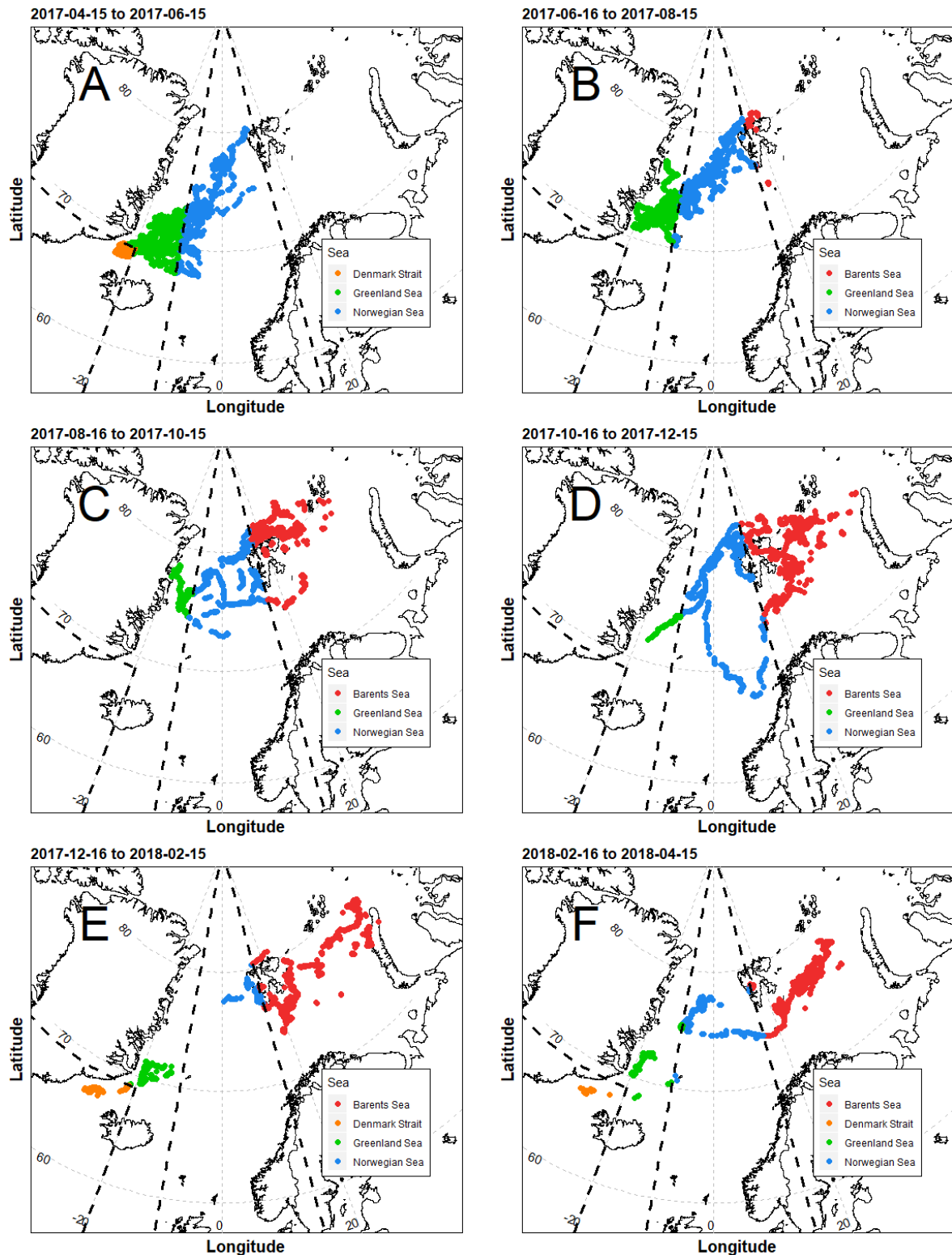
Figure 6: Overall distribution. Overall movements of all seal pups (n=26) in the period from tagging (April 12, 2017) to the last transmissions of all seal pups (May 17, 2018). The last known location of the animal at the end of a track and marked with the animal ID. Green hues to yellow hues on the tracks, indicates animals tagged with the SMRU tags (n=16), and orange, red and pink hues indicate animals tagged with SPLASH tags (n=10).

3.1.2 Seasonal distribution

For a more nuanced picture of the distribution, see **Fig. 7**, which shows all locations within a period of two months, from the day after release in April of 2017 until a year after release in the middle of April of 2018.

In **Fig. 7** the distribution of the seal pups throughout the first year of life can be observed. The first two months after they are released (**Fig. 7A**) they first drifted with the ice a little bit southward. After, this drifting they soon began to move east/north-east. Some animals followed the pack-ice northwards, and some animals went straight east or south into the open Norwegian Sea. Within these two months there are animals which actually migrated all the way to the Svalbard archipelago. In the summer, June to August (**Fig. 7B**), pups kept close to the pack ice, and moved further north following this. Most animals were in the Norwegian Sea, over deep water and were associated with the pack ice. Some animals did reach the Barents Sea, both on the south side and the north side of Svalbard. Early autumn (**Fig. 7C**) the pups move even more north-east and into the Barents Sea. One animal went to the east coast of Greenland. Most of the activity in this period was concentrated on the north side of Svalbard. In the autumn/early winter (**Fig. 7D**) the pups were mostly in the Barents Sea, with

15

most of the activity in the northern part of the Barents Sea. One seal (W715, can be seen on **Fig. 3**) went on a roundtrip from the north of Svalbard and all the way down to Lofoten archipelago on the coast of Norway and back up again to the Barents Sea within these two months. This roundtrip is at least 1900 km and happened within a period of two months. One seal was also moving from the ice-edge outside Svalbard and down the coast of Greenland into the Greenland Sea. Winter distribution (**Fig. 7E**) did show a divided population, with most of the activity in the Northern Barents Sea and around Svalbard, but also some activity in the Denmark Strait and the Greenland Sea. In the late winter and early spring pups were still in split into two parts, one in the Barents Sea and one in the Denmark Strait/Greenland Sea. Curiously both the individuals in the Barents Sea and the individuals in the Denmark Strait/Greenland Sea moved toward the Greenland Sea. In late April and the beginning of May, the seals moved further into the Greenland Sea pack ice (**Fig. 20,** in the appendix) this movement coincide with the moulting (Folkow et al., 2004; Nansen, 1924).
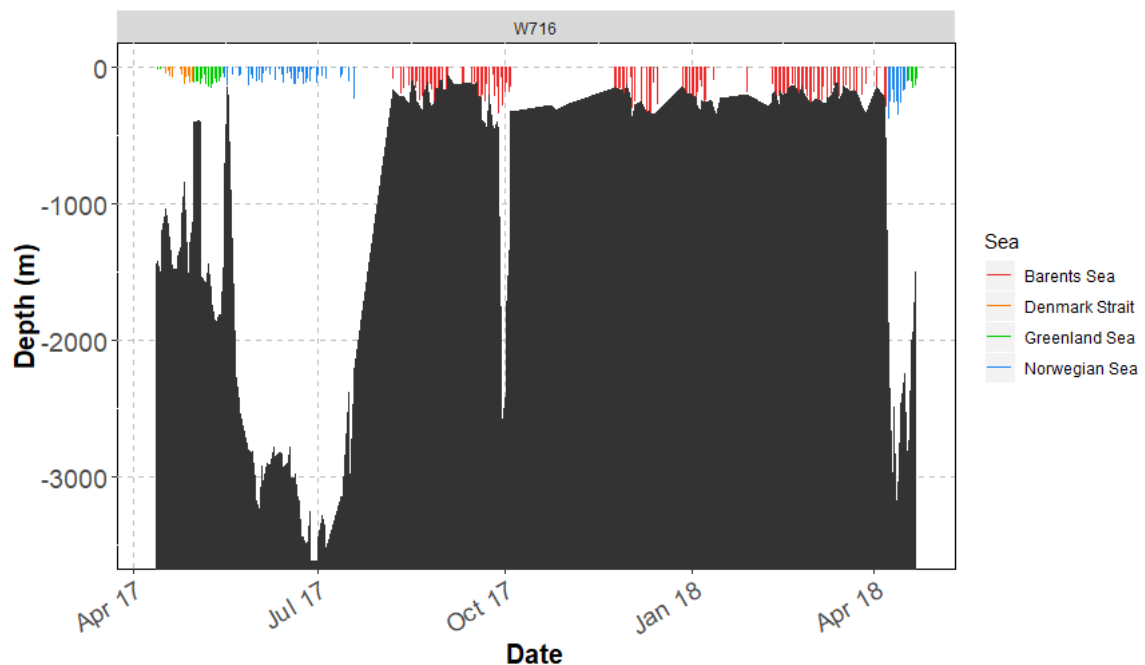
Figure 7: Distribution every 2 months. *All sub-figures show all observations within a 2 months priod. A: April 15 to June 15, 2017 (n=16), B: June 16 to August 15, 2017 (n=10), C: August 16 to October 15, 2017 (n=7), D: October 15 to December 15, 2017 (n=7), E: December 16, 2017 to February 15, 2018 and F: February 16 to April 15, 2018 (n=5).*

3.2 Diving behaviour

The diving behaviour is both the use of the water column (**Fig. 8, 9 and 10),** and the duration of the dives **(Fig. 11, 12 and 13).** The diving performance is how the seal pup dives, and in this case how deep it dives and the duration of these dives.
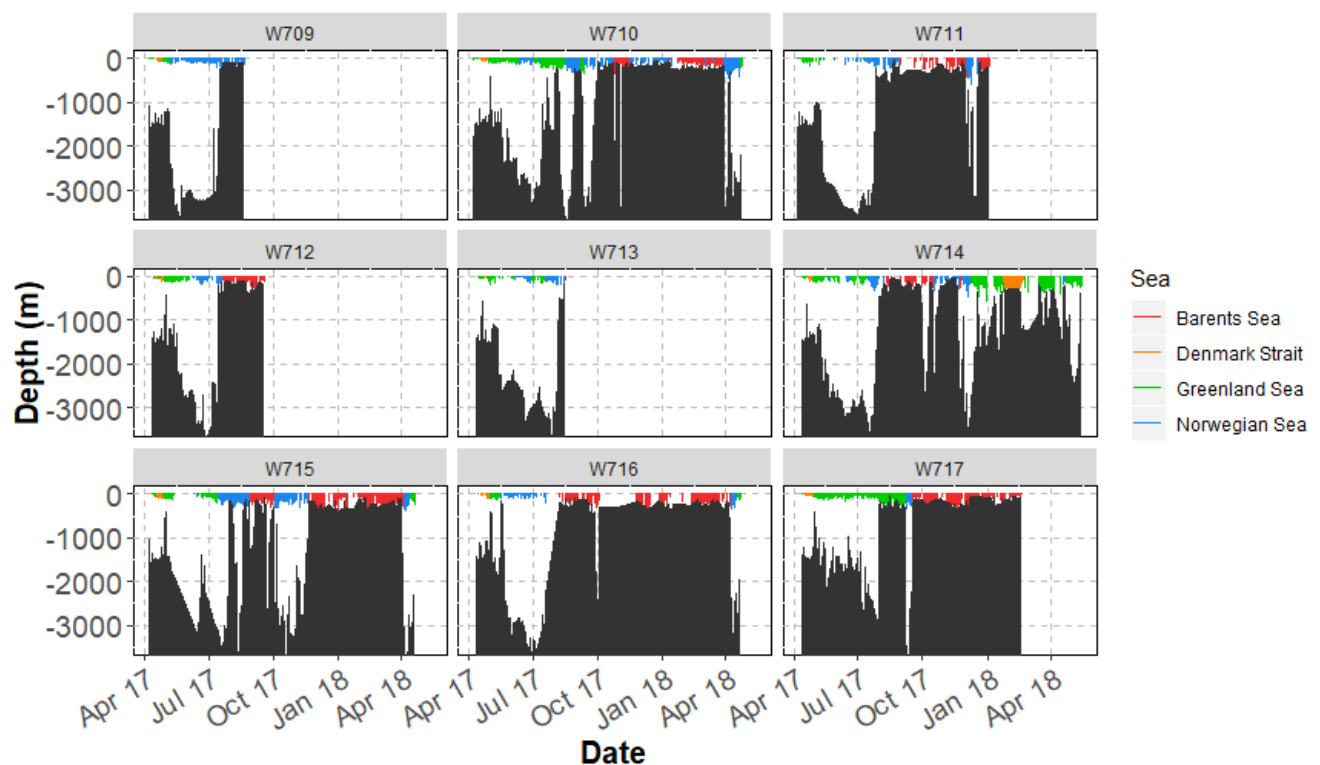
3.2.1 Depth

To show how the harp seal pups dive and use the water column, one example is shown in **Fig. 8,** which shows a seal who stay in the Barents Sea the whole winter. This seal shows a move from open water onto the shelf sea in the middle of October and stays in shallow water over the winter. There were some gaps in the diving record of this animal, but it is reasonable to assume that the seal is in the Barents Sea in these periods because it was there before and after the gaps. **Fig. 17** in the Appendix shows the migratory path of this specific seal, it can also be seen in **Fig. 6** as the red track. W716 enters the Barents Sea shelf in the end of July, but the first diving record is a bit later. The pup (W716) then stays in the Barents Sea for the whole autumn and winter, before returning to the West Ice in the spring of 2018. **Fig. 8** shows the seal departs from the shallow Barents Sea in the start of April 2018. While in the Barents Sea, at age of ~5 months, the seal regularly dives down to the bottom, which is at approx. 230 meters depth (Loeng, 1991). All the coloured segments are the max dives, and therefore does not show the exact use of the water column.
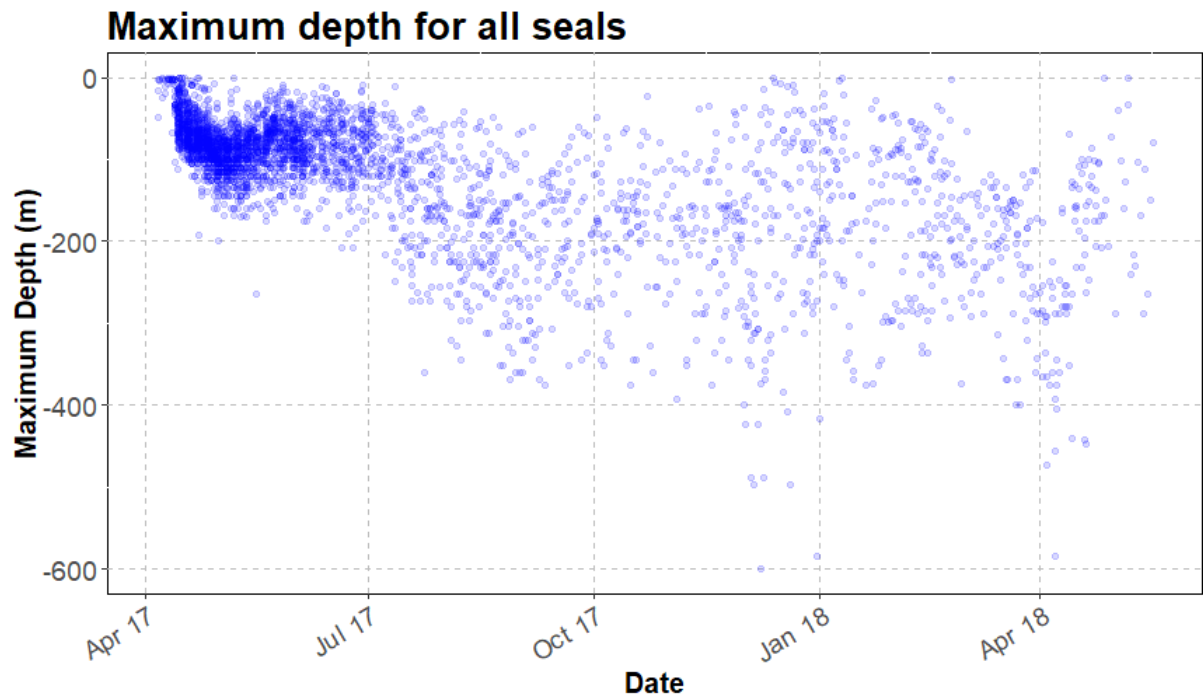

Figure 8: Absolute diving depth one animal (Animal id W716). The black area on the figure is the bottom, and the coloured segments are the deepest dives within a 4-hour period. The colours of the segments represent different subareas, with Barents Sea in red, Denmark Strait in orange, Greenland Sea in green and Norwegian Sea in blue. Gaps in the data is periods where the tag for some reason did not transmit (See discussion 4.3).

18

The use of the water column for all SPLASH seals is shown in **Fig. 9**. The seal from **Fig. 8** (W716) can be seen in the middle bottom panel. All the SPLASH seals reached the shelf sea before the transmitters stopped transmitting. The seals were able, and regularly dove to the bottom of the of the sea, this happened in the Greenland Sea (green section in subplot W717), the Norwegian Sea (blue section in subplot W710), the Denmark Strait (orange section in subplot W714) and lastly in the Barents Sea (red sections in most subplots in **Fig. 9**). Comparative figures for SMRU animals can be found in the **Fig. 18**, in the appendix. Because of the short longevity of the SMRU-tags in this study, very few (n=2) of the SMRU animals came into the shallower seas in the western Norwegian Sea and Barents Sea. All of the dives in both **Fig. 9** and **Fig. 18** are maximum dives within a summary period(4h SPLASH, and 24h for SMRU animals)

Fig. 9: Absolute diving depth all SPLASH-animals. Sub plots for all SPLASH-animals with diving and spatial data (n=9). The black area on the figure is the bottom, and the coloured segments are records of the deepest dives within a 4-hour period. The colours of the segments represent different subareas, with Barents Sea in red, Denmark Strait in orange, Greenland Sea in green and Norwegian Sea in blue.
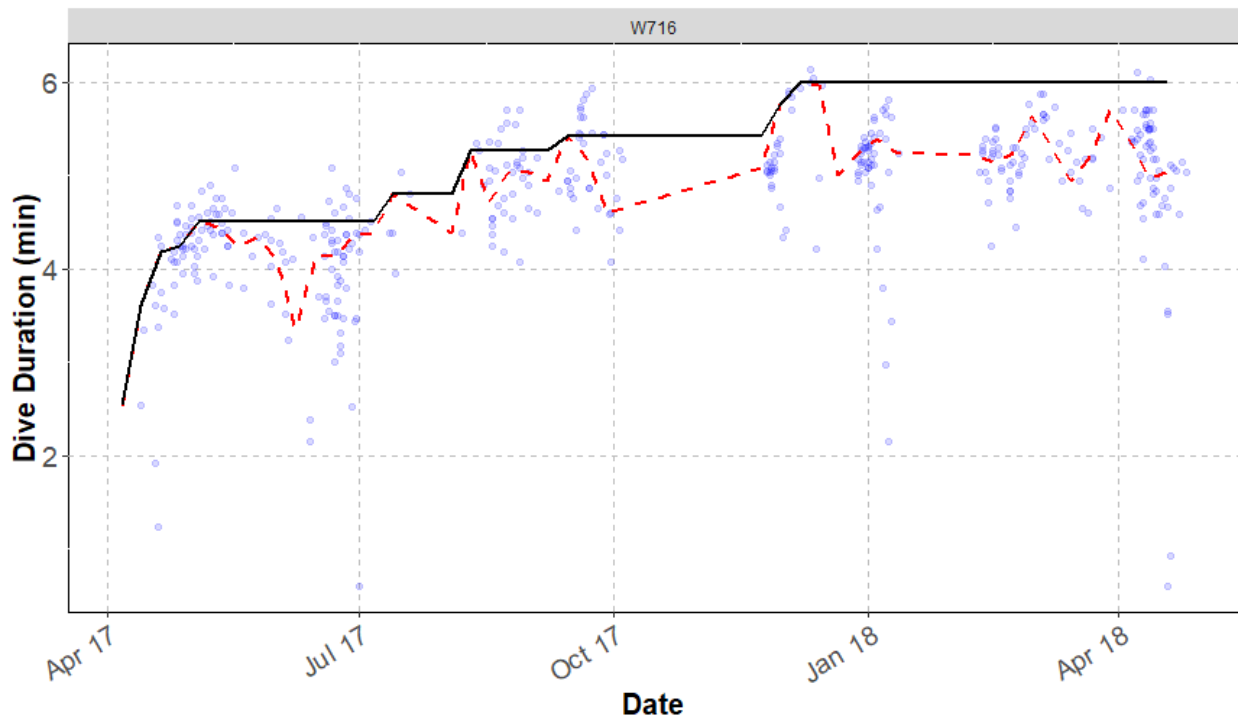
The maximum dive depth recorded was 600 meters (**Fig. 10**), with very few records of depth over 400 meters. Most maximum depth records were around 200 meters, which is also the mean depth of the Barents Sea. The higher density of dives in the start is because of a higher number of active transmitters.

Figure 10: Maximum diving depth for all animals. Maximum dives per period (Period for SMRU is 24 hours and period for SPLASH is 4 hours) for all seals. Blue dots are the observations.
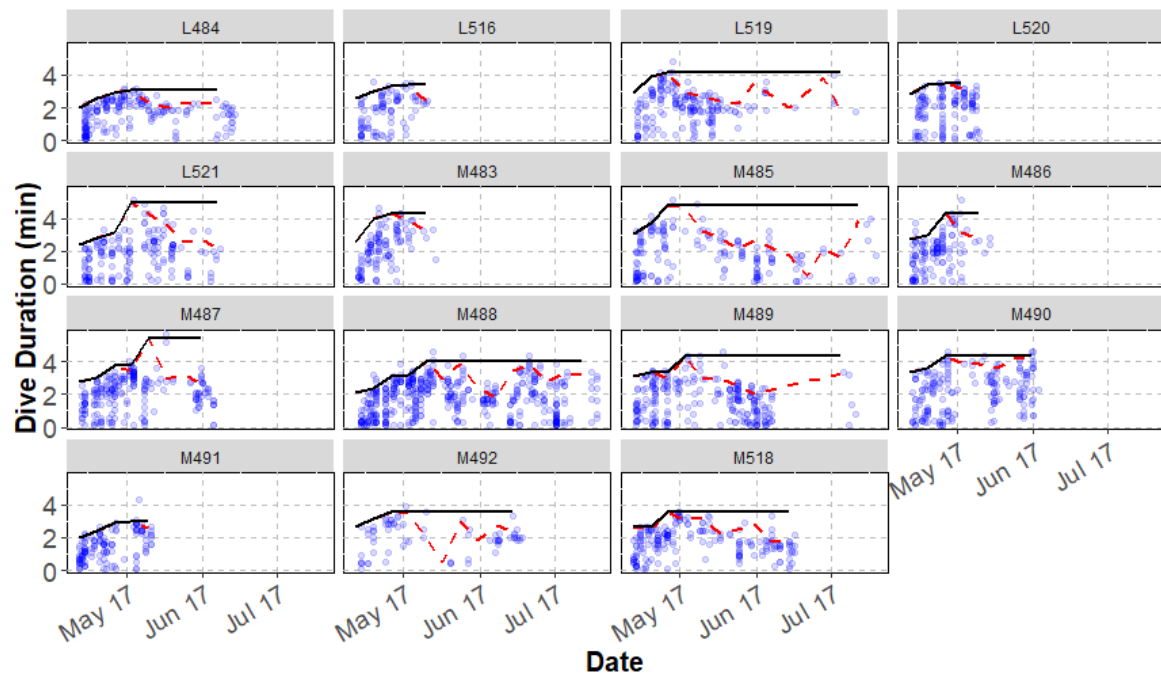
3.2.2 Duration

Fig. 11 shows the modelling of dive duration (see Methods 2.4.1) of the chosen seal, W716, the same seal as in **Fig. 8**. The median of the data is used as the model output gives a prediction on the 0.95 quantile in the SMRU animals, see Methods 2.4.1. As can be seen **Fig. 11**, the 0.5 quantile rapidly reaches 4.5 minutes, and continues in a stepwise progression until it plateaus again at 6 minutes. There is a rapid increase in the duration in the start, which plateaus after a few weeks. There is still another increase after July 2017, which is slower, and plateaus off again in December 2017. This increase after July 2017 corresponds nicely with the arrival at the Barents Sea (**Fig.8**).

Figure 11: W716 Dive duration performance. The blue dots are observations predicted from the duration of the dives, based on the 0.95 quantile between diving depth and diving duration on the SMRU animals. The red dashed line is the 0.5 quantile, i.e. the median. As the red dashed line is dynamic and follows the diving duration modelling data, the solid black line shows the maximum of the 0.5 quantile and is what will be used in the estimation of the diving performance, see next chapter (3.3 Diving Performance).
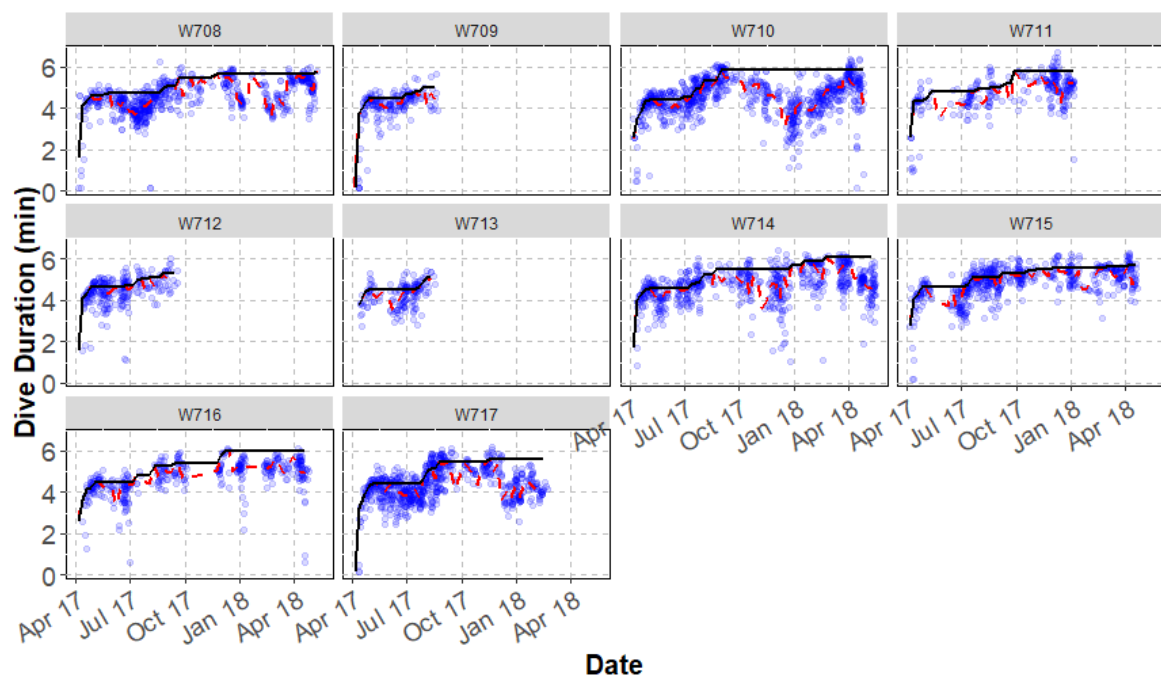
Fig. 12 shows the dive duration data for the SMRU animals (n=15), as in **Fig. 11,** but this is duration data directly from the tag and not a model like the SPLASH animals, and therefore the red line goes in the 0.95 quantile. The black line is the maximum of the 0.95 quantile. Note the short tag longevity compared to the SPLASH animals (see **Table 1**). All of these pups show a very early diving pattern, and all start diving to ~2- 3 minutes right after they are released. Later, after a few weeks they plateau at approx. 4 min. There is no second plateau as in **Fig.8,** this is because of the short longevity of these tags compared to the SPASH animals.

Figure 12: SMRU Dive duration performance. *All dives plotted in blue. Red dashed line is quantile regression and follows 0.95 quantile. The solid black line follows the maximum of the 0.95 quantile. Note there is only one plateau at around 4 minutes of dive duration.*

Fig. 13 is as the **Fig. 11**, as this is again the model duration of the SPLASH animals (n=10). These animals also have a plateau within a few weeks, and keeps that until after July, for then to stepwise increase over the autumn and winter. Some animals (W714 and W715, see **Fig. 13**) has an increase in the diving performance all the time until the tag was lost in April/May 2018. The animal from **Fig. 11** is in the bottom left of the figure.
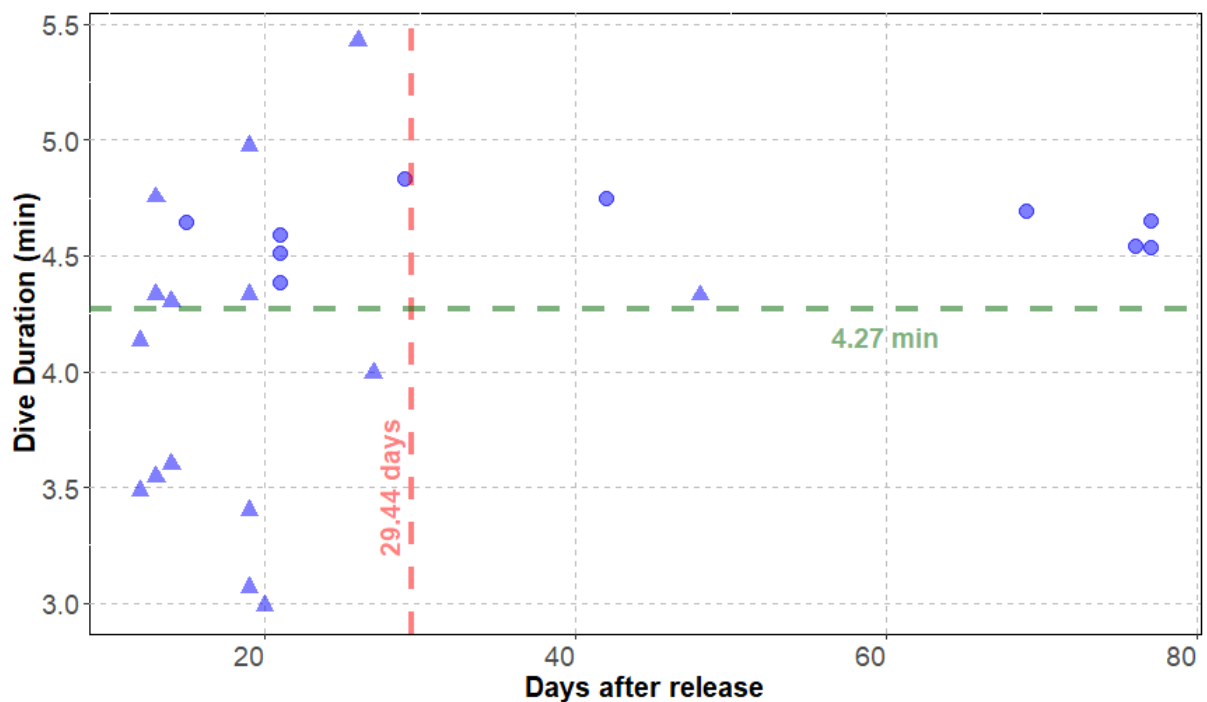

Figure 13: SPLASH Dive duration performance. Modelled dives plotted in blue. Red dashed line is quantile regression and follows 0.5 quantile. The solid black line follows the maximum of the 0.5 quantile. These animals show a plateau within the first weeks of release, and then a subsequent increase in diving capacity later in the year.

3.3 Diving performance

Diving performance is the 0.95 quantile of the dives, i.e. the top 5% of the dives, in diving duration. In **Fig. 12** the 0.95 quantile is the red dashed line that follows this 0.95 quantile throughout the plot. In **Fig. 11** and **Fig. 13** the median of the data is used, as the predicted values in the SPLASH-model are the equivalent to the 0.95 quantile in the real data, i.e. the SMRU data. In this analysis the black line in the former figures (**Fig. 11, 12 and 13**) is used. This line shows the maximum reached diving performance at that point.

From the dive duration performance figures, the point where the first plateau is was selected, see **Figure 8**. The first plateau is the first time there is no further uninterrupted

23

increase in diving performance, before it starts rising again. The SMRU animals do not have any transmitters with a longevity longer than July 2017, and therefore to keep the timescales comparable, the SPLASH data were cropped to only include June of 2017. All the animals had their first plateau before July of 2017. The mean plateau is 4.27 (SD= 0.61) min and the plateau were reached with a mean of 29.44 (SD= 22) days. SPLASH animals with a model duration are indicated with circles and SMRU animals are indicated by triangles.
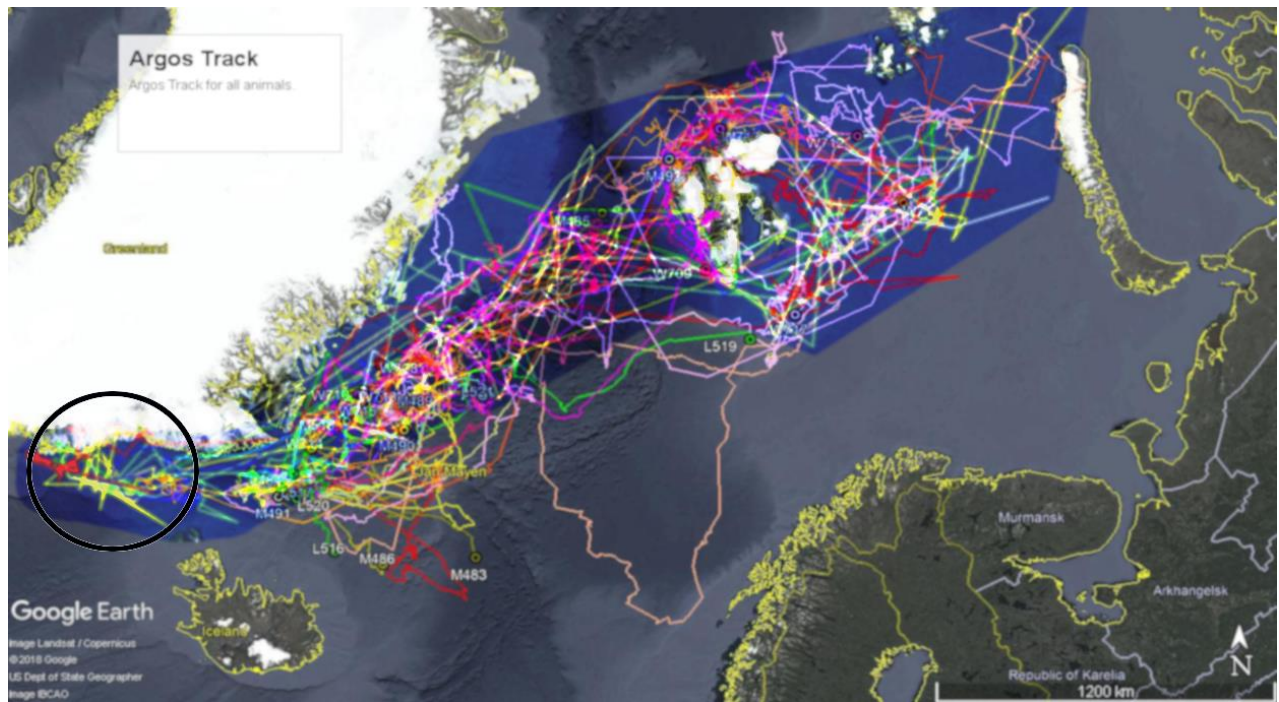

Figure 14: Plateau points for all animals. Triangles (Δ) indicate SMRU animals, and circles (●) indicate model SPLASH animals. The green horizontal dashed line indicates the mean plateau time, and the red vertical dashed line indicate the mean plateau date.

4 Discussion:

4.1 Distribution:

The harp seal pups seem to be very proficient at migrating in the first year of life, and their overall distribution, see **Fig. 6**, seems to mostly coincide with the distribution patterns shown in Folkow et al, 2004, as can be seen in **Fig. 1** and **15,** and with time resolution in **Fig. 19** (Appendix). The latter figure (**Fig. 19** in the Appendix) shows that from the release point, most animals went northwards following the sea ice edge, until approx. 75° latitude, were the animals go away from the ice and goes into the Barents Sea to feed. But the whole time there are some stragglers, who stay by the sea ice edge, or goes southwest into the Denmark Strait and stays there to feed. The same trend can be seen in the harp seal pups in this project, see **Fig. 7**, but there are some major differences. The adult seals in 1999/2000 went to the Denmark Strait in the winter, with all animals collected there in February of 2000 (**Fig. 15**

24

(inside the black circle) **and Fig. 19C**). The seal pups in this study remained in the Barents Sea throughout the winter, and at a comparable time, see **Fig. 7, E** in February, most of the pups stay in the Barents Sea, with just one individual staying in the Denmark Strait where the adult animals in Folkow, et al. 2004 were located.

Figure 15: Overlap figure of the tracks from Folkow et al. (2004) and the tracks of all the pups in this study. The darker blue area is where the adult animals from Folkow et al. (2004) went. They overlap almost perfectly, except for the area in the Denmark Strait where the adult animals went (see the black circle).

In February, see **Fig. 7 E**, most of the pups are still in the Barents Sea, with one seal in the Denmark Strait. This is contrary to the adult animals in 2000 (Folkow, et al., 2004) who all were in the Denmark Strait (**Fig. 19 C**). In the whelping period, the end of March and start of April, the adult animals reached the whelping areas in the Greenland Sea from the south (**Fig. 19D**). The pups are not sexually mature yet, so they do not have to be in the West Ice in the whelping period. Most of the pups uses this period of the season to eat, either by the ice edge in the Barents and Norwegian Sea, or in the Denmark Strait (**Fig. 7 F**). All the harp seals do however have to moult, and therefore congregate on the see ice in the Greenland Sea in May. This is probably the reason the pups are in their way back in the middle of April (**Fig. 7F** and **Fig. 20** in the Appendix).
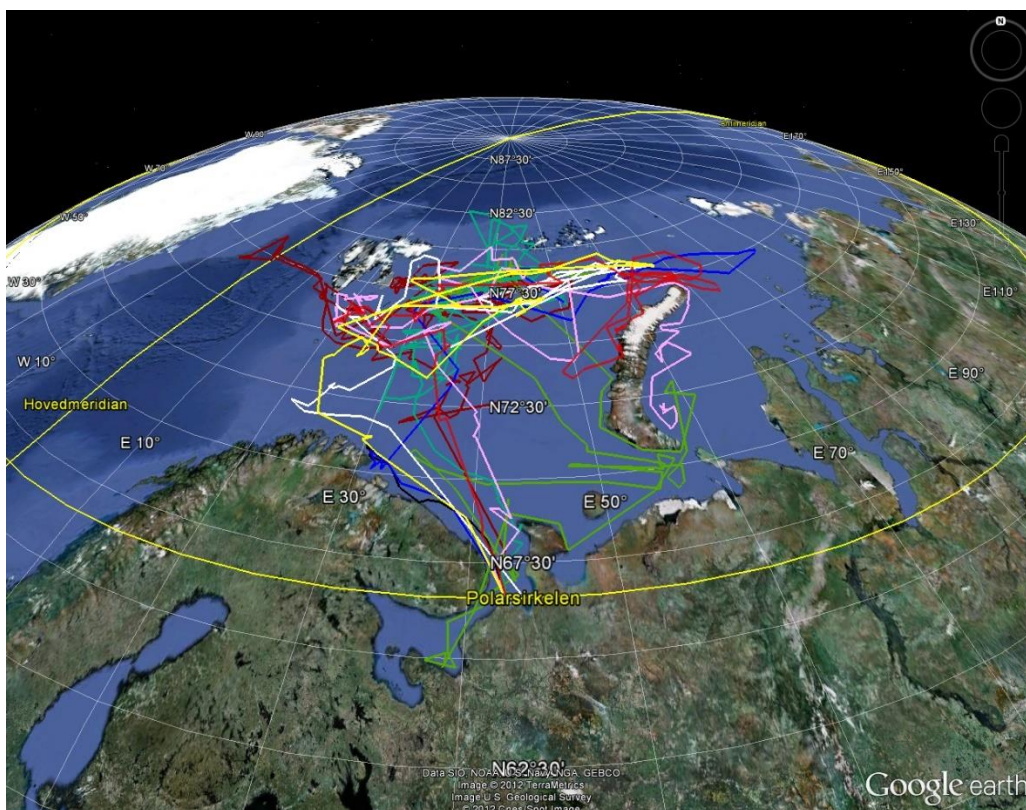
4.1.1 Focal areas
The harp seal pups showed a clear pattern in distribution when feeding. Pups seem to either follow the high productivity belt by the pack ice edge or go pelagic in the north-western

Barents Sea over the Svalbard Bank and around Bjørnøya. **Fig. 7** is the figure which shows the highest temporal resolution distribution. Most of the activity in these areas is by the ice edge, and the north-western Barents Sea (**Fig. 7C, D and E**). The use of these focal areas corresponds nicely with the distribution of the adult harp seals from the Greenland Sea population (**Fig. 1, 15** and **Fig. 19** with temporal scale).

4.1.2 Overlap with White Sea population

It is reasonable to assume that the seals will share their feeding grounds in the Barents Sea with the Harp seals from the White Sea population. The White Sea breeding population also uses the Barents Sea as a feeding area (Nordøy et al., 2008) (**Fig. 16**). It appears that the Barents Sea/White Sea population uses more of the south Barents Sea than the animals from the Greenland Sea population does. Due to the high amount of activity in the northern Barents Sea it appears that the Barents Sea/White Sea population follow the same high productivity belt as shown in the discussed previous.

Figure 16: *Distribution of seals from the Barents Sea/White Sea population. (Blix et al., 2013) (adapted from Nordøy et al., 2008).*

Øien and Øritsland (1995) showed that seals marked in the Greenland Sea were recaptured in the Barents Sea, and some were recaptured on the west side of Greenland and by the coast of Canada, in the Labrador Sea. The results from both Folkow and colleagues (2004) (**Fig. 1**)

and my results in this study (**Fig. 6; Fig. 7; Fig. 15**) shows that the seals certainty move into the Barents Sea, but no animals were observed to go into the Labrador Sea.

4.2 Diving

There is a record (**Fig. 10**) of all dives made in this project. These are both the SPLASH animals and the SMRU animals. The SMRU animals shows every dive that was recorded, while the SPLASH animals show only the deepest diving depth for each animal every 4-hour bin. The end of the figure will therefore mislead a little bit, giving the impression that all the dives were deep, when in reality there would be a lot of shallower dives not represented because of the way these tags were set up. **Fig. 10** shows a rather unexpected dive of -600 meters. This is rather remarkable for a seal pup of this size. Adults are known to dive down to over 500 meters (Folkow et al., 2004; Nordøy et al., 2008). This shows that the seal pups of under a year can dive as deep as the adults, but most of the time the diving depth is governed by the depth of the relatively shallow shelf seas on which they forage. The diving performance can be seen on **Fig. 12** and **Fig. 13,** consider that the dates in the x-axis is not the same in both figures. On **Fig. 13**, the dive duration also reaches a higher level on the autumn and over the winter. **Fig. 14** shows that the seals are quickly reaching up to a mean of 4.27 (SD = 0.61) minutes of dive duration. And this happens within mean of 29.44 (SD = 22.00) days.

4.2.1 Comparison with other species

A shallower diving species is the harbour seal (*Phoca vitulina*), which live in shallow coastal water. They are unusual in that they often enter the water right after birth (Bigg, 1981, as cited in Jørgensen et al., 2001). Due to this behaviour, they start diving right after birth. The pups mostly dive for durations <1 minute within the first two weeks of life (Jørgensen et al., 2001). Less than 1% of their dives exceeded their cADL of 3.25 minutes, using a diving metabolic rate of twice their basal metabolic rate (Kleiber, 1961, as cited in Jørgensen et al., 2001). Weaned harbour seals had an average dive duration of ~1 minute which increased to a mean dive duration of 3.09 minutes when the pups were 2-3 months old (Bekkeby & Bjørge, 2000). Unfortunately, the mean diving duration was not explored in for the harp seal pups in this study but should be a little bit higher than the 3.09 minutes reported in the harbour seal since harp seals live at deeper waters and store more oxygen than the harbour seal (Burns et al., 2007). This is also reflected in the cADLs at 3.25 and 4.3 minutes for the harbour and the harp seal, respectably (Burns et al., 2007; Jørgensen et al., 2001).

The eastern population of hooded seals share the same whelping grounds as the harp seals, but they are completely different in their diving and distribution. They are deep divers, which as adults can dive for over 50 minutes and over 1000 meter (Folkow & Blix, 1999). They are usually distributed in the Greenland Sea, Norwegian Sea, and the northern Atlantic (Folkow et al., 1996). Weanling hooded seals also goes trough the post weaning fast like the harp seal, and during this time they quickly develop a remarkable diving capacity. Hooded seal pups had a very rapid initial diving development and were diving to depths >100 meters, and durations >15 minutes after only 3 weeks of diving (Folkow et al., 2010). Most dives were however under 6 minutes in this period. The cADL of hooded seal pups is 6.0 minutes (Burns et al., 2007). This development of diving capacity is much faster than the harp seal weanlings in this study (**Fig. 12, 13 and 14**) which was able to dive for 4 - 5 minutes and to a depth of > 100 as well (**Fig. 10**) after the same time 3 weeks. Folkow and colleagues (2010) also showed that the diving development also plateaued after 3 weeks, just as in this study (**Fig. 12 and 13**). They hypothesise that the hooded seal pups are foraging shallow in this period of the year, and do not therefore have to dive much deeper. The weanlings did show a similar diving capacity to that of adult harp seals after a year, with many dives in the 10 – 15-minute duration (Folkow et al., 2004; Folkow et al., 2010; Nordøy et al., 2008).

4.2.2 Physiological development

The cADL (calculated aerobic diving limit) of harp seal weanlings is 4.3 minutes (Burns et al., 2007). This cADL is remarkable close to the diving performance in this study at 4.27 minutes (Fig. 14). This is approx. a third that of the adult harp seals were cADL is 12.1 minutes (Burns et al., 2007).

4.2.3 Ontogeny of diving

When harp seals are born, their oxygen stores are much lower than the adults, and they only get worse throughout the terrestrial nursing period (Burns et al., 2007). How does then the newly weaned pups manage to be proficient divers? They train for it, and they become better and better. This training seems to happen in the post weaning fast, i.e. the 4-6 weeks after they are weaned (Worthy & Lavigne, 1983). This training can also be observed in fig. 12 and 13, were in the first weeks after release, i.e. within the period of this post weaning fast the pups dives a lot with dives of 2 – 4 minutes of duration. All this diving training will make the seals experience regularly hypoxia (lack of oxygen in the tissues). Hypoxia, in turn prevent the degradation of Hypoxia-inducible factor 1α (HIF-1α), which then interact with its

constitutive protein Hypoxia-inducible factor 1β(HIF-1β) and producing the dimer Hypoxia-inducible factor 1(HIF-1) (Vázquez-Medina et al., 2011). HIF-1 is a transcription factor which then translocate into the nucleus and is involved in the upregulation of genes involved in angiogenesis (production of new blood vessels), erythropoiesis (production of new red blood cells, erythrocytes), energy metabolism and other effects (Semenza, 1999). Production of myoglobin is also observed to be upregulated in response to hypoxia (Kanatous & Mammen, 2010). Myoglobin in the swimming muscles of weanling harp seal pups were only ~25% of the adults (Lestyk et al., 2009). Lestyk and colleagues (2009) concluded that muscle function (training) has a stronger influence on the maturation of the muscles than the life history strategy. Kanatous and colleagues (2008) concluded that muscle activity is vital, and not only hypoxia is needed to produce myoglobin.

4.2.4 Extrinsic development

Harp seals eat a variety of fish and crustaceans when they are foraging. Depending on were they are harp seals eat different prey. In the Northern Barents Sea, the harp seal mostly eats crustaceans, as krill (*Thysanoessa* sp.) and amphipods (*Themisto* sp.), in the pelagic zone and some species lower down in the water column: like polar cod (*Boreogadus saida*), capelin (*Mallotus villosus*) and northern prawn (*Pandalus borealis*) (Nilssen et al., 1995a). In the Southern Barents Sea, the harp seals eat a more piscivorous diet with more gadoid fishes and flatfish, and pelagic species like herring and capelin and sand eels (Nilssen et al., 1995b).

They use the whole water column (Fig. 9) in the Barents Sea. This means that the weanlings probably have no problem in reaching the same food as the adults. Acoustic studies (Lindstrøm et al., 2012) show that there is a lot of krill, and amphipods, were in the upper pelagic side, and polar cod (*Boreogadus saida*), and long rough dab (*Hippoglossoides platessoides*) in the lower 50 meters of the northern Barents Sea. They showed that juvenile animals primarily ate crustaceans, while the adult animals ate a more piscivorous diet (Lindstøm et al., 2012). As all the seals remained in the Northern Barents Sea during the study, the pups most likely had a diet primarily consisting of krill and amphipods. There are however a lot of dived down to the bottom in the Barents Sea, and this indicates that the seals at least ate substantial amounts of benthic species like polar cod, northern prawn and long rough dab. Krill is a very important food source for the harp seal (Lindstrøm et al., 2012). Folkow and colleagues (2004) and Nordøy and colleagues (2008) suggested that the capelin could be a substantial food source since the seal distribution overlaps pretty well with the distribution of capelin. The capelin stock of 2017 was at ~3.3 million tonnes, which is

substantial, but only half of what the stock was 5 years prior (Institute of Marine Research, 2019).

4.3 Tag performance

The SPLASH-tags does record duration, but this is divided into bins, and gives number of dives for each bin in each recording interval (4 hours or 24 hours). The bins are two minutes large, except the first ones of 30 sec and 1 minute respectively, and the last bin is everything over 22 minutes. The data from the SPLASH-tags on these duration bins show highest frequency in the bin over 22 minutes, meaning that the dives was over 22 minutes of duration. If one looks at all the other data, the 22 minutes diving record are completely unlikely, especially when the longest record were around 5-6 minutes (**Fig. 12 and 13**).

To explain this, we must look how the tags were set up, how they were programmed. These SPLASH-tags define a dive with submersion, i.e. the tag is wet, and end the dive when the tag again is over the water. Dives shorter than 30 secs and shallower than 2 meters are also ignored. My explanation of the unrealistic duration data reported by these tags, is that, for some reason, the tags stayed wet when the animals surfaced and, thus counted several consecutive dives into the same dive.

One reason for this is the location of the tags, on the upper back (**Fig. 3**). This makes it possible for the pups to surface and breathe without surfacing the tag. Adults animals have the tags on top of the head, and this makes it much more reliable for measuring the diving duration by the wet/dry switch. There just is not enough area on top pf the head of these pups to mount the transmitters without increasing drag excessively or interfering too much with their behaviour. Previous studies with harp seals and using SPLASH-tags does not have this bias (Folkow et al., 2004; Nordøy et al., 2008). They mounted the tags on top of the head and on the neck/back (between shoulders) and were able to use the data from bins without this bias. It could be that the tags on the pups were placed a bit too far back on the back, and the tag did not surface. Or the pups could have a different behaviour that keeps the tags submerged for long periods of time.

An example of these behaviours is swimming on the back. Harp seals are also known to swim extended periods on their back (Sergeant, 1991). Seals have their eyes placed more on the top of the head than other carnivorans and live in essentially zero-gravity. Therefore, many seals often swim on their back in the water (Pelletier, 2011). They do this to keep an eye out for predators and food. Seals have little use of looking up when they cruise in the

surface, except to look at persons in boats, and other predators on land, like the polar bear (*Ursus maritimus*). Therefore, when the harp seals migrate they sometimes swim on their backs to look for food and to look for their main pelagic predator, the killer whale (*Orcinus orca*) (Nansen, 1924).

The modelled SPLASH duration data (mSPLASH duration) (M&M 2.4.1. and **Fig. 4**) are based on the 0.95 quantile of the real SMRU data and fits that well. As the mSPLASH duration is equivalent to the 0.95 quantile of the SMRU diving data, the median of the data is used, i.e. the 0.50 quantile. The model that was selected (M&M 2.4.1. and **Fig. 4**), is a predicted variable which is equivalent to the 0.95 quantile.

As seen here in **Fig. 14** the mSPLASH duration data lies quite close to the mean duration of 4.27 minutes. The time it takes for the SPLASH animals the plateau is later than the SMRU animals. This will pull the mean later and gives the impression that the SPLASH animals are slower to dive deeper, and slower to mature.

There are advantages and disadvantages with both types of tags used in this study. Both tag types provide nice and reliable spatial data, but the SPLASH tags used in this study used the much more accurate GPS system, which is superior in every way. But for my study the Argos positioning system is more than satisfactory. The data format in the SMRU tags is far superior than the format of the SPLASH tags for studying diving development ad performance. One headache was the way SPLASH tags define the dive, which made the whole duration data for the SPLASH tags unusable for any analysis. For unknown reasons the SMRU tags depleted their battery after just ~3 months, which was quite unfortunate. SPLASH tags had much less problem with battery longevity.

6 References

Argos (2016). Argos User's Manual © 2007 -2016 CLS Last updated on June 15, 2016. (2016).

Bekkby, T., & Bjørge, A. (2000). Diving behaviour of harbour seal Phoca vitulina pups from nursing to independent feeding. *Journal of Sea Research*, *44*, 267–275. Retrieved from www.elsevier.nl/locate/seares

Blix, A. S. (2005). *Arctic animals and their adaptations to a life on the edge.* Trondheim: Tapir Academic Press.

Blix, A. S., Folkow, L. P., & Nordøy, E. S. (2013). Changing the Look on Seals from Pole to Pole with Satellite Technology. In C. Verde & G. di Prisco (Eds.), *From Pole to Pole: Adaptation and Evolution in Marine Environments. Vol. 2.* (pp. 113–126). Springer-Verlag, Berlin Heidelberg. https://doi.org/10.1007/978-3-642-27352-0_7

Bowen, W. D., Oftedal, O. T., & Boness, D. J. (1985). Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Canadian Journal of Zoology*, *63*(12), 2841–2846. https://doi.org/10.1139/z85-424

Bradshaw, C. J. A., McMahon, C. R., & Hays, G. C. (2007). Behavioral Inference of Diving Metabolic Rate in Free-Ranging Leatherback Turtles. *Physiological and Biochemical Zoology*, *80*(2), 209–219. https://doi.org/10.1086/511142

Burns, J. M., Lestyk, K. C., Folkow, L. P., Hammill, M. O., & Blix, A. S. (2007). Size and distribution of oxygen stores in harp and hooded seals from birth to maturity. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *177*(6), 687–700. https://doi.org/10.1007/s00360-007-0167-2

Costa, D. P., Gales, N. J., & Goebel, M. E. (2001). Aerobic dive limit: How often does it occur in nature? *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *129*(4), 771–783. https://doi.org/10.1016/S1095-6433(01)00346-4

Defant, A. (1961). *Physical oceanography* (Vol 1). New York, NY: Macmillan.

Folkow, L. P., & Blix, A. S. (1999). Diving behaviour of hooded seals (Cystophora cristata) in the Greenland and Norwegian Seas. *Polar Biology* (Vol. 22). https://doi.org/10.1007/s003000050391

Folkow, L. P., Mårtensson, P. E., & Blix, A. S. (1996). Annual distribution of hooded seals (Cystophora cristata) in the Greenland and Norwegian seas. *Polar Biology* (Vol. 16). https://doi.org/10.1007/BF02329206

Folkow, L. P., Nordøy, E. S., & Blix, A. S. (2004). Distribution and diving behaviour of harp seals (Pagophilus groenlandicus) from the Greenland Sea stock. *Polar Biology*, *27*(5), 281–298. https://doi.org/10.1007/s00300-004-0591-7
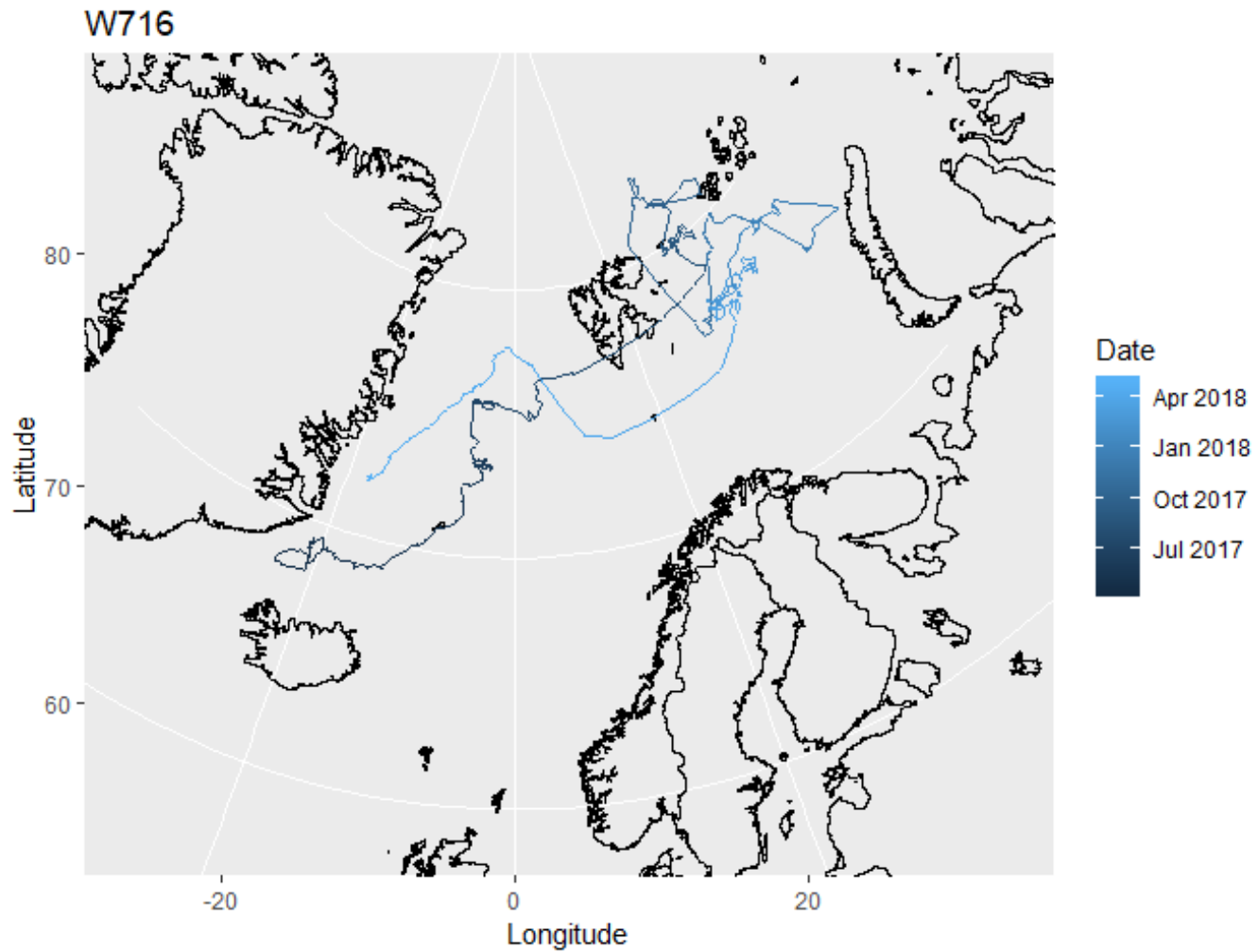
Folkow, L. P., Nordøy, E. S., & Blix, A. S. (2010). Remarkable development of diving performance and migrations of hooded seals (Cystophora cristata) during their first year of life. *Polar Biology*, *33*, 433–441. https://doi.org/10.1007/s00300-009-0718-y

Freitas, C., Lydersen, C., Fedak, M. A., & Kovacs, K. M. (2008). A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science*, *24*(2), 315–325. https://doi.org/10.1111/j.1748-7692.2007.00180.x

Freitas, Carla (2012). argosfilter: Argos locations filter. R package version 0.63. https://CRAN.R-project.org/package=argosfilter

ICES. (2008). *Report of the working group on harp and hooded seals (WGHARP)*. 27 - 30 August 2008, Tromsø, Norway. ICES CM 2008/ACOM:17. 63pp

ICES. (2014). *Report of the ICES/NAFO Working Group on Harp and Hooded Seals (WGHARP)*. 17-21 November 2014, Quebec City, Quebec, Canada. ICES CM 2014/ ACOM:20. 62 pp.

ICES. (2016). *Report of the ICES/NAFO/NAMMCO Working Group on Harp and Hooded Seals (WGHARP)*. 26-30 September 2016, ICES HQ, Copenhagen, Denmark. ICES CM 2016/ACOM:21. 85 pp

Institute of Marine Research. (2019). Capelin stock in the Barents Sea. Environmental monitoring of Svalbard and Jan Mayen (MOSJ). Retrieved from0 http://www.mosj.no/en/fauna/marine/capelin.html

Jørgensen, C., Lydersen, C., Brix, O., & Kovacs, K. M. (2001). Diving development in nursing harbour seal pups. *Journal of Experimental Biology*, *204*(22), 3993–4004. Retrieved from http://jeb.biologists.org/cgi/reprint/204/22/3993.pdf

Kanatous, S. B., & Mammen, P. P. A. (2010). Regulation of myoglobin expression. *Journal of Experimental Biology*, *213*(16), 2741–2747. https://doi.org/10.1242/jeb.041442

Kanatous, S. B., Hawke, T. J., Trumble, S. J., Pearson, L. E., Watson, R. R., Garry, D. J., … Davis, R. W. (2008). The ontogeny of aerobic and diving capacity in the skeletal muscles of Weddell seals. *Journal of Experimental Biology*, *211*(16), 2559–2565. https://doi.org/10.1242/jeb.018119

Koenker, R., & Bassett, G. (1978). *Regression Quantiles*. *Econometrica* (Vol. 46). Retrieved from http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.470.9161&rep=rep1&type=pdf

Kooyman, G. L. (1964). *TECHNIQUES USED IN MEASURING DIVING CAPACITIES OF WEDDELL SEALS*. *The Polar Record* (Vol. 12). Retrieved from https://www.cambridge.org/core/services/aop-cambridge-core/content/view/ABD5262D6ABA9A69C02B7FAEBE4877C8/S003224740005484Xa.pdf/techniques_used_in_measuring_diving_capacities_of_weddell_seals.pdf

Kooyman, G. L., Castellini, M. A., Davis, R. W., & Maue, R. A. (1983). Aerobic Diving Limits of Immature Weddell Seals. *J. Comp. Physiol*, *151*, 171–174. Retrieved from https://link.springer.com/content/pdf/10.1007%2FBF00689915.pdf

Kooyman, G. L., Wahrenbrock, E. A., Castellini, M. A., Davis, R. W., & Sinnett, E. E. (1980). Aerobic and Anaerobic Metabolism During Voluntary Diving in Weddell Seals: Evidence of Preferred Pathways from Blood Chemistry and Behavior. *J. Comp. Physiol*, *138*, 335–346. Retrieved from https://link.springer.com/content/pdf/10.1007%2FBF00691568.pdf

Kovacs, K. M., & Lavigne, D. M. (1985). Neonatal growth and organ allometry of Northwest Atlantic harp seals (Phoca groenlandica). *Canadian Journal of Zoology*, *63*(12), 2793–2799. https://doi.org/10.1139/z85-418

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., Ugarte, F. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology*, *29*(3), 724–737. https://doi.org/10.1111/cobi.12474

Lestyk, K. C., Folkow, L. P., Blix, A. S., Hammill, M. O., & Burns, J. M. (2009). Development of myoglobin concentration and acid buffering capacity in harp (pagophilus groenlandicus) and hooded (cystophora cristata) seals from birth to maturity. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *179*(8), 985–996. https://doi.org/10.1007/s00360-009-0378-9

Lindstrøm, U., Nilssen, K. T., Pettersen, L. M. S., & Haug, T. (2012). Harp seal foraging behaviour during summer around Svalbard in the northern Barents Sea: diet composition and the selection of prey. https://doi.org/10.1007/s00300-012-1260-x

Loeng, H. (1991). Features of the physical oceanographic conditions of the Barents Sea. *Polar Research*, *10*(1), 12–16. https://doi.org/10.3402/polar.v10i1.6723

McConnell, B. J., Chambers, C., & Fedak, M. A. (1992). Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science*, *4*(4), 393–398. https://doi.org/10.1017/S0954102092000580

Nansen, F. (1924). *Blant sel og bjørn*. Jacob Dybwads Forlag, Oslo

Nilssen, K. T., Haug, T., Potelov, V., & Timoshenko, Y. K. (1995a). Feeding habits of harp seals (Phoca groenlandica) during early summer and autumn in the northern Barents Sea. *Polar Biology, 15*(7), 485–493. https://doi.org/10.1007/BF00237462

Nilssen, K. T., Haug, T., Potelov, V., Stasenkov, V. A., & Timoshenko, Y. K. (1995b). Food habits of harp seals (Phoca groenlandica) during lactation and moult in March-May in the southern Barents Sea and White Sea. *ICES Journal of Marine Science, 52*(1), 33–41.

Nordøy, E. S., Folkow, L. P., Potelov, V., Prischemikhin, V., & Blix, A. S. (2008). Seasonal distribution and dive behaviour of harp seals (Pagophilus groenlandicus) of the White Sea–Barents Sea stock. *Polar Biology*, *31*(9), 1119–1135. https://doi.org/10.1007/s00300-008-0453-9

Øien, N., & Øritsland, T. (1995). Use of mark-recapture experiments to monitor seal populations subject to catching. *Developments in Marine Biology*, *4©*, 35–45. https://doi.org/10.1016/S0163-6995(06)80007-7

Pelletier, T. C. (June 4, 2011). WHY DO THE SEALS SWIM UPSIDE DOWN ? Retrieved May 6, 2019, from http://askanaturalist.com/why-do-the-seals-swim-upside-down/

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rasmussen, B., & Øritsland, T. (1964). Norwegian tagging of harp and hooded seals in North Atlantic waters. *Fiskeridirektoratets Skrifter*, *13*(7), 43–55.

Sakshaug, E. (1997). Biomass and productivity distributions and their variability in the Barents Sea. *ICES Journal of Marine Science*, *54*(3), 341–350. https://doi.org/10.1006/jmsc.1996.0170

Sakshaug, E., & Holm-Hansen, O. (1984). Factors governing pelagic production in polar oceans. In O. Holm-Hansen, L. Bolis, & R. Gilles (Eds.), *Lecture notes on coastal and estuarine studies: Vol.8. Marine Phytoplankton and Productivity* (pp. 1–18). Springer, Berlin. https://doi.org/10.1029/ln008p0001

Sakshaug, E., & Slagstad, D. (1992). Sea ice and wind: Effects on primary productivity in the Barents Sea. *Atmosphere-Ocean*, *4*(30), 579–591. https://doi.org/10.1080/07055900.1992.9649456

Sea Mammal Research Unit. (n.d. a). Argos & GPS/Argos SRDL Tags. University of St Andrews. Retrieved from http://www.smru.st-andrews.ac.uk/Instrumentation/downloads/SRDL_Tag_version_300.pdf

Sea Mammal Research Unit. (n.d. b). GPS Phone Tags. University of St Andrews. Retrieved from http://www.smru.st-andrews.ac.uk/Instrumentation/downloads/GPS_Phone_Tag22.pdf

Semenza, G. L. (1999). Regulation of mammalian O2 homeostasis by hypoxia-inducible factor 1. *Annu. Rev. Cell Dev. Biol. 15, 15*, 551–578.

Sergeant, D. E. (1991). Harp Seals, Man and Ice. *Canadian Special Publication of Fisheries and Aquatic Sciences, 114*. 153.

Smedsrud, L. H., Halvorsen, M. H., Stroeve, J. C., Zhang, R., & Kloster, K. (2017). Fram Strait sea ice export variability and September Arctic sea ice extent over the last 80 years. *Cryosphere*, *11*(1), 65–79. https://doi.org/10.5194/tc-11-65-2017

Smith, S. L., Smith, W. O., Codispoti, L. A., & Wilson, D. L. (1985). Biological observations in the marginal ice zone of the East Greenland Sea. *Journal of Marine Research*, *43*(3), 693–717. https://doi.org/10.1357/002224085788440303

SPLASH10-F TAG PRODUCT SHEET. (n.d.). Wildlife Computers. Retrieved from https://static.wildlifecomputers.com/product-pages/SPLASH10-F-Product-Sheet.pdf
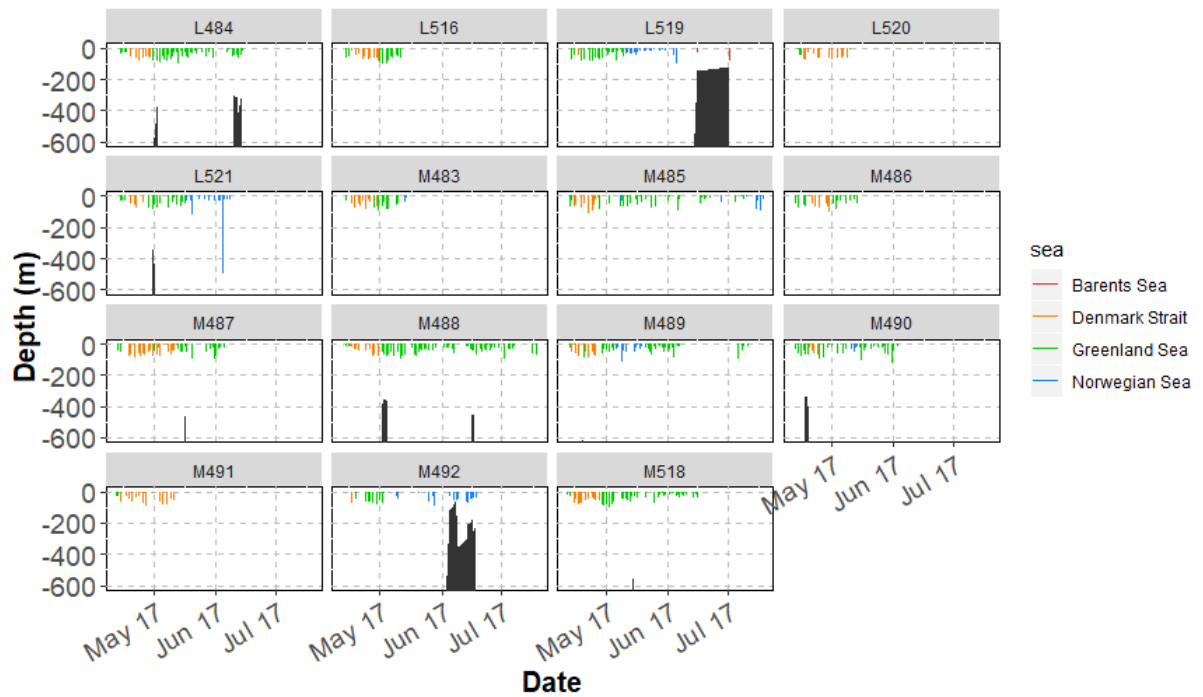
Stewart, R. E. A., & Lavigne, D. M. (1980). Neonatal Growth of Northwest Atlantic Harp Seals, Pagophilus groenlandicus. *Journal of Mammalogy*, *61*(4), 670–680. https://doi.org/10.1644/09-MAMM-A-232.1.Key

Tanaka, S. (1987). Satellite Radio Tracking of Bottlenose Dolphins Tursiops truncatus. *Nippon Suisan Gakkaishi*, *53*(8), 1327–1338.

Vázquez-Medina, J. P., Zenteno-Savin, T., Tift, M. S., Forman, H. J., Crocker, D. E., & Ortiz, R. M. (2011). Apnea stimulates the adaptive response to oxidative stress in elephant seal pups. *Journal of Experimental Biology*, *214*(24), 4193–4200. https://doi.org/10.1242/jeb.063644

Vincent, C., McConnell, B. J., Ridoux, V., & Fedak, M. A. (2002). Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. *Marine Mammal Science*, *18*(1), 156–166. https://doi.org/10.1111/j.1748-7692.2002.tb01025.x

Wickham, H. (2017). tidyverse: Easily Install and Load the 'Tidyverse'. R package version 1.2.1. https://CRAN.R-project.org/package=tidyverse

Worthy, G. A. J., & Lavigne, D. M. (1983). Energetics of fasting and subsequent growth in weaned harp seal pups, *Phoca groenlandica*. *Canadian Journal of Zoology*, *61*(2), 447–456. https://doi.org/10.1139/z83-059
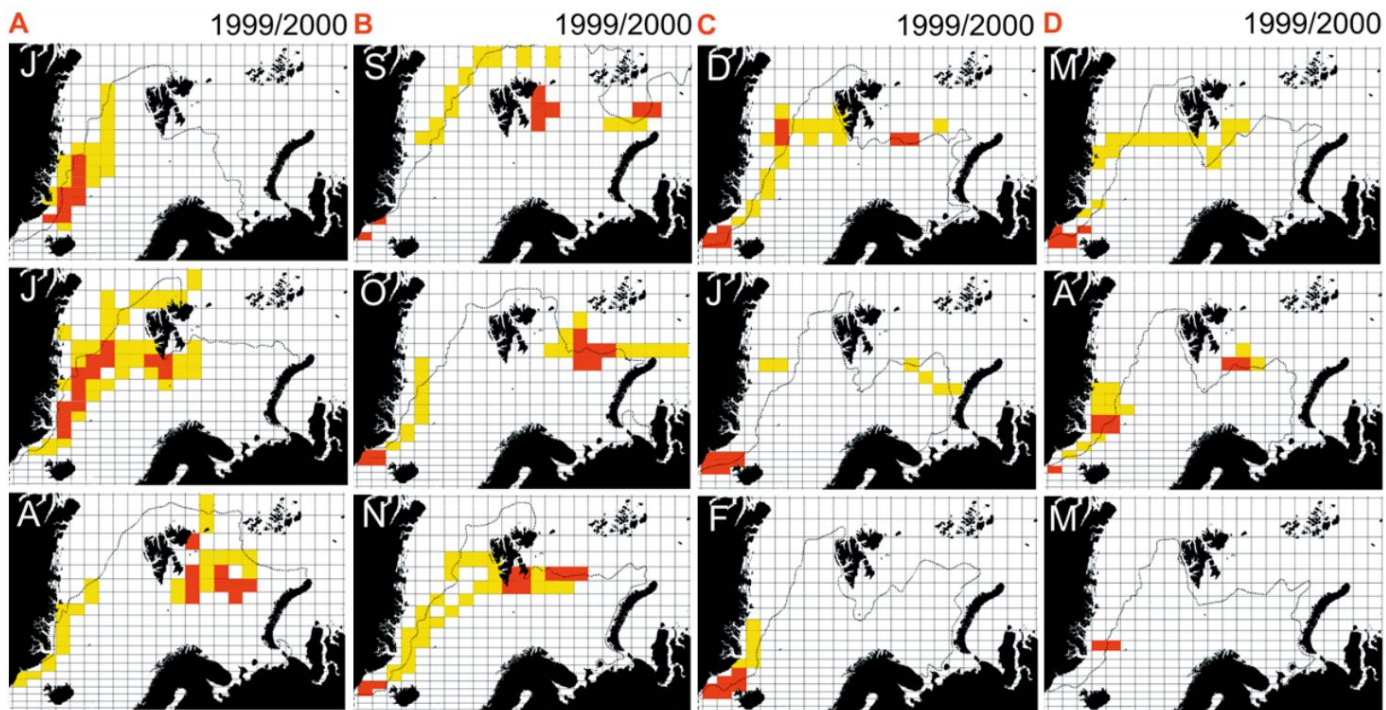
7 Appendix:

Figure 17. Total distribution of the representative seal, W716, from the 14th of April of 2017 until 25th of April 2018. The date of the location of the track is represented by the colour gradient from dark blue to light blue. There are some gaps in the transmissions and they can be seen as strait long lines.
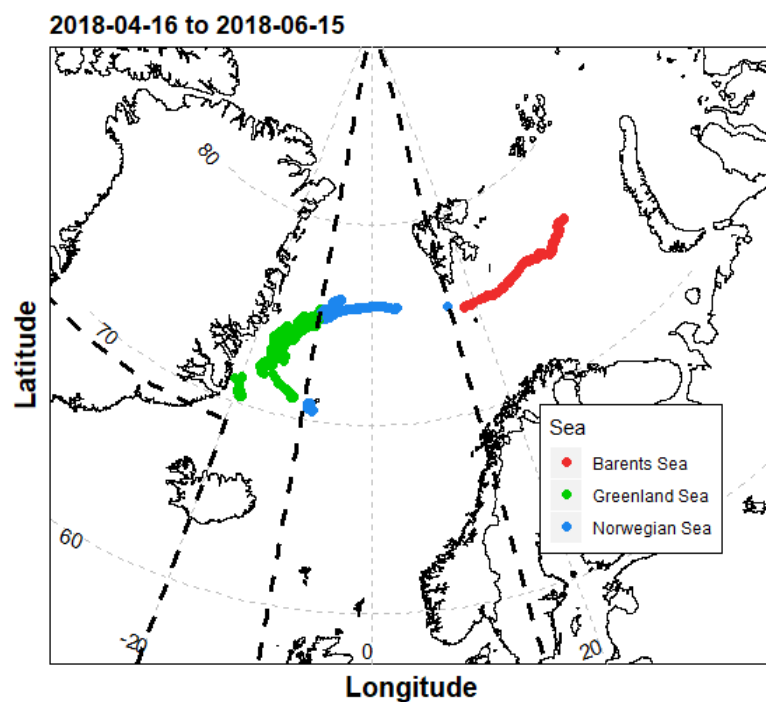
Figure 18. Absolute diving depth of all SMRU seals with diving data(n=15), notice the Y-axis is cropped to -600 meter to be able to see any of the dives, and the X-axis is much shorter than the SPLASH animals in *Fig. 9.* The coloured segments represent single dives and the colour represent the sea where the diving is going on. The black is the bottom of the ocean. Most of the duration all these seals are in waters deeper than 600 meters. These are all maximum dives within a 24-hour period.

Figure 19: Monthly distribution of 10 adult harp seals in 1999/2000. The subfigures are vertical with 3 plots in each. A: June, July and August 1999, B: September, October and November 1999. C: December 1999, January and February 2000. D: March, April and May 2000. Red denote high density of animals, and yellow denotes that at least 1 seal was in that area in that months. The dotted line is the monthly average ice distribution. Adapted and modified from Folkow, et al., 2004.

2018-04-16 to 2018-06-15

Fig. 20: Pup distribution after April 15, 2018. Here most of the pups are concentrated in the drift ice off the coast of Greenland, and one is still on its way back from the Barents Sea.