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Challenges for ice-associated top trophic Arctic animals in a changing climate

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A dissertation for the degree of Philosophiae Doctor – December 2016

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Summary

The Arctic is currently in a rapid state of change, with temperature increases in this region being three times the rate of the global average and sea-ice extent declining rapidly. Differential responses of species to these rapid environmental changes are leading to changes in biological interactions, which are having ramifications for the wider marine and terrestrial ecosystems. Ice-obligate marine mammal and seabird species, including ringed seals (*Pusa hispida*), polar bears (*Ursus maritimus*) and ivory gulls (*Pagophila eburnea*), are dependent on sea ice for a variety of purposes and as such are sensitive to declines in this habitat. In 2006, a sudden shift in the sea-ice regime in Svalbard, Norway, occurred with the altered sea-ice conditions persisting to the present day. Following the shift in sea-ice conditions, the position of the offshore sea-ice edge (the marginal ice zone, MIZ) shifted from remaining over the productive continental shelf of the Barents Sea to being located over the less productive waters of the Arctic Ocean Basin. Additionally, the amount of fast-ice forming in the fjords, especially on the west coast of Spitsbergen, the largest island of this Arctic Archipelago, sharply declined. In order to study the impacts of the environmental changes occurring in the Svalbard region, the movement patterns, behaviour and degree of spatial overlap for ringed seals (n=60), polar bears (n=160) and ivory gulls (n=40) were investigated using data from biotelemetry devices equipped on these species before (2002 – 2004; ringed seals and polar bears) and after (2010 – 2013; all three species) the shift in the sea-ice regime occurred. These three species are trophically linked; ringed seals are the primary prey of polar bears and ivory gulls scavenge on polar bear kills. Both polar bears and ringed seals in Svalbard have two movement strategies; they either remain coastal or seasonally follow the retreating offshore sea-ice edge. Ivory gulls that breed in Svalbard travel to the offshore sea-ice edge of the Barents Sea post-breeding.

Ringed seals following both movement strategies utilised the same habitat both before and after the change in sea-ice conditions. Ringed seals that took offshore foraging-migration trips were in areas with similar sea-ice concentrations and similar proportions of first-year sea ice to multi-year sea ice and coastal ringed seals spent similar amounts of time close to tidal glacier fronts. However, ringed seals that took offshore foraging-migration trips spent a decreased amount of time hauling out (i.e. resting) following the shift in the sea-ice extent. Ringed seals with both movement strategies had an increase in foraging effort and thus energetic costs and also a change in foraging behaviour following the sea-ice collapse. These changes indicate that alterations in the invertebrate and fish species composition, abundance or density have occurred throughout the Svalbard region.

Coastal polar bears in Svalbard spend between 30 – 50 % of their time close to tidal glacier fronts depending on season. This space use pattern was similar between the two time periods in the spring (Mar – May), but following the sea-ice collapse polar bears spent significantly less time close to tidal glacier fronts in the summer (Jun – Aug) and autumn (Sep – Nov). However, coastal ringed seals did not change the percentage of time they spent close to glacier fronts or hauled out (i.e. exposed to polar bear predation) in the summer. Coastal ringed seals must increasingly be using calved pieces of glacier ice as haul-out platforms after

the change in sea-ice conditions decreased the amount of fast-ice in coastal areas; polar bears killing seals on floating ice pieces has been suggested to be a specialty hunting strategy. The dichotomy in the response of these two species to the change in environmental conditions has led to large changes in the amount of spatial overlap between coastal polar bears and ringed seals on the east coast of Svalbard during the summer. Spatial overlap values have decreased in coastal areas with tidal glacier fronts and increased slightly in coastal areas where no tidal glacier fronts are present. Following the sea-ice collapse and the decreased “availability” of their traditional prey source, coastal polar bears moved greater distances per day in the summer and spent more time close to ground-nesting bird colonies, indicating increased predation on terrestrially-based prey sources.

Polar bears, ringed seals and ivory gulls in Svalbard travel to the MIZ in the summer and autumn, which due to its high and extended time period of productivity is a profitable foraging area. All three species preferred areas with sea-ice concentrations between 40 – 80 % and were more closely associated with the 50 % than the 15 % sea-ice contour. The highest spatial overlap between these three species between August and October occurred in areas slightly north of the 50 % sea-ice contour. These three species will likely continue to track their preferred habitat in the MIZ further north as the MIZ continues to retreat, as long as the energetic benefits outweigh the energetic costs. If ringed seals that take offshore foraging-migration trips continue to decrease the amount of time spent hauled out, opportunities for polar bear predation and ivory gull scavenging will likely be impacted.

The MIZ is predicted to further retreat and ultimately seasonally disappear. This will likely result in an increased proportion of each species being associated with coastal tidal glacier fronts. An additional concern is that glaciers in Svalbard are in negative mass balance and that the total number and length of tidal glacier fronts has decreased in recent decades; both of these declines are expected to continue. The decline in both of these ice features will almost certainly increase intra- and interspecific competition in these areas and have consequences for the growth, distribution, survival of different age classes and abundance of ringed seals, polar bears and ivory gulls in Svalbard. The level of plasticity each of these species has to cope with the environmental changes taking place is currently unknown. The effects on each of these ice-obligate, top trophic Arctic animals and the resultant changes in biological interactions will have ramifications for the wider Arctic marine and terrestrial ecosystems.

List of papers

- I. Hamilton CD, Lydersen C, Ims RA, Kovacs KM. 2015. Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice. *Biol. Lett.* **11**, 20150803, doi:10.1098/rsbl.2015.0803
- II. Hamilton CD, Lydersen C, Ims RA, Kovacs KM. 2016. Coastal habitat use by ringed seals *Pusa hispida* following a regional sea-ice collapse: importance of glacial refugia in a changing Arctic. *Mar. Ecol. Prog. Ser.* **545**, 261-277
- III. Hamilton CD, Kovacs KM, Ims RA, Aars J, Lydersen, C. Submitted. An Arctic predator-prey system in flux: climate change impacts on coastal space use by polar bears and ringed seals. *J. Anim. Ecol.*
- IV. Hamilton CD, Kovacs KM, Ims RA, Aars J, Strøm H, Lydersen C. Submitted. An Arctic predator, prey and scavenger system in a changing climate. *Mar. Ecol. Prog. Ser.*

1. Introduction

(a) Species interactions

No species exists in isolation. Each species has a multitude of interactions with both the abiotic and biotic realm. The range of physically habitable conditions (i.e. its fundamental niche) a species is able to live and reproduce in are for the majority of species not fully realized (i.e. its realized niche), due in part to species interactions (Whittaker et al. 1973).

Species interactions can be positive, negative or have no effect for a given species. Well-known examples of species interactions, for example parasitism and predation, have clear winners and losers. In competitive interactions, both species involved are seen as losers as both experience a contraction of their fundamental niche. The realized niche can also differ among individuals in the same species. Competition can be both intra- and interspecific and the risk of predation may differ depending on factors such as age or size. Each species in an ecological community is involved in many interactions, leading to the formation of complicated food webs (Lavigne 1996). This web of interactions can make determining the effects of a change in a species' abundance or distribution on the wider ecosystem difficult to predict.

(b) Climate change

The earth's climatic system is in a constant state of flux. The earth has gone through multiple ice ages and during the last 800,000 years numerous glacial and interglacial periods have occurred (Lüthi et al. 2008, Encyclopaedia Britannica 2016). However, the current rate of warming is unprecedented when compared to warming events in the earth's geological past. Both present CO₂ levels in the atmosphere (> 400 ppm) and the rate of CO₂ increase are higher than at any time during the last 800,000 years (Lüthi et al. 2008, IPCC 2013a).

The average global surface temperature has increased by 0.85°C between 1880 and 2012. Additionally, the warmest 30 year period in the last 1400 years likely occurred between 1983 and 2012 (IPCC 2013b). Ecological impacts of climate change, including species range shifts, changes in abundance, shifts in activity patterns and effects on genetics, physiology and morphology have been recorded in every natural system on all continents for a variety of terrestrial, marine and freshwater species (IPCC 2014, Scheffers et al. 2016). However, different species are being impacted at different rates, leading to trophic mismatches and temporal and spatial changes in species interactions (Thackeray et al. 2010, Doney et al. 2012, IPCC 2014, Scheffers et al. 2016). Disrupted trophic interactions will impact the abundance and realized niche of affected species as well as how they in turn are affected by climate change (Gilman et al. 2010, Doney et al. 2012, Van der Putten et al. 2012). The effects of altered trophic interactions will also ripple throughout the ecosystem (Doney et al. 2012).

Climate change is not the only threat currently facing global ecosystems. Flora and fauna are also being impacted by invasive species, habitat alteration and fragmentation,

chemical and plastic pollution, industrial developments and varying intensities of hunting pressure. The interaction of these stressors can be merely additive or synergistic, the latter meaning that the resultant impact is greater than the sum of the different stressors. Whereas a species might have enough plasticity to cope with a single stressor acting alone, the additive or synergistic effect of multiple stressors might be greater than the amount of plasticity a species has.

If a species does not have enough plasticity to cope with the combined effects of climate change and other stressors, the species can either move, adapt or go extinct. Species are predicted to move towards the poles or to higher altitudes in response to increases in global temperatures, tracking their preferred physical habitat. There can be large variability in the ability of different species to shift their distribution, depending both on traits of the species themselves and the external drivers of change (Chen et al. 2011). For example, range shifts in the marine system (19 km/yr) are occurring an order of magnitude faster than in the terrestrial system (0.6 km/year; Sorte et al. 2010). Distributional rates of change may also depend on the geographic location, as in some regions boreal species are shifting polewards at a faster rate than southern counterparts (Virkkala & Lehikoinen 2014). Polar animals already occupy the northernmost or southernmost regions of the globe and thus have a limited ability to extend their distribution polewards. For some species, such as polar species that occupy the continental shelves, there may not be favourable habitat polewards of their present distributional range. An additional challenge is that some polar species have a limited tolerance to changes in physical conditions (Doney et al. 2012). Projected rates of fauna change with low greenhouse gas emission scenarios predict that the tundra regions will gain more species and have higher rates of species turnover than other regions; present and future ecological communities in the tundra will thus bear little resemblance to each other (Lawler et al. 2009). The fast rate at which the climate is changing may also limit the adaptation potential of long-lived species, as large changes in the environment are occurring over the lifetime of only one or two generations (Lüthi et al. 2008, IPCC 2013a).

(c) Arctic

The Arctic is currently warming at a rate three times greater than the global average, due to a phenomenon known as Arctic amplification (Comiso & Hall 2014). Arctic amplification is not a new phenomenon; during the Quaternary period (2.6 million years ago (mya) to the present day), the temperature change in the Arctic during both warming and cooling periods was consistently 3 – 4 times greater than the Northern Hemisphere average (Miller et al. 2010). Furthermore, during the last 65 million years, changes in vegetation, temperature and ocean characteristics have been greater in the Arctic than other latitude ranges in the Northern Hemisphere (Miller et al. 2010). Although Arctic amplification has many causes operating on a variety of spatial and temporal scales, a primary cause is changes in Arctic sea-ice conditions (Miller et al. 2010, Serreze & Barry 2011).

Since satellite measurements began in 1979, sea-ice extent has declined at 3.8 %/decade with summer sea-ice extent declining at a rate of 11.5 %/decade (Comiso & Hall

2014). Between 2005 and 2008, there was a > 40 % loss of multi-year sea ice in the Arctic Ocean. There has also been a reversal in the dominance of the two different sea-ice types; between 2003 and 2008 the volume of sea ice in the Arctic Ocean shifted from being dominated by multi-year sea ice to first-year sea ice. (Kwok et al. 2009). Concomitant with the loss of multi-year sea ice has been a decrease in the thickness of sea ice over the Arctic Ocean. Data collected by submarines indicates that sea-ice thickness decreased by 48 % between 1980 (3.64 m) and 2008 (1.9 ± 0.5 m; Kwok & Rothrock 2009). The most recent suite of climate models (i.e. CMIP5) predict that the Arctic will be seasonally sea-ice free in the summer by as early as the 2030s (Wang & Overland 2012).

Sea ice in the Arctic possibly appeared around 47 mya. Multi-year sea ice potentially formed around 13 – 14 mya with sea ice likely being the most widespread for the past 2 – 3 million years (Polyak et al. 2010). During interglacial periods in the Quaternary period, seasonal sea-ice extent was likely less than at present. In Northeast Greenland, wave-generated beach ridges indicate that areas as far north as 83°N had seasonally open water, meaning that the area of seasonal melt was around 500 km north of its present position (Polyak et al. 2010). It is possible that the Arctic Ocean was seasonally sea-ice free during an interglacial period in the Quaternary period, but more information from sediment cores and climate proxies are needed to conclusively determine the history of sea ice in the Arctic (Polyak et al. 2010). However, data from sediment cores and climate proxies indicate that the current sea ice loss likely exceeds shifts in sea-ice conditions that have occurred over the last few thousand years and has certainly been unprecedented over the past 1,450 years (Polyak et al. 2010, Kinnard et al. 2011).

Although the Arctic ecosystem has a greater complexity and connectivity than was previously believed (Post et al. 2009), the Arctic ecosystem still contains relatively few species compared to many other ecosystem types. Understanding the effects of climate change may thus be easier for the Arctic ecosystem than for ecosystems that have a greater faunal richness. Conversely, the low biological diversity in the Arctic also increases the risk of ecological change occurring, as higher biological diversity within ecological functional groups and a higher diversity of responses to change within functional groups are linked to higher ecosystem resilience (Elmqvist et al. 2003).

Declines in Arctic sea ice have resulted in ramifications for both the marine and terrestrial Arctic realms, as well as for wider regions of the globe. Decreases in Arctic sea-ice cover have been linked to increases in summer temperatures in the Arctic coastal tundra region, resulting in increased values of the Normalized Difference Vegetation Index (NDVI); the increased plant productivity will have a multitude of impacts on the Arctic ecosystem (Bhatt et al. 2010). The reduced sea-ice extent is also clearly linked to the high rates of warming that have occurred over the Arctic Ocean in the autumn and winter over the last decades (Serreze & Barry 2011). Arctic sea-ice declines have also had large consequences for Arctic terrestrial and marine ecological dynamics (Post et al. 2013). These include both direct effects, such as loss of habitat for ice-associated flora and fauna and mismatches between primary producers and primary consumers, as well as indirect effects, such as effects on

migration and movement patterns and the likelihood of pathogen transmission (Post et al. 2013). Sea ice serves as both a platform facilitating dispersal for some species while it represents a barrier to dispersal for other; declines in sea ice will thus have consequences for the degree of genetic isolation experienced by different species (Post et al. 2013). Reduced sea-ice extent has also been linked to changes in large-scale atmospheric circulation patterns, the strength and path of the polar and subtropical jet streams and weakening of the polar vortex (Budikova 2009, Overland & Wang 2010, Kim et al. 2014). One effect of these changes has been an increased likelihood of severe winters over the northern mid-latitudes (Petoukhov & Semenov 2010, Kim et al. 2014). Arctic amplification is expected to intensify over the coming decades as sea-ice loss continues and accelerates, further impacting both the Arctic and other global regions (Serreze & Barry 2011).

Arctic marine mammals and seabirds are at or near the top of their respective food chains. The species that live in the Arctic year-round are sea-ice obligate with sea ice serving a variety of functions. Sea ice is used as a foraging area, a transport and hunting platform for polar bears (*Ursus maritimus*), as protection from open-water predators (i.e. killer whales, *Orcinus orca*) and storm events and as a platform for birth, nursing and resting for ice-associated seals (Kovacs et al. 2011). Reduced sea ice is believed to be a serious threat to this species assemblage, although the sensitivity of each species to reduced sea ice varies (Laidre et al. 2008, Moline et al. 2008, Kovacs et al. 2011). Consequences of reductions in sea ice include population isolation due to loss of sea ice as a dispersal and movement platform, increased competition with Arctic migrants that will extend their range northwards and be in the area for extended time periods, exposure to novel pathogens and parasites, increased accessibility for hunters and predators, loss of breeding, nursing and resting platforms and changes in species composition, abundance and density in prey bases due to changes in the food web (Moline et al. 2008, Kovacs et al. 2011, Post et al. 2013).

Although present Arctic marine mammal species have survived numerous interglacial periods in the Quaternary period when the sea-ice extent was less than at present, it is possible that these species have never experienced an Arctic that was seasonally sea-ice free. Although the ancestors of the harp (*Pagophilus groenlandicus*), hooded (*Cystophora cristata*) and ringed seals (*Pusa hispida*) are believed to have adapted to Arctic conditions around 12 mya (due to the appearance of a white natal coat (shed *in utero* in hooded seals)), present species appeared in the Pliocene period (2.6 – 5.3 mya) during a cooling period in the North Atlantic (Arnason et al. 2006, Harington 2008). The bearded seal (*Erignathus barbatus*) and a single circumarctic walrus species (*Odobenus rosmarus*) likely appeared in the Pleistocene period (2.6 million to 11,700 years ago), with the earliest fossils of the bowhead (*Balaena mysticetus*), narwhal (*Monodon monoceros*) and beluga whale (*Delphinapterus leucas*) dating from 40,000 to 6,000 years ago (Harington 2008). Although there has been debate about the date of divergence between polar bears and brown bears (*Ursus arctos*), a recent study suggests that divergence between these two species occurred between 4 to 5 mya, noting a decline in numbers has taken place the last 500,000 years (Hailer et al. 2012, Miller et al. 2012, Cahill et al. 2013). During the Quaternary period, species such as bowheads, walruses, ringed seals and harp seals shifted their ranges in response to glacial and interglacial periods,

with radiocarbon-dated bowhead remains used as a proxy for sea-ice conditions over the last 10,000 years (Harington 2008, Polyak et al. 2010).

Box 1: Ecosystem sentinels

Marine mammals and seabirds can act as ecosystem sentinels; they can integrate and reflect changes that have occurred over large spatial and temporal scales, which may otherwise be hard to detect (Moore 2008). Changes in stable isotope and fatty acid profiles as well as shifts in the abundance, distribution, diet and space use patterns of marine mammals and seabirds can warn of changes that have occurred in lower trophic levels as well as wider changes in the environment (Moore 2008). Repeated sampling of pollutant levels in the tissues of marine mammals and the use of multiple tissues with different turnover times also provides a way to track exposure to different contaminants over multiple time scales (Moore 2008, AMAP 2009). Using ecosystem sentinels may be especially important in logistically challenging regions such as the Arctic, where the remoteness, extreme weather, darkness and large expanses of sea ice impacts the feasibility of observations and sampling regimes over long intra- and inter-annual time scales.

(d) Ringed seal

Five subspecies of ringed seals are recognized; the Arctic ringed seal, *P. h. hispida*, inhabits the Arctic Ocean and the Arctic continental shelf seas. The Arctic ringed seal is an ice-obligate species in the Arctic ecosystem. It has a circumpolar distribution; the highest densities of ringed seals occur over the Arctic continental shelves but individuals have also been observed close to the North Pole (Reeves 1998). Ringed seals are thought to number in the millions, although no exact number or trends are known due to a lack of repeated abundance estimates throughout most of its range (Laidre et al. 2015).

Ringed seals are able to make and maintain breathing holes in the fast-ice using their claws, facilitating their wide distribution (McLaren 1958). Ringed seals dig out subnivean lairs above their breathing holes in the winter and spring which are used for birth and nursing by adult females and for general rest by all age classes of both sexes (Figure 1; Smith & Stirling 1975, Lydersen & Gjertz 1986, Smith et al. 1991). Ringed seals give birth around late-March to April to pups weighing ~4.5 kg, with lactation lasting for an average of 39 days (Lydersen & Kovacs 1999). Subnivean lairs offer pups both thermal and predator protection, with high levels of predation occurring in years when conditions are not suitable for subnivean lair formation or when rain-on-snow events or high temperatures causes the lairs to melt prematurely (Smith & Stirling 1975, Lydersen & Gjertz 1986, Lydersen & Smith 1989, Smith et al. 1991, Stirling & Smith 2004). Females usually have a complex of lairs (2 – 3 lairs) with the pup switching between them, either facilitated by the mother or independently depending on pup age, in response to predation attempts (Smith & Stirling 1975, Smith et al. 1991, Lydersen & Hammill 1993).

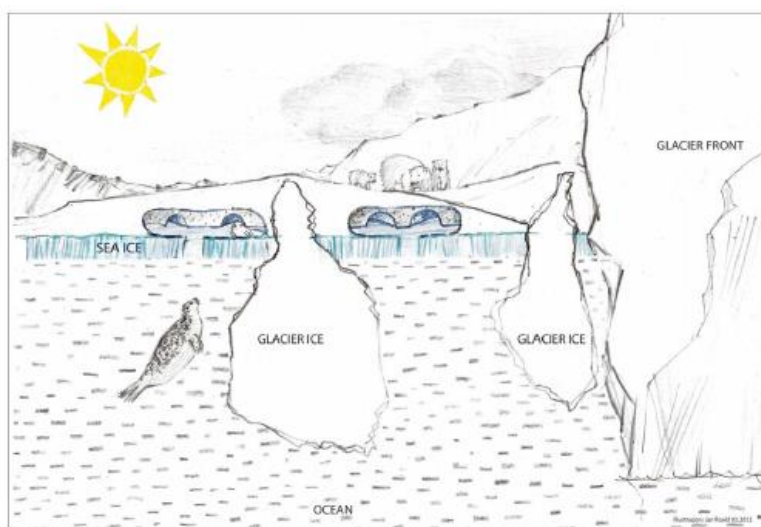


Figure 1: Ringed seal subnivean lair complex. Taken from Lydersen et al. (2014).

Sea ice is used as a moulting platform between mid-May and mid-July and as a haul-out platform throughout the year. Additionally, adult body condition and female pregnancy rate are affected by sea-ice conditions at large spatial scales (Stirling 2002, Stirling 2005, Chambellant et al. 2012). Ringed seals are opportunistic foragers but most of the foraging targets ice-associated prey (Reeves 1998, Labansen et al. 2007).

(e) Polar bears

Polar bears are the top predators in the Arctic ecosystem. They have a circumpolar distribution, with the highest density of bears occurring over the Arctic continental shelves. Polar bears also occur in low densities over the Arctic Ocean Basin (Amstrup 2003). Numerous consequences of sea-ice declines have been documented for this species, with its long-term viability seen as uncertain (Stirling & Derocher 2012). Presently, 19 sub-populations of polar bears are recognized with a global population size of 20,000 – 25,000. Eight sub-populations are declining for a variety of reasons including changes in habitat due to sea-ice declines and overharvest (trends in seven are unknown due to a lack of data; Obbard et al. 2010, Stirling & Derocher 2012). Additionally, Population Viability Analyses (PVA) run on each sub-population indicated that the risk of future decline in the next 10 years was high (60 – 80 %) or very high (80 – 100 %) for seven sub-populations (nine could not be estimated due to lack of data; Obbard et al. 2010).

Polar bears are dependent on sea ice in a variety of ways. Sea ice is used as a transport and breeding platform with bears in some sub-populations also denning in multi-year ice (Fischbach et al. 2007, Stirling & Derocher 2012). Arguably the most important function that sea ice serves is a platform for hunting ice-associated prey. Common prey items, depending on area, are hooded seals, harp seals, harbour seals (*Phoca vitulina*), bearded seals, narwhal, walrus and beluga whales (Derocher et al. 2002, Thiemann et al. 2008, Iversen et al. 2013). The most important prey species throughout most of their range is ringed seals (Derocher et al. 2002, Thiemann et al. 2008, Iversen et al. 2013). Ringed seals are important prey in the

spring when females emerge from their dens (Freitas et al. 2012). Although polar bears can swim long distances, cubs of the year (COYs) shortly after den emergence do not have the fat stores of older individuals and will quickly become hypothermic if submersed in cold water (Blix & Lentfer 1979). Predation attempts occur frequently on ringed seal subnivean lairs (14 – 30 % of subnivean lairs in an area show evidence of a polar bear attack); success rates vary between 6 and 34 %, depending on local snow conditions (Stirling & Archibald 1977, Lydersen & Gjertz 1986, Hammill & Smith 1991). Polar bear predation can remove up to 44 % of the local pup production with this number likely being much greater during years when subnivean lairs cannot be formed or melt prematurely (Hammill & Smith 1991, Stirling & Smith 2004). Not surprisingly, pup production of ringed seals and survival and natality of polar bears are linked and are sensitive to sea-ice conditions (Stirling 2002).

(f) Ivory gulls

Ivory gulls are quite a rare seabird, numbering ~14,000 pairs globally. (Gilchrist et al. 2008). Although they were first discovered in 1609, they remain one of the most poorly known seabird species in the world (Gilchrist et al. 2008). However, recent, large-scale biotelemetry tagging efforts have begun to fill in some of the knowledge gaps for this species, including identifying migratory paths and key wintering areas (e.g. Gilg et al. 2010, 2016, Spencer et al. 2016).

Ivory gulls are sea-ice specialists with a patchy, circumpolar distribution (Gilchrist et al. 2008). They are associated with drifting sea ice for most of the year; they rarely fly over land and have been suggested to avoid areas with open water (Gilchrist et al. 2008, Gilg et al. 2010, Spencer et al. 2014, Gilg et al. 2016, Spencer et al. 2016). Their affinity to areas with high sea-ice concentration varies on an intra-annual basis, with ivory gulls found more routinely in areas with high sea-ice concentration in the summer than during the migratory and winter seasons (Gilg et al. 2016). Ivory gulls in different circumpolar regions have differences in their intra-annual patterns of proximity to open water and the sea-ice edge, due to variations in the timing of migration, breeding colony location and the proximity of different types of feeding areas during the breeding season (Gilg et al. 2016).

Ivory gulls are opportunistic foragers. They forage primarily in association with drifting sea ice on ice-associated fish and invertebrates. They are also scavengers and are regularly observed scavenging on polar bear kills, on marine mammal placentas and at human settlements (Divoky 1976, Gilchrist et al. 2008). Their breeding colonies are situated on nunataks, steep cliffs or on flat ground but have also been observed on ice floes. The remoteness of their often monospecific breeding colonies likely limits predation on eggs and chicks (Gilchrist & Mallory 2005, Gilchrist et al. 2008, Boertmann et al. 2010). They usually lay 1 – 2 eggs and are thought to reach maturity after their second year (Gilchrist et al. 2008)

(g) Svalbard

Svalbard is a Norwegian High Arctic Archipelago ($74^{\circ} - 81^{\circ}\text{N}$, $10^{\circ} - 35^{\circ}\text{E}$) situated between the Greenland Sea, the Barents Sea and the Arctic Ocean (Figure 2). Approximately 60 % of the 61,022 km² land mass of Svalbard is covered with glaciers. The glaciers in Svalbard are in negative mass balance with the present rate of thinning being approximately four times the thinning rate observed in the 20th century (Kohler et al. 2007). Although the high proportion of surge glaciers in Svalbard (i.e. 29 % of glaciers) complicates analyses of glacier retreat, the number of glaciers with tidal glacier fronts and the total length of tidal glacier fronts have both decreased over the last decades (Jiskoot et al. 2000, Błaszczuk et al. 2009). Surface air temperature increases during the last three decades are also higher in Svalbard than elsewhere in the Eurasian Arctic (Nordli et al. 2014).

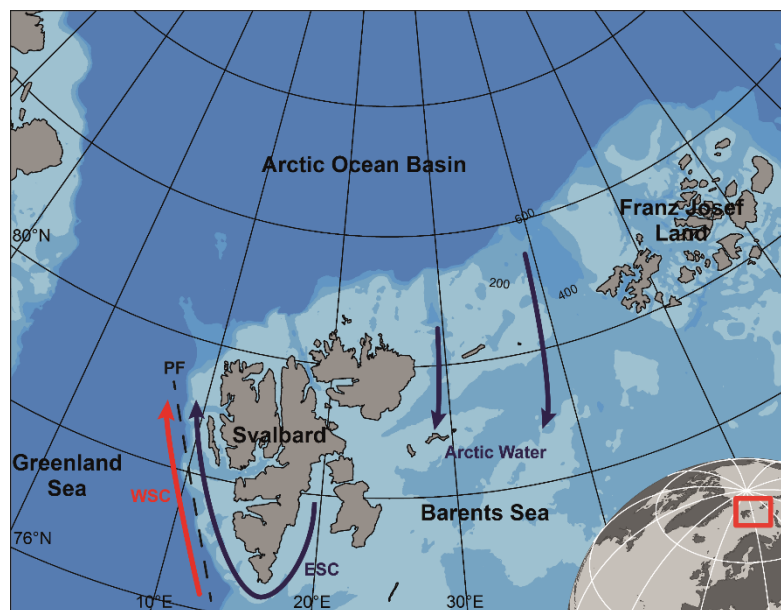


Figure 2: Map of Svalbard showing the main water masses, ocean currents and location of the archipelago.

The West Spitsbergen Current (WSC), a branch of the North Atlantic Current, flows northwards on the western coast of Svalbard along the continental slope (Figure 2). The WSC transports warm, saline water and is the main source of oceanic heat for the Arctic Ocean (Aagaard & Greisman 1975). Arctic water masses enter the Barents Sea from the Arctic Ocean Basin between Svalbard and Franz Josef Land, Russia. The Eastern Spitsbergen Current (ESC) transports colder, less saline Arctic water around the southern tip of Svalbard, northward along the western side of Svalbard (Ingvaldsen & Loeng, 2009; Figure 2). A polar front (PF; Figure 2) exists between the WSC and the ESC on the western coast of Svalbard. Water mass exchange across the polar front with resulting intrusion of Atlantic water into fjords on the west coast of Svalbard is mainly wind driven. The magnitude of Atlantic water intrusion varies both intra- and inter-annually, switching the west coast fjords between a “warm” or “cold” mode (Svendsen et al. 2002, Cottier et al. 2005, Pavlov et al. 2013, Blanchet et al. 2014, Tverberg et al. 2014). The oceanographic conditions in Svalbard fjords are also affected by glacier melt water, river run-off and processes relating to the formation and melting of sea ice (Svendsen et al. 2002, Cottier et al. 2005). The temperature of the WSC

increased by 0.06°C/yr between 1997 and 2010 (Beszczynska-Möller et al. 2012). The water temperature in fjords on the western coast of Svalbard has also increased over the last century (Pavlov et al. 2014). Additionally, the Arctic Water masses in the northern Barents Sea have increased in temperature since the early 2000s (Lind & Ingvaldsen 2012). Annual monitoring of zooplankton in a western Svalbard fjord indicates that the fjord has been in a “warm” mode for the vast majority of years since 2006. (Environmental monitoring of Svalbard and Jan Mayen, www.mosj.no).

The Barents Sea is the deepest of the Arctic continental shelf seas with an average and maximum depth of 230 m and ~500 m, respectively (Ingvaldsen & Loeng 2009). There is large inter-annual variation in the amount of sea-ice cover in the Barents Sea due to a variety of factors such as the magnitude of the Atlantic Water inflow, the North-Atlantic Oscillation (NAO) index and the degree of solar radiation during the summer months (Gloersen et al. 1993, Vinje 2009). However, the sea-ice extent has retreated greatly over the last decades. Historically, the minimum summer sea-ice extent occurred over the productive continental shelf of the Barents Sea, but it has now shifted to being located over the less productive deep Arctic Ocean Basin (Norwegian Ice Service, Norwegian Meteorological Institute, <http://polarview.met.no/>). The seasonal duration of Barents Sea sea-ice cover was 20 weeks shorter in 2013 compared to 1979, a rate of decrease which is 2 – 4 times the magnitude of other Arctic areas (Laidre et al. 2015).

Concomitant with the abiotic changes in this region have been changes in the biotic realm. Between 2004 and 2012, a rapid “borealization” of the Barents Sea occurred, with boreal fish communities extending their distribution northwards at a pace similar to the abiotic changes occurring in this region. The Arctic shelf fish community has also moved northward and is now limited to deep areas bordering the Arctic Ocean Basin (Fossheim et al. 2015). Fish and invertebrate species typically associated with Atlantic water masses have also begun to appear in and dominate water masses in the WSC and in western Svalbard fjords over the recent years (Jensen et al. 2014, Weydmann et al. 2014, Berge et al. 2015)

Svalbard and the Barents Sea are home to a wide variety of ice-obligate and ice-associated species and are also the destination of many seasonal migrants (Kovacs 2006, Sakshaug et al. 2006). Both the ringed seal and polar bear populations in Svalbard have two movement strategies: they either remain coastal in Svalbard or they are seasonally associated with the offshore sea ice (Mauritzen et al. 2002, Freitas et al. 2008a). Ivory gulls that breed in Svalbard, as well as ivory gulls from breeding colonies in Northeast Greenland and Franz Josef Land, Russia, migrate to the offshore sea ice of the Northeast Atlantic post-breeding and remain there for several months until continuing their migration in November (Gilg et al. 2010). Svalbard was most likely a refugium for polar bears and other Arctic species during past interglacial periods (Miller et al. 2012). It is not known if changes in the Svalbard region occurred at a faster rate than other Arctic areas in the past, but currently, Svalbard is serving as the “canary in the coal mine” for the impacts of climate change, with changes observed in Svalbard expected to spread to other Arctic areas over the coming decades.

Box 2: Biotelemetry

Biotelemetry translates to “remote measurement” of “life”. Biotelemetry devices record and transmit information about an animal and its surroundings. Biologging is a parallel field that necessitates that the animals are re-caught after a certain time interval to retrieve the information which the biologging device stores. Both biotelemetry and biologging devices produce large amounts of data for a rapidly growing number of species (see Evans et al. 2013).

Biotelemetry is a rapidly growing field. For example, the number of aquatic telemetry studies increased over six-fold between 1986 and 2014 (Hussey et al. 2015). Information recorded by the devices can either be transmitted acoustically to acoustic receivers or by radio waves to satellite systems (i.e. Argos satellite system) or radio receivers. Biotelemetry has transformed the study of animal movement, as the movements of many individuals can be tracked over large spatial and temporal scales (see for example Block et al. 1998, Sharples et al. 2012, Kissling et al. 2013). Technological developments such as Fastloc-GPS have improved the location accuracy, even for diving marine mammals that spend small amounts of time at the surface (Costa et al. 2010). Biotelemetry devices can record and transmit information not only about an animal’s locations, but also data about its behaviour (e.g. dive depth and duration), physiology (e.g. heart rate and swim speed) and surroundings (e.g. light level and temperature; Lydersen et al. 2002, Cooke et al. 2004, Ponganis 2007). Ongoing miniaturization and technological developments are allowing more parameters to be measured on an increasing number of species. For example, technological advancements have recently allowed the tracking of neonate baby turtles and soft-bodied marine invertebrates such as squid and jellyfish (Mansfield et al. 2014, Mooney et al. 2015). Business-card tags have also been developed that allow the transmission of information between different tagged animals (Holland et al. 2009).

Biotelemetry has revolutionized the study of animals that are difficult to track (e.g. aquatic animals and birds) and of animals that live in remote, inaccessible, logistically challenging regions (e.g. polar areas; Lydersen et al. 2001, Egevang et al. 2010, Hamilton et al. 2014). Environmental data collected by animals equipped with biotelemetry devices has also greatly increased the amount of data available in under-sampled areas. For example, seals equipped with biotelemetry devices are responsible for 70% of the CTD profiles ever collected south of 60°S and provide data during the polar winter, when no or few other data sources are available (Fedak 2013). Maximum dive depth data from animals equipped with biotelemetry devices have also improved bathymetry maps in under-sampled areas (Padman et al. 2010). Ecosystem level studies, via tagging of many species in a region simultaneously, and studies investigating the impacts of climate change or other ecological disturbances (e.g. habitat fragmentation), via tagging over long time scales, are other areas where biotelemetry is currently having a large impact (Papers I – IV, Block et al. 2011).



Figure 3: Biotelemetry devices deployed on a polar bear, ivory gull and ringed seal.
Photo credit: Jon Aars (polar bear) & Hallvard Strøm (ivory gull)

2. Objectives

An opportunity for a natural experiment presented itself when the sea-ice regime in Svalbard and the Barents Sea underwent a sudden shift in 2006, with the altered sea-ice conditions persisting to the present day. Both ringed seals and polar bears in Svalbard had been equipped with biotelemetry devices before the shift in sea-ice conditions occurred. As part of the Norwegian Polar Institute's ICE program, ringed seals, polar bears and ivory gulls were equipped with biotelemetry devices after the shift in the sea-ice regime. These three species are trophically linked. Ringed seals are the primary prey of polar bears and ivory gulls scavenge on polar bear kills.

The objective of this PhD project on a grand scale was to determine the challenges for ice-obligate top trophic level species in a changing climate, particularly in regards to the declining Arctic sea ice. This was accomplished by investigating:

- How have the two movement strategies of ringed seals been affected by the change in sea-ice conditions that occurred in 2006?
- What defines the habitat of the coastal movement strategy of polar bears and how have the bears with this strategy been affected by the change in sea-ice conditions?
- How has the predator-prey relationship between coastal polar bears and ringed seals been affected in a spatial context by the change in sea-ice conditions?
- What are the habitat requirements of the polar bears, ringed seals and ivory gulls when they travel offshore to the marginal ice zone (MIZ) in the summer and autumn?
Additionally, what defines the main spatial overlap areas for this species assemblage in the MIZ?
- What are likely future scenarios for this species assemblage?

3. Materials and Methods

(a) Biotelemetry devices

Ringed seals, polar bears and ivory gulls were equipped with biotelemetry devices in various locations around Svalbard, Norway between 2002 and 2014 (Figure 4, Table 1). Locations were transmitted for all three species using the Argos (CLS 2016) or Iridium (McLean, VA, USA, www.iridium.com) satellite systems. A variety of behavioural data, such as information on dives, haul outs and water temperature for ringed seals and information on temperature for polar bears, were also transmitted.

Table 1: The number of individuals equipped with biotelemetry devices in Svalbard, Norway for each species and time period.

Species	Time period	Number of individuals tagged	Paper
Ringed seals	2002 – 2003	22	I,II,III
Ringed seals	2010 – 2012	38	I,II,III,IV
Polar bears	2002 – 2004	21	III
Polar bears	2007 – 2014	139	III,IV
Ivory gulls	2010 – 2013	40	IV

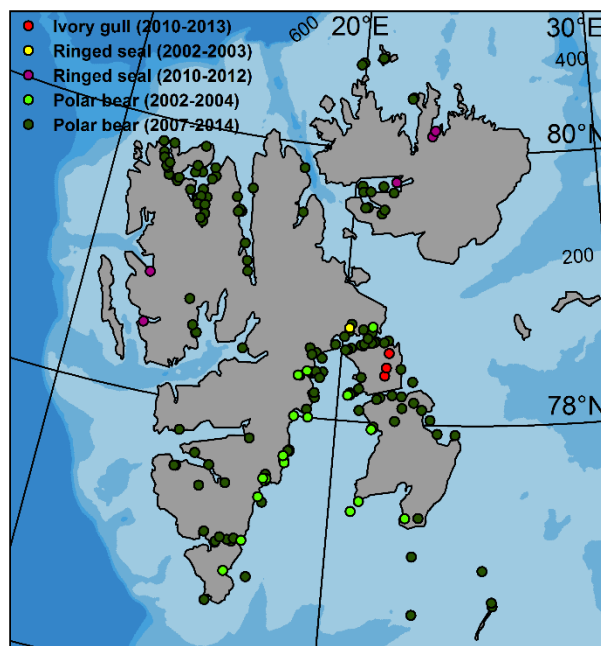


Figure 4: Tagging locations for the ivory gulls, ringed seals and polar bears equipped with biotelemetry devices in Svalbard, Norway.

(b) Location filtering

Locations transmitted by the Argos satellite system have variable accuracy levels due to a number of reasons including the number of transmissions received by the satellite, the

distribution of the messages along the satellite pass, animal motion and the altitude of the animal (CLS 2016). The highest location accuracy class (i.e. class 3) has a location error of < 100 m while the lowest accuracy classes (classes A and B) do not have an error estimated by Argos. Comparative studies using Fastloc-GPS have found that the error of classes A and B ranges between 4 and 100 km, depending on factors such as animal behaviour (Costa et al. 2010, CLS 2016). Transmitted GPS locations have greater accuracy than Argos locations, although variable location error also occurs, especially for older devices. The variable location accuracy and resultant spikes in the movement paths necessitated that the transmitted locations for each individual were filtered.

Polar bear and ringed seal locations were filtered using a combination of the speed-distance-angle (SDA) filter and the continuous-time correlated random walk (CRAWL) model, with a stopping model implemented for the ringed seal CRAWL models to account for time spent hauled out (Freitas et al. 2008b, Johnson et al. 2008). Ivory gulls were filtered only using the SDA filter, as the CRAWL model and other models such as Ian Jonsen's *bsam* package (Jonsen et al. 2005) which were developed using marine mammal datasets, did not adequately capture the movement path of this seabird species. Locations were extracted from the CRAWL models for polar bears and ringed seals and the SDA filtered tracks for ivory gulls at relevant time stamps.

(c) Single species approach

Investigating whether habitat use and behaviour of ringed seals and polar bears were impacted by the rapid environmental changes that occurred in the Svalbard region was a central objective of this PhD. For the coastal movement strategy of polar bears, a characterization of habitat was not previously available.

The filtered positions were compared to aspects of the environment recorded and transmitted by the biotelemetry devices as well as to a variety of environmental variables that were available at the appropriate spatial and temporal resolution (Figure 5). Additional movement, behaviour and space use metrics that were investigated include the distance travelled per day, home range size, Time Spent in Area (TSA), proportion of time spent haul out and various dive variables (see Figure 5 for additional details). Statistical models such as linear mixed-effect models (LMEs), generalized linear mixed-effect models (GLMMs) and generalized additive mixed-effect models (GAMMs) were used to investigate how these various response variables changed in response to a variety of temporal (e.g. time period, month), environmental (e.g. distance to glacier fronts, bathymetry) and biological (e.g. sex, mass) predictor variables. (Figure 5). Standard techniques for data exploration, model selection and model validation were followed (Burnham & Andersen 2000, Zuur et al. 2009, Zuur et al. 2010).

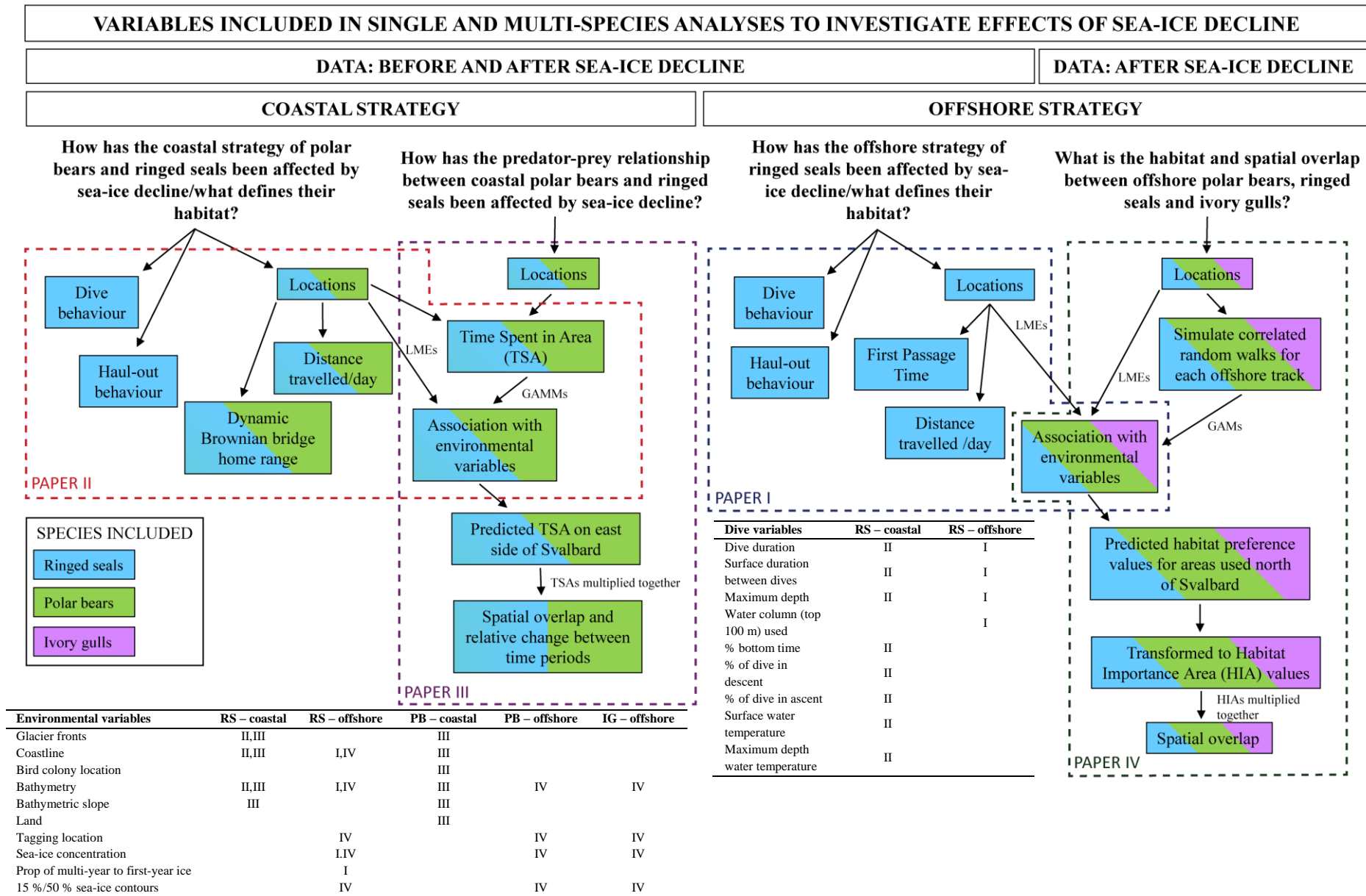


Figure 5: Schematic showing the outline of the single and multi-species analyses conducted for the ringed seals (RS, blue), polar bears (PB, green) and ivory gulls (IG, purple) equipped with biotelemetry devices before (2002 – 2004) and after (2007 – 2014) a decline in the sea-ice conditions in Svalbard, Norway. The tables highlight which environmental and dive variables were used for each species and movement strategy with the roman numerals indicating which paper these analyses are included in.

(d) Multi-species approaches

A variety of statistical packages and approaches have been developed to investigate niche overlap or species distribution overlap (e.g. nicheOverlap function in the dismo R package (<https://cran.r-project.org/web/packages/dismo/dismo.pdf>), niche overlap methods using EcoSim (<https://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html>) or pairwise species association using Pairs (<http://www.keib.umk.pl/pairs/?lang=en>)). However, these methods require input based on presence/absence data, species abundance data or require that the habitats/areas used can be split into discrete categories, making them inappropriate for the biotelemetry data collected from these three species. Biotelemetry devices enables the locations of the tagged animals to be known at different points in time. The absence of one of the tagged ringed seals from a fjord when one of the tagged polar bears was present does not equate to the absence of ringed seals at this location (i.e. an untagged ringed seal could have been present). The habitat variables interesting for polar marine species (e.g. glacier fronts, coastline, bathymetry) can also not be split into discrete categories (i.e. if a species is close to a glacier front it is also close to a coastline and likely has shallow bathymetry). This necessitated the use of alternative methods to investigate the spatial overlap between the ringed seal, polar bear and ivory gull species assemblage.

An approach based on Time Spent in Area (TSA; Sumner 2015) was used to investigate whether the amount of spatial overlap between coastal ringed seal and polar bear changed between 2002 – 2004 and 2010 – 2013. TSA was related to environmental variables and used to predict the proportion of time spent in 2.5 X 2.5 km grid cells for the east side of Svalbard (Figure 5). These predicted values for ringed seals and polar bears in each time period were multiplied to calculate the degree of spatial overlap. The two spatial overlap plots were used to assess the relative change in spatial overlap between the two time periods (Figure 5). This approach is similar to Hunsicker et al. (2013)'s method of investigating changes in spatial overlap between two fish species in the Bering Sea.

In order to investigate the spatial overlap in the MIZ between offshore ringed seals, polar bears and ivory gulls, the actual track of each individual (i.e. utilized habitat) was compared to simulated tracks of where each individual could have gone (i.e. available habitat). The starting location, number of steps and distributions of step lengths and turning angles for the simulated tracks (i.e. correlated random walks) were based on the actual track from each individual (Żydelis et al. 2011, Raymond et al. 2015). A binomial generalized additive model (GAM) was used to model the habitat characteristics of the actual tracks (response variable value of 1) and simulated tracks (response variable value of 0) in order to find the preferred habitat characteristics (Figure 5). The GAM model for each species was used to predict the habitat preference for the area these species utilised north of Svalbard and Franz Josef Land using sea ice data from 2012. In order to conduct an inter-species comparison, the predicted values were transformed into habitat importance percentiles for each species and multiplied to find the areas that had the greatest spatial overlap (Raymond et al. 2015; Figure 5). Another common approach used to investigate habitat preference is to generate pseudo-absences based on where each individual could have moved to in a given

time step. This approach was not suitable for the temporal resolution of the biotelemetry data available (i.e. 4 hours), as the habitat characteristics between pseudo-absences and actual positions at this time scale are very similar. Decreasing the temporal resolution to obtain differences between the actual positions and pseudo-absences was not desirable as it would degrade the power of the dataset.

4. Main Findings

(a) Paper I: Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice

Numerous movement and behaviour indices for ringed seals that took offshore foraging-migration trips were impacted by the summer sea-ice extent shifting from over the productive Barents Sea continental shelf to over the less productive deep Arctic Ocean Basin. It was primarily juvenile individuals that took offshore trips, with larger, older individuals remaining coastal in association with tidal glacier fronts. Ringed seals that took offshore foraging-migration trips were in areas with similar sea-ice concentrations and similar proportions of first-year sea ice to multi-year sea ice in both time periods, indicating that they sought this habitat. But following the sea-ice retreat, ringed seals had to travel further to reach the MIZ, reaching sea ice for the first time ~1 degree of latitude further north, and swam greater distances per day, even when in areas with high sea-ice concentration. They also exhibited different offshore trip strategies, such as travelling to the shallow areas of the Kara Sea or travelling to Franz Josef Land, Russia. Ringed seals also had dives of longer duration, had shorter surface intervals between dives, spent less time resting on sea ice and had less clear area-restricted search (ARS) behaviour following the sea-ice collapse. Whereas peaks in the First-Passage Time analysis that indicate ARS were clearly visible for the majority of seals in 2002 – 2004 that took offshore trips, only three of the 11 seals that took offshore trips in 2010 – 2013 had clear peaks. Taken together, these findings indicate that following the retreat in sea-ice conditions an increase in foraging effort occurred which increased the energetic costs of finding sufficient food resources. If the increased costs are not compensated for by increased energetic returns, growth, age-at-maturity, reproduction and ultimately survival rates will be impacted.

(b) Paper II: Coastal habitat use by ringed seals Pusa hispida following a regional sea-ice collapse: importance of glacial refugia in a changing Arctic

Coastal ringed seals spent the majority of their time in areas close to tidal glacier fronts. These areas are foraging “hotspots” in the summer and autumn. In the winter and spring calved pieces of glacier ice frozen into the annual fast-ice accumulate snow to sufficient depths for ringed seals to be able to make subnivean lairs. The association with tidal glacier fronts did not change between the two time periods for the seals tagged on the east coast. Seals tagged on the west coast in the second time period spent significantly more time close to glacier fronts than seals tagged on the east coast in either time period (Figure 6). High intraspecific competition likely occurs in close proximity to glacier fronts, causing ringed seals that had taken offshore foraging-migration trips, which were mostly smaller, younger individuals, to be located further from these features on their return to the Svalbard coastline compared to the ringed seals resident in these areas year-round (Figure 6). Distance travelled per day and monthly home range size decreased towards the winter and spring. Ringed seals are spatially restricted once the fast-ice forms due to their need to make and maintain a network of breathing holes. However, this spatial restriction was delayed in 2010 – 2013 compared to 2002 – 2004, especially for seals tagged on the west coast, due to the delay in fast-ice formation.

Ringed seals had dives of longer durations, had shorter surface intervals between dives, spent an increased proportion of the dive descending and a decreased proportion of time at the bottom of dives after the shift in sea-ice conditions occurred. These changes were similar for seals tagged on both the east and west coasts of Svalbard, even though environmental changes to date have been much more drastic on the west coast of Svalbard. These changes indicate that foraging effort increased and a shift in foraging behaviour occurred for Svalbard ringed seals following the change in sea-ice conditions, indicating that changes in prey species composition, abundance and distribution have occurred Svalbard wide, likely due to decreases in the thickness and extent of sea ice (Figure 6).

(c) Paper III: An Arctic predator-prey system in flux: climate change impacts on coastal space use by polar bears and ringed seals

Coastal polar bears spent between 30 – 50 % of their time close to tidal glacier fronts and moved between 0.3 and 40 km/d depending on season. Time spent close to glacier fronts did not change in the spring (Mar – May) between the two time periods. In the summer (Jun – Aug) and autumn (Sep – Nov), polar bears spent significantly less time close to glacier fronts after the sea-ice collapse (Figure 6). However, ringed seals did not change the percentage of time they spent close to glacier fronts or hauled out in the summer between the two time periods. This resulted in a significant change in the spatial overlap between ringed seals and polar bears on the east side of Svalbard in the summer (Figure 6). The highest spatial overlap values in 2002 – 2004 were ~150 % higher than the highest values in 2010 – 2013. The spatial overlap values greatly decreased in coastal areas close to glacier fronts after the change in sea-ice conditions, with small increases in coastal areas where no glacier fronts are present.

The decrease in spatial overlap indicates that an alteration in the intensity of the predator-prey relationship between ringed seals and polar bears has occurred during the summer season. Following the sea-ice collapse, ringed seals are likely hauling out on calved pieces of glacier ice during the summer instead of fast-ice, which has likely decreased their availability to polar bears. The primary hunting methods of polar bears are still-hunting at a breathing hole or stalking on sea ice; although polar bears have been observed successfully catching seals on ice floes by approaching them aquatically, this is assumed to be a speciality hunting technique (Stirling 1974). The biotelemetry data indicates that the percentage of bears that spent greater than 50 % of their time close to tidal glacier fronts fell from 73 % (11 out of 15 bears) to 22 % (5 out of 23 bears) following the shift in sea-ice conditions.

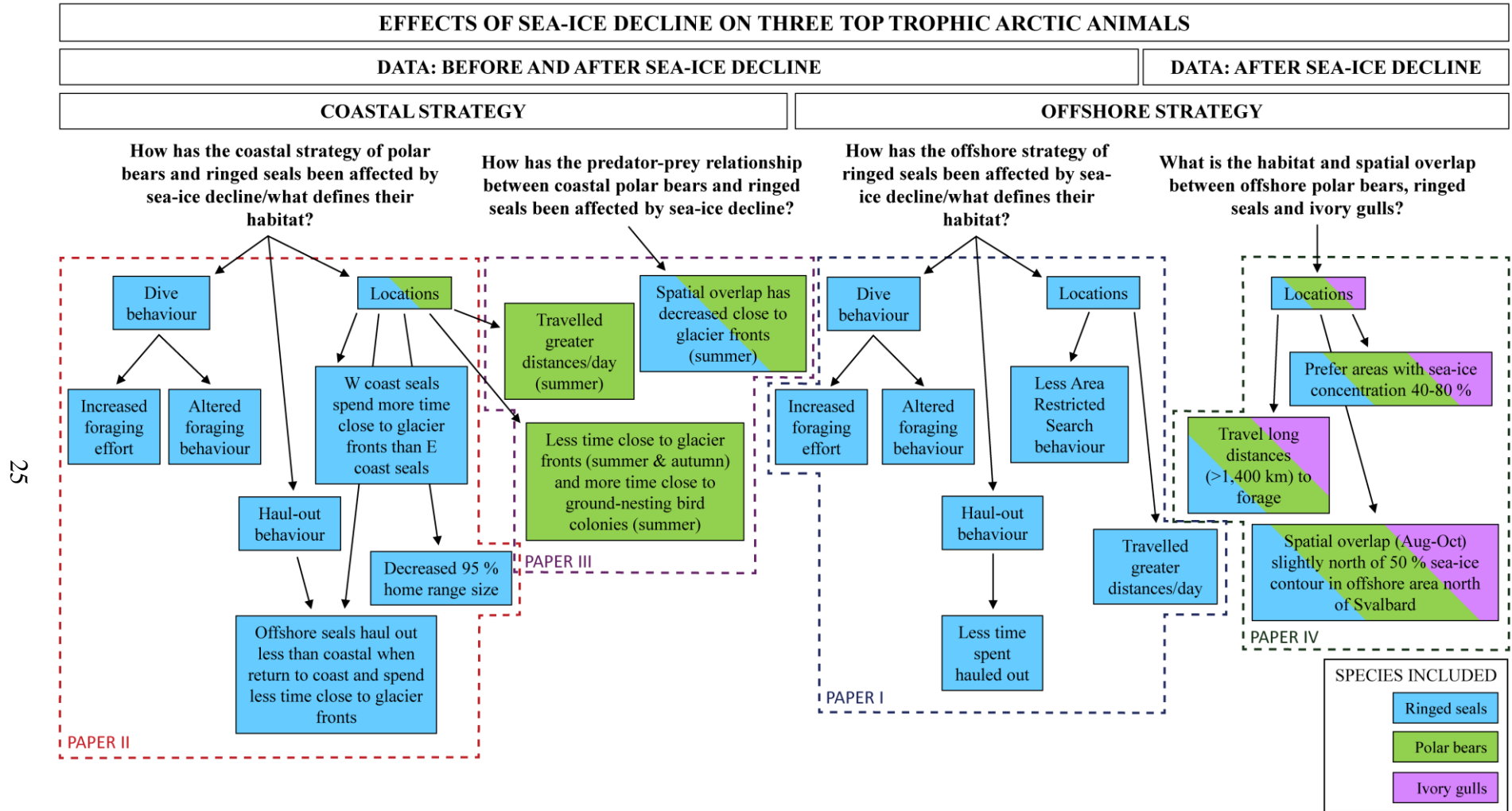
The decreased “availability” of polar bear’s traditional food source has likely resulted in them using more alternative food sources after the sea-ice decline. Polar bears moved greater distances per day in the summer and spent more time close to ground-nesting bird colonies in 2010 – 2013 than in 2002 – 2004, highlighting the linkages that exist between the terrestrial and marine ecosystems in most Arctic regions (Figure 6). Population sizes of pink-footed geese (*Anser brachyrhynchus*) and barnacle geese (*Branta leucopsis*) have greatly increased over the past decades (Goosemap 2012, Madsen & Williams 2012), likely increasing their importance as alternative food sources.

This paper has quantitatively shown that a deterioration in sea-ice conditions over a large spatial scale in Svalbard has altered the predator-prey relationship between ringed seals and polar bears. Following the decreased “availability” of their traditional food source, polar bears are utilising alternative prey sources, such as ground-nesting bird colonies, to a larger degree, with resultant implications for the wider Arctic marine and terrestrial ecosystems.

(d) Paper IV: An Arctic predator, prey and scavenger system in a changing climate

Portions of the Svalbard ringed seal and polar bear populations and all of the ivory gulls equipped with biotelemetry devices in Svalbard travelled to the MIZ of the Barents Sea in the summer and autumn. Productivity in the MIZ is high and extended as the bloom follows the retreat of the sea-ice, making it an important foraging area for species that are able to track its progression. Over 90 % of the individuals that travelled offshore in all three species spent the majority of their time (≥ 50 %) in areas with sea-ice concentrations over 15 %, while only 20 – 50 % of individuals were in areas with sea-ice concentrations greater than 90 %. All three species preferred areas with sea-ice concentrations between 40 – 80 % (Figure 6). Ringed seals, polar bears and ivory gulls were more closely affiliated with the 50 % than the 15 % sea-ice contour. Individuals of all three species travelled long distances to forage in the MIZ, with the maximum distance travelled from the tagging location exceeding 1,400 km (great circle distance) for all three species (Figure 6).

The highest spatial overlap for this species assemblage between August and October occurred in areas slightly north of the 50 % sea-ice contour (Figure 6). As the sea ice continues to retreat, all three species will likely track their preferred habitat further north. How far these species will track the MIZ into the Arctic Ocean Basin depends on the varying costs of movement for all three species and the relative energetic gains from foraging. This will in turn be dictated by the degree to which primary productivity increases in the Arctic Ocean Basin as well as corresponding changes in invertebrate and fish stocks. An isolated, ephemeral population of polar bears might be established in the MIZ when the sea ice retreats too far away from land for them to swim, dependent on adequate food resources being available in this region year round. Lack of suitable denning sites in the MIZ over a long time scale will limit this population's persistence to one or a few generations. The predicted disappearance of sea ice in the Arctic Ocean Basin will result in spatial overlap for this species assemblage existing only in coastal areas in Svalbard, with an increased proportion of each species likely associated with tidal glacier fronts. Increases in intra- and interspecific competition in these areas as well as continued declines in sea ice and snow conditions and the number of tidal glacier fronts will likely lead to range shifts and population decreases in each species, which will have effects on the wider Arctic ecosystems.



25

Figure 6: Schematic showing the main results of the single and multi-species analyses investigating the effects of sea-ice decline for ringed seals (blue), polar bears (green) and ivory gulls (purple) equipped with biotelemetry devices before (2002-2004) and after (2007-2016) a sea-ice decline in Svalbard, Norway.

5. Conclusions and future perspectives

The deterioration of sea ice in the Svalbard and Barents Sea area has had numerous impacts on ringed seals and polar bears. Foraging behaviour has been altered and the energetic costs of foraging have increased for both movement strategies of ringed seals (Papers I, II). Coastal polar bears have also altered their foraging behaviour during the summer and autumn, with resultant consequences for the magnitude of spatial overlap and the intensity of the predator-prey relationship between polar bears and ringed seals (Paper III). Coastal polar bears increasingly utilising “alternative” marine and terrestrial food sources will have ramifications for the wider Arctic ecosystems. Offshore polar bears, ringed seals and ivory gulls have the highest spatial overlap in areas slightly north of the 50 % sea-ice contour in the MIZ between August and October (Paper IV). Further retreat of the MIZ, reductions in the number of tidal glacier fronts and deterioration of sea ice in coastal areas pose a serious threat to the growth, reproduction, survival, distribution and abundance of all three top trophic, ice-obligate species.

(a) Effects on single species

Following the collapse of the sea-ice conditions in 2006, fast-ice in the fjords of Svalbard now forms later and melts earlier than it did previously or fails to form at all, especially on the west coast of Svalbard (Norwegian Ice Service, Norwegian Meteorological Institute, <http://polarview.met.no/>). Fast-ice needs to form early enough for snow to accumulate to sufficient depths for ringed seals to be able to make subnivean lairs (Smith & Stirling 1975, Lydersen & Gjertz 1986, Lydersen & Smith 1989). As Svalbard receives little snow fall, ringed seals are dependent on calved pieces of glacier ice frozen into fast-ice that can accumulate snow to sufficient depths for subnivean lair formation (Smith & Lydersen 1991). The retreat of tidal glacier fronts onto land over the past decades and the predicted continued retreat of these features in the future (Błaszczuk et al. 2000) is likely to decrease the areas in which successful pup production can occur.

Ringed seals give birth directly on the sea ice when there is not enough snow for subnivean lair formation, leading to very high levels of pup mortality (Lydersen & Smith 1989). An almost complete failure of ringed seal pup production on the western coast of Svalbard has occurred since 2006 due to a lack of adequate sea ice and snow cover (Kit Kovacs & Christian Lydersen, pers. comm.). Male ringed seals usually maintain underwater territories in the fast-ice habitat in the spring, mating with females at the end of the nursing period (Smith & Hammill 1981, Reeves 1998). Given the high site fidelity documented among the coastal ringed seals, both intra- and inter-annually, and the genetic substructure that exists between different Svalbard fjords (Paper II, Kit Kovacs & Christian Lydersen, unpublished data), it is unknown if ringed seals will move to other areas where sea-ice conditions are suitable for breeding or if there has been a breakdown in the breeding system. Continued failures in pup production will ultimately lead to a decreased abundance and distribution shifts of ringed seals in Svalbard.

The ringed seals caught in 2010 – 2012 on the western coast of Svalbard were among the heaviest seals caught on Svalbard since research began on this population in the 1980s (Lydersen & Gjertz 1986, Krafft et al. 2006). Females lose ~0.65 kg/day during the ~39 day nursing period, despite feeding extensively (Lydersen & Kovacs 1999). A female that loses her pup shortly after birth will not deplete her energy stores to the same extent as a female that successfully weans her pup. Males also have high energetic costs during this period due to the defence of their underwater territories; their energetic balance has likely also been altered by the decline in sea-ice conditions. The high masses observed in these ringed seals are most likely a result of the breeding failures documented in this area since 2006, although potential improvements in foraging conditions may also play a role.

The changes in behaviour and movement documented for ringed seals indicates that energetic costs while foraging have likely increased for both movement strategies following the sea-ice collapse (Papers I, II). It is not known whether ringed seals are recouping these extra energetic costs through concurrent energetic gains. As ringed seals are not central place foragers and because of the logistical demands of working in remote and inaccessible areas of Svalbard, the vast majority of ringed seals equipped with biotelemetry devices are never seen or captured again. The lack of a subsistence harvest in Svalbard means that samples are not available to determine if the increases in energetic costs, as indicated by changes in behaviour and movement patterns, have led to changes in parameters such as reproductive rate, age at first breeding or survival of different age classes.

Ringed seals are also being negatively impacted by sea-ice declines in other Arctic regions. In Hudson Bay and Prince Albert Sound, Canada, changes in reproductive parameters, condition, survival of pups and diet have been observed in recent decades and linked to changes in sea ice and snow conditions (Harwood et al. 2000, Ferguson et al. 2005, Stirling 2005, Chambellant et al. 2013). It is likely that negative impacts on ringed seals are also ongoing in other areas of the Arctic but have not been detected due to a lack of monitoring throughout a large part of the ringed seals' range. For example, abundance trends for ringed seals are unknown for all Arctic regions (Laidre et al. 2015). A circumpolar monitoring plan for ringed seals has been developed as ringed seals are highly abundant throughout their circumpolar range, are sensitive to sea-ice conditions and are key components of the Arctic ecosystem (Kovacs 2008). Based on this they have been recommended as an “indicator species” (i.e. ecosystem sentinel) for monitoring the impacts of climate change by both the Arctic Monitoring and Assessment Programme (AMAP) and the Conservation of Arctic Flora and Fauna (CAFF). However, lack of funding has prevented international monitoring programs from being implemented.

The movement strategy that a polar bear in Svalbard follows is individually specific, with an animal following the same strategy every year if possible (Mauritzen et al. 2001, Jon Aars, unpublished data). However, under some circumstances polar bears do switch strategies. For example, early sea-ice retreat can turn bears that usually have the offshore strategy into coastal bears (Jon Aars, unpublished data). Studies investigating condition, reproduction rates and survival of Svalbard polar bears have not found a consistent decline in these parameters

over time, although variations in reproduction and condition have been linked to the Arctic Oscillation (AO; Environmental monitoring of Svalbard and Jan Mayen, www.mosj.no, Andersen & Aars 2016). High AO values (i.e. milder springs with less sea ice) have been linked to reduced body condition of males and also to a reduced proportion of females with COYs the following year (Environmental monitoring of Svalbard and Jan Mayen, www.mosj.no, Andersen & Aars 2016). Delays in the timing of sea ice freeze-up also impacts the ability of pregnant females to reach islands that were historically important denning areas. Lower body mass of females and their cubs upon den emergence has also been reported on the denning island of Hopen when sea ice freeze-up has been delayed the preceding autumn (Derocher et al. 2011, Aars et al. 2013). Further effects of sea-ice declines may become apparent in the future as suitable polar bear habitat in the Barents Sea is predicted to decline substantially during the 21st century (Durner et al. 2009).

Polar bears throughout their range are increasingly spending more time on land due to earlier dates of sea ice break-up and later dates of sea ice freeze-up, which is negatively impacting condition, survival of different age classes, reproductive rate and abundance for multiple sub-populations including the Western Hudson Bay and Southern Beaufort Sea sub-populations (Regehr et al. 2007, Towns et al. 2009, Stirling & Derocher 2012, Rode et al. 2015). Delays in sea ice freeze-up have also been linked to an increase in the number of human-bear conflicts (Towns et al. 2009). Similar to ringed seals, polar bears are also at risk of warm weather and rain-on-snow events during winter, as this can collapse subnivean lairs and maternity dens, in some cases killing the occupants (Clarkson & Irish 1991, Stirling & Smith 2004, Stirling & Derocher 2012)

Ivory gulls are distributed in relation to drifting sea ice for the majority of the year (Paper IV, Gilg et al. 2010, Spencer et al. 2014, Gilg et al. 2016, Spencer et al. 2016). Ivory gulls from colonies in Svalbard, Northeast Greenland and Franz Josef Land, Russia, travel to the MIZ of the Northeast Atlantic post-breeding (Paper IV, Gilg et al. 2010). Nearly half of the ivory gulls tagged in Svalbard also made trips to the MIZ from the breeding colonies throughout the breeding season (Hallvard Strøm, unpublished data). Ivory gulls are opportunistic feeders. In addition to foraging on ice-associated invertebrates and fish, they also scavenge on polar bear kills (Divoky 1976, Gilchrist et al. 2008, Gilg et al. 2010, Lydersen et al. 2014). It is not known how important scavenging is in regards to annual energy intake or if there are individual foraging strategies, but the frequency with which ivory gulls are observed at polar bear kill sites indicates that scavenging is likely an important foraging strategy, at least for some individuals or during some parts of the year. The energy content of ringed seal blubber (which is nearly 100 % fat) is up to 10 X larger than the energy content of polar cod (*Boreogadus saida*) and their invertebrate prey (ringed seal fat: 34 – 39 kJ/g w.w. (Stirling & McEwan 1975), polar cod: 4 – 7 kJ/g w.w. (Harter et al. 2013; Hop & Gjørseter 2013), *Themisto libellula*: 4 kJ/g w.w. (Hop et al. 1997)).

Ivory gull abundance has declined by 80 % in the Canadian Arctic since the early 1980s. Although the exact cause is unknown, changes in sea ice or marine conditions in their wintering grounds are likely explanations due to the large spatial scale over which the decline

has occurred (Gilchrist & Mallory 2005). Population trends in the remainder of ivory gulls' circumpolar range are uncertain (Greenland and Svalbard) or stable (Russia) with colony size fluctuating inter-annually due to factors such as sea-ice condition (Gilchrist et al. 2008).

Climate change is not the only stressor currently impacting the species assemblage of ringed seals, polar bears and ivory gulls. Long-range transport of persistent organic pollutants (POPs) to the Arctic takes place by atmospheric, riverine and oceanic pathways (AMAP 2009). Some of the contaminants bioaccumulate in Arctic organisms. Biomagnification in food webs can occur, with top trophic level animals having higher concentrations of pollutants than lower trophic level animals. This is especially a problem in the marine food web, as it has multiple trophic levels and many animals with a high fat content (AMAP 1998). POP concentrations can vary across species in similar trophic levels and can also vary within a species across various Arctic regions, due to differences in the ability of different species to metabolize the various POPs and the type and degree of industrial and agricultural activity in the pollutant source regions (Wolkers et al. 1998, Wolkers et al. 2004, Lucia et al. 2015). Although specific studies on the effects of POPs for Arctic ringed seals are not available, levels are high enough to raise concerns for immune function, reproduction and vitamin A levels when compared to known effect levels in other species (AMAP 2009). POP levels in polar bears are high enough to negatively impact immune response, metabolism, retinol and thyroid hormones and to potentially cause reproductive disorders (AMAP 2009, Andersen & Aars 2016). Ivory gulls also show contaminant levels exceeding thresholds known to affect reproduction in other avian species, including the highest egg mercury concentrations documented in any Arctic bird (Bond et al. 2015, Lucia et al. 2015). Additionally, climate change and the effect of POPs may interact, as climate change may affect the transport pathways and the impacts of POPs (AMAP 1998). Additional stressors for this species assemblage include oil development, maritime shipping, tourism and commercial fishing, which are likely to expand and intensify their activity in Arctic areas as sea-ice declines continue.

(b) Effects on species interactions

Predator-prey interactions between ringed seals and polar bears and the resultant scavenging opportunities for ivory gulls have likely been affected both offshore and coastally in Svalbard by the decline in sea-ice conditions. Hunting ringed seals and their pups on fast-ice is especially important for female polar bears with COYs in the spring (Freitas et al. 2012). Thus, an increased proportion of pups born outside of the protective subnivean lairs due to deteriorating snow and sea-ice conditions will positively impact polar bears, as long as ringed seal abundance and density remains at levels similar to the present day. The amount of energy gained from ringed seals pups depends on the age of the pups killed. Ringed seal pups increase from ~5 % fat at birth to 36 – 45 % fat based on wet weight at the end of the lactation period (Stirling & McEwan 1975, Lydersen et al. 1992). As polar bears usually only eat the fat (Stirling & McEwan 1975), polar bears are expected to obtain less energy overall if they prey on most ringed seal pups shortly after birth (Rosing-Asvid 2006).

Tidal glacier fronts are foraging “hotspots” for many marine mammal and seabird species during the summer and autumn; sub-surface plumes of meltwater released from glaciers entrap 10 – 100X the volume of seawater as they rise to the surface. Lower trophic level prey (i.e. invertebrates and polar cod) either die or are stunned due to osmotic shock or become trapped at the bottom, creating rich foraging conditions for higher trophic levels (Lydersen et al. 2014). Ringed seals and polar bears that have the coastal movement strategy concentrate their time close to tidal glacier fronts and ivory gulls are regularly observed feeding at these features (Papers II, III, Freitas et al. 2008a, Lydersen et al. 2014). The increase in foraging effort and change in foraging behaviour of coastal ringed seals after the sea-ice collapse indicates that changes in invertebrate and fish species composition, abundance or distribution have likely occurred across the Svalbard Archipelago (Paper II). Fish species typically associated with Atlantic water masses have begun to appear in fjords in western Svalbard in recent years (see for example Jensen et al. 2014, Berge et al. 2015); interestingly, ringed seals tagged in these areas spent significantly more time close to tidal glacier fronts than seals tagged on the east coast of Svalbard (Paper II). Data are lacking to determine what changes have occurred in the prey community in eastern Svalbard. Water temperatures recorded by the seals were similar between 2002 – 2004 and 2010 – 2013; the defining difference between these two time periods was the deterioration of sea-ice conditions (Paper II).

The earlier break-up of sea ice has led to a decrease in spatial overlap between coastal ringed seals and polar bears in Svalbard, which will likely have consequences for polar bear energetic gain and ivory gull scavenging opportunities (Paper III). Polar bears in most areas are thought to accumulate the majority of their annual energetic needs in the late spring and early summer (Stirling & Derocher 2012). Earlier break-up of the sea ice will shorten the time available to accumulate these essential fat reserves, as it will cause bears to prematurely cease hunting seals. Decreased “availability” of their traditionally most important food resource may result in polar bears increasingly using alternative food resources. Paper III quantitatively documented that coastal polar bears in Svalbard spent more time close to ground-nesting bird colonies after the sea-ice collapse than before, highlighting that changes in the marine ecosystem can affect the terrestrial ecosystem due to the linkages that exist between these two systems in most Arctic regions. An increase in the occurrence probability of polar bears has also been documented at ground-nesting bird colonies in the west coast of Svalbard and in the Canadian Arctic and linked to longer ice-free seasons in these areas (Iverson et al. 2014, Prop et al. 2015). The effect of polar bears in ground-nesting bird colonies can be quite substantial, with predation levels over 90 % recorded (Smith et al. 2010, Prop et al. 2015). High predation rates over time can impact bird abundance, affecting not only the wider Arctic marine and terrestrial ecosystems but also ecosystems over the birds’ migratory routes. Impacts can include the amount of agricultural damage and the amount of food available to predators at stopover and wintering sites (Jonker et al. 2010). Other alternative food sources for polar bears include hunting and scavenging carcasses of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and scavenging whale carcasses (Derocher et al. 2000, Iversen et al. 2013, Aars et al. 2015). The documented increase in daily movement rates of Svalbard coastal polar

bears in the summer after the sea-ice collapse could increase the chances of finding these carcasses (Paper III).

The northward retreat of the MIZ led to an increase in foraging effort and a change in foraging behaviour for ringed seals that took offshore foraging-migration trips (Paper I). Ringed seals are opportunistic predators but they do show a preference for polar cod and lipid-rich pelagic invertebrates (Reeves 1998, Labansen et al. 2007). Polar cod are distributed in relation to cold ($< 0^{\circ}\text{C}$), Arctic water masses, occupying sympagic, pelagic and benthic habitats (Hop & Gjørseter 2013). Juvenile polar cod (ages 1 and 2) occupy cracks in the sea ice, where they get some protection from predators (Hop & Gjørseter 2013). Polar cod abundance has decreased in the Barents Sea and the distribution of the 0-age class has shifted northeastward over the last decade, concomitant with the rapid “borealization” of the Barents Sea fish communities (McBride et al. 2014, Fossheim et al. 2015). Furthermore, both polar cod and sea-ice associated invertebrates are found in higher densities over the Barents Sea continental shelf than in the Arctic Ocean Basin (Gulliksen & Lønne 1989, David et al. 2016). The amount of multi-year sea ice in the Arctic Ocean Basin decreased by $> 40\%$ between 2005 and 2008, which likely reduced habitat quality for the sympagic fish and invertebrate community (Kwok et al. 2009). The shift of the MIZ from over the Barents Sea continental shelf to over the Arctic Ocean Basin, as well as the decrease in multi-year sea ice, are most likely related to the increased foraging effort and less spatially concentrated foraging activity documented for the offshore ringed seals (Paper I).

Ringed seals that took offshore foraging-migration trips to the MIZ spent less time hauled out (i.e. less time exposed to polar bear predation) after the MIZ shifted to being located over the Arctic Ocean Basin (Paper I). If this has resulted in fewer kills of ringed seals by polar bears, both the energy balance of polar bears and the scavenging opportunities for ivory gulls may be impacted. The extent to which polar bears are impacted depends on the availability of alternative prey in the MIZ. In addition to breeding in the fast-ice that forms coastally in Svalbard, ringed seals have also been documented breeding in the pack ice of the Barents Sea (Wiig et al. 1991). Not much is known about these ringed seals, but they likely provide an additional source of food for offshore polar bears. Harp seals and bearded seals are also present in the MIZ of the Barents Sea during the summer and autumn and are found in polar bear scat samples in these areas (Derocher et al. 2002, Nordøy et al. 2008). Their larger body masses makes them important prey to polar bears in terms of biomass, although ringed seals are numerically the most important prey source (Derocher et al. 2002).

(c) Future outlook

A key factor when predicting the future outlook for Arctic species is the extent to which decreases in Arctic sea-ice extent will impact the level of primary production in this region. Future predictions of primary production in the Arctic range from quite modest (10 – 30 %) to substantial increases (doubling to tripling; Arrigo et al. 2008, Slagstad et al. 2011, Lawrence et al. 2015). Sea-ice declines in the Arctic Ocean Basin to date have not led to large increases in primary production, potentially due to nutrient limitation, but primary production

has increased over the Arctic continental shelves (Bluhm et al. 2015). Nutrient concentrations are not homogenous across the Arctic Ocean, with some regions (i.e. Eurasian Basin) having higher nitrate fluxes than others (i.e. Canada Basin), suggesting that the potential for increases in primary production varies across the Arctic Ocean (Bluhm et al. 2015, Randelhoff & Guthrie 2016).

An additional concern for Arctic marine mammals and seabirds is the future species composition, biomass and distribution of their prey base (i.e. invertebrates and fish) in an Arctic that has less sea ice or is seasonally sea-ice free. This is dependent on future levels of primary production in this region, as well as the degree of plasticity and adaptation capabilities of present Arctic inhabitants and the number, size and identity of southern species that will expand their distribution northwards. Large-scale ecosystem studies in the Barents Sea found that large changes in the distribution of fish communities and structure of the food web occurred between 2004 and 2012 (Fossheim et al. 2015, Kortsch et al. 2015). A rapid “borealization” of this region occurred due to the expansion of boreal fish communities northwards with the Arctic shelf community now retracted to deeper areas bordering the Arctic Ocean Basin. High bathymetric depth might limit further expansion of the Arctic shelf community northwards (Fossheim et al. 2015). Polar cod and a number of invertebrate species are currently found throughout the Arctic Ocean Basin, but they occur at lower densities in this region than over the Arctic continental shelves (Gulliksen & Lønne 1989, David et al. 2016). Polar cod in the Arctic Ocean Basin likely originate from the continental shelf areas (David et al. 2016), likely necessitating healthy coastal populations for the present abundance of polar cod in the Arctic Ocean to be maintained. The concentration of different species of sea-ice associated invertebrates and the younger year classes of polar cod varies greatly from ice floe to ice floe, but there are generally higher concentrations of these species in multi-year sea ice (i.e. thicker ice) and in areas with high sea-ice concentration. In addition, multi-year sea ice acts as “seeding platforms” for first-year sea ice (Arndt et al. 2009, David et al. 2016). Thus, the disappearance of multi-year sea ice and the replacement of multi-year sea ice with first-year sea ice as the dominant sea-ice type in the Arctic Ocean Basin is a great threat to this sympagic community (Kwok et al. 2009, Wang & Overland 2012). The future composition of the lower trophic levels in a seasonally sea-ice free Arctic is currently unknown.

Ringed seals, polar bears and ivory gulls will likely continue to travel to the MIZ during the summer and autumn as the sea-ice extent continues to retract as long as the energetic gains outweigh the energetic costs. A modelling study suggested that the offshore foraging-migration trips of ringed seals should remain profitable as long as the sea-ice retreats no further than 600 – 700 km (i.e. sea-ice edge approximately situated around 86°N) from the Svalbard coast, given adequate prey resources (Freitas et al. 2008c). Ivory gulls are likely to continue to travel to the MIZ as it retreats as long as there continues to be adequate prey resources in this area, given their lower costs of movement and the large distance presently covered in their yearly migration. A concern for polar bears with the offshore movement strategy is whether the sea ice is within swimming distance of the Svalbard coastline. Polar bears can swim long distances (> 50 km) with dependent young (including COYs several

months after emergence), but this likely has higher energetic demands than moving the same distance over sea ice (Pagano et al. 2012). Additionally, although COYs several months after den emergence (Jul to Sep) do survive long distance swims, they have a higher mortality rate than COYs that do not take long distance swims (Pagano et al. 2012). The longest documented continuous swim of a female polar bear was a 687 km swim over nine days. The consequences of making this swim were large, as she lost 22 % of her body mass as well as her yearling cub (between recaptures; Durner et al. 2011). Polar bears are also vulnerable to weather conditions during long distance swims. Following a period with high winds and rough sea conditions, four polar bear carcasses were found floating in open water, with the authors estimating that a total of 27 bears may have died as a result of this single storm event (Monnett & Gleason 2006). When the distance between the sea-ice edge and Svalbard is too far for polar bears to swim, a permanent offshore group of polar bears may result, dependent on adequate food resources existing in this region on an annual basis. This population will likely be limited to one or a few generations (given the persistence of the Arctic ice cap year-round), due to a lack of suitable denning areas over a long time scale. Polar bears in the Barents Sea den on land; polar bears in other regions of the Arctic do den on drifting sea ice but the proportion of dens in sea ice has declined over recent decades due to the deterioration of sea-ice conditions (Fischbach et al. 2007). The general decline in Arctic sea-ice conditions will likely limit the feasibility of the permanent offshore polar bears switching to denning in drifting sea ice over a long time scale. Finding adequate amounts of prey when the distance between the coast and sea-ice edge decreases the proportion of the ringed seal population making offshore foraging-migration trips is another key concern for offshore polar bears. Less ringed seals that will potentially further decrease the proportion of time spent hauled out will affect both the energy budget of offshore polar bears and the scavenging opportunities for ivory gulls.

As the MIZ continues to decline and ultimately seasonally disappears (Wang & Overland 2012, IPCC 2013a) the interaction between these three species in this area will naturally cease to exist. There will be serious consequences for the offshore (potentially permanent) group of bears; polar bears in Svalbard will be restricted to the coastal movement strategy. High intraspecific competition among ringed seals already occurs at glacier fronts, as it is primarily juvenile individuals that take offshore foraging-migration trips and these individuals are further from tidal glacier fronts upon their return to coastal areas than year-round residents (Papers I, II). Intraspecific competition may continue to cause juvenile ringed seals and ivory gulls to leave the Svalbard coastline when the Arctic is seasonally sea-ice free to search for alternate foraging areas offshore; however, their ability to find adequate prey resources at accessible depths in the rapidly changing Barents Sea ecosystem will determine the future success of this strategy. The ability of these two species to remain offshore for several months without resting platforms available is also uncertain at this time.

The disappearance of summer sea ice in the Arctic Ocean, potentially as early as the 2030s (Wang & Overland 2012), will increase the importance of coastal areas for these species, particularly areas close to tidal glacier fronts. These coastal areas will become the dominant place where trophic interactions between these three species occurs. Intra- and

interspecific competition at glacier fronts will likely increase, which will have consequences for the abundance and distribution of these three species around Svalbard. Further deterioration of sea ice coastally in Svalbard is likely to continue to affect the amount of spatial overlap during the summer between coastal polar bears and ringed seals. As ringed seals will increasingly use calved pieces of glacier ice as haul-out platforms, an increased proportion of polar bears may learn the aquatic hunting technique (i.e. sneaking up on hauled out seals from the water) which previously was viewed as a speciality (Stirling 1974). Increased usage of both terrestrially- and marine-based alternative food resources by polar bears, such as Svalbard reindeer, whale carcasses, ground-nesting and cliff-nesting bird colonies, is also likely to occur.

An additional concern is that glaciers in Svalbard are in negative mass balance, and both the number and total length of tidal glacier fronts have decreased over the past decades (Kohler et al. 2007, Błaszczuk et al. 2009). The decrease in the number of tidal glacier fronts as well as the decline in sea ice and snow conditions will decrease the area where ringed seal pup reproduction can successfully occur. The continued decline in glacier fronts will also increase the competition occurring in these areas and likely lead to a decrease in the number of ringed seals, ivory gulls and polar bears these areas can support. The environmental changes ongoing in Svalbard will have consequences for the condition, reproductive rates, survival, distribution and ultimately abundance of each species on Svalbard. Changes in these three species will have rippling effects throughout the wider Arctic marine and terrestrial ecosystems.

Polar bears, ringed seals and ivory gulls all have the ability to be ecosystem sentinels for the Arctic marine ecosystem. Their circumpolar distribution allows them to indicate changes for the entire Arctic as well as highlight potential differences between the various Arctic regions. Ecosystem sentinels are especially useful for the Arctic region. Large areas of the Arctic are unpopulated and conducting research on long intra- and inter-annual time scales is logistically challenging due to the remoteness, large expanses of sea ice, extended periods of darkness and harsh environmental conditions. Additionally, environmental variables derived from passive satellite sensors that detect reflected sunlight radiation, such as chlorophyll *a* concentration, are not available for the polar night period. Present studies on these three species demonstrates their usefulness as ecosystem sentinels. Changes in ringed seal movement, behaviour and diet have the ability to warn of changes occurring in lower trophic levels or the environment (Papers I, II, Chambellant et al. 2012, 2013). Changes in the intensity of the predator-prey relationship between polar bears and ringed seals indicates a likely increased predation pressure on alternative marine and terrestrial food sources, at least for some periods of the year (Paper III). In addition, a 130-year feather record for ivory gulls that shows a 45 X increase in methyl mercury values in the absence of dietary changes indicates that bioavailable mercury has increased in the Arctic as a result of human activities (Bond et al. 2015). The use of all three species to warn of and detect rapid changes that will be occurring in the Arctic over the coming decades should be expanded by scientific and management groups.

The amount of plasticity that ringed seals, polar bears and ivory gulls will exhibit to changes in their environment is presently unknown. All three species will need to increasingly use alternative food sources. Alterations in the species composition, abundance or density of their prey bases and inaccessibility of traditionally important food sources for some periods of the year are expected to occur over the coming decades as environmental change continues. The primary concern for ringed seals is their dependence on a stable sea-ice platform with ample snow cover for successful reproduction. Even if ringed seals show plasticity in foraging behaviour and the use of haul-out platforms, declines in abundance will likely occur if pups are born outside the protective subnivean lairs. One of the primary concerns for polar bears is having a stable and predictable food supply in the spring when females that have been fasting for several months emerge from their dens with dependent cubs. They currently rely on ringed seals (Freitas et al. 2012) and the population size of ringed seals will likely decrease in the coming decades. Ivory gulls are currently associated with drifting sea ice for the majority of the year; this species will have to show behavioural plasticity to persist in an Arctic that is seasonally sea-ice free. Other Arctic seabird species (e.g. black-legged kittiwakes, *Rissa tridactyla*) are not distributed in association with sea ice throughout the year, indicating that alternative foraging areas do exist (Frederiksen et al. 2011).

If ringed seals, polar bears and ivory gulls do not have enough plasticity to cope with the rapid environmental changes occurring in the Arctic, their only options are to move, adapt or go extinct. The capacity for these species to move further north is limited. These species already inhabit the northernmost areas of the globe; land masses do not exist further north of their present range and the MIZ is predicted to seasonally disappear during the coming decades (Wang & Overland 2012). Additionally, the environment is changing at an unprecedented rate when compared to earlier periods of change in the earth's geological past (Lüthi et al. 2008, Polyak et al 2010, Kinnard et al. 2011, IPCC 2013a). This limits the potential for adaptation in these three long-lived species as large changes in their environment are occurring over a few generations.

All species are constantly involved in a web of trophic interactions. This web changes through time, according to factors such as season, life cycle stage and external environmental influences. Understanding the effects of these interactions and how they vary over time can be difficult as interactions can change in non-linear and unexpected ways, raising the importance of long time scale and multi-species studies. Enhanced understanding of how present biological interactions operate and how these interactions are changing over the course of an individual's lifespan and as a response to environmental perturbations will improve predictive capacity as well as management and amelioration efforts.

6. References

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