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At-sea behaviour of the world's northernmost harbour seal *(Phoca vitulina)* population in a changing Arctic

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Cover Photo: Harbour seal *(Phoca vitulina)* instrumented with a Conductivity-Temperature-Depth Satellite-Relay-Data-Logger (CTD-SRDL) used in the present study. © Kit Kovacs and Christian Lydersen, NPI

The most exciting phrase to hear in science, is not "Eureka!", but "That's funny…".

Isaac Asimov

Nothing can be more improving to a young naturalist than a journey in a distant country.

Charles Darwin

AT-SEA BEHAVIOUR OF THE WORLD'S NORTHERNMOST HARBOUR SEAL

(PHOCA VITULINA) POPULATION IN A CHANGING ARCTIC

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A DISSERTATION FOR THE DEGREE OF PHILOSOPHIAE DOCTOR

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SUMMARY

The earth is experiencing warming at a rate that challenges the adaptive capacities of many animal species. Temperatures are increasing more rapidly in the Arctic than in any other region on the globe and predictions suggest that the degree of change is expected to be the greatest in this biome. The Northern Barents Region, including the waters surrounding the Svalbard Archipelago, has experienced the most dramatic environmental changes recorded to date, with effects cascading through the entire ecosystem. Because marine mammals can integrate and reflect ecological variation across various spatial and temporal scales, they are prime sentinels of marine ecosystem change. This thesis explores movement patterns and foraging behaviour, and the ontogeny of these behaviours, in harbour seals *(Phoca vitulina)* from the world's northernmost population in Svalbard, Norway, in the context of local environmental conditions.

Sixty harbour seals, including pup, juvenile and adult age classes, were instrumented near the main breeding site for this population on Forlandsøyene, west of Prins Karl Forland in 2009 and 2010 (30 animals each year; 15 adults/juveniles and 15 pups) with Conductivity-Temperature-Depth Satellite-Relay-Data-loggers (CTD-SRDLs) for the adults and juveniles and smaller Satellite-Relay-Data-loggers (SRDLs) for the pups. These instruments collected information on at-sea movement, diving, haul-out behaviour and ocean temperature; additionally the CTD-SRDLs collected oceanographic parameters including conductivity. The adult and juvenile seals were instrumented after the annual moult in September while the pups were instrumented towards the end of the nursing period in late June. The seals showed a strong preference for the west side of the archipelago, where they stayed within 50 km of the coast on the shelf, seldom entering the fjord systems especially in the winter. Habitat selection analysis showed that the adult and juvenile seals avoided heavy ice concentrations and preferred shallow waters (<100 m) and steep bathymetric slopes. Some pups ventured out of the west coast shelf area occasionally, with individuals that explored the Bjørnøya region or the east coast of Spitsbergen. The transition from maternal dependence to independent foraging occurred at a young age and was quite abrupt; marked changes in movement and diving patterns thought to accompany the

end of the post-weaning fast were observed when the pups were approximately 50 days of age.

The core area occupied by the seals is characterized by complex oceanographic conditions and intense mixing between masses of Arctic Water and Atlantic Water from the West Spitsbergen Current (WSC), which drives the high primary productivity and dynamism in this region. The adult and juvenile seals diving behaviour had a marked seasonality and was influenced by local wind-driven upwelling phenomenon. During upwelling events, the West Spitsbergen Shelf is flooded by Atlantic Water masses, which were specifically targeted by the seals. Presumably these water masses brought Atlantic fish species close to shore and within the seals' foraging depth-range. However, no strong correlation between dive parameters and upwelling events was found for the pups suggesting that they might not be able to exploit prey associated with Atlantic Water masses early in their lives.

This study strongly suggests that the influence of the WSC on the western part of the Svalbard Archipelago is a determining factor for the presence of this harbour seal population in the High Arctic. Although environmental stressors are strong on this population currently, the predicted warming will likely favour an increased abundance and a broader distribution of harbour seals through a borealization of the marine ecosystem in the coastal areas of the Svalbard Archipelago.

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Blanchet M. A, Lydersen C., Ims R., Kovacs K.M. (2015). Seasonal oceanographic and atmospheric drivers of diving behaviour in a temperate seal species living in the High Arctic. *PLOS ONE.* doi: 10.1371/journal.pone.0132686

Paper III

Blanchet M. A, Lydersen C., Ims R., Kovacs K.M. (*Submitted*). Making it through the first year: Ontogeny of movement and diving behaviour of harbour seals pups *Phoca vitulina* from Svalbard, Norway. *Marine Mammal Science*

I INTRODUCTION

A. The harbour seal

a. General ecology and life cycle

The harbour seal, or common seal *(Phoca vitulina* Linnaeus 1758), is one of the most studied Phocid species mainly due to its broad coastal distribution, visibility and site fidelity. Centuries of interactions with humans through harvest, conflicts with fisheries or more recently tourism have given the species its common name (Bonner 1989). The harbour seal is a small Phocid seal that has an average body length of 150 cm and an average mass of 70-100 kg (King 1983), although these parameters do vary between populations with the largest seals occurring in the North Pacific (Burns 2009). Harbour seals alternate periods on a solid substrate (hauled out on land or ice) with foraging trips at sea. They remain tied to solid substrates for birthing, nursing their young and resting (Bartholomew 1970; King 1983, Riedman 1990). New-born pups average 80 cm in length and weigh an average of 11 kg (Bowen, Oftedal et al. 1994, Coltman, Bowen et al. 1998, Burns 2009). Pups are born on land or on ice in the late spring or early summer. They usually shed their lanugo *in-utero* and are born with the same colour pattern as the adults. Harbour seals give birth on platforms (sandy beaches, intertidal rocks, or glacial ice) that can be unstable or flooded rapidly and pups are therefore extremely precocial at birth. They are able to swim within a few hours after birth and are active at sea during the entire nursing period (Boulva and McLaren 1979, Jørgensen, Lydersen et al. 2001). Weaning occurs around 30 days of age and is followed by a post-weaning fast that lasts approximately 15 days (Muelbert and Bowen 1993). Adults moult once a year in mid-summer to early fall, depending on sex and age. During this period they feed little and spend most of their time out of the water (Burns 2009). Female harbour seals reach sexual maturity when they are three or four year old while males usually reach sexual maturity at four or five years of age. Once sexually mature, females can produce one pup per year for the rest of their lives. The maximum life span is around 35 years although few animals reach that age in the wild (Burns 2009).

b. Distributional range

Harbour seals have one of the broadest distributions among the pinnipeds, ranging from temperate areas as far south as southern California and France to arctic waters of the North Atlantic (Bigg 1969, Thompson 1989, Bjørge, Desportes et al. 2010) (Figure 1). This species covers a latitudinal spread from 20° N through to nearly 80° N, including the entire longitudinal range of the coasts of the Northern hemisphere. The species thus encounters vast amounts of variation in environmental parameters, ranging from temperate to arctic conditions.

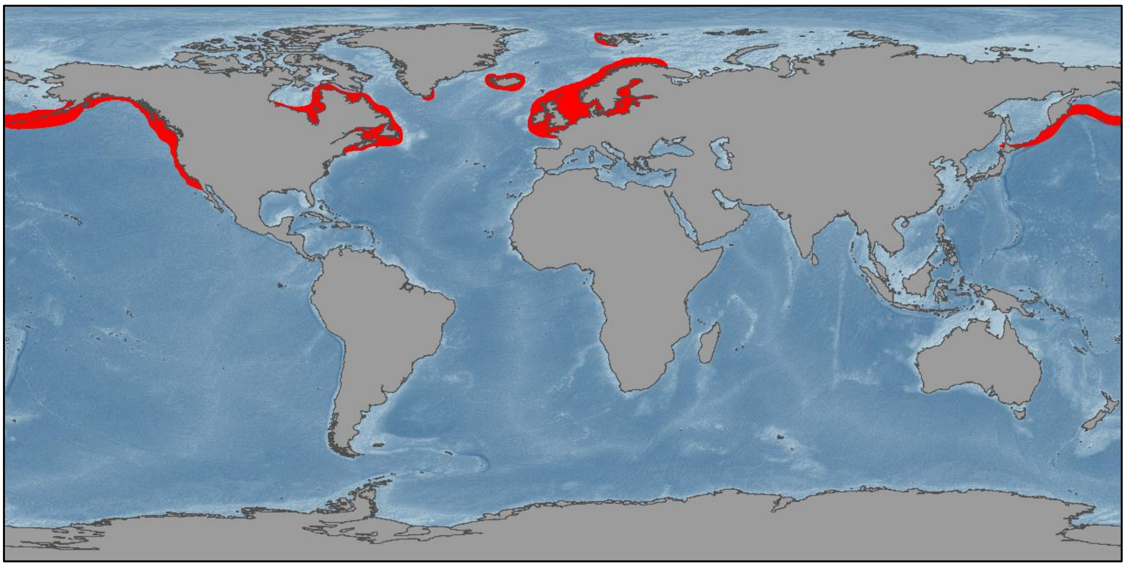

Figure 1. Worldwide distribution of harbour seals (adapted from IUCN, Thompson and Härkonen, 2008).

c. Subspecies and population structure

Oceans basins and land masses act as distributional barriers for the coastal harbour seal and the species has evolved into five subspecies (Scheffer 1958, Wiig 1989). Two subspecies occur in the North Pacific, *P. v. stejnegeri* with a range that stretches from Japan to the western Aleutians, and *P. v. richardii* which occurs from the eastern Aleutians to southern California (Shaughnessy and Fay 1977). In the eastern North Atlantic, *P. v. vitulina* extends from Brittany to the Barents Sea reaching the coasts of north-western Russia, Iceland and north to the Svalbard Archipelago. A small population in south-east Greenland also appears to belong to this subspecies receiving migrants from Iceland and Svalbard (Andersen, Lydersen et al. 2011). *P. v. concolor* is found in the western North Atlantic ranging from the Canadian Arctic to New Jersey on the northern coast of the US. This subspecies is also thought to occupy the west coast of Greenland, though no specific genetics testing has confirmed this assumption (Rice 1998). A third isolated subspecies *P. v. mellonae* lives in a series of land-locked, inter-connected freshwater lakes on the Ungava Peninsula in northern Quebec, although it is thought that the seals' distribution is now limited to only three lakes (Smith 1997, DFO 2009 revised 2011). In addition, a small, apparently isolated population of freshwater harbour seals occupy the Iliamna Lake in Alaska on a year-round basis; this population is not recognized as a sub-species (Hauser, Allen et al. 2008).

Genetic analysis have revealed differentiation between harbour seal populations in the Pacific and Atlantic at the broad ocean basin scale but also at a more local scale with genetic differentiation occurring even between neighbouring colonies (Stanley, Casey et al. 1996, Westlake and O'Corry-Crowe 2002, Herreman, Blundell et al. 2009, Andersen and Olsen 2010). Harbour seals are generally considered to be a relatively sedentary species that exhibit small scale movements and long-term site-fidelity, which likely account for the observed population subdivisions within large-scale regions despite the absence of major geographical barriers. Genetic differentiation among groups of *P. vitulina* has been detected on a scale of only a few hundred kilometres in the northeastern Pacific (Stanley, Casey et al. 1996, O'Corry-Crowe, Martien et al. 2003) and it appears that dispersal patterns of harbour seals are mainly behaviourally restricted, limiting the gene flow between more distant regions (Brown and Mate 1983). Observed genetic differences do increase with geographic distance suggesting that dispersal, when it occurs, is among neighbouring subpopulations (Westlake and O'Corry-Crowe 2002). Detailed genetic studies are still lacking for the worldwide population of harbour seals, and a more specific approach at local scales is needed in order to detect sub-structuring within larger genetically separated groups (Andersen and Olsen 2010) and to identify suitable functional units for describing populations dynamics (Härkönen and Harding 2001).

d. Status and current threats

The harbour seal was listed as “Least concern” on the IUCN Red List in 2008; at the time the global population was estimated to be between 350 000 and 500 000 individuals (Thompson and Härkönen 2008). Major declines have been documented for some populations in the last 20 years (Bjørge, Desportes et al. 2010, Kovacs, Aguilar et al. 2012) while others harbour seal populations appear to be stable or increasing. Dramatic differences exist between subspecies, regions and populations in terms of available information regarding population status, population dynamics and national management schemes.

Conservation concerns have led to the protection of harbour seals under the Marine Mammals Protection Act (MMPA 1972) in the USA and the Habitat Directive in Europe (1992). However, harbour seals are targeted sporadically by culling programmes at local levels in Canada (NOAA 2014), Norway (Nilssen, Skavberg et al. 2010) and Iceland (Hauksson and Einarsson 2010) while they have been recently protected in Russia (Zyryanov and Egorov 2010) and Greenland (Boertmann and Rosing-Asvid 2014; NAMMCO 2011). They are also part of indigenous subsistence programmes in Alaska (Wolfe, Fall et al. 2009). The effect of hunting pressure on local populations is not always known but in some cases, such as in Iceland it is believed to be unsustainable (Hauksson 2010). Other threats to harbour seal populations cover a vast variety of causes ranging from direct human-associated takes and disturbances to climate-related influences. They include predation (Springer, Estes et al. 2003), interactions with fisheries (NAMMCO 2014), chemical pollution (Shaw, Berger et al. 2012, Shaw, Berger et al. 2014), diseases (Hall, Jepson et al. 2006, Härkönen, Dietz et al. 2006), changes in food availability and quality (Trites and Joy 2005, DeMaster, Trites et al. 2006, Lonergan, Duck et al. 2007), decreases in available habitat (Womble, Pendleton et al. 2010) and occurrence of harmful algal blooms (Jensen, Lacaze et al. 2015).

B. The world's northernmost population on Svalbard

The Svalbard Archipelago is located in the European High Arctic, laying between 76° N and 81° N (Figure 2). It hosts the world's northernmost population of harbour seals (Wiig 1989, Prestrud and Gjertz 1990), which is the only population of this species that occurs above the Arctic Circle (Henriksen, Gjertz et al. 1997).

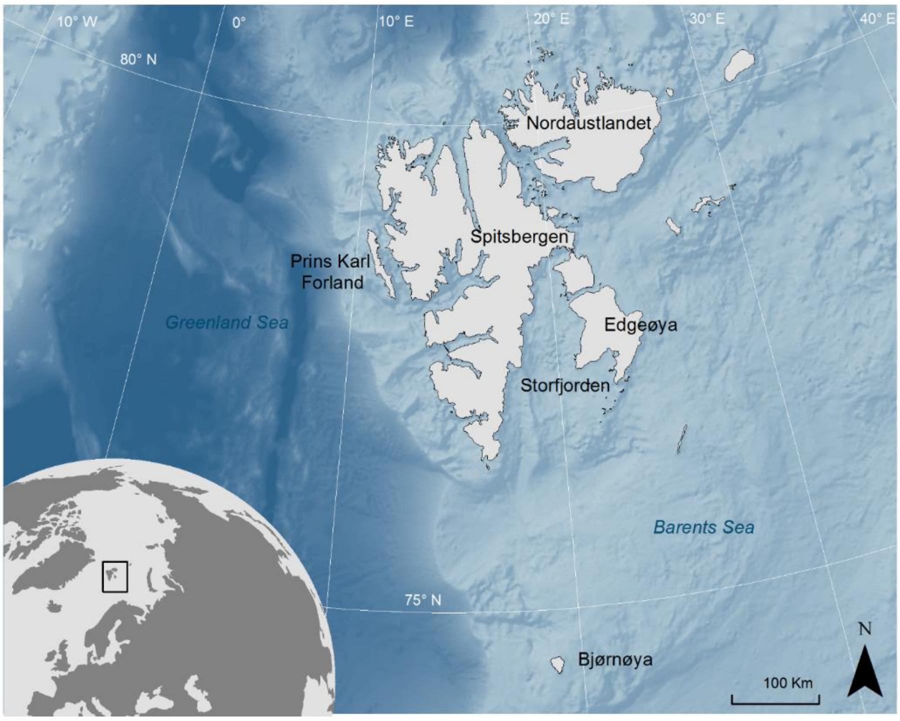

Figure 2. Map of the Archipelago of Svalbard. The inset shows the archipelago in a larger geographical context.

a. Genetic diversity and population structure

The Svalbard harbour seal population is highly genetically distinct from neighbouring populations and shows a significantly reduced allele richness as well as indications of a bottleneck resulting from a recent population decline (Andersen, Lydersen et al. 2011). There seems to be very limited gene flow from other populations to Svalbard indicating a closed, distinct population that rarely receives migrants. Some records of Svalbard animals recovered in nets in northern Norway do exist (Gjertz, Lydersen et al. 2001) and genetic analyses suggest that this population supplies individuals to at least the south-east Greenland population (Andersen, Lydersen et al. 2011). Harbour seals on Svalbard are shorter and fatter than their southern counterparts, suggesting an adaptation to a colder environment through a thicker blubber layer in order to stay within their thermoneutral zone (Lydersen and Kovacs 2005). Individuals from this population exhibit a high degree of size dimorphism between sexes compared to many other populations of this species. Males are longer and heavier than females which might be beneficial during the mating period when males hold underwater territories for long periods of time (VanParijs, Thompson et al. 1997, Lydersen and Kovacs 2005). The longevity of Svalbard harbour seals is short compared to harbour seals in other regions. The lack of old individuals, with almost no animal older than 16 years is surprising given the limited negative human-seal interactions (Lydersen and Kovacs 2005). The lack of old individuals might however be linked to strong predation pressure from terrestrial predators like polar bears *(Ursus maritimus)* or marine predators such as killer whales *(Orcinus orca)* or Greenland sharks *(Somnius microcephalus)* (Lydersen and Kovacs 2005). Greenland sharks are abundant in the region and recent studies show that this large fish does prey on harbour seals (Yano, Stevens et al. 2007, Leclerc, Lydersen et al. 2012). Their Northwest Atlantic counterparts are thought to have heavily impacted harbour seals population demography on Sable Island (Lucas and Stobo 2000). Killer whales are reported only irregularly in Svalbard and no observation of predation by them on harbour seals has been reported (Øien 1988, Lydersen and Kovacs 2005). Alternatively, harsh environmental conditions might exert long-term low levels of stress that could reduce the life span (Lydersen and Kovacs 2005).

b. Population size

A recent population abundance survey was conducted for harbour seals in Svalbard in 2009 and 2010 (Merkel, Lydersen et al. 2013); the estimated size of the population was about 2000 individuals, based on counts from Prins Karl Forland. This count is believed to be a minimum estimate as only individuals on Prins Karl Forland, the main haulout site within the archipelago were counted. In recent years an increasing number of harbour seals have been observed on land in other areas of Svalbard during the summer (Hop, Pearson et al. 2002; The Norwegian Polar Institute's Marine Mammal Sighting Database). Assessments of the total population of harbour seal in Svalbard in the future will have to encompass a larger geographical area to take into account the expanding distribution of harbour seals in this region.

c. Diet

Information is scarce regarding the diet of harbour seals in Svalbard. Currently, dietary information is available for only the period from early summer through fall (Andersen, Lydersen et al. 2004, Colominas 2012), leaving the whole of the dark period unknown. Based on analysis of hard-parts from scats and blubber fatty acid, harbour seals on Svalbard appear to be opportunistic, polyphagous feeders (Andersen, Lydersen et al. 2004, Colominas 2012), similar to elsewhere in the species' range. Fish dominates the diet with members of the cod (Gadidae) and sculpin families (Cottidae) being the most abundant, likely reflecting the relative abundance of these prey species at a local scale. The relative abundance of Atlantic cod *(Gadus morhua)* compared to polar cod *(Boreogadus saida)* has shown an increase between samples collected in the late 1990’s and 10 years after (Colominas 2012), likely reflecting changes in the fish community structure of the west coast region in Svalbard. Atlantic fish species such as haddock *(Melanogrammus aeglefinus)* and Atlantic wolfish *(Anahichas lupus)* have appeared in the latter period indicating a dietary shift.

d. Distribution and movements

In Svalbard harbour seals are mainly found on Prins Karl Forland, an 86 km-long island on the West coast of Spitsbergen (Lydersen and Kovacs 2010). This island is currently the only documented pupping site for harbour seals in this region and one of the main haulout sites throughout most of the year (Lydersen and Kovacs 2010, Hamilton, Lydersen et al. 2013). Adults and juveniles from this population are observed along the west coast of Spitsbergen up to the northeastern corner of Spitsbergen, with the northernmost record being 80.5 ° N (Wiig 1989, Prestrud and Gjertz 1990, Henriksen, Gjertz et al. 1997, Hop, Pearson et al. 2002, Lydersen, Krafft et al. 2002).

e. Main threats and conservation status

Svalbard harbour seals are on the Red List because of the small size of this population and are protected from exploitation. There are no gillnet fisheries in the distribution range of harbour seals limiting potential negative human-seal interactions. The main breeding site occurs within a bird-reserve, so access to this region is extremely limited during the whole of the summer. Studies on contaminants show that the seals are exposed to a wide range of environmental pollutants including pesticides, both legacy and currently used persistent organic pollutants (POP’s) as well as their metabolites (Wolkers, Lydersen et al. 2004). But, concentrations in Svalbard harbour seals are much lower than in other populations of this species found further south. Animals from Svalbard contain 5-10 times less contaminant compared to seals in the Norwegian mainland and their concentrations are 30 times lower than those of harbour seals from more industrialized areas such as in the Gulf of St Lawrence (Wolkers, Lydersen et al. 2004). A more recent study confirms a precipitous decline in legacy POP’s, with a drop in concentrations of 60-90 % over the period of a decade (Routti, Lydersen et al. 2014). Both of these studies conclude that the current levels of contaminants are not a threat to harbour seals on Svalbard. However the high levels of metabolites (hydroxy PCBs) found in individuals from this population suggest an efficient PCB biotransformation and this might represent a risk for thyroid homeostasis (Routti, Lydersen et al. 2014); potential signs of endocrine disruption should be closely monitored.

C. Climate change in the Barents Sea and its effects

Climate change has already caused warming of the atmosphere and oceans; sea ice has declined markedly and sea level has risen (IPCC 2013) changing the physical and biological characteristics of both the terrestrial and marine environments occupied by harbour seals over their wide distributional range. Warming is occurring more rapidly in the Arctic than in any other region on the globe and predictions suggest that the degree of change is expected to be the greatest in this ecosystem (Kovacs and Lydersen 2008, Onerheim, Smedsrud et al. 2014).

a. Physical changes

i. Changes in sea ice

Arctic sea ice cover is part of the polar heat sink and is considered a key component of the global climate system (Comiso and Hall 2014). As the ice retreats, more heat is absorbed into the ocean causing a warmer surface that in turn causes more ice melting. The total extent of sea ice cover in the arctic and sub-arctic seas has shown a sharp declining trend in recent decades, reaching a minimum in 2012 which represented the lowest areal expanse since 1978 (Parkinson and Comiso 2013). A significant reduction of old, thick multiyear ice has led to increased rates of loss of annually formed sea ice under the influence of winds and currents (Maslanik, Fowler et al. 2007). This occurs particularly at the ice edge where thin ice is prone to breaking under the mechanical action of sea waves and winds, leading to an increase in the production of drift ice available for transport i.e. losses from the arctic system (Falk-Petersen, Pavlov et al. 2014) and a retreat of the ice edge. Drift ice is principally wind-driven and its concentration varies very quickly both in time and space causing the sea ice landscape to change rapidly (Ingvaldsen et al. 2004). In the Barents Sea, ice cover variation is additionally influenced by the amount of heat transported by the West Spitsbergen Current (Vinje 2009). In recent years, an increase of the heat and flux transported into the Arctic Ocean by the West Spitsbergen Current has caused profound changes in sea ice cover in the Svalbard Archipelago. Land-fast ice used to occur in all fjords, along most of the east coast, in the innermost part of Storfjorden and in shallow areas while nowadays the west coast and most of its fjords are virtually ice-free throughout winter (Vinje 2009). Changes in sea ice phenology (timing of freezing and ice-break up) have also been particularly marked in the Barents Sea region where the summer open-water period has increased by >20 weeks between 1979 and 2013 (Regehr, Lunn et al. 2006, Laidre, et al. 2015) causing changes that are cascading through the entire ecosystem.

ii. Increased temperatures and alteration in ocean circulation

The rise in arctic air temperatures has been almost twice as large as the global average in recent decades (Screen and Simmonds 2010). In Europe, the Svalbard Archipelago has experienced the greatest water temperature increase during the last three decades (Nordli, Przybylak et al. 2014). The West Spitsbergen Current, which flows along the shelf edge, represents the main source of heat entering the Arctic Ocean rendering the Barents Sea region crucial to the understanding of heat fluxes through the Arctic Ocean (Sakshaug and Kovacs 2009, Pavlov, Tverberg et al. 2013). Since 1979, a 0.3°C per decade warming of the West Spitsbergen Current has been observed concurrently with winter sea ice losses in this area of close to 10% per decade (Onerheim, Smedsrud et al. 2014). Increased temperatures in the fjords on the west coast of Spitsbergen have been linked to an increase of the temperature of the core West Spitsbergen Current and of the flux of Atlantic Water flowing through it (Pavlov, Tverberg et al. 2013). Wind driven upwelling is known to occur along the shelf break on the west coast of the Archipelago; this phenomenon sustains large ice-free areas along the coast even in the winter (Falk-Petersen, Pavlov et al. 2014). Multiyear ice generally impeded the influence of wind-driven upwelling along the shelf break north of Svalbard but the present trend of diminishing amounts of thick ice will likely increase the influence of such upwelling phenomenon in the future (Sakshaug and Kovacs 2009). Indeed, in January 2012 strong upwelling phenomenon were observed at the ice edge north of the archipelago sustaining a large ice-free zone throughout the winter (Falk-Petersen, Pavlov et al. 2014). A strong summer air temperature warming trend has also been observed in Svalbard, influencing negatively the mass balance of glaciers among other things (Kohler, James et al. 2007). Tidewater glaciers are of importance to sea birds and marine mammals as feeding hotspots and the current glacial retreat suggests a future reduction of the length of calving fronts that is likely to affect the distribution of top predators in this region (Lydersen, Assmy et al. 2014). Recently, melting glaciers have been shown to produce noise well above other natural oceanic environments potentially causing displacement of local marine mammals (Pettit, Lee et al. 2015).

b. Biological changes

i. Changes in primary production

Although the recently observed climate-related changes have clearly modified the physical environment in high latitude regions, the consequences on key biological processes remain largely unknown. Sea ice has a dual role in terms of primary production in polar seas, providing both a habitat for ice algae and associated fauna and regulating the available light for primary production (Søreide, Leu et al. 2010, Geoffroy, Robert et al. 2011). In the Barents Sea, warm nutrient-rich water of Atlantic origin drives the high primary productivity (Sakshaug 1997) which is the basis for a lipid-driven food chain via *Calanus sp.* (Falk-Petersen, Pavlov et al. 2014). The absence of sea ice cover enables primary production to take place as soon as the sun returns in March/April. This in turns supports a high biomass of grazing zooplankton such as the ones that have recently been observed North of Svalbard (Falk-Petersen, Pavlov et al. 2014). However, earlier ice break up and consequently earlier onset of the phytoplankton bloom might also cause a potential mismatch between the peak of primary production, the reproductive cycle of key arctic grazers and their associated predators with consequences for the entire lipid-driven Arctic marine ecosystem (Søreide, Leu et al. 2010). The strong seasonal pulse of energy through ice-associated and pelagic marine food webs directly influences the abundance of top trophic levels, represented by marine mammals and sea birds populations (Engelsen, Hegseth et al. 2002).

ii. Shifts in species' ranges

Temperate and boreal species are already becoming more established in arctic regions, and might potentially displace or replace resident taxa in the future (Parmesan 2006). Polar species have tended to be stable or decline in abundance while temperate species at the same site have increased in abundance and/or expanded their distributions (Parmesan and Yohe 2003). This is of particular importance when displaced species play key roles in the ecosystem such as the polar cod, which is a dominant species on arctic shelves (Renaud, Berge et al. 2012). This small arctic fish is a central part in the diet of seabirds, marine mammals and commercial fish species (Gjøsæter 2009, Loseto, Stern et al. 2009) and transfers up to 75% of the energy from lower trophic levels to top predators (Geoffroy, Robert et al. 2011). In the past decade Atlantic cod, haddock, herring (*Clupea harengus)* and capelin *(Mallotus villosus)*, all boreal/temperate fish species, have expanded their ranges well into the Barents Sea and the coastal waters of the Svalbard Archipelago competing with the local arctic endemic species, potentially leading to competitive exclusion.

Northwards range shifts are not only affecting predator-prey relationships but also pathogens-host dynamics (Brooks and Hoberg 2007, Burek, Gulland et al. 2008, Tryland, Godfroid et al. 2009, Kovacs, Aguilar et al. 2012). Pathogens can be transmitted to new immunologically naïve host populations via invasive species, seasonal migrations, migrations caused by nutritional stress or changes in the host population behaviour (Tryland, Godfroid et al. 2009, Kutz, Checkley et al. 2013). For example warmer sea temperatures in the Svalbard Archipelago have resulted in the presence of temperate marine species that could serve as vectors for the coccidian parasite *Toxoplasma gondii,* and this pathway might explain the high prevalence of this parasite in top predators in this region (Berge, Johnsen et al. 2005, Jensen, Aars et al. 2010). Furthermore, pathogens tend to generally grow faster and survive better when temperatures are warmer, therefore a warmer climate could simply result in higher survival rates of these organisms in environments that were previously too cold.

iii. Pollution and direct human disturbances

Although no major sources of pollution are typically found in the Arctic, this region is nevertheless exposed to pollutants through atmospheric transport, river runoffs and marine currents (Gabrielsen and Sydnes 2009). Climate-related changes are known to affect these pathways and these changes could alter the amount of pollutants transported to the Arctic. There is also compelling evidence that increasing temperature could be deleterious to wildlife exposed to pollutants through an alteration of contaminants biotransformation rates (Noyes, McElwee et al. 2009). Reductions in arctic sea ice are resulting in new trans-arctic shipping lanes and increased ship traffic in the Arctic (Smith and Stephenson 2013). This will increase potential disturbances, ranging from increased ocean noise to potential oil spills and direct emission of pollutants (Corbett, Lack et al. 2010) affecting marine biota in the vicinity.

D. Harbour seals as ecosystem sentinels

Worldwide climate change and resource development especially in the Arctic impose a growing pressure on biodiversity which requires that managers have access to up-to-date information on ecosystems in order to make timely informed decisions. Because marine mammals can integrate and reflect ecological variation across various spatial and temporal scales, they are a prime sentinels of marine ecosystem changes (Boyd, Wanless et al. 2006, Moore 2008). For example changes in individual body condition, offspring survival, population demography or spatial distribution can demonstrate shifts in food web structure, resources distribution, pathogens pathways or local environmental conditions. However, single indicators are unlikely to be influenced by climate change alone and groups of indicators are needed to demonstrate efficiently how climate change is affecting marine systems (Philippart, Anadon et al. 2011). Monitoring programs should therefore favour a multidisciplinary approach integrating biological and physical aspects of the ecosystem. An account of the variability of the monitored parameters should also be estimated and links between observed changes and potential drivers should be explored in order to be able to detect changes.

In the perspective of global climate change, harbour seals are particularly interesting as ecosystem sentinels due to their broad distribution in the northern hemisphere and the variety of environmental conditions this species encounters. This offers the possibility for worldwide inter-populations comparison and for identifying drivers influencing population dynamics. The case of the northernmost harbour seal population on Svalbard is especially interesting because this species is essentially temperate, not ice-affiliated and is not a true Arctic species. Therefore harbour seals on Svalbard might have a competitive advantage over local arctic species under warmer conditions. Alternatively this isolated, highly genetically distinct population could be at risk of extinction through stochastic events such as epizootic episodes or oil spills. Therefore, exploring the drivers influencing the seals' behaviour is essential to predict the consequences of the unprecedented warming in this region

II OBJECTIVES

The main objectives of this thesis were the following:

1. Investigate movement patterns and quantify habitat selection using telemetry data from adult and juvenile harbour seals from Svalbard in relation to environment parameters. This is essential to establish a baseline of movement patterns and to explore possible consequences of further climate change on this northernmost population (**Paper I**).
2. Characterize the diving and foraging behaviour of adult and juvenile harbour seals on a seasonal basis and explore the oceanic drivers affecting these behaviours. Climate is changing rapidly, especially in the Svalbard region. It is thus crucial to understand how environmental variables influence the foraging behaviour of top predators such as harbour seals in order to understand how they might be affected by changes in large-scale ocean circulation patterns in the coming decades (**Paper II**).
3. Explore the ontogeny of movement patterns and diving behaviour in harbour seals pups through the period of transition into independence. Adult mortality is an essential driver in long-lived animals' population dynamics, but mortality is generally highest during the first year of life. Therefore it is important to identify the factors influencing pups' behaviour and to understand how this age class might react under in a changing environment (**Paper III**).

III MAIN FINDINGS

Figure 3. Harbour seal from Svalbard instrumented with a Conductivity-Temperature-Depth Satellite-Relay-Data-Logger (CTD-SRDL) (Photo Kit Kovacs and Christian Lydersen, NPI)

A. Habitat selection by adult harbour seals (Paper I)

We explored post-moulting at-sea movements of 30 adult and juvenile harbour seals using Conductivity-Temperature-Depth Satellite-Relay-Data-Loggers deployed in the autumn 2009 and 2010 through the whole year. All of the seals showed a strong preference for the west side of the archipelago, staying mainly in coastal areas (<50 km over the continental shelf), but seldom entering the fjord systems especially in the winter. Distance swam per day, individual home range size, and trip duration increased throughout the winter to a peak that was reached when drifting sea ice in the region was at a maximum. No effect of age was observed, but sex differences were significant; males occupied larger areas than females. Habitat selection was quantified by modelling the time spent in areas of 2.5 x 2.5 km as a function of environmental parameters using Cox proportional hazard models. The harbour seals avoided heavy ice concentrations (>50%) but did occupy areas with substantial amounts of drifting ice (5 to 25%). Shallow water (<100 m) and steep bathymetric slopes were preferred to deep water or flat-bottom areas.

B. Influence of seasonal atmospheric and oceanographic processes on the foraging behaviour of adult harbour seals (Paper II)

We explored diving and foraging behaviour of 30 adults and juveniles harbour seals using Conductivity-Temperature-Depth Satellite-Relay-Data-Loggers deployed in the autumns of 2009 and 2010 through the whole year. These multi-sensors instruments collected data both on the animals' own behaviour and the environment they are experiencing at the same spatial and temporal scale. There was a strong seasonal variation in the diving behaviour with dives being deeper, longer, less numerous and more pelagic during the winter/early spring compared to the fall. Animals also spent proportionally less time at the bottom of their dives suggesting that the prey type or concentration was different in winter. Influxes of warm saline water, corresponding to Atlantic Water characteristics, were observed intermittently at depths ~100 m during both winters in this study. The seasonal changes in diving behaviour were linked to average weekly wind stresses from the north or north-east, which induced upwelling events onto the shelf through offshore Ekman transport. During these events the shelf became flooded with Atlantic Water from the West Spitsbergen Current, which presumably brought Atlantic fish species close to shore and within the seals' foraging depth-range.

C. Ontogeny of movement patterns and foraging behaviour through the first year of life (Paper III)

In phocids, the period of maternal dependence is usually short and weaning abrupt leaving a short period for transmission learning from mother to pup. We explored at-sea and diving behaviour of harbour seals' pups during their first year of life using Satellite-Relay-Data-Loggers deployed during the nursing period in June/July 2009 and 2010. Abrupt change in movement patterns was observed at 47 ± 9 days corresponding to the end of the post-weaning fast when the pups initiate their independent life. At the same age sharp changes were also observed in the activity budget and diving patterns. Pups spent progressively more time diving and less time at the surface and hauled out on land. They improved dramatically their diving skills; dives became deeper, longer, and more numerous with a higher percentage of bottom time and faster descent and ascent rates. They also needed less time to recover from a dive suggesting a rapid development of total body oxygen store. Movement type changed with age from resident-like movement corresponding to the period during which pups followed their mothers to a correlated random walk-like (CRW) movement during the beginning of the independent period when pups started wandering on their own. The CRW-like movement type was the dominant movement type until ca 80 days of age when pups started settling down into a more adult-like movement. Pups generally dispersed within the limits of the West Spitsbergen Shelf where the majority of the adults/juveniles staid. However, a few pups travelled south to Bjørnøya, to the East coast of Spitsbergen and southwest almost reaching the Island of Jan Mayen. Through winter and spring the number of dives decreased markedly as depth and duration increased. This change in diving behaviour was also observed in adults/juveniles and was linked to the occurrence of upwelling events. However few clear effects of environmental parameters were detected on the pups diving behaviour. This suggests that harbour seal pups in Svalbard prey upon different items compared to the adults/juveniles or that they are physically or behaviourally unable to exploit the same resource. Estimated first year survival was surprisingly low compared to other harbour seal populations perhaps because of strong environmental stressors this northernmost population experiences.

IV CONCLUSIONS AND FUTURE PERSPECTIVES

A. Conclusions from tracking data and future research paths

The first year-round observations of at-sea movements and diving behaviour of pups, juveniles and adult harbour seals from the world's northernmost population are presented in this thesis. The seal behavioural data is integrated with remote sensing environmental information and oceanographic data collected by the seals themselves at the same geographic and temporal scales, allowing comparison to be made among the three age classes. The tracking data provides a solid baseline for understanding how individuals of different age classes in this population currently use their environment and it also provides a basis for predicting how they might react to environmental changes in the future.

1. Tracking data revealed that all three age classes showed a strong preference for the West Spitsbergen Shelf through all seasons, indicating favourable conditions for this species in this region on a year-round basis. None of the instrumented adult or juvenile animals travelled to the east coast of Spitsbergen suggesting that they do not find sufficiently favourable conditions on this coast despite the absence of sea ice for large parts of the year and the presence of available platforms to haulout. Alternatively, given the small size of the population, and the favourable conditions on the west coast of Spitsbergen; there might not be any need for individuals to travel to the east coast at greater distance from the main haulout and pupping site. Harbour seal movements on Svalbard should be studied again in a few years in order to explore the relationship between their use of space and changing sea ice concentrations.

2. The influx of warm saline Atlantic Water that occurs close to the coast on the west side of the Svalbard Archipelago is essential for maintaining high productivity via intense mixing of water masses at the polar front. Seasonal changes in diving behaviour of harbour seals linked with upwelling phenomenon were observed for adult and juvenile animals that reside year-round on the West Spitsbergen Shelf, showing that Atlantic Water masses and associated prey were targeted by the seals under such conditions. Harbour seals are essentially a temperate species that is not normally found in the High Arctic. But, the presence of Atlantic Water is a factor that makes it

possible for a population of this species to reside at this high latitude. No information regarding the winter diet of harbour seals in this region is available currently; such data would be valuable to directly link the changes in foraging behaviour with targeted prey. Additionally, information on the distribution of potential prey species such as Atlantic cod in Svalbard's coastal areas would allow enhance further exploration of the prey – predator – environment relationship.

3. Pup tracking data allowed the exploration of the ontogeny of at-sea movements and foraging behaviour through the weaning period and the examination of possible environmental drivers. Most pups remained in the vicinity of their birth place, remaining close to Prins Karl Forland, close to the coast along the West Spitsbergen Shelf. However, some pups showed a wider dispersion pattern than older animals with some individuals travelling well outside of the range used by the adults. Pups do not seem to react as strongly as the adults to upwelling phenomenon, which highlights the importance of instrumenting different age classes that are likely to react in different ways to environmental variables.

4. Estimated first year survival of pups on Svalbard was surprisingly low compared to southern populations. Because temperatures in the Svalbard Region are predicted to increase further, with positive mid-winter temperatures by 2050, the physical environmental conditions might become more favourable for harbour seals. This could result in increased first-year survival. Regular surveys and estimates of annual pup production would yield information regarding the trajectory of this population.

5. Harbour seals are rarely used as oceanographic platforms due to their restricted ranges, coastal habitat, non-migratory habits and moderate diving depth range. Understanding spatial and temporal variations in coastal zones can be challenging because conventional monitoring platforms such as research vessels or Argo buoys are limited in accessing these regions (Villar-Guerra, Cronin et al. 2012). Therefore some recent effort has been made to use coastal seals, such as harbour seals, as oceanographic samplers in restricted areas like estuaries and coastal areas (Villar-Guerra, Cronin et al. 2012, Brown, Jeffries et al. 2013, Lerczak 2013). Polar Regions in particular present considerable logistical challenges for the collection of data on hydrographic properties and bathymetry, especially during winter in ice-filled waters under rough meteorological conditions. In this context Svalbard harbour seals, residing year-round in a very dynamic ocean region along the West Spitsbergen Shelf

might prove to be valuable adaptive samplers for monitoring changes occurring in the West Spitsbergen Current, the frequency of upwelling events and fine-scale oceanographic processes. Data collected by the seals in the present study have already been used to quantify the influence of ice melt in transforming the shelf water masses during the winter in relation to other mixing processes (Tverberg, Nøst et al. 2014). The continuing development of techniques combining GPS and the Argos system will undoubtedly yield more precise locations and are promising for fine-scale coastal hydrographic studies at high latitudes.

B. Harbour seals in Svalbard: an isolated population at risk or a temperate species with a foothold in the Arctic?

a. An isolated population at risk in a changing environment?

The Svalbard harbour seal population is small, numbering around 2000 individuals (Merkel, Lydersen et al. 2013) with low genetic diversity that shows possible signs of inbreeding (Andersen, Lydersen et al. 2011). Low genetic diversity in such a small population could reduce its adaptive capabilities and resilience to sudden environmental changes and stochastic events such as epidemic outbreaks or oil spills. Viruses, bacteria and parasites of marine mammals are predicted to shift their distribution northwards and might affect the health of immunologically naïve populations. Some boreal fish species have already become established in the Barents Sea and it is reasonable to assume that a significant number of their pathogens will follow them. Among these pathogens, those with a broad host specificity might infect established populations (Tryland, Godfroid et al. 2009). Epidemic outbreaks have wiped out entire populations of harbour seals in the past. For example in 1988, up to 60% of the North Sea harbour seals died from a Phocine Distemper Virus (PDV) epidemic (Harding, Härkönen et al. 2002). Changes in haulout patterns due to the reduction of availability of sea ice platforms may also increase the risk of direct contact between different species, favouring the transmission of pathogens. In the case of the PDV, epidemics are thought to have started through contact between harbour seals, grey *(Halichoerus grypus)* and harp seals *(Pagophilus groenlandicus)*; grey seals acting as carriers (Härkönen and Harding 2010, Duignan, Bressem et al. 2014).

In the recent years, predation events by polar bears on harbour seals on Svalbard have been documented. Bears were observed killing pups on Prins Karl

Forland during both years of the present study (including one of the study animals) and some instrumented bears are known to spend prolonged periods on Prins Karls Forlandet, right around the time of harbour seal pup nursing/weaning (Lydersen, Aars and Kovacs pers. comm.). Several of the data streams from instrumented pups ceased at an early stage while the pups were on land. Some of the instruments were subsequently found further inland, which suggests that the pups had been killed close to shore and then dragged inland by a bear or by an arctic fox. Harbour seals are not a typical prey for polar bears which generally hunt ringed seals, harp seals or bearded seals *(Erignathus barbatus)* on ice. However, due the reduction of sea ice polar bears are spending more time on shore during the summer and the predation pressure on harbour seals is likely to increase in the future in Svalbard. Reduced sea ice might also favour increased visitation to the region by killer whales *(Orcinus orca),* which might become a significant predator of harbour seals, as it is thought to be the case in Hudson Bay in Canada (Ferguson, Higdon et al. 2010).

Direct human-related disturbances such as increased ship traffic, contaminant levels and ocean noise could also affect this remote population negatively under reduced sea ice conditions. A small population occupying a limited geographical area might therefore be at risk (Corbett, Lack et al. 2010).

b. A temperate species with competitive advantages?

The Arctic is expected to have the largest species turnover with respect to invading species and local extinction of species, with a modelled invasion intensity that is five times the global average (Cheung, Lam et al. 2009, Fossheim, Primicerio et al. 2015). The diminishing trend of sea ice cover observed in the Arctic will put pressure on pagophilic (ice-loving) top predators, mainly due to a dramatic reduction of their habitat. In addition, they will face nutritional stress if their typical prey are also ice-associated and if their niche overlaps with another species that have a competitive advantage. In Svalbard, ringed seal and harbour seal distributions overlap in the western parts of the archipelago. Ringed seals are obligate ice-associated seals that forage either close to the coast at glacier fronts or offshore at the ice edge; this species uses only sea ice for pupping, moulting and resting (Freitas, Kovacs et al. 2008). Harbour seals on the contrary tend to avoid areas with high concentrations of drift ice or fast ice and prefer to haulout on land (Lesage, Hammill et al. 2004, Bajzak, Bernhardt et al. 2013, Blanchet, Lydersen et al. 2014). This species is therefore likely to benefit from reduced sea ice cover, while ringed seals will lose habitat that is essential to them. The profound changes occurring in arctic fish communities will also likely benefit harbour seals who are generalist opportunistic foragers, while ringed seals are less flexible, ice-associated fauna specialists (Gjertz and Lydersen 1986). Harbour seals will also likely benefit from the predicted increase in influxes of Atlantic Water through the West Spitsbergen Current as they have been shown to target this water mass and its associated fish and invertebrate community (Blanchet, Lydersen et al. 2015). Warmer air and water temperatures will likely be beneficial to some extent to harbour seals by decreasing thermic stress both on land and at-sea.

Based on aerial surveys and sporadic observations, harbour seals numbers are thought to be increasing in Svalbard and their distribution is thought to be expanding (Merkel, Lydersen et al. 2013). Harbour seals have been observed in Kongsfjorden in recent years (Hop, Pearson et al. 2002) and are thought to be present year-round in this area, although they are not known to breed within the fjord. Reduction of land-fast ice and influxes of Atlantic Water could however favour the future establishment of a permanent colony in this fjord. If warmer conditions prevail over the entire archipelago, this will favour the growth and geographic expansion with new breeding sites of this harbour seal population. Indeed, pups have been shown to disperse over wider areas than adults (Blanchet, Lydersen et al. Submitted) and can reach areas inside deep fjords and even travel to the east coast.

Climate predictions indicate a unilateral warming of the atmosphere and oceans that will cause major shifts in the earth’s ecosystems, especially at high latitudes. Although diseases and other threats could compromise the world northernmost harbour seal population, mainly due to its small size and limited geographical distribution; it is likely that this temperate species with a foothold in the Arctic will mainly benefit from the current warming, making it an ecological winner in this region.

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