A life after Research? First Release of Harp Seals *(Phoca groenlandica)* after Temporary Captivity for Scientific Purposes

Marie-Anne Blanchet[1], Mario Acquarone[1,2], Martin Biuw[3] , Roger Larsen[1], Erling S. Nordøy[4] and Lars P. Folkow[4]

[1] *The Norwegian College for Fishery Science, UiT The Arctic University of Norway, Tromsø, Norway*

E-mail: marie-anne.e.blanchet@uit.no

[2] *Present address: The Marine and Freshwater Research Institute, Reykjavik, Iceland*

[3] *Institute for Marine Research, Tromsø, Norway*

[4] *Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway*

Abstract

Three wild-caught female harp seals *(Phoca groenlandica)* from the Greenland Sea stock were brought into temporary captivity in connection with a controlled validation study on energetics. The two pups and one adult were kept in two indoor and outdoor experimental facilities approved by the Norwegian committee on animal experimentation. They were trained daily using operant conditioning to participate in experiments and husbandry and were regularly fed live fish. After 2.5 y, the seals were instrumented with satellite transmitters and released in the Barents Sea under a Norwegian Food Safety Authority permit. The tags transmitted for 45, 67 and 162 d for the juveniles and adult, respectively. The two juveniles remained into the Barents Sea east of the Svalbard Archipelago while the adult female migrated to the Greenland Sea following a pattern consistent with that observed in wild seals from the same stock. They all performed regular deep dives (>100 m) and exhibited signs of foraging comparable to wild seals. Our results suggest that it is possible to conduct temporary captive studies with wild adult and juveniles harp seals. Study animals can be trained and subsequently released, if they meet a set of criteria. This framework combines advantages of

captive study design with traditional field methods and follows European animal experimentation ethical guidelines with respect to the re-homing of experimentation animals.

Key words: Harp seal, *Phoca groenlandica*, temporary captivity, satellite telemetry, release, rehabilitation

Introduction

Studying marine mammals in the wild is challenging mainly due to logistic constraints that can limit the quantity and quality of data (Mellish et al., 2006; Thomton et al., 2008). It is especially true when studying Arctic marine mammals' fine-scale behavior such as foraging and feeding events that occur at sea and for which direct observation is practically impossible. The use of animal-borne satellite linked data recorders or biologgers can help overcome some of these challenges by transmitting information on the animal's behavior or its physiological state (Wilmers et al., 2015). Such instruments are becoming increasingly sophisticated and can collect a wealth of high quality data facilitating estimation of metrics such as energy intake (Williams et al., 2014), metabolic rate (Wilson et al., 2006; Ponganis et al., 2007; Goldbogen et al., 2010; Ropert-Coudert et al., 2012; Fahlman et al., 2013), foraging effort and body condition (Lesage et al., 1999; Biuw et al., 2003; Richard et al., 2014; Miller et al., 2016), and the measurements of environmental variables (Biuw et al., 2007; Laidre et al., 2010). However, sensors and built-in algorithms must be calibrated and validated in order to allow correct interpretation of these complex data. This often involves captive studies in controlled environments prior to deployments in the wild (Wilmers et al., 2015; Williams et al., 2014). The use of surrogate species is not always possible – or relevant – when species-specific data are collected. Some species are available in very limited numbers in zoological collections across the world and they are not always accessible for research purposes. This is the case for harp seals (*Pagophilus groenlandicus*) for which less than 10 individuals are presently kept in zoological facilities worldwide (www.zootierliste.de access date 1.01.2018). The harp seal is a major top predator in the northeast Atlantic ocean and its prey consumption is estimated at a few million tons annually in the Barents Sea (Nordøy et al., 1995; Nilssen et al., 2000; Lindstrøm et al., 2013). Understanding their foraging behavior and providing more accurate estimates of their food intake is of high importance for fishery and ecosystem management. They are highly mobile predators undertaking extensive migrations (Folkow et al., 2004; Nordøy et al., 2008; Svetochev et al., 2016), warranting the use of biologgers and species-specific calibration of sensors and instruments algorithms. This was the approach developed in the COEXIST project (The Norwegian Research Council grant no: 234411) aiming at estimating energy expenditure, body condition, and prey consumption of wild harp seals, based on data derived from calibrated animal-borne satellite linked data recorders.

In addition to the main aim of the project, we also wanted to assess whether temporary captivity and habituation to humans of individual harp seals were compatible with their successful release and readjustment to the wild. A similar approach was tested successfully with Steller sea lions (*Eumetopia jubatus*) (Mellish et al., 2006; Thomton et al., 2008), grey seals (*Halichoerus grypus*), and harbor seals (*Phoca vitulina*) (Vincent et al., 2002; M. Fedak pers. comm, 15 January 2018). However, published accounts on the behavior of animals after release is limited to the above-mentioned studies and one study on rehabilitated harbor seals who were not habituated to human contact (Morrison et al.,2012). At-sea behavior of the formerly captive harp seals in this study was analyzed and compared with previously published harp seal movements and diving patterns.

Methods

Capture and handling methods of the animals were approved by the Norwegian Animal Research Authority (Permits 6646 and 6093) and by the Danish Ministry of Foreign Affairs (including approval for the expedition into Greenlandic waters). Release was carried out under permit from the Norwegian Animal Research Authority (Permit 9065).

Animal capture and transport

Three female harp seals (one adult and two pups, hereafter juvenile 1 and 2 when they were released at 2.5 y old) were captured in the whelping patches (Figure 1 a, b, c) located on drift ice off the east coast of Greenland (approximately 71°01'N - 17°36'W) during a research cruise led by the University of Tromsø in April 2014. Pups were captured as whitecoats at a weight that was consistent with weaning and were estimated to be approximately two weeks old (Stewart & Lavigne, 1980; Kovacs 1987) (Table 1). The adult had given birth and her pup was weaned prior to her capture. Based on the color and marking of the coat, this adult female was estimated to be approximately 6-7 y-old (Stewart & Lavigne, 1980). The animals were transported in open crates placed on the deck of the R/V *Helmer Hanssen* to the University of Tromsø where the experiments were carried out (Figure 1).

Place Figure 1 here

Facilities

Indoor facility — After capture and transport to Tromsø, the seals were placed into two separate (one for the pups and one for the adult) indoor seawater tanks (42 000 L each; 5.6 x 5.8 for 1.6 m depth), each with a 1.5 m wide wooden haul-out platform along one side of the tank. The tanks were continuously supplied with fresh seawater (> 60 $L.min^{-1}$), pumped from 70 m depth in a nearby fjord. This secured a stable salinity and a continuously low water temperature (4 - 10 °C, depending on season). The air temperature varied between 7 and 10° C throughout the year. Artificial light was set to simulate light conditions at 70° N, including 24 h of light during the summer and only civil twilight for 3 h per day during the polar night period, when the sun does not rise above the horizon.

Outdoor facility —Part of the experiment was undertaken in a nearby fjord where the animals were transported individually by road in a kennel. The facility was constructed from a repurposed aquaculture pen (Figure 1 d, e). The pen's float ring was 80 m in circumference and fully enclosed with a standard aquaculture net bag with a nominal depth of 18 m. The surface of the pen was covered by a net attached to the external perimeter of the net bag at 2 m depth, and to a central floating pontoon, where a hole through the top net allowed the seals to surface and breathe as well as haul out on the platform to rest. During experiments, the hole in the floating pontoon was covered by a Plexiglas dome used to measure respiratory gas exchange.

Husbandry

The seals were trained using operant conditioning and positive reinforcement (Skinner, 1951; Pryor & Ramirez, 2014). The application of positive reinforcement allowed voluntary access to the research animals by desensitizing the animals and minimized the use of physical or chemical restraint thereby improving their welfare and the validity of the data acquired (Desportes et al., 2007). The animals were trained for husbandry behaviors (weighing, morphometric measurements, voluntary injections, and blood sampling), as well as research-related behaviors. The juvenile animals were trained to enter a kennel for transport to and from the experimental sea pen and accept the attachment and removal of data logging instruments and other experimental devices without being restrained while the adult animal was restrained for these procedures (Figure 1 g). Animals were fitted with neoprene and Velcro ® patches glued onto their fur, upon which instruments/devices could be attached for the duration of the experiment. For parts of the experiment that required a long immobilization (gluing of the neoprene patches and injection of tritium for body condition measurements), the animals were lightly sedated using tiletamine-zolazepam (50 $mg.ml^{-1}$ tiletamine and 50 $mg.ml^{-1}$ zolazepam, Zoletil® Forte 102 Vet, Virbac Laboratories, France) at a dose rate of 0.8 - 1.0 $mg.kg^{-1}$ body mass. The juveniles were lightly sedated once they voluntarily entered the transport kennel, while the adult was lightly sedated once the indoor pool was drained. Freshly thawed fish, herring *(Clupea harengus)* and capelin *(Mallotus villosus),* were offered between one and three times a day on a varied schedule during training or enrichment sessions, according to the physiological needs of each animal. Gelatin was also offered as a secondary reinforcer (Pryor & Ramirez, 2014) and as an enrichment item. Each animal was observed to successfully catch live fish in the outdoor experimental pen while they were still fed their full ration of frozen fish.

Release protocol

The three animals were kept under human care for 2.5 y before they were released back to the wild. By this time, the pups matured to juveniles. Prior to release, the animals' morphometric measurement were recorded (Table 1) and were fed *ad libitum* the preceding week. Human-animal interactions were also kept to a minimum during that period. The three animals were transported from Tromsø to the release site onboard the R/V *Helmer Hanssen* in open wooden crates placed on the vessel's trawl deck (Figure 1 h, i, j), following the same basic protocol as at capture. They were released on the 12 November 2016, at 10.00 AM at 75°70'N - 31°10'E in the Barents Sea south east of Spitsbergen (Figure 2). Once the ship was stationary and drifting at the release position, the sides of the cages were opened, allowing seals to voluntarily step onto the trawl slide and to enter the water on their own. All three animals entered the water within 10 min of opening the crates (Figure 1 i, j). The release location was chosen based on a previous satellite tracking study of Greenland Sea harp seals, which showed that this region was frequented by wild harp seals at a similar time of year (Folkow et al., 2004).

Instruments

The animals were all fitted with satellite-linked data recorders. The adult was fitted with a Conductivity-Temperature-Depth Satellite Relay Data Logger ((CTD-SRDL), Sea Mammal Research Unit (SMRU), University of St Andrews, St Andrews, Scotland http://www.smru.st-andrews.ac.uk/Instrumentation/CTD); juvenile 1 was fitted with a standard non-CTD SRDL from the same manufacturer while juvenile 2 was fitted with a Splash 10 satellite-linked data recorder (Wildlife Computers (WC), Seattle, WA, USA, https://wildlifecomputers.com/our-tags/splash/). The tags were glued onto the fur mid-dorsally in the neck area (adult and juvenile 1) or onto the top of the head (juvenile 2) using super glue (Loctite ® Henkel Ltd, UK) (Figure 1 i). The collected data were all relayed via the Argos satellite system (System Argos, Toulouse, France) and the location estimates were also calculated by Argos. The transmission regime as well as the structure and resolution of the behavioral and dive data varied substantially between the three instruments. For the SMRU tags, a dive was defined as a period of submersion at least 8 s long and at least 6 m deep. If either the depth or the total duration of a period of submersion was less than these values but the animal was wet, this time was recorded as surface time. If the saltwater switch was dry for more than 10 min, the time was recorded as a haul-out event, which then lasted until the instrument was again continuously wet for at least 40 min. The dive data stored and transmitted by these instruments fell into two categories 1) summaries that included the percentage of time spent diving, at the surface, and hauled out for 6 h periods, and 2) a randomly chosen subset of dives for which a dive profile represented by four inflection points was transmitted along with the maximum dive depth and the dive duration. Dive parameters (average maximum depth and average dive duration) were extracted from the subset of dives received and relayed via Argos while the maximum depths were taken from the received summaries or the maximum depth of the CTD casts. This is due to the fact that SMRU instruments store different types of information in different "pages" that are randomly selected from a transmission buffer at the time of transmission. When the instrument transmits, it randomly chooses a "page" resulting in the reception of either a summary, a dive profile, or a CTD profile. In addition, it is important to note that the distribution of CTD depths is biased towards deeper dives, as the instrument selects deeper dives in order to have the most information on the water column. The instruments were programmed to send data whenever possible.

The WC tag stored and transmitted dive data in a very different way. Dive depth and duration were split into bins as follows: 0 – 5 m, 5 – 10 m, 10 – 15 m, 15 - 20 m, 20 – 25 m, 25 – 50 m, 50 – 75 m, 75 – 100 m, 100 – 150 m, 150 – 200 m, 200 – 250 m, 250 – 300 m, and > 300 m for depth bins and 0 – 1 min, 1 – 2 min, 2 – 3 min, 3 – 4 min, 5 – 6 min, 6 – 7 min, 7 – 10 min, 10 – 15 min, 15 – 20 min, and 20 – 25 min for duration bins. The percentage of time spent in the various depth and duration bins and the total number of dives for a 6 h period were transmitted throughout the tracking period. WC tag depth sensor resolution was 0.5 m.

Data analysis

All data processing and analyses were done using the R statistical framework (R Development Core Team 2016). Satellite derived locations were first filtered using a Kalman filter under a state-space framework using the R package "crawl" (Johnson et al., 2008). The filter assumes data are imperfect observations from an underlying correlated random walk process, and incorporates a covariate for Argos location error (when available) for each of the six Argos location classes (LC—3,2,1,0,A,B). Processing the raw location estimates in this manner resulted in a model of the most likely track, from which point location estimates could be interpolated for any specific time. Hourly locations were estimated by interpolation using this model; these positions were used for further calculations. No additional covariate representing the haul-out behavior was used due to the paucity of received haul-out data. Dive and CTD-cast locations were also estimated from the fitted model based on the time of occurrence of these events. Movement parameters were calculated for each seal, maximum distance from the release point using the great circle distance (km), total cumulated distance (km), average speed ($m.s^{-1}$) calculated over the entire track, and average daily distance ($km.day^{-1}$). The daily speed was calculated over the track and smoothed using a moving average with a window of 3 d. The time spent by the seals along various portions of their tracks was calculated using the First Passage Time (FPT) method (Fauchald & Tveraa, 2003), using the implementation in the "adehabitat" R package (Calenge, 2006). Here, FPTs (i.e., the time period between first entry and last exit of a circle with a specific radius) were calculated along the path of each animal on 5 km interpolated locations from radii ranging from 5 through 30 km at 5 km intervals. The variance of the log (FPT) was then calculated for each animal in order to identify the radius corresponding to the maximum variance and hence the spatial scale at which each animal concentrated its time (see Fauchald & Tveraa (2003) for details). Each of the interpolated locations along an animal's path then receives an FTP score based on the selected radius, essentially indicating the degree to which an animal focused in a specific area or if it merely transited through an area. The ascent and decent rates of dives were only calculated for the two animals carrying SMRU instruments and were defined as the vertical transit rate between, respectively, the surface and the first inflection point and between the last inflection point and the surface.

Environmental variables

Daily sea ice concentration was downloaded from the reanalysis products from ERA-Interim project from the European Center for Medium Range Weather Forecast (Dee et al*.,* 2011). Sea ice concentration was calculated at a scale of 0.75 ° deg * 0.75 ° as the daily proportion of a cell covered by ice ranging from 0 to 1 based on the ERA model. Average sea ice concentration (the proportion of a grid cell covered by sea ice) was calculated between December and April on the east coast of Greenland to produce the sea ice extent as the 15% sea ice coverage using R package "raster" (Hijmans et al., 2017).

Results

Tag performance/transmission rate

The tags placed on the three seals yielded 162 d, 67 d, and 45 d of data for the adult, juvenile 1, and juvenile 2, respectively (Table 1). The average daily transmission rate was very different between the animals with 4, 12, and 32 daily received locations for the adult, juvenile 1, and juvenile 2, respectively. For SMRU-tagged animals, the 6-h summary data were available for 49% and 40% of the deployment duration for the adult and juvenile 1, respectively.

Place Table 1 here

Movement data

The movements and migration pathways varied dramatically between the three seals, with the two juveniles remaining in the Barents Sea during the entire tracking duration (i.e., 67 d and 45 d) while the adult migrated towards the Denmark Strait on the east coast of Greenland about 12 days after release (Figure 2). The two juveniles travelled north, reaching the Svalbard Archipelago and then headed south again towards the central Barents Sea and to Bear Island for juvenile 1, until the tags stopped transmitting. The adult travelled in a generally S-SW direction from the release point, ending up within 100 km from the Norwegian mainland before crossing the northeast Atlantic towards the Greenland coast. This crossing took 11 d, at which time she reached heavy pack ice at the edge of the Greenlandic continental shelf. She then headed south following the ice edge along the continental shelf and spent nearly four months in heavy drift ice in the Denmark Strait. Her speed decreased markedly throughout her path with the highest values registered while in the Barents Sea and crossing the northeast Atlantic (Figure 3a). Her average speed was higher during the first part of the track (mean = 0.63 +/- 0.4 $m.s^{-1}$) compared to when she reached the pack ice off the east coast of Greenland (mean = 0.48 +/- 0.34 $m.s^{-1}$). The travelling speed of juvenile 1 increased throughout the tagging period, reaching a peak at the end of December when swimming in a seemingly directed movement towards Bear Island (Figure 3b). Juvenile 2 showed peaks of speed at the end of November and mid-December, though she markedly slowed at the end of November (Figure 3c).

Place Figure 2 here

Place Figure 3 here

The three animals displayed area restricted search effort (ARS, indicated by high FPT values) in several discrete patches along their pathways. The adult and juvenile 2 moved within ARS patches with a radius of 10 and 11 km, respectively, while juvenile 1 moved at a much larger scale of 35 km. The adult spent significantly more time (>48 h) within such ARS patches while she was operating along the edge of the Greenlandic shelf, compared to in other regions along the track (Figure 3 a, d). The adult spent 85% of the total track duration in ice of concentration >15%. Both juveniles showed the highest FPT values (>96 h and >48 h for juvenile 1 and 2, respectively) in the central Barents Sea. These longer residency times included some haul out events on the east side of the Svalbard Archipelago; however, given the paucity of the received haul-out data (e.g., only 3 out of a minimum of 9 haul-outs known to have occurred for juvenile 1 were actually received), it is difficult to estimate how these data may have influenced the residency time. No drift ice was obviously available for hauling out through the tracking period in this region.

Dive and CTD data

Due to the very different nature of the dive data between the three instruments, they were analyzed separately. For the adult seal, the number of received dives was 222, and based on the received summary data this represents ~1.3% of all dives with a further 116 CTD profiles recorded. Her mean dive duration was 10.5 +/- 4.2 min with a maximum duration of 25 min recorded (Table 1). The average dive depth was 209 +/- 109 m with a maximum depth (including depths recorded in CTD casts) of 499 m. The distribution of dive durations was relatively unimodal with most dives lasting between 10-15 min with an average depth of ~300 m (Figure 4a). CTD cast depths also averaged ~300 m. All received dives and CTD casts occurred on the edge or on the Greenlandic continental shelf in drift ice. For juvenile 1, the percentage of received dives was 1.5% (N = 82 dives), based on the received summary with a further 47 CTD profiles. The mean dive duration was 2.8 +/- 2.2 min with a maximum duration of 9 min; however, the majority of dives lasted for 5 min or less. Average dive depth was 41 +/- 36 m with a maximum recorded depth (including depths recorded in CTD casts) of 331 m; the majority of dives were shallower than 150 m (Table 1). Most of the dives were short (<5 min) and relatively shallow (<100 m). CTD cast depths were centered around 100-150 m (Figure 4b). For juvenile 2, the transmission of dives summaries covered 100% of the tracking period, which accounted for all 17,418 dives performed by this animal. This yields an average diving rate of 396 +/- 118 dives/d (Table 1). Dives lasted for a maximum of 20 - 25 min for a maximum depth of 300 - 350 m (Figure 3c) with most dives shorter than 5 min. Maximum dive depths varied during the tracking period but dives deeper than 150 m occurred on a regular basis. The highest proportion of diving time was spent between 50 and 100 m and this remained consistent throughout the tracking period for this animal (Figure 4c).

Place Figure 4 here

Discussion

We followed the movements and diving behavior of three females harp seals from the Greenland Sea stock after temporary captivity for a 2.5 year period; animals were housed in both indoor and outdoor facilities. Our first objective was to assess how these animals behaved compared to their wild counterparts. General migration patterns for various harp seal stocks have been suggested based on direct observations (Haug et al., 1994; Lacoste & Stenson, 2000) and in part confirmed by tracking studies (Folkow et al., 2004; Nordøy et al., 2008; Svetochev et al., 2016). Information on detailed movement and diving patterns of harp seals is scarce and mainly based on two tracking studies of adult animals from the Greenland Sea and the Barents Sea stocks (Folkow et al., 2004; Nordøy et al., 2008). Information about the movements of pups and juveniles is limited to four pups tagged in the White Sea in 2010 (Svetochev et al., 2016). Harp seals from the Greenland Sea stock migrate from the east coast of Greenland to the Barents Sea after the annual molt and return to East Greenland to forage in the pack ice (Potelov et al., 2000; Folkow et al., 2004; Nordøy et al., 2008; Haug et al., 1994). Adult seals generally return to the Greenland Sea by late December and follow the ice edge into the Denmark Strait (Folkow et al., 2004). They remain in this area until March foraging in heavy ice at the edge of the continental shelf before hauling out onto the pack ice to breed. The adult seal in the present study followed exactly this pattern after her release into the Barents Sea. She first headed west and south then veered west across the North Atlantic arriving on the east coast of Greenland in early December (Figure 1). No position estimates were received during transit, so we do not know how directed this transit was. However, given the duration (~11 d) and distance (~1,600 km), the estimated minimum sustained straight-line swim speed was ~1.2 m s^{-1} (~2.4 knots). This appears to be a reasonable sustained swimming speed for an 11-d period, so it is likely that the transit followed a relatively directed great circle course. Moreover, the movement pattern and travel rate are consistent with those recorded from the instrumented adults from the same stock as documented by Folkow et al. (2004), where all instrumented seals returned to the Greenland Sea by the end of December. The daily speed (47 km.d^{-1}) and cumulated distance (7,645 km in 162 d) were also consistent with results from the same previous study. As seen in Figure 3a, the travel rate of the adult seal was substantially higher during the earlier part of the tracking period, in the Barents Sea and during transit (~1.15 m s^{-1}), associated also with relatively low FPT values. Once she reached the pack ice, her speed decreased (~0.5 m.s^{-1}) and she spent substantially more time in restricted areas, as shown by the highest values of FPT. These high FPT values are in part due to the animal hauling out on ice floes but she also performed numerous dives in this area at the edge of the continental shelf. Many of the dives were relatively deep (>200m) and long (10-15 min), close to or above the 12 min theoretical Aerobic Dive Limit (ADL) estimated for a harp seal of similar mass (Lydersen & Kovacs, 1993; Burns et al., 2007). This suggests that she was foraging in this zone in tight association with ice and the edge of the continental shelf. This is consistent with observations from the Barents and White Seas where seals are often observed foraging at the edge of the pack ice during winter (Haug et al., 1994; Lawson et al., 1998; Haug et al., 2004; Lindstrøm et al., 2013). Harp seals feed on a variety of prey, ranging from fish such as capelin (*Mallotus villosus*), polar cod (*Boreogadus saida*) and herring (*Clupea harengus*) to smaller preys such as euphausids (krill) and amphipods (*Parathemisto* spp.) (Lindstrøm et al., 2013). However, their diet varies seasonally and spatially with amphipods, capelin, and krill being the most important items for harp seals along the east coast of Greenland (Haug et al., 2004). Pelagic amphipods of the *Parathemisto* genus are sympagic species and could explain the foraging behavior in heavy ice concentration. However, this prey item is typically found in the upper layers of the water column and given the proportion of long, deep dives close to the seafloor performed by this adult, it is possible that she was also targeting more benthic prey such as Greenland halibut (*Reinhardtius hippoglossoides*), a known prey item from Svalbard (Lydersen et al., 1991; Wathne et al., 2000). In addition, large capelin stocks are also present in the Denmark Strait area (ICES, 2016), so this is another likely prey species to have been targeted by this female.

The limited available information on movements of juvenile harp seals (Svetochev et al., 2016) showed that, after being tagged during the breeding season in March-April, these pups dispersed from the White Sea into primarily the eastern Barents Sea, spending long periods apparently feeding along the ice edge between Svalbard and Frans Josef Land. One of the pups appears to have subsequently circumnavigated Svalbard before returning towards the White Sea along the west coast of Svalbard. Preliminary data from a recent tracking study of juvenile harp seals from the Greenland Sea stock suggest primarily northeastward migration pathways, also into the Barents Sea (M. Biuw, pers. comm., 15th December 2017). Furthermore, pup and juvenile phocids from other species such as harbor seals and hooded seals *(Cystophora cristata)* are known to disperse widely and sometimes occupy larger areas than adults suggesting that harp seal pups can reach the Barents Sea region shortly after weaning (Folkow et al., 2010; Blanchet et al., 2016; Vacquie-Garcia et al., 2017; Carter et al., 2017). Harp seals are observed year round in the Barents Sea both in offshore and coastal areas (R. Larsen, pers. comm. 1st December 2017) and such animals may belong to either stock (Greenland Sea or Barents Sea), since both use the area (Folkow et al., 2004; Nordøy et al., 2008; Svetochev et al., 2016). As was shown by Svetochev et al. (2016), juveniles from the White Sea stock can also occupy this area year round, where they can mix with adults and most likely also juveniles from the Barents Sea population (Lydersen et al., 1991; Folkow et al., 2004). It is not known whether juveniles exhibit a yearly migration pattern between breeding/molting grounds along the east coast of Greenland and the Barents Sea, like the adults, but given that corresponding patterns are exhibited by White Sea harp seal pups, it is highly likely that pups also from the Greenland Sea undertake such migrations. However, females do not breed before the age of 5-6 years and juveniles, therefore, do not need to reach the breeding grounds at the same time as other individuals, decreasing the need for a tight synchronicity (Kovacs, 1987). This could explain why none of the juveniles undertook a direct migration across the northeast Atlantic after their release, at least not while the tags were still transmitting the first ~2 months. Both exhibited signs of area restricted search in the Barents Sea suggesting foraging behavior. They both performed a few deep benthic dives (>200 m), especially juvenile 2, for which we have the most complete dive record. The 50 – 100 m layer of the water column was the most consistently used throughout the tracking period suggesting that they were targeting a certain prey type. As observed by Folkow et al. (2004), adult harp seals forage in this area during the winter in open waters at depths of about 50 m to 300 m where capelin is usually found. Lindstrøm et al. (1998) also showed that harp seals prefer fish over crustaceans in the Barents Sea despite the overwhelming availability of the latter. It is therefore likely that both juveniles were also targeting capelin.

Rehabilitation programs are considered successful if the rehabilitated individuals displays behaviors similar to those of wild conspecifics (Morrison et al., 2012) and are able to successfully forage. In the case of the released adult female, our results suggest that she was behaving remarkably similar to wild harp seals after a captive period of 2.5 years. Her navigational sense was not impaired by captivity considering that she undertook a direct migration back to the Greenlandic shelf returning to a location just 150 km south of the capture location. This might be due to the highly migratory nature of this species that undertakes foraging trips between the Greenlandic coast and the Barents Sea every year (Folkow et al., 2004). The captivity period did not seem to affect her swimming, diving, and foraging abilities. Within hours of release, she was able to perform a 280 m dive, suggesting that she still had the physical capabilities of reaching great depths despite not having been able to dive this deep for 2.5 years. She was regularly diving close to or exceeding her theoretical ADL, as shown by the distribution of dive duration, and was likely foraging successfully. The tracking duration of 162 d provide a minimum estimate of short-term survival and the end of April when the tag ceased transmitting is consistent with the beginning of the annual molting period (Folkow et al., 2004).

Short-term survival results are more difficult to interpret for the juveniles, as the tags stopped transmitting after a limited period. The reasons for unexpectedly short tagging durations are not easily determined (Hays et al., 2007). In the present case, tracking duration was 67 and 45 d for juvenile 1 and 2, which is shorter than the expected tag life span. Diagnostic data transmitted by the tag carried by juvenile 1 did not provide any information on whether the tag was failing (e.g., reduction in battery voltage), although antenna failure or tag detachment is always a possibility. However, if the animals had died a non-traumatic death (due to exhaustion, starvation, or disease), we should have seen a gradual change in their behavior and especially their diving abilities. This was not the case, especially for juvenile 2 that transmitted continuous dive records. Both juveniles were swimming at a speed consistent with those registered for wild adult harp seals and for the adult animal in the present study. They both covered large horizontal distances of 2,749 km and 2,489 km in 67 and 45 d, respectively. They also showed signs of area restricted search patterns suggesting that they were foraging or at least actively searching for food. Moreover, they were targeting the depth layer (50 – 300 m) where most of the capelin is found in the Barents Sea during this period (Lindstrøm et al., 2013), strongly suggestive of active feeding. The development of their diving abilities was rapid after release and did not seem to have been impaired by the captive period. In particular, continuous dive records from juvenile 2 show that she was diving routinely to depths greater than 100 m within the first week post-release. Both juveniles were diving consistently at depths greater than 100 m for up to 15 min throughout the tracking period. The development of diving abilities is crucial for rehabilitated animals and can serve as an indicator of their fitness (Morrison et al., 2012). In our case, this was a special concern as both animals had been captured as whitecoats. They had never dove in open water and did not have mature oxygen stores (Burns et al., 2007). However, they could display swimming and diving behavior in captivity, particularly in the outdoor experimental pen where they regularly dived to depths of 14 m, all of which might have contributed to their physiological development (Burns et al., 2007; Geiseler et al., 2013). We cannot exclude that the animals died due to a traumatic event such as predation, but behavioral indicators such as swimming patterns and diving abilities suggest that both juveniles had capabilities compatible with good fitness. These abilities were persistent throughout the tracking period and have served as a proxy for fitness in successfully rehabilitated harbor seals (Lander et al., 2002; Morrison et al., 2012).

The rehabilitation and "re-homing" of research animals is explicitly mentioned in the European Directive 2010/63/EU on the protection of animals used for scientific purposes (http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32010L0063). Article 19 requires that "Member States may allow animals used or intended to be used in procedures to be (…) returned to a suitable habitat or husbandry system appropriate to the species, provided that several conditions are met.” Therefore, dedicated efforts should be made to return wild research animals to nature when possible and plans for this should be included in the original experimental design. Several criteria must be met before releasing seals that have been in captivity for a prolonged period: they must be in good health and body condition and be able to capture live prey (Whaley, 2009; Morrison et al., 2012; Gaydos et al., 2013). In the present case, all three animals met the above-mentioned criteria; they were all healthy, had a weight consistent with their age, and were all able to capture live fish that had been presented at regular intervals through the captivity period. Young animals with no previous foraging experience, such as our two juveniles, must be evaluated with extra attention prior to release. Maternal dependency varies greatly in pinnipeds (Kovacs & Lavigne, 1986) but in the case of harp seals there is no transfer of maternal information during the nursing period (Kovacs, 1987). Pups are weaned at approximately two weeks of age; do not dive with their mothers, and start feeding independently shortly after weaning (Kovacs, 1987; Haug et al., 2000). This behavioral trait increased our confidence that the juveniles would be prone to rapid experience-based learning and were good candidates for release. However, this assessment should be made on a case-by-case basis. Aberrant behaviors in released animals that might compromise their survival can be a concern and should also be evaluated prior to release. These include the attraction and desensitization to the presence of humans (Whaley, 2009). In our case, all animals had been trained and desensitized to the presence of humans during the captive period; however, they were released in a zone with extremely scarce human presence in coastal and off-shore areas. We concluded that the likelihood for encounters with humans that could compromise the rehabilitation process in the first weeks after the release was very low.

In summary, our results suggest that it is possible to conduct temporary captive studies with wild adult and juveniles harp seals, followed by their release, as previously shown for other pinnipeds (Mellish et al., 2006; Thomton et al., 2008). Study animals from this species can be trained and ultimately released, provided that they meet certain release criteria and that the likelihood of encountering humans in the release zone is low. This framework combines the advantages of a captive study design and traditional field methods while also respecting European ethical guidelines on animal experimentation.

Acknowledgements

This study was a part of the COEXIST project financed by the Norwegian Research Council (NFR grant no: 234411). The training and husbandry of the seals would not have been possible without the invaluable help of the Arctic and Marine Biology technical staff Hans Lian, Hans-Arne Solvang, Renate Thorvaldsen and dedicated volunteers and students: Ann-Isabel Algera, Anja-Helene Alvestad, Stine Fiskaa, Johanna Pedersen, Sophie Scotter and Judith Ullmann. We are grateful to the crew of the R/V Helmer Hansen who were instrumental in the both the capture and the release process; in particular Daniel Appenroth and Ivan Tatone.

Literature cited

Biuw, M., B. McConnell, C. J. A. Bradshaw, H. Burton, and M. Fedak. 2003. Blubber and Buoyancy: Monitoring the Body Condition of Free-Ranging Seals Using Simple Dive Characteristics. Journal of Experimental Biology 206 (19):3405 LP – 3423. http://jeb.biologists.org/content/206/19/3405.abstract.

Blanchet, M-A., C.,Lydersen, R.A. Ims and K.M. Kovacs. 2016. Making It through the First Year: Ontogeny of Movement and Diving Behavior in Harbor Seals from Svalbard, Norway. Marine Mammal Science 32 (4):1340–69. https://doi.org/10.1111/mms.12341.

Burns, J. M., K. C. Lestyk, L. P. Folkow, M. O. Hammill, and A. S. Blix. 2007. Size and Distribution of Oxygen Stores in Harp and Hooded Seals from Birth to Maturity. Journal of Comparative Physiology B 177 (6):687–700. https://doi.org/10.1007/s00360-007-0167-2.

Calenge, C. 2006. The Package 'adehabitat' for the R Software: A Tool for the Analysis of Space and Habitat Use by Animals. Ecological Modelling 197 (3):516–19. https://doi.org/https://doi.org/10.1016/j.ecolmodel.2006.03.017.

Carter, M. I. D., Russell, D. J. F., Embling, C. B., Blight, C. J., Thompson, D., Hosegood, P. J., & Bennett, K. A. (2017). Intrinsic and extrinsic factors drive ontogeny of early-life at-sea behaviour in a marine top predator. Scientific Reports, 7(1), 1–14. https://doi.org/10.1038/s41598-017-15859-8

Dee, D.P., S.M. Uppala, A. J. Simmons, P. Berrisford, P. Poli, S. Kobayashi, U. Andrae, *et al.* 2011. The ERA-Interim Reanalysis: Configuration and Performance of the Data Assimilation System. Quarterly Journal of the Royal Meteorological Society 137 (656). John Wiley & Sons, Ltd.:553–97. https://doi.org/10.1002/qj.828.

Desportes, G., Buholzer L., Anderson-Hansen K., Blanchet M.A., Acquarone M., Shephard G., Brando S., Vossen A., and U. Siebert. 2007. Decrease Stress; Train Your Animals: The Effect of Handling Methods on Cortisol Levels in Harbour Porpoises *(Phocoena Phocoena)* Under Human Care. Aquatic Mammals 33 (3):286–92.

Fahlman, A., Svärd, C., Rosen, D., Wilson, R., & Trites, A. (2013). Activity as a proxy to estimate metabolic rate and to partition the metabolic cost of diving vs. breathing in preand post-fasted Steller sea lions. Aquatic Biology, 18(2), 175–184. https://doi.org/10.3354/ab00500

Fauchald, P. and T. Tveraa. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84 (2). Ecological Society of America:282–88. https://doi.org/10.1890/0012-9658.

Folkow, L.P., E.S. Nordøy, and A.S. Blix. 2004. Distribution and Diving Behaviour of Harp Seals *(Pagophilus groenlandicus)* from the Greenland Sea Stock. Polar Biology 27 (5):281–98. 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 Biol 33:433-441.

Gaydos, J. K., L. I. Vilchis, M.M. Lance, S.J. Jeffries, A. Thomas, V. Greenwood, P. Harner, and M.H. Ziccardi. 2013. Post-release movement of rehabilitated harbor seal *(Phoca vitulina richardii)* pups compared with cohort-matched wild seal pups. Marine Mammal Science 29 (3):E282–94. https://doi.org/10.1111/mms.12002.

Geiseler S.J., Blix A.S., Burns J.M., Folkow L.P. (2013) Rapid postnatal development of myoglobin from large liver iron stores in hooded seals. Journal of Experimental Biology 216:1793-1798.

Goldbogen, J. A., Calambokidis, J., Oleson, E. M., Potvin, J., Pyenson, N. D., Schorr, G., & Shadwick, R. E. (2010). Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. Journal of Experimental Biology, *214*(1), 131–146. https://doi.org/10.1242/jeb.048157

Haug, T., K.T. Nilssen, and L. Lindblom. 2000. First Independent Feeding of Harp Seal

(Phoca groenlandica) and Hooded Seal *(Cystophora cristata)* Pups in the Greenland Sea. NAMMCO Scientific Publications 2.

Haug, T., K.T. Nilssen, and L. Lindblom. 2004. Feeding Habits of Harp and Hooded Seals in Drift Ice Waters along the East Coast of Greenland in Summer and Winter. Polar Research 23:35–42. https://doi.org/10.1111/j.1751-8369.2004.tb00127.x.

Haug,T., K.T. Nilssen, N Øien, and V. Potelov. 1994. Seasonal Distribution of Harp Seals *(Phoca groenlandica)* in the Barents Sea. Polar Research 13:163–72. https://doi.org/10.1111/j.1751-8369.1994.tb00446.x.

Hays, G.C., C.J.A. Bradshaw, M.C. James, P. Lovell, and D.W. Sims. 2007. Why Do Argos Satellite Tags Deployed on Marine Animals Stop Transmitting? Journal of Experimental Marine Biology and Ecology 349 (1):52–60. https://doi.org/https://doi.org/10.1016/j.jembe.2007.04.016.

Hijmans, R. J. (2017). raster: Geographic Data Analysis and Modeling. R package version 2.5-8. https://CRAN.R-project.org/package=raster

ICES (2016) Report of the North-Western Working Group (NWWG), ICES CM 2016/ACOM:08, ICES HQ, Copenhagen, Denmark, 27 April-4 May 2016, 703 pp.

Johnson, D.S., J.M. London, M-A. Lea, and J.W. Durban. 2008. Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–15. https://doi.org/10.1890/07-1032.1.

Kovacs, K.M. 1987. Maternal Behaviour and Early Behavioural Ontogeny of Harp Seals, *(Phoca groenlandica)*. Animal Behaviour 35:844–55. https://doi.org/https://doi.org/10.1016/S0003-3472(87)80120-3.

Kovacs, K.M, and D.M. Lavigne. 1986. Maternal Investment and Neonatal Growth in Phocid

Seals. Journal of Animal Ecology 55:1035–51.

Lacoste, K.N, and G.B. Stenson. 2000. Winter Distribution of Harp Seals *(Phoca groenlandica)* off Eastern Newfoundland and Southern Labrador. Polar Biology 23:805–11. https://doi.org/10.1007/s003000000155.

Laidre, K.L, M.P. Heide-Jørgensen, L. Logsdon, L. Delwiche, and T.G. Nielsen. 2010. A Whale of an Opportunity: Examining the Vertical Structure of Chlorophyll-a in High Arctic Waters Using Instrumented Marine Predators. Marine Biology Research 6:519–29.

Lander, M.E., J.T. Harvey, K.D. Hanni, and L.E. Morgan. 2002. Behavior, Movements, and Apparent Survival of Rehabilitated and Free-Ranging Harbor Seal Pups. The Journal of Wildlife Management 66:19–28.

Lawson, J.W., J.T. Anderson, E.L. Dalley, and G.B. Stenson. 1998. Selective foraging by harp seals *(Phoca groenlandica)* in nearshore and offshore waters of Newfoundland, 1993 and 1994. Marine Ecology Progress Series 163:1-40.

Lesage, V., M.O. Hammill, and K.M. Kovacs. 1999. Functional Classification of Harbor Seal *(Phoca vitulina)* Dives Using Depth Profiles, Swimming Velocity, and an Index of Foraging Success. Canadian Journal of Zoology 77:74–87. https://doi.org/10.1139/z98-199.

Lindstrøm, U., K.T. Nilssen, L.M.S. Pettersen, and T. Haug. 2013. Harp Seal Foraging Behaviour during Summer around Svalbard in the Northern Barents Sea: Diet Composition and the Selection of Prey. Polar Biology 36:305–320. https://doi.org/10.1007/s00300-012-1260-x.

Lydersen, C., L.A. Angantyr, Ø. Wiig, and T. Øritsland. 1991. Feeding habits of northeast

Atlantic harp seals *(Phoca groenlandica)* along the summer ice edge of the Barents sea. Canadian Journal of Fisheries and Aquatic Sciences 48:2180–83. https://doi.org/10.1139/f91-257.

Lydersen, C., and K.M. Kovacs. 1993. Diving behaviour of lactating harp seal, *Phoca groenlandica*, females from the Gulf of St Lawrence, Canada. Animal Behaviour 46:1213–21. https://doi.org/https://doi.org/10.1006/anbe.1993.1312.

Mellish, J-A. E., D.G. Calkins, D.R. Christen, M. Horning, L.D. Rea, and S.K. Atkinson. 2006. Temporary captivity as a research tool: comprehensive study of wild pinnipeds under controlled conditions. Aquatic Mammals 32:58–65. https://doi.org/10.1578/AM.32.1.2006.58.

Mestre, F., M.P. Bragança, A. Nunes, and M.E. dos Santos. 2014. Satellite Tracking of Sea Turtles Released after Prolonged Captivity Periods. Marine Biology Research 10:996

Miller, P., Narazaki, T., Isojunno, S., Aoki, K., Smout, S., & Sato, K. (2016). Body density and diving gas volume of the northern bottlenose whale *(Hyperoodon ampullatus)*. The Journal of Experimental Biology, l, jeb.137349. https://doi.org/10.1242/jeb.1373491006. https://doi.org/10.1080/17451000.2013.872801.

Morrison, C., C. Sparling, L. Sadler, A. Charles, R. Sharples, and B. McConnell. 2012. Postrelease Dive Ability in Rehabilitated Harbor Seals. Marine Mammal Science 28:110–123. https://doi.org/10.1111/j.1748-7692.2011.00510.x.

Nilssen, K.T., O.P. Pedersen, L.P. Folkow, and T. Haug. 2000. Food consumption estimates of Barents Sea harp seals. NAMMCO Scientific Publications 2:9–27.

Nordøy, E.S., P.-E. Mårtensson, A.R. Lager and A.S. Blix. 1995. Food consumption of the Northeastern Atlantic stock of harp seals. In: Whales, seals, fish and man. Proceedings of an International Symposium on the Biology of Marine Mammals in the Northeast Atlantic. (eds. Blix, A.S., L. Walløe & Ø. Ulltang), Elsevier Publisher B.V., Amsterdam, pp. 255-260.

Nordøy, E.S., L.P. Folkow, V. Potelov, V., and A.S. Blix. 2008. Seasonal distribution and dive behaviour of harp seals *(Pagophilus groenlandicus)* of the White Sea-Barents Sea stock." Polar Biology 31:1119–35. https://doi.org/10.1007/s00300-008-0453-9.

Ponganis, P.J., T.K. Stockard, J.U. Meir, C.L. Williams, K.V. Ponganis, R.P. van Dam, and R. Howard. 2007. Returning on empty: extreme blood depletion underlies dive capacity of emperor penguins. Journal of Experimental Biology 210:4279 – 4285.

Pryor, K and Ramirez K. 2014. "Modern Animal Training A Transformative Technology." In The Wiley Blackwell Handbook of Operant and Classical Conditioning, First Edition, 737 pp.

Richard, G., J. Vacquié-Garcia, J. Jouma'a, B. Picard, A. Génin, J.P.Y. Arnould, F. Bailleul, and C. Guinet. 2014. Variation in body condition during the post-moult foraging trip of southern elephant seals and its consequences on diving behaviour. The Journal of Experimental Biology 217:2609 – 2619.

Ropert-Coudert, Y., A. Kato, D. Gremillet, and F. Crenner. 2012. Bio-Logging: Recording the ecophysiology and behaviour of animals moving freely in their environment. In Bio-Logging: Recording the Ecophysiology and Behaviour of Animals Moving Freely in Their Environment Centre National de La Recherche Scientifique (CNRS), Paris, France, 43–62.

Skinner B. F. 1951. How to teach animals? American Psychologist 185:26–29.

Stewart, R.E.A., and D.M. Lavigne. 1980. Neonatal growth of northwest Atlantic harp seals, pagophilus groenlandicus. Journal of Mammalogy 61 (4):670–80.

Svetochev, V. N., Kavtsevich, N. N., & Svetocheva, O. N. (2016). Satellite tagging and seasonal distribution of harp seal (juveniles) of the White sea-Barents sea stock. Czech Polar Reports, 6(1), 31–42. https://doi.org/10.5817/CPR2016-1-4

Thomton, J.D., J-A.E. Mellish, D.R. Hennen, and M. Horning. 2008. Juvenile Steller sea lion dive behavior following temporary captivity. Endangered Species Research 4:195–203.

Vacquie-Garcia, J., C. Lydersen, M. Biuw, T. Haug, M.A. Fedak, and K.M. Kovacs. 2017. Hooded seal *Cystophora cristata* foraging areas in the northeast Atlantic ocean investigated using three complementary methods.PLOS ONE https://doi.org/10.1371/journal.pone.0187889.

Vincent, C. B. J. Mcconnell, V. Ridoux, M.A. Fedak. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. Marine Mammal Science. 18:156-166 10.1111/j.1748-7692.2002.tb01025.x

Potelov V., K.T. Nilssen, V. Svetochev, T. Haug. 2000. Feeding habits of harp (Phoca groenlandica) amd hooded seals (Cystophora cristata) during late winter spring and early summer in the Greenland Sea. NAMMCO Scientific Publications Volume 2, 40–49.

Wathne, J.A., T. Haug, and C. Lydersen. 2000. Prey preference and niche overlap of ringed seals Phoca hispida and harp seals Phoca groenlandica in the Barents Sea. Marine Ecology Progress Series 194:233–39.

Whaley, J.E. 2009. Policies and best practices: marine mammal stranding response, rehabilitation, and release. Standards for realease. NOAA Report 114 pp.

Williams, T.M., L. Wolfe, T. Davis, T. Kendall, B. Richter, Y. Wang, C. Bryce, G. Hugh Elkaim, and C.C. Wilmers. 2014. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. Science 346:81– 85.

Wilmers, C.C., B.N., C.M. Bryce, J.A. Smith, R.E. Wheat, and V. Yovovich. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology.Ecology 96:1741–53. https://doi.org/10.1890/14-1401.1.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *The Journal of Animal Ecology*, *75*(5), 1081–90. https://doi.org/10.1111/j.1365-2656.2006.01127.x

Figure 1. Visual summary of the handling of the harp seals. The map (a) shows the location of the capture, experiments and release sites. The pictures show the capture procedure (b, c), handling during the experiments (d, e, f, g) and release (h, i, j).

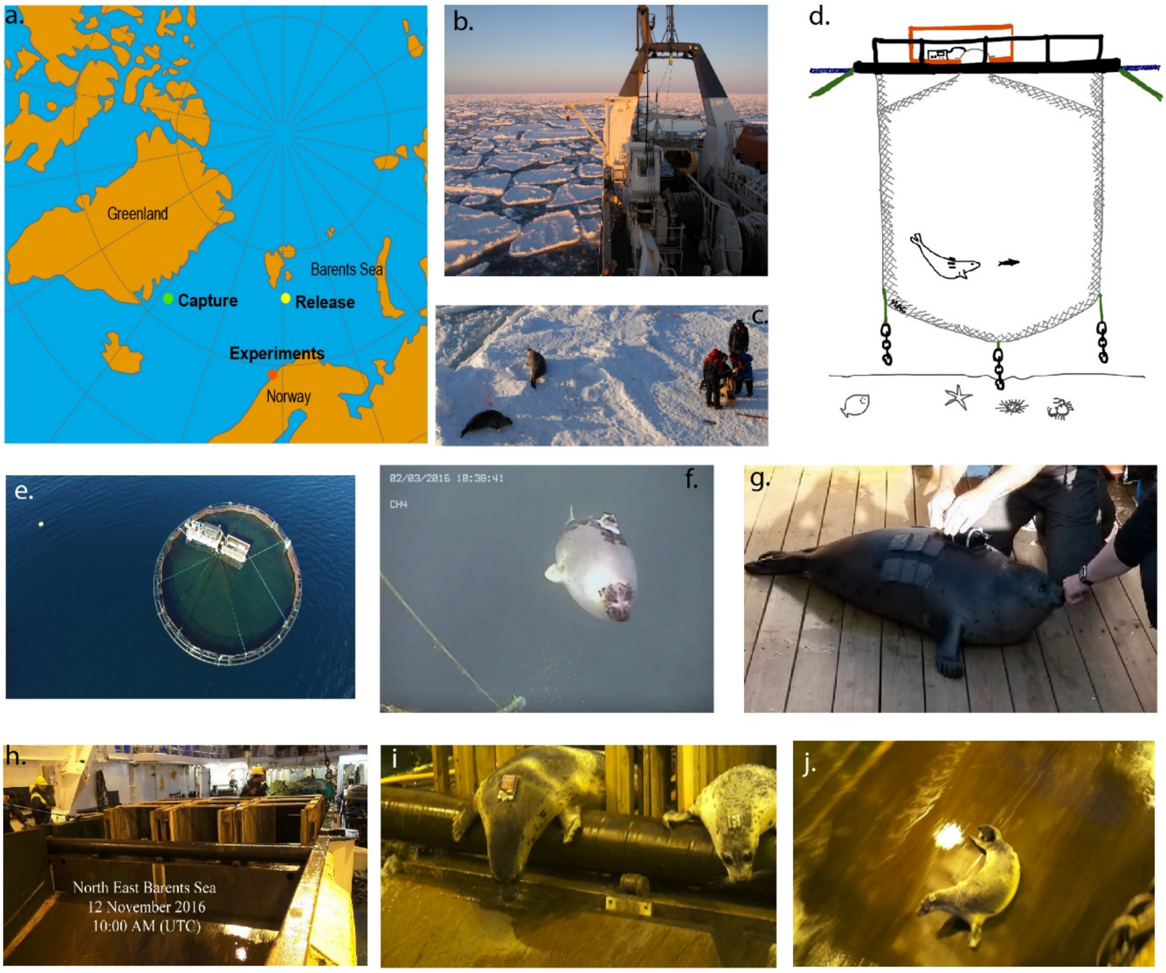

Figure 2. Filtered tracks of the three released harp seals *(Phoca groenlandica).* The dots represent the locations of the capture (green), experiments (red) and release (yellow) sites. The tracks were filtered using a Kalman filter.

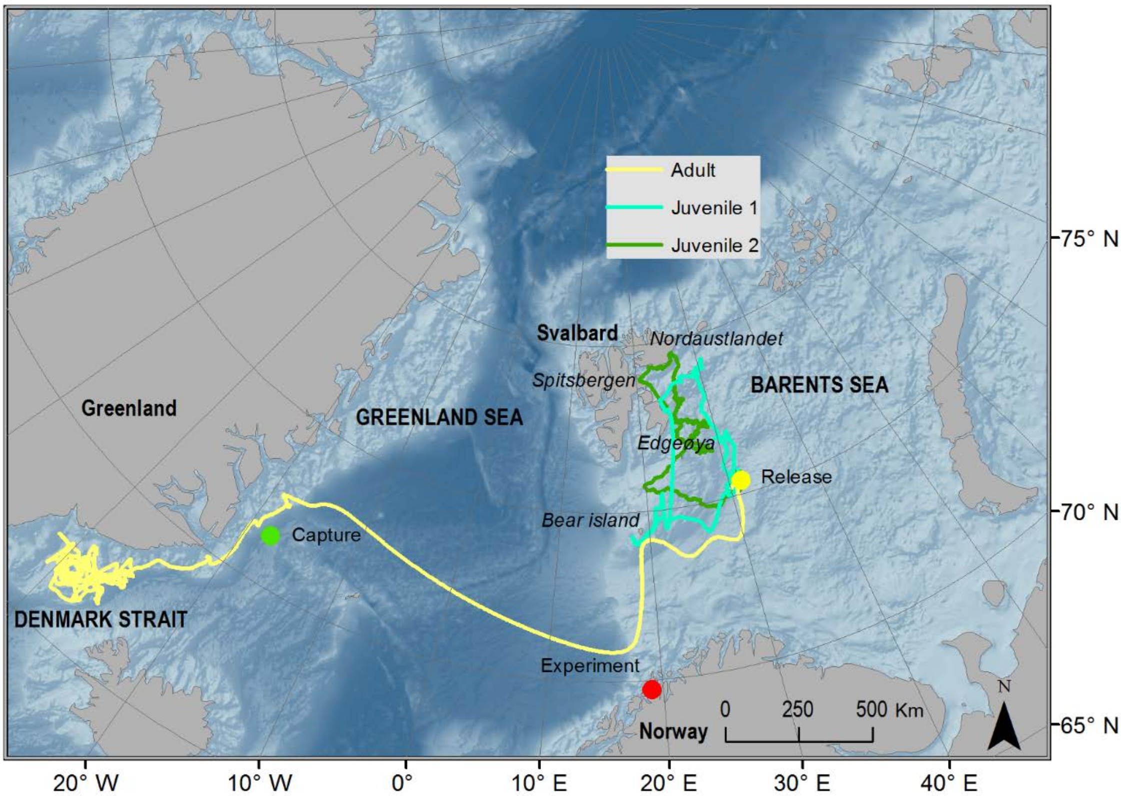

Figure 3. Speed along the track (in grey) and distance from the release site (in red) as a function of the date for the adult (a), juvenile 1 (b), and 2 (c). The blue dots at the top of the first two graphics represent the transmitted dives and the bottom colored circles represent the duration of the first passage time (FPT) for each animal at their individual scale. The map (d) represents the first passage time for each animal at their individual scale along each track. The color scale and scheme are consistent for all graphs. Warmer colors represent longer FPT. The black solid line on the map represents the 15% sea ice concentration limit averaged between December and April.

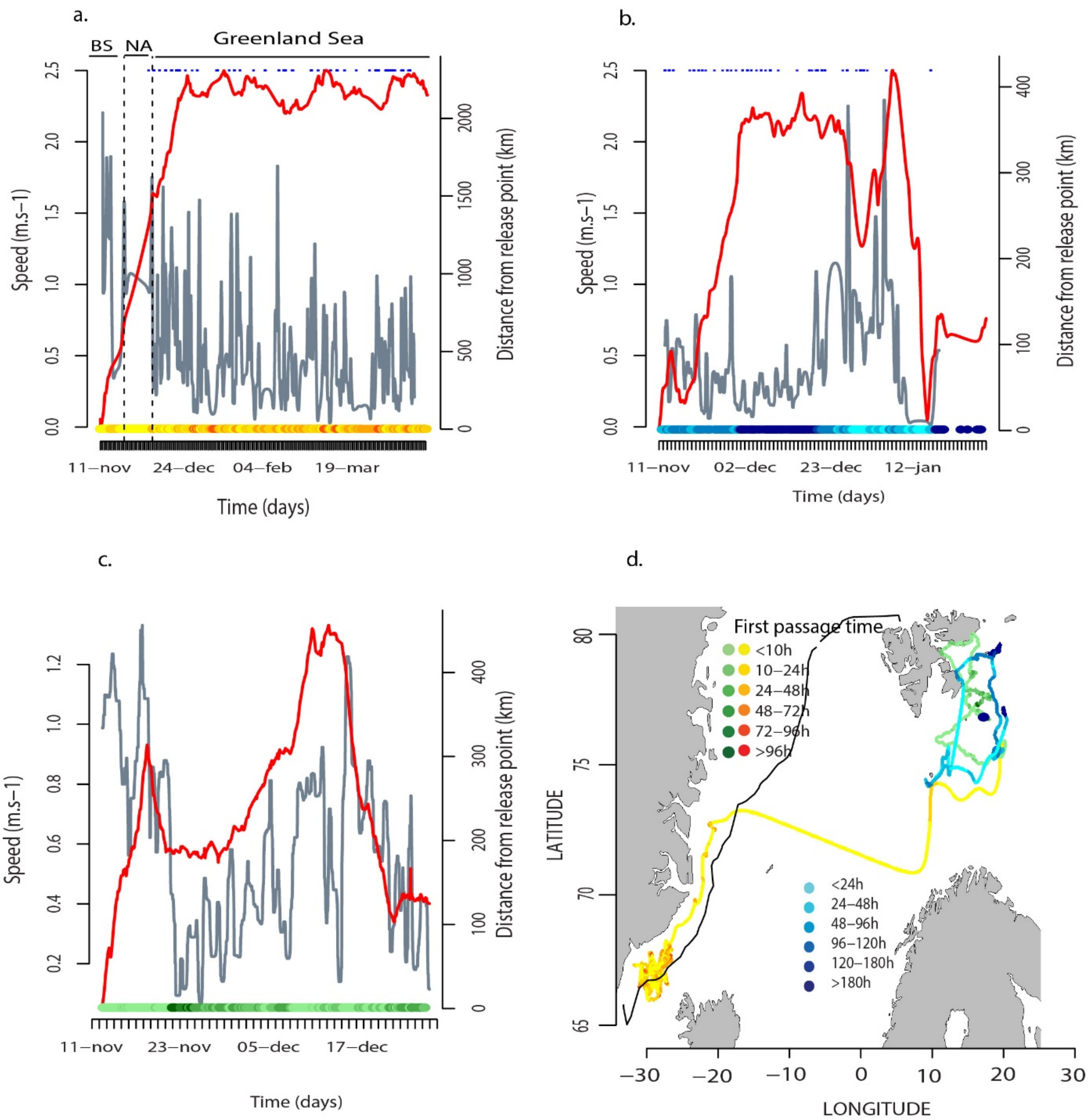

Figure 4. Distribution of the dive duration (top panels) and dive depth (side panels) for the released adult (a), juvenile 1 (b) and juvenile 2 (c) harp seals. For the first two animals (a and b) each black dot on the middle panel represents a transmitted dive and each red dot the depth of each transmitted CTD cast. The width of the duration and depth bins is constant (1 minute and 5 m) and corresponds to the x-axis and y-axis respectively. For juvenile 2 (c) the middle panel represents a heat map of the time spent within various depths bins. The depth bins are represented by the horizontal histogram, with bin ranges as follows: 0 – 5 m, 5 – 10 m, 10 – 15 m, 15-20 m, 20 – 25 m, 25 – 50 m, 50 – 75 m, 75 – 100 m, 100 – 150 m, 150 – 200 m, 200 – 250 m, 250 – 300 m, and > 300 m. The duration bins (vertical histogram) have the following ranges: 0 – 1 min, 1 – 2 min, 2 – 3 min, 3 – 4 min, 5 – 6 min, 6 – 7 min, 7 – 10 min, 10 – 15 min, 15 – 20 min, and 20 – 25 min. The width of the bins is proportional to depth or duration range. The width of the depth bins correspond to the y-axis scale.

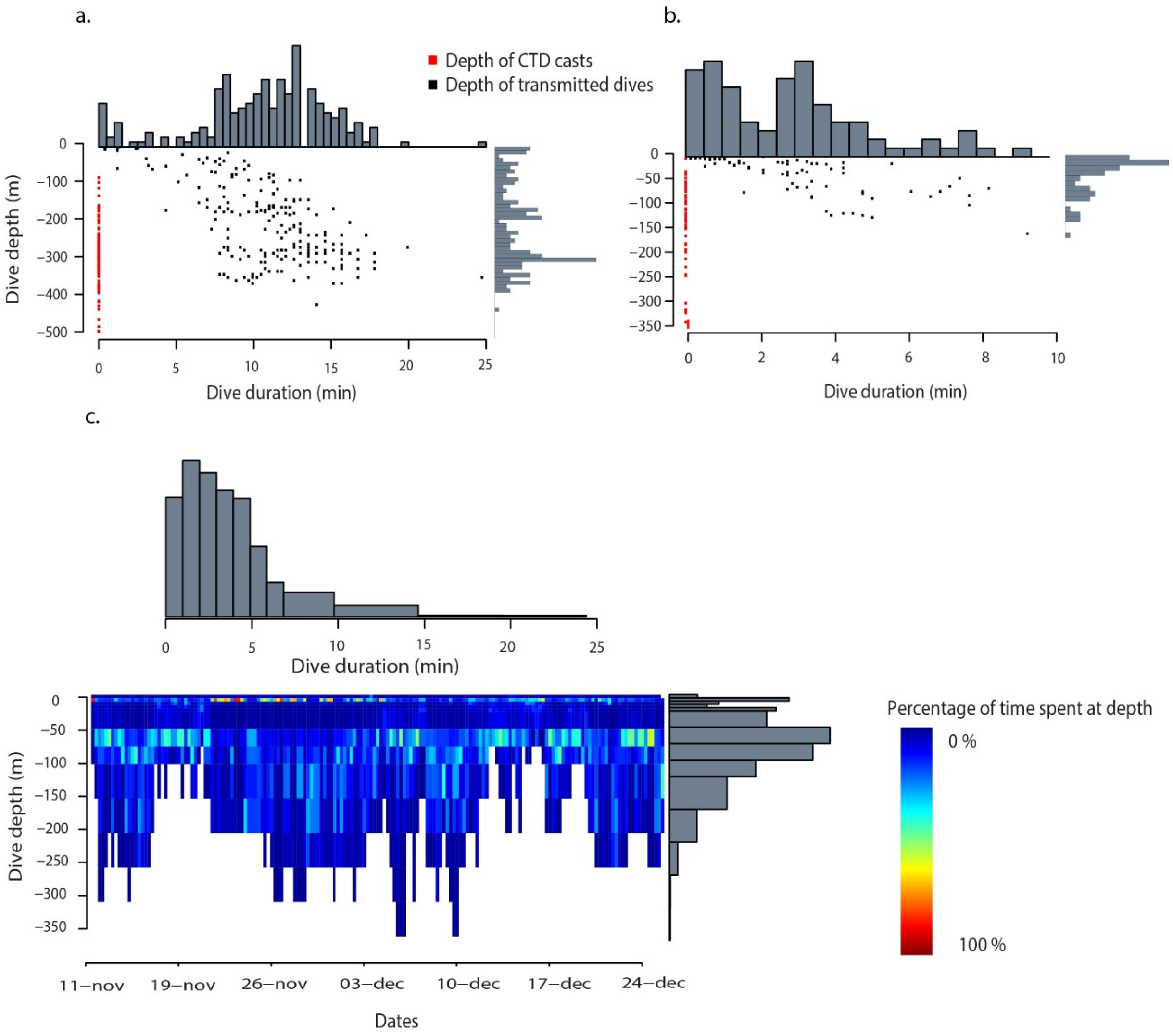

Table 1. Description of each animal and summary statistics based on the records transmitted by each instrument

Metrics	Adult	Juvenile 1	Juvenile 2
Mass at capture	86	27	31
Mass at release	120	88	64
Estimated age at capture	ca. 6 y	ca 15 d.	ca 15 d.
Tracking duration (d)	162	67	45
Max dist. from release point (km)	2308	419	456
Av. Daily dist. ($km.d^{-1}$)	47	41	56
Av. Speed ($m.s^{-1}$)	0.54	0.47	0.65
Total cumulated distance (km)	7645	2749	2489
Av. dive depth +/- sd - max (m)	210 +/- 108 (475)	41 +/- 36 (331)	NA (250-300)
Av. dive dur +/- sd - max (min)	10,5 +/- 4,2 (25)	2,8 +/- 2,2 (9)	NA (20-25)
Av. Decent rate +/- sd - max ($m.s^{-1}$)	1,45 +/- 0,49 (2,9)	1,76 +/- 0,94 (6.14)	NA
Av. Ascent rate +/- sd - max ($m.s^{-1}$)	1,02 +/- 0,44 (2,62)	0.79 +/- 0,6 (3,05)	NA
Daily diving rate +/- sd - max (dive. day^{-1})**	NA	NA	396 +/- 118 (730)
Percentage Time haulout*	4	1.5	NA
Percentage Time diving*	77	69.0	NA
Percentage Time surface*	19	30.0	NA

* These percentages are calculated based on the transmitted summaries (ca. 45%) for each animal

**This metric can only be calculated for juvenile 2