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Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf seas

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ABSTRACT

In a warmer Arctic, endemic marine mammal species will face extreme levels of habitat change, most notably a dramatic reduction in sea ice. Additionally, the physical environmental changes, including less ice and increased water (and air) temperatures will result in alterations to the forage base of arctic marine mammals, including density and distributional shifts in their prey, as well as potential losses of some of their traditionally favoured fat-rich prey species. In addition they are likely to face increased competition from invasive temperate species, increased predation from species formerly unable to access them in areas of extensive sea ice or simply because the water temperature was restrictive, increased disease risk and perhaps also increased risks from contaminants. Over the coming decades it is also likely that arctic marine mammals will face increased impacts from human traffic and development in previously inaccessible, ice-covered areas. Impacts on ice-associated cetaceans are difficult to predict because the reasons for their affiliation with sea ice are not clearly understood. But, it is certain that ice-breeding seals will have marked, or total, breeding-habitat loss in their traditional breeding areas and will certainly undergo distributional changes and in all probability abundance reductions. If species are fixed in traditional spatial and temporal cycles, and are unable to shift them within decadal time scales, some populations will go extinct. In somewhat longer time frames, species extinctions can also be envisaged.

Keywords: *Arctic, cetaceans, climate change, ice, pinnipeds, seals, walrus, whales*

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Introduction

Evidence for unidirectional climate warming, with increased air and sea temperatures and circumpolar reductions in arctic sea ice are now unequivocal[1,2]. Warming is occurring more rapidly in the Arctic than in any other region on the globe, and predictions for the future suggest that the degree of change is expected to be greatest in this biome. It is estimated that by as early as 2040 multi-year sea ice will be restricted to a small region in the northernmost part of West Greenland and the Eastern Canadian Archipelago, if there is any ice at all left in summer[1,3]. The earliest warning signs of climate change in the Arctic gave cause for concern for the potential impacts on marine mammals of the region[4,5]. These concerns have escalated, in parallel with more extreme predictions for change, and predictions of increasing rates at which the changes will occur.

Arctic marine mammals are ''K-strategists'' that are adapted to an environment that routinely experiences a great deal of seasonal and inter-annual change. They have conservative life-strategies, reaching sexual maturity relatively late in life, having few young per reproductive episode (that receive significant amounts of maternal care), having high survivorship especially in adult age classes and long lives. Typically, they exhibit quite stable population numbers. Their morphology, life history and behaviour patterns are all finely tuned to deal with cold temperatures, a very high degree of seasonality in both their biotic and abiotic environments, as well as high degrees of inter-annual variability, and all important to many species, the presence of extensive areas of sea ice.

Arctic endemics have experienced repeated periods of cooling and warming over evolutionary time and there is evidence of quite dramatic distributional shifts in their ranges with changing environmental conditions in the past. However, rapid, long-term unidirectional change, as opposed to large-scale inter-annual variation, presents a particularly difficult challenge to arctic marine mammals because such changes are likely to result in permanent habitat change, if not complete habitat loss in some cases[6]. Habitat change or loss is critical when a species is highly specialized or dependent on particular ecological conditions at specific times of the year. And, the life histories, behaviours and feeding patterns of arctic marine mammals are temporally fine-tuned to specific ecological conditions in specific seasons, often with a high degree of spatial precision as well. Seasonal variability in temperature and food availability and the presence of extensive seasonal sea ice are fundamental environmental parameters with which these animals have evolved. Top trophic arctic animals are heavily dependent on a food chain that has at least seasonally abundant prey that is rich in lipids; the prey themselves being evolved to survive periods of low food availability and cold temperatures. Arctic marine mammals have become specialists that deal very well with an environment that is harsh in many ways and thus excluding to many other species. They are members of communities with few species and thus relatively simple food webs and low levels of interspecific competition. They live in regions that are too cold for many disease vectors to survive. Therefore, they are not likely to withstand competition or exposure to new pathogenic agents particularly well. Arctic marine mammals are particularly vulnerable to changes in climate that are sudden, unidirectional or unusually large in magnitude. They are likely to be quite sensitive indicators of significant changes in ocean environments.

Species-specific responses to climate change are likely to be variable across the circumpolar Arctic, with rates of change varying with prevailing local rates of change in the environment. Regionally, species are exposed to somewhat different environmental conditions and temperature shifts, ice reductions, freshwater inputs and other environmental factors influenced by changing climate regimes will not occur at the same rates across the entire Arctic[5,7–9]. Interspecifically, it is likely that a lot of variance will be seen in terms of adaptive flexibility to a changing environment. Negative impacts of climate change are likely to be visible first in the southern parts of the ranges of arctic species, or in regions that are showing the strongest signals of warming currently[10] and among species with narrow niches[11]. Specificity for a particular food type, or particular habitat type, makes species vulnerable to environmental change. Climate signals are certainly already being detected in the dynamics of some arctic marine mammals as well as marine mammals in other areas[12–16]. But, poor base-line data on even the most basic population parameters, such as population size, will make tracking global changes in arctic marine mammal populations due to alterations to the environment challenging.

There is particular concern for pagophilic (‘‘ice-loving’’) arctic marine mammals, given the scenarios outlined for the future regarding sea ice[5,6,12,14,17–27]. Habitat loss for pagophilic species and the sympagic community of which they are part will include: (1) reduction in total habitat area available; (2) habitat fragmentation (*i.e.* discontinuous pack ice); (3) habitat deterioration (*i.e.* thinner ice and less multiyear ice); and (4) unidirectional change in the timing of seasonal distribution and abundance of sea ice. All of these forms of degradation are likely to affect the availability of resources, and in the longer term, impact foraging success, increase mortality, reduce fertility, and over time decrease fitness[6]. The responses of ice-associated cetaceans to climate-induced perturbations are less certain than those for ice-breeding pinnipeds[5], although it has been suggested that climate change may have grave implications for cetaceans in the Arctic[28].

Quantifying habitat loss or change in arctic marine environments, and understanding the significance of how the changes affect marine mammals is not a straightforward task because marine environments in general are complex and arctic marine environments are poorly documented. Cycles such as North Atlantic Oscillation (NAO) and the Arctic Oscillation (AO) have influences on different time scales and there are often time-lags of varying temporal magnitude at different trophic levels. Native hunters in the North, commercial whaling and sealing operations, naturalist observations and ecological investigations over hundreds of years have of course accumulated a lot of basic knowledge regarding what sorts of habitats are preferred by different species of marine mammals, regional differences in relative abundances, diet is known in some areas, seasonal patterns of movements of some species *etc*. But, the reasons for changing patterns of distribution and abundance are not well understood, off-shore pelagic behaviour is poorly documented, and the winter period when the Arctic is in 24 hour darkness has until recently been a ‘‘black-box’’ regarding marine mammal behaviour.

Vibe’s[29] analysis in the 1960s of the relationship between multi-decadal environmental fluctuations and harvest success in West Greenland was one of the first studies to explore long-term patterns of distributions of arctic marine mammals. He clearly showed the importance of different types of ice in determining the distribution of marine mammals of the region. But, documentation of precise movement patterns of these highly mobile animals is a very recent phenomenon that has paralleled the technological development of satellite-linked tracking devices. Putting movement and behavioural data together with the (often dynamic) local environmental conditions the animals are experiencing, and presumably making habitat choices within, is of course the next step in understanding habitat requirements of these animals. Such studies are in their infancy, but environmental data collected via satellite observations (*e.g.* ocean colour, ice cover *etc*.) are now becoming more commonly available for ecological investigations[22,25,30–33]. Additionally, newly developed satellite-linked tags borne by the animals, which contain environmental sensors (*e.g.* temperature, conductivity (salinity, density), light level *etc.*), will undoubtedly advance our understanding of marine mammal habitat utilization in the Arctic and elsewhere rapidly in the decade to come[34–36]. However, our current understanding of habitat choice by arctic marine mammals is limited, in fact very limited for some species.

Arctic resident whales

The three cetaceans that live year-round in the High Arctic, bowhead whales *Balaena mysticetus*, white whales *Delphinapterus leucas* and narwhals *Monodon monoceros* live in tight association with sea ice through much of the year, using edges, leads and polynyas to surface to breath (Figure 1). These animals travel through areas that satellite images suggest are 10/10th cover, but obviously must find, or create, open water in these areas to breathe. Bowhead whales, belugas and narwhals are all capable of breaking young ice with their backs so that they can breathe in ice covered areas, but generally they seem to prefer to be in areas containing leads or polynyas and open-water areas at the periphery of the pack-ice zone. All three species have all ''lost'' their dorsal fins, and developed very thick blubber layers as adaptations to ice-living. They can all be defined as ice-associated whales. But, the actual linkages that bind these species to sea ice are not well understood; all three species do spend time in ice-free water. All of the northern whales exhibit modestly specific habitat selection with varying amount of ice cover, depths, bathymetric structure *etc.* playing a role[30], but there is also considerable flexibility across their ranges in the habitat types chosen on a seasonal basis, and in their patterns of movements. One commonly cited suggestion for the attractiveness of ice to these whales is avoidance of killer whale *Orcinus orca* predation, but the extent of their movements into sea ice areas appears to be excessive for what would be needed to avoid this predator[37] and in the case of white whales and narwhals, can actually expose them to predation by polar bears *Ursus maritimus* as well as potentially increasing the risk of entrapment in the ice[19]. Thus, it seems likely that food availability in ice-filled waters might be the major attractant, rather than the ice *per se*[30], although few data are available to test this hypothesis.

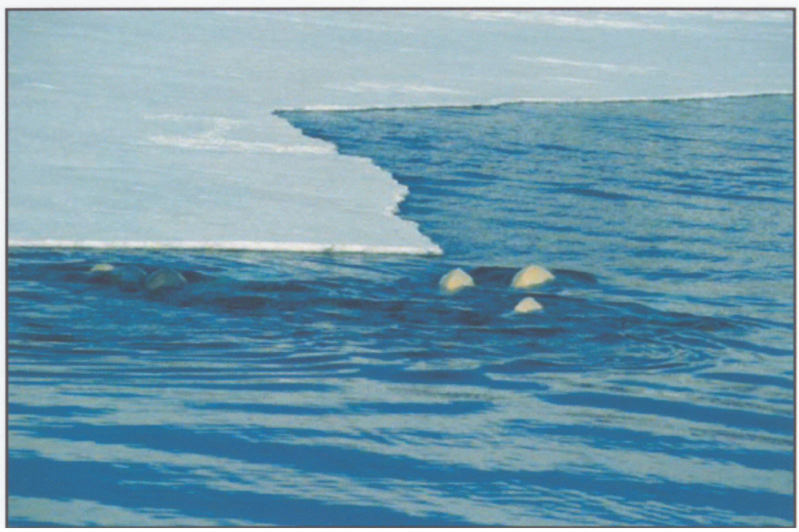

Fig. 1. *White whales are often found in association with sea ice, but the coupling between them and this habitat is poorly understood.*

Bowhead whales

Bowhead whales are perhaps the most ice-adapted cetacean. They have evolved over millions of year to become ‘‘ice-whales’’, with elevated rostrums and blow-holes that allow them to breathe more easily in ice and they have developed the thickest blubber of any of the whales. Additionally, they have the longest baleen among the mysticetes which presumably enhances their ability to capture large amounts of concentrated, seasonally available prey, which allows them to take advantage of the brief, intense productivity surge along arctic ice edges in spring and summer. They have extreme longevity, living to 200 years of age, and it takes 25 years to reach sexual maturity. They have long periods of maternal dependence, and long inter-calf intervals for a baleen whale. Bowheads are specialist feeders that consume high arctic copepods and euphausids along the southern perimeter of the northern pack-ice and the distribution of these prey species largely determines their movements and distribution. However, in the North Pacific their diets do vary somewhat regionally and over time. They feed on both pelagic and epibenthic crustaceans, presumably based on availability of the different species of prey. Their low-trophic feeding habits shelter them to a degree from contaminants that concentrate up the food chain. The bowhead is the only mysticete whale that remains in the Arctic on a year-round basis.

Bowhead whales in northern Alaska are known to exhibit a marked pattern of migration, but movement patterns have only been followed using satellite tracking in Greenland and Canada. Available information suggests that all of the populations exhibit a marked annual pattern of migration that might be learned from their mothers and hence fixed and somewhat independent of actual environmental conditions. Increasing abundance in several bowhead populations in recent years, with concomitant increases in body condition in harvested stocks, suggest a counter-intuitive, positive demographic response during a period of reduced sea ice[38–40]. It has been hypothesized that these responses have been due to improved feeding opportunities that have arisen via local increases in primary production[6] and severe reductions in sea ice in some areas facilitating access to coastal areas, hence inflating coastal counts. But the improvement in food availability might be temporary; as lower-lipid, temperate zooplankton make their way north, arctic species are likely going to be displaced by smaller, less-lipid-rich species[41].

Bowheads are an endangered species in the North Atlantic, particular so in the eastern stock between East Greenland and Frans Josef Land; despite many decades of protection from commercial hunting activities their numbers remain very low. Little is known about any aspect of their current distribution, abundance, diet *etc*. Sightings have taken place only rarely in recent decades, opportunistically during general cetacean surveys, but a single dedicated attempt to locate them on the former whaling grounds in ‘‘Whalers Bay’’, west of Svalbard was successful[42]. Echo-sounder signals and the simultaneous sightings of large numbers of little auks when bowheads were sighted, suggest that the whales were feeding on copepods. Additionally, they have been sighted in Svalbard fjords several times in recent years, but their numbers are unquestionably still very low.

Learmonth and colleagues[23] suggest that climate change will cause declines in bowhead whales and Laidre and colleagues[6] rank them in a sensitivity analysis with respect to climate change as being moderately sensitive in a global perspective. However, the depressed population abundance in the Atlantic Arctic, especially within the Spitsbergen stock, probably warrants a more conservative evaluation for this population. The bowhead whale’s dependence on lipid-rich species of *Calanus* and euphausiids for their food makes it likely that changes in sea-ice conditions will have a major impact on bowhead whale foraging in this area. Additionally, their low reproductive potential, their vulnerability to predation in more open water because of their low swimming speeds and their likely sensitivity to increased development (boat strikes *etc*. if they are similar to their close relatives the northern right whales, *Eubalaena glacialis*) make them a species of concern with regard to climate change. Tynan and DeMaster's[5] conclusion, that it is not known whether this species could adjust to ice-free waters, seems warranted.

White whales

White whales have a patchy, circumpolar distribution in the Arctic; they also extend into sub-Arctic regions in some areas. A small, threatened, population of belugas is resident in the Gulf of St Lawrence, well below the Arctic Circle but they have been challenged by industrial pollution and habitat disturbance in this southern locale. Among the arctic-resident cetaceans, white whales are the most numerous and widely spread species. Arctic white whales spend a lot of their time associated with sea ice and are known to forage at ice edges and cracks, and at glacier fronts. But, they also sometimes feed in open water areas. They display highly variable degrees of seasonal movements, with some populations migrating vast distances, while others exhibit only seasonal toward-shore/away-from-shore movements. From the west coast of Greenland westward to Alaska, white whales populations undertake seasonal migrations that can be thousands of kilometres long while in other areas such as Svalbard, Cumberland Sound, and Cooke Inlet, white whales remain in coastal areas throughout the year, moving offshore only when the shore-fast ice forces them into deeper water. In many places white whales move into estuaries and rivers in summer, occupying brackish or even fresh water for protracted periods (such as in the White Sea population in the Russian Arctic). There are a variety of explanations for these departures from the sea including, warmer water being important to young calves, fresh water aiding the summer moult, alternate prey availability *etc*. But, some populations do not have accessible rivers (*e.g.* Svalbard), so it is clearly not essential for their survival.

White whales are largely fish eaters with polar cod (*Boreogadus saida*) and arctic cod (*Arctogadus glacialis*) being among their most important prey species across their arctic range. However, they also consume invertebrate prey, and at times a wide variety of other fishes. It has been suggested that white whales are generalist feeders that take the prey that is most abundant and available. They are known to eat squid and octopus (*Cephalopoda*), shrimp (*Pandalus* *borealis*) and other crustaceans (*e.g. Mesidothea entomon*, *Mesidothea sabini*, *Gammaridae* spp), Greenland halibut (*Reinhardtius hippoglossoides*), capelin (*Mallotus villosus*), saffron cod (*Eleginus gracilis*), lantern fishes (*Myctophidae*), redfish (*Sebastes* spp.), sculpins (*Cottidae*), herring (*Clupea harengus*), smelt (*Osmerus mordax*), char (*Salvelinus alpinus*), Pacific salmon (*Oncorhynchus* spp.) and even Atlantic cod (*Gadus morhua*) when it is available.

Laidre and colleagues[6] suggest that white whales are susceptible to changing patterns of production, which cause shifts in prey distribution, and timing and distribution of sea ice formation. They are also vulnerable to increases in pollution levels as they are not effective at metabolising contaminants, and have been locally threatened by pollution problems in the past at the southern end of their range. Tynan and DeMaster[5] predict that arctic belugas might be forced to alter the timing and geographical patterns of seasonal migrations given retraction of the southern edge of the ice, particularly in the Canadian Arctic Archipelago. Vibe[29] documented that historical distributions of this species have been intimately tied with wind, current and ice conditions along the Greenlandic coast. The changes that are predicted for northern ice over the next decades may promote genetic exchange between stocks of white whales that are currently isolated due to the geographic barrier the southern ice edges represent[43]. Learmonth and colleagues[23] suggest that climate change will cause declines in white whales, while Laidre and colleagues[6] suggest that their sensitivity is only moderate. The flexibility that white whale populations display regarding food choices, habitat choices and ability to deal with non-invasive interactions with humans (places such as Churchill Manitoba) bodes well for their ability to deal with climate change in the Arctic. However, several white whale populations are currently being harvested beyond sustainable limits and pollution represents a threat to these odontocetes. White whales have recently been classified by the IUCN[44] as being vulnerable, declining, and at risk due to climate change.

Narwhals

Narwhal are closely related to white whales, but are less numerous and have a significantly more restricted distribution. They occupy arctic shelf seas in the North Atlantic region, as far east as Frans Josef Land in Russia. They spend most of their time associated with sea ice. In winter they are usually in completely ice-covered off-shore areas along continental shelf slopes where there are only cracks and leads for breathing. No other cetacean species occupies such dense winter sea ice cover for such long periods of time[6]. The areas they occupy usually have deep-water and complex bathymetry. In the summer months, they come into shallow coastal areas and fjords[45], but some are also seen along the southern edge of the arctic ice far from land, at least in the Barents Sea. The reason for the inshore migrations is uncertain, though it has been suggested that they come in to feed along glacier fronts. Seasonal movement patterns in some areas involve migrations over a period of months and distances in excess of 1000 km[46].

It is generally thought that narwhal feed most heavily in winter during their off-shore period on Greenland halibut at depths over 1000 m[22], but they also eat cephalopod prey and polar cod. When they are available for hunting in coastal areas, they are not feeding heavily, so dietary information for this species is likely incomplete.

Based on ice density records in West Greenland between 1978 and 2001, Laidre and Heide-Jørgensen[22] expressed concern that climate-change induced reductions in open water areas might threaten narwhal populations. But, this prediction is somewhat counter-intuitive, given the more global predictions of drastic reductions in ice cover in the decades to come. Learmonth and colleagues[23] suggest that climate change will cause declines in narwhal and Laidre and colleagues[6] rank them among the three most sensitive species to climate change, among the arctic endemics they analysed. Current contaminant loads in narwhal, compared to white whales occupying the same areas, suggest that their preferences for deep dwelling, lipid-rich, long-lived fishes puts them at somewhat greater risk related to impacts from pollution[47]. Additionally, narwhal appear to be less flexible in their choice of habitats and food types than their close relatives, the white whales, but they do have the ability to access very deep dwelling prey and retract into the protective cover of extensive ice cover when it is available. Climate change impacts on this species are likely to be mediated through ice distribution patterns and their effects on key prey species.

Dolphins and porpoises

White-beaked dolphins (*Lagenorhyncus albirostris*) also reside in arctic waters throughout the year in the Barents and Greenland Seas, right up to the ice edge in summer. This cold-water dolphin occupies shelf seas of less than 200 m depth and consumes small, schooling fish. Based on reductions in stranding of this species in northwest Scotland, MacLeod and colleagues[15] suggest that the species range has already retracted northward. Further these authors suggest that a lack of suitable shelf waters further north may lead to a decline in abundance or its distribution becoming fragmented. However, our virtually total lack of knowledge regarding even basic biological parameters for this species, precludes any attempt to predict climate-induced changes to their distribution, abundance, *etc*. with any precision. The only obvious prediction is the likelihood of increased competition from species such as the white-sided dolphin (*Lagenhorhynchus acutus*) or bottlenose dolphin (*Tursiops truncatus*) as water temperatures increase and these other dolphins and north-temperate fish species shift northward. There is already evidence of recent north-ward range expansion of the bottlenose dolphin in the North Atlantic that might be related to climate change[48].

Harbour porpoise (*Phocoena phocoena*) also reside well above the Arctic Circle on both sides of the North Atlantic. A single individual has been sighted repeatedly in Svalbard in recent years. However, this small, north temperature cetacean is not normally ice-associated. Warmer sea temperatures may allow the northward spread of the range of this species, as long as forage species, such as herring and capelin remain abundant. Substantial declines in sand eel spawning in recent years in the North Sea have resulted in marked increases in incidences of starvation among harbour porpoises[49].

Migratory whales

Increases in the number of summer-visiting baleen whales, or increases in their duration of stay, might represent increased competition for the smaller resident odontocetes in the southern parts of the North Atlantic Arctic as some of the baleen whales consume small schooling fish in addition to krill prey (*e.g*. fin whales (*Balaenoptera physalus*), minke whales (*B. acutorostrata*), humpback whales (*Megaptera novaeangliae*) and sei whales (*B. borealis*). These species currently migrate long distances to take advantage of summer peaks of productivity in northern waters (as does the blue whale (*Balaenoptera musculus*), though it is almost exclusively a krill feeder). Climate change will have its most likely impacts on these migratory species in terms of distribution changes due to geographic shifts in the locations of frontal and up-welling areas that concentrate their food. Such large scale oceanographic changes are likely to affect most marine mammals, but they are currently very difficult to predict.

Migrating odontocetes that occupy the North Atlantic Arctic seasonally include killer whales, sperm whales (*Physeter macrocephalus*) and northern bottlenose whales (*Hyperoodon ampullatus*), as well as pilot whales (*Globicephala melas*) in the northern Norwegian Sea and southern areas of the Barents Sea. Changes in water temperature might encourage northward range expansions by these species if projected production increases provide appropriate food for them. However, it has been suggested that long-distant migrants among these summer residents, that expend considerable amounts of energy moving from their summering grounds at times that coincide with maximum prey abundance, do face some risk. If shifts in timing of the availability of their prey occur, these species could encounter ‘‘mismatch’’ *i.e.* their timing of arrival not matching prey peaks[23].

Killer whales are part of the summer marine mammal community as far north as northern Svalbard in the Atlantic Arctic. Warmer water and less ice are likely to result in higher frequencies of visitation to northern areas by this species. The number of killer whale sightings in the eastern Canadian sub-arctic has been increasing steadily for many decades; the same is true within arctic waters in recent decades as well as in the northwest Atlantic region (S. Ferguson, unpublished data). Higher prevalence of killer whales in an Arctic with less ice would almost certainly result in higher rates of predation among endemic arctic marine mammals. Killer whales readily prey on seals, walruses and baleen whales and are thought to have had quite major impacts recently on some arctic marine mammal populations in the North Pacific[50].

Ice-dependent seals

Ringed seals

Ice-living seals are particularly vulnerable to changes in the extent and character of arctic ice because they depend on the ice as a pupping, moulting and resting platform, and some species also forage on ice-associated prey species[5]. Ringed seals are in many respects the ‘‘classical’’ arctic ice-seal in that their unique ability to maintain breathing holes in thick sea-ice enables this seal to occupy areas vast distances from ice edges that other pinniped species are unable to use (Figure 2A). They are distributed throughout all arctic oceans all the way to the North Pole and number in the millions.

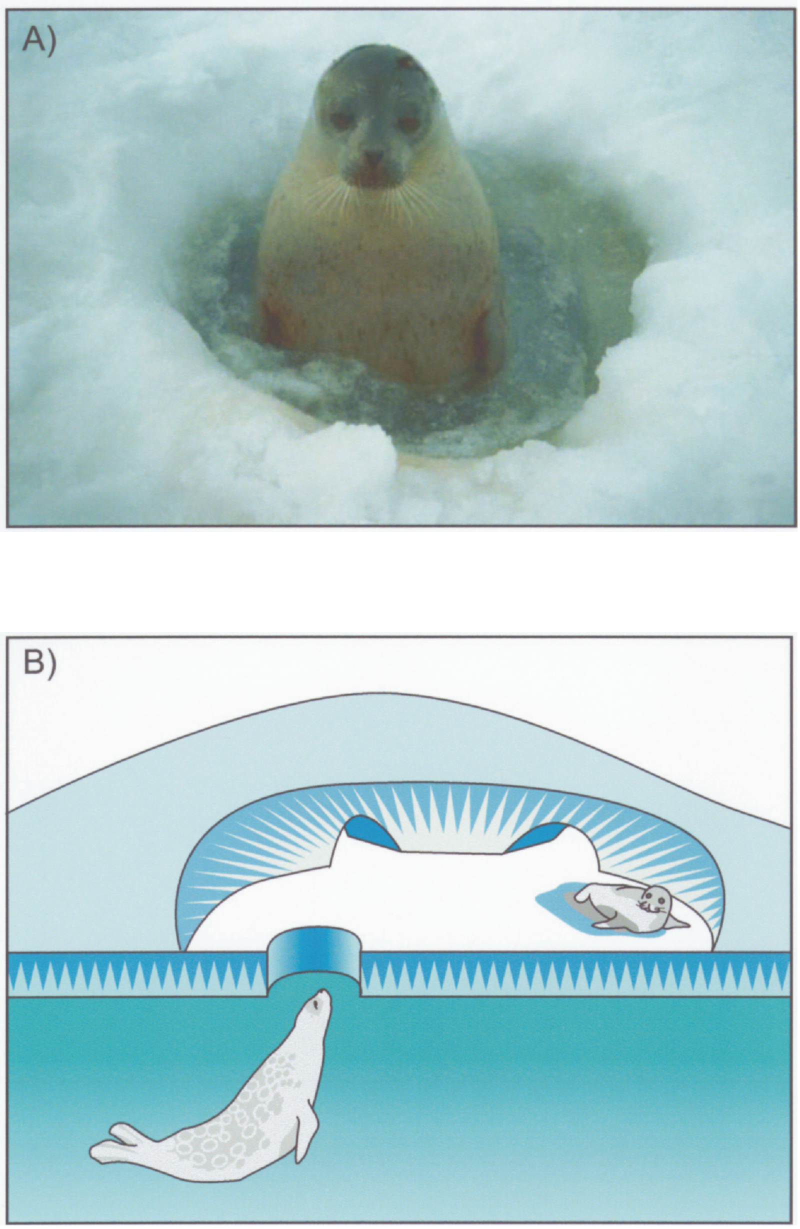

Fig. 2. *The ringed seal's unique ability to maintain holes in thick sea ice has resulted in their broad circumpolar distribution* **(A)**. *The lairs used for birthing and winter haulout afford this small, arctic seal protection from inclement weather, and some protection from surface predation* **(B)**.

Within its arctic range this species uses sea ice exclusively as its breeding, moulting and resting (haul-out) habitat; rarely do ringed seals come onto land. Ringed seals occupy fast-ice areas in the late fall/early winter in preparation for early spring. Their principle winter habitat is land-fast ice in fjords. But, they are also known to breed in at least three regions on free-floating pack ice, in the Sea of Okhotsk, the Barents Sea and Davis Strait. During the fast-ice season ringed seals show preferences for areas with stable ice, over medium-depths (10–35 m) of water. Significant snow cover is required for lair construction; these structures are usually constructed in snow drifts that form downwind of ice ridging or behind glacier ice pieces frozen into annual ice (Figure 2B). The lairs are important for pup survival; these small snow caves provide a thermally sheltered environment with some protection from polar bears (*Ursus maritimus*), foxes (*Lagopus alopex*) and other potential predators. Prime habitat is occupied by breeding adults, while reproductively inactive animals including immature individuals are usually found in peripheral areas.

Outside the annual land-fast ice season ringed seals show considerable diversity in their distribution patterns. Some animals remain in the general vicinity of their breeding sites while others disperse along coastlines where ice from glaciers is available, some spend time pelagically in areas containing sea ice and yet others move north to the southern edge of the permanent ice. The common feature to all of these areas is the availability of sea ice. During the summer and early fall ringed seals seem to maintain their preference for annual ice (as opposed to multiyear ice), and are usually found at highest densities over shallow-mid-depths (100–200 m) of water in areas where the ice cover is 40–80%[33]. Despite the variable patterns of space use, mobility and the size of the area used by ringed seals is consistently greater during the open water season[51].

Many studies of ringed seal diet have been conducted across the species' range and although this seal feeds on a variety of fishes and invertebrates several strong tendencies with respect to prey selection are found among ringed seals across the Arctic. Most ringed seal prey is small and preferred prey tends to be schooling species that form dense aggregations. Fishes are usually in the 5–10 cm range and crustacean prey in the 2–6 cm range. Typically, a variety of 10–15 prey species are found in a given area, but 2–4 dominate strongly. Fishes are generally preferred over invertebrate prey, but diet is regionally determined to some extent by availability of various types of prey at particular seasons as well as preference, which in part is guided by energy content of various prey species[52,53]. Polar cod is often reported to be the most important prey species for ringed seals. This small fish occurs in both ice-free and ice-covered waters and especially at ice edges. It is an important prey species not only for ringed seals but also for a wide range of other marine mammals, sea birds and other species of fish in arctic waters. Ringed seals also eat arctic cod, redfish, capelin and herring as well as Greenland halibut, *Liparis* sp. and a variety of other fish in small amounts. Invertebrate prey seems to become more important to ringed seals during the open-water season, from late spring through the summer months and into the early fall, in areas where sampling across seasons has been performed, and is often found to dominate the diet of young animals. Large amphipods (*e.g. Themisto libellula*), ‘‘krill’’ (*e.g. Thysanoessa inermis*), mysids (*e.g. Mysis oculata*), shrimps (*e.g. Pandalus* spp., *Eualus* spp., *Lebbeus polaris*, *Crangon septemspinosa*) and cephalopods (*e.g. Gonatus* spp.) are all important in some regions at least seasonally in the Northeast Atlantic.

Learmonth and colleagues[23] suggest that climate change is likely to cause declines in ringed seals, while Lairdre and colleagues[6] classify ringed seals within their ‘‘least sensitive’’ category. Although ringed seals are flexible in their food choice, and breed on ice of somewhat different types, they have very specific snow and ice requirements for breeding and remain associated with sea ice throughout the year. The distribution and annual duration of sea ice cover and snow availability on ice in areas with sufficient food nearby in spring are essential for successful reproduction. Ringed seals require sufficient snow cover to construct lairs in which they rest, give birth and care for their young, which are born weighing only 4 kg. Both ice and snow must be stable enough in the spring season to successfully complete the 6 week long period of lactation[54]. Premature break-up of the land-fast ice can result in separation of mothers from their dependent pups and hence high neonatal mortality. Spring rains or high temperatures in spring can cause the roofs of lairs to prematurely collapse leaving ringed seals subject to increased predation and exposure risks. When insufficient snowfall takes place prior to breeding, a similar phenomenon occurs.

Ringed seals in some areas are already showing relatively long-term downward trends in reproductive rates and survival of young that are thought to be linked to changes in sea ice conditions and other major ecosystems shifts, the pathways of which are poorly understood[14,55]. During 2006 and 2007 many of the fjords on the west coast of Svalbard did not freeze for the first time in recorded history. Ringed seal reproduction was virtually non-existent in areas where many hundreds of pups are normally born. It is not known if the seals that normally pup in this region established themselves elsewhere early enough to set up territories and build lairs, *etc*., but it seems highly unlikely. If the extremes predicted for losses of sea ice do occur, it is difficult to envisage how this ice-breeding seal will survive beyond the small refugia-areas where ice-cover will remain, despite its currently broad range and high abundances. Arctic ringed seals do not normally haul out on land and performing this behaviour would be a rather dramatic change to the species behavioural repertoire. Baltic ringed seals and Saimma and Ladoga ringed seal subspecies do perform this behaviour on islands and have survived at low population densities over an extended period of time; however, there is little or no predation risk in their ranges. Land-breeding would expose the ringed seals' small neonates to much higher predation rates in the Arctic even in a best case scenario[56]. Marked decreases in ringed seal abundance are likely to have cascading effects in arctic food webs. They are the most important species in the diet of polar bears and are themselves top trophic consumers of significant magnitude.

Bearded seals

Bearded seals (*Erignathus barbatus*) have a patchy circumpolar Arctic distribution. They are normally associated with sea ice on a year-round basis. However, they do occasionally haulout on land during the summer months. In the Atlantic Arctic bearded seals are quite sedentary, though some young animals disperse broadly, at least for a time after weaning and are occasionally found on mainland Norway. In the Pacific Arctic some bearded seals follow the retraction of the pack ice northward during the summer and southward once again in the late fall and winter. Bearded seals avoid heavy ice areas; they use ice edges and leads for haulout. During winter they concentrate in areas that contain polynyas or in areas where leads in the ice tend to be a regular feature, or they remain along the outside of pack-ice areas. The global population of bearded seals cannot be accurately assessed; but it is likely that this species numbers in the hundreds of thousands in the Arctic.

Bearded seals use drifting annual ice, over shallow water within arctic shelf seas for breeding (Figure 3). They often give birth in coastal areas, but in the Barents Sea they can be found throughout the free-floating pack ice. This large phocid seal gives birth to

Fig. 3. Bearded seals give birth to, and nurse their young in relative isolation, on small, free-floating pack-ice floes in shallow, coastal areas. (Female on the left with her 3-week old pup on the right).

disproportionately large, precocial young that swim within hours of their birth, affording mother-pup pairs the freedom to move back into ice-filled areas near shore (or over shallow water), if the ice they are on is carried over deep water by winds or currents. The large body size of the new born pups (37 kg) allows them to deal with exposure to the environment more easily than the neonates of ringed seals. Bearded seal pups travel with their mothers for the three-week long lactation period, though they often sleep on floes while the mothers dive. These characteristics afford them considerable flexibility in finding suitable haul-out platforms.

Bearded seals are for the most part benthic feeders, eating a wide variety of crabs, clams, shrimp, and other invertebrates and well as a wide assortment of benthic fish, and occasionally more pelagic fish species. The bearded seals elaborate whiskers allow them to find prey in soft-bottom sediments. They are suction feeders that also use hydraulic jetting to access prey when it resists suction, similar to walruses. Their benthic dietary preference restricts their functional range to relatively shallow areas, but this includes much of the North Atlantic Arctic. Learmonth and colleagues[23] suggest potential declines in bearded seals, while Laidre and colleagues[6] rank them similarly to ringed seals, as least sensitive. Their distribution, density, and reproductive success certainly appear to be dependent on the maintenance of suitable sea ice conditions in shallow, often coastal, areas. But, although the distribution of bearded seal is more restricted than that of ringed seals, and their numbers fewer, they might have more flexibility in terms of adapting to a warmer Arctic with less ice. They do come onto land in many parts of their range, and the young are large and highly mobile.

Harp seals

Harp seals (*Pagophilus groenlandicus*) are a gregarious, North Atlantic/Arctic species. They are highly migratory, moving southward in the late fall and early winter into three breeding sites off the east coast of Canada, between Jan Mayen and Svalbard (West Ice), and in the White Sea (East Ice) for the birthing period in March, and then each stock moves somewhat northward into traditional moulting areas approximately one month later, before dispersing further north for the remainder of the year. Harp seals from the eastern and western Atlantic are genetically distinguishable. West Ice and East Ice animals overlap in their summer ranges, but are also likely separate populations. Harp seals remain in association with sea ice much of the year, preferring drifting, first-year ice with large open leads. They are however flexible about the nature of summer-ice habitats, and can at times be found in ice-free waters. Their distribution in the late summer and early fall in the North East Atlantic Arctic overlaps that of capelin[57]. But, during breeding they make very specific choices that are related to ice type and geographic location. They travel to traditional sites in southern waters where they form vast herds in extensive seasonally-formed drifting pack ice. Breeding is highly synchronized and occurs at the same time each year at remarkably precise locations. Through active use they maintain holes when leads freeze so that there are multiple access points to the water around each floe making up a pack. The white-coated pups are born weighing 10 kg and grow rapidly during the 12 day lactation period[54]. The pups are left on the ice floes upon weaning, where they moult prior to entering the water to move northward into the Arctic for their sub-adult years. Upon reaching sexual maturity they return to their natal areas for breeding. Harp seals number close to eight million animals when the three populations are combined. All of these animals are concentrated within the North Atlantic Arctic from late spring until late autumn.

Harps seals usually feed over continental shelves, at depths of less than a few hundred meters. Adult harp seals feed primarily on small marine fish such as capelin, herring, sculpins, sand lance, polar cod and arctic cod. They also eat significant amounts of invertebrate prey on a seasonal basis in some areas, including krill (euphausids), mysids, amphipods and shrimps. Invertebrate prey makes up about one-third of the biomass of the diet while harps seals are in the Barents Sea; this prey is particularly important to young age classes.

Learmonth and colleagues[23] suggest possible declines in harp seal due to climate change and Laidre and colleagues[6] rank their sensitivity as moderate. However, the situation in recent years, when ice did not form in the Gulf of St Lawrence breeding area (1976, 1981, 2001 and 2002) suggests severe consequences for harp seals if spring sea ice condition continue to follow current and predicted trends[21]. In 2007, the ice was again thin in the Gulf and storms broke it up while the young were still dependent (M. Hammill, personal communication); 100% mortality was likely. The incidence of light ice (or no ice) years is increasing in this area, yet harp seals return to breed there each spring. It is not known whether repeated reproductive failure will induce them to remain on more northerly, thicker ice, or whether they will continue to return to their natal sites. This will be an essential factor in determining their resilience to climate change.

Hooded seals

Hooded seals (*Cystophora cristata*) are a large, pack-ice breeding northern phocid that ranges through a large sector of the North Atlantic Region. They follow an annual movement cycle that keeps them in close association with drifting pack ice much of the year, similar to harp seals. During the spring the adults concentrate for breeding purposes in three locations: one group forms off the east coast of Canada (in two areas – the Gulf of St Lawrence and the ‘‘Front’’, north of Newfoundland); a second group congregates in the Davis Strait; and a third comes together on the West Ice, east of Greenland. They disperse after breeding for an intensive feeding period, often coming south into subarctic waters before congregating loosely to moult in traditional areas for each group; Front animals move north of their breeding area, Davis Strait animals moult in areas southeast of Greenland and West Ice animals moult in waters off east Greenland. Hooded seals often occupy heavy multi-year ice during the moult in northern areas. All stocks then disperse broadly for the summer and autumn months, preferring areas along the outer edges of pack ice. Somewhat surprisingly, recent genetics work suggests no biological distinction between the groups[58]. The global population size of hooded seals is very difficult to estimate because this species is difficult to survey, but it is almost certainly in excess of half a million animals.

Although otherwise solitary, hooded seals aggregate during breeding in traditional areas. They breed several weeks later than harp seals, just prior to the start of the seasonal ice break-up. Similar to harp seals, breeding is highly synchronised. In the Gulf of St Lawrence hooded seals choose heavier ice than harp seals, selecting areas where the ice floes are the largest available. Females are spaced at 50 + m intervals within the loose herd. Hooded seals are born weighing about 25 kg and double their body mass during their short 4-day nursing period (Figure 4A,B). The pups are born moulted, but remain on the ice for days or weeks following weaning before they enter the water and make their way northward.

Hooded seals are deep divers that fed on a variety of deep-water fishes including Greenland halibut and a variety of redfish species as well as squid, capturing their prey at considerable depths. They also consume large quantities of *Themisto* and polar cod in northern areas and Atlantic cod and prawns when they are in the southern parts of their range. Satellite-tracking records suggest that their foraging is concentrated along continental shelf edges, presumably taking advantage of the high productivity caused by the up-welling at the shelf.

Learmonth and colleagues[23] suggested potential declines in hooded seals due to climate change, while Laidre and colleagues[6] ranked them among the most sensitive category due to their narrow range, low relative abundance and narrow food preferences. However, despite the fact that hooded seals prefer thick ice, they will use flat, annual ice (such as that in the southern parts of the Gulf of St Lawrence) when thicker ice is not available for breeding, and they require it for a relatively short period of time to breed successfully. They are also capable of remaining pelagic for long periods of time in areas without ice outside the breeding and moulting periods. Yet, similar to the situation for harp seals, when ice conditions are poor, pup mortality is extremely high. The situation in recent years, when ice did not form in the Gulf of St Lawrence breeding area (see above) suggests severe consequences for both harp and hooded seals if spring sea ice conditions continue to follow current and predicted trends.

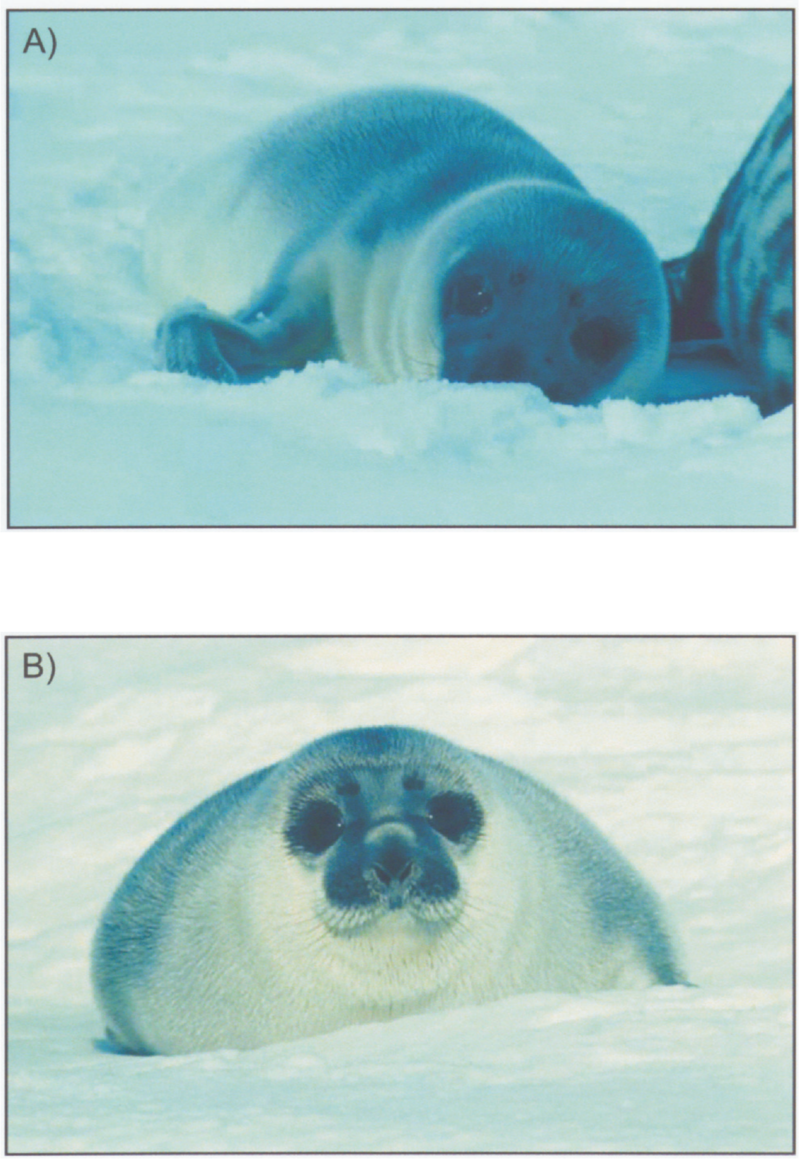

Fig. 4. *Hooded seals are highly adapted to breeding on pack-ice; they double their birth mass during their 4-day long lactation period – the shortest lactation of any mammal (***(A)***, newborn;* **(B)***, 4-day old, weaned pup). But, they still require predictable, extensive fields of sea-ice for breeding and moulting.*

Walruses

Walruses (*Odobenus rosmarus*), have a range that is restricted to the Arctic. Their distribution is circumpolar, but is somewhat disjointed; two sub-species are recognised, the Pacific walrus (*O. r. divergens*) and the Atlantic walrus (*O. r. rosmarus*). The global population of walruses is estimated to be about 250,000 animals, of which 220,000 belong to the Pacific sub-species. The Atlantic walrus is distributed from the central and eastern Canadian Arctic eastward all the way to the Kara Sea; several more or less well-defined sub-populations exist within this range. Walruses haul-out on pack ice during most months of the year, using land-based sites only during the summer months when sufficient ice is unavailable in traditional summering areas (Figure 5). They over-winter in areas of pack ice where the ice either has enough leads to allow breathing, or where it is thin enough between floes that they can break through to maintain breathing holes, and yet the ice itself must be thick enough to support the weight of groups of these highly gregarious animals. Walruses often over-winter in areas with polynyas that provide access to open water. They exhibit seasonal movement patterns on an annual cycle occupying some haulout sites only during specific months of the year; most adult and subadult males remain together, separate from flocks with females and young. Mating takes place aquatically, near wintering haulout groups on the ice.

Walruses have a narrow ecological niche. They depend on the availability of large areas of shallow waters (less than 80 m) with suitable bottom substrate that will support productive bivalve communities. Walruses are benthic foragers that feed primarily on molluscs. In the Svalbard area *Mya truncata* is a favourite food[59]. Walruses eat large quantities in a single meal and consume approximately 60 kg of food per day when they are in their at-sea phases[60]. Some walruses do hunt seals, but it is thought that this behaviour is performed by only a small proportion of male animals. Hence, a healthy, productive benthic community is required to support a walrus population. Additionally, they must have access to haul-out areas relatively close to feeding areas, which for some parts of the year means an ice platform near foraging grounds, while in summer it means coastal areas on islands in the Arctic near shallow banks that produce molluscs in sufficient densities. During summer, male walruses spend 75% of their time in water, hauling out for several days at a time to rest between aquatic excursions[61]. There is little data available for female walruses, but observational

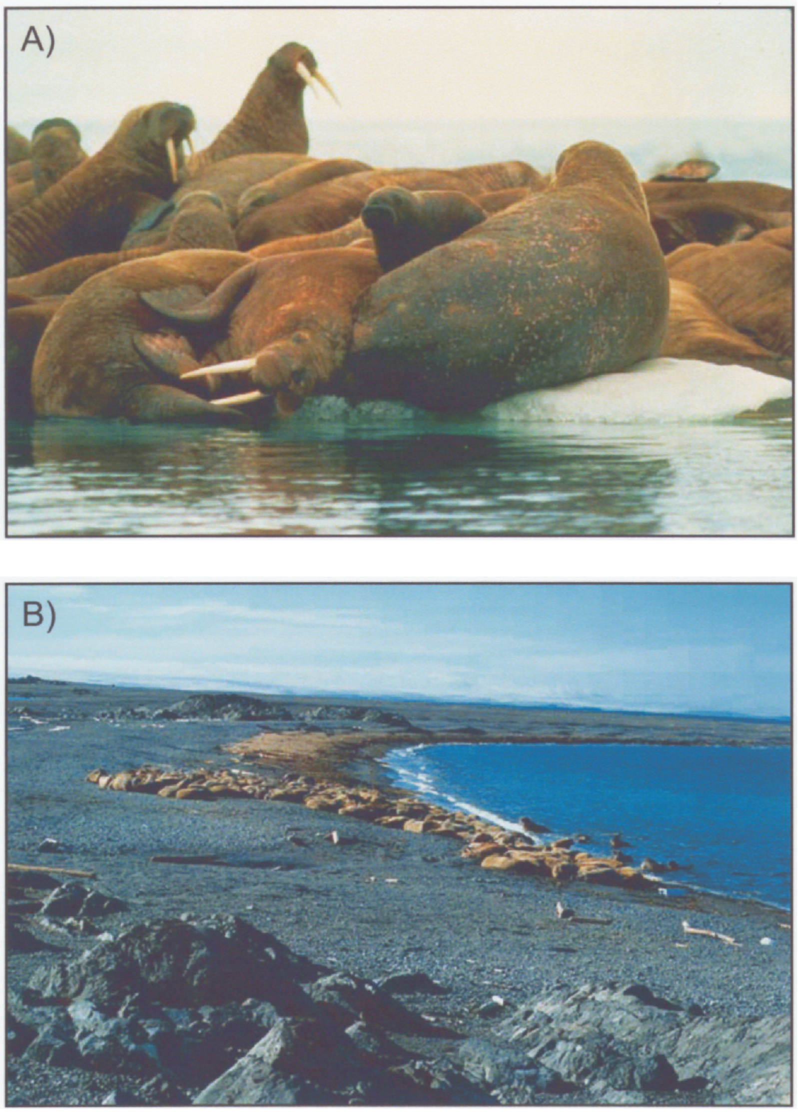

Fig. 5. *Walruses haul out readily on sea ice* **(A)** *or land* **(B)***, usually in dense aggregations. Their future abundance and distribution in a changing Arctic will depend largely on the well-being of benthic bivalve communities in coastal areas where walruses can haulout between feeding trips.*

studies and the few satellite tracking efforts done on females suggest a similar pattern to males, with a few days ashore followed by time at sea. The calves accompany their mothers on foraging expeditions from the time they are only a few weeks old, and remain with them for 2–2.5 years. Thus, females only have a calf every 3 or 4 years.

Retraction of the arctic ice cap could result in much of the remaining ice being located over water that is too deep for these benthic foragers. This is likely to be a significant concern at least for Pacific walruses in the not-too-distant future[18,62]. An additional concern, relevant for both subspecies, is that the predicted decline in the sympagic ice community will result in a decrease in the flux of carbon to the benthic community, upon which walruses and other benthic foragers depend[5]. Predicted increases in overall production in arctic shelf seas that are ice-free, is likely to be captured by the pelagic community, with little fall-out to the benthos. But, walruses should adapt more easily to a terrestrial haulout habitat than the other arctic pinnipeds discussed above and are likely to survive into the future, at least at numbers permitted by the available biomass of benthic resources in areas where suitable haulout sites are close enough to potential feeding areas. Born[63] was optimistic regarding the future of walruses in this regard, while Laidre and colleagues[6] rank them as ‘‘moderately sensitive’’ to the impacts of climate change. The many islands in the Northwest Atlantic Arctic may afford walruses more terrestrial habitat than in the Northeast Atlantic Arctic, where the Svalbard-Frans Josef Land population resides. Learmonth and colleagues[23] suggested possible declines in walruses due to climate change. However, historically, walruses have occurred in areas with only seasonal or no predictable sea ice *e.g.* in the Gulf of St Lawrence and on Sable Island in Nova Scotia, as well as in Iceland and northern Norway. Their current distribution is thought to be heavily influenced by human hunting[64].

Coastal seals

Harbour seals

Harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) are for the most-part temperate species, but they have sufficiently broad niches that they occupy some warm-spots in the Arctic. Unlike the seals discussed above, these species are not dependent on ice-platforms. In most parts of their ranges they use islands for breeding and daily rest periods ashore; though some grey seal populations breed on ice.

Harbour seals have one of the broadest distributions among the pinnipeds and range into both the Pacific and the Atlantic Arctic. Harbour seals in the Atlantic Arctic occur in very small numbers in southern Greenland, and are somewhat more numerous in Iceland and the north coast of Norway; there is also a small population that breeds on the west coast of Spitsbergen, Svalbard. They are a coastal, non-migratory, species that aggregates in small numbers on rocky outcrops, beaches or inter-tidal areas. It is unusual for harbour seals to haul out on ice, but they appear to do so when shore-based sites are inaccessible in winter in some areas.

Harbour seals are shallow divers that feed on a wide variety of fish species, as well as cephalopods and crustaceans. Foraging studies have been conducted across much of their broad geographic range. A few prey species tend to dominate the diet at a given location for a given season, but prey types vary regionally and seasonally as well as inter-annually. Harbour seals seem to prefer small, schooling prey, which they capture based somewhat on availability, although they do also exhibit specific preferences in some areas. This species shows considerable flexibility in feeding modality. Diet information is available for harbour seals at their northernmost location, in Svalbard, only from the autumn; during this season members of the cod family dominate the diet, with polar cod being numerically most abundant and Atlantic cod being the most important prey species in terms of biomass[65].

Based on their haul out requirements and foraging preferences, one would predict that harbour seals would likely increase in abundance and expand their distribution in a warmer Arctic. However, harbour seal populations have recently declined markedly in the North Pacific (at several locations in Alaska, with the most severe declines in the Gulf of Alaska[18,66–69]), the Northwest Atlantic (Sable Island on the east coast of Canada[70,71] and most recently in the Northeast Atlantic (with widespread declines within the United Kingdom ranging from Shetland to the Wash[72,73]). These recent declines are not associated with the phocine distemper virus epidemics that swept European coasts in 1988 and again in 2002[74] and pollution burdens in northern harbour seals are quite low compared to their southern counterparts, so contaminant effects are unlikely to be involved in these declines. The precipitous declines in these northern populations have been attributed to climate-change-induced regime shifts, concomitant shifts in predator-induced mortality on harbour seals, altered competitive stresses and unknown causes[75,76]. Low population numbers in Greenland, Iceland and Norway (mainland) are attributable to harvesting and culling programmes, but, human harvests are not performed at the other north temperate locales. Harbour seals have expanded northward in the past during warm periods[77] and might do so again if interspecific interactions and food availability permit. They are reported by Stirling[55] to be occurring in greater numbers in open water harvests by Inuit hunters in western Hudson Bay in recent years. The precipitous declines in northern populations, in combination with northward range expansion, make predictions for the future of this species with respect to climate change challenging.

Grey seals

Grey seals are another temperate species that makes its way into the Arctic in several areas of the North Atlantic. Their principle range occurs in north temperate waters off the east coast of Canada and in the United Kingdom; populations in both areas seem to have stabilised following a period of several decades of significant population increase[78]. Baltic populations are also increasing, following reductions in unsustainable hunting levels, as are populations at the southern fringes of the distribution of this species[79,80]. Historically, grey seals were abundant in Iceland and along the coastal regions of northern Norway and North-eastern Russian. But, they have been depleted through hunting and government culling programmes and in some areas have been extirpated. A crude estimate of the global population size of this species is 400,000 animals. But only some few thousand occur within the Atlantic Arctic currently; surveys of the northern Norwegian mainland and Murman (western Russia) coasts suggest that there were some 4,500 animals in this area when this region was last surveyed[81]. Grey seals are not migratory; they remain within relatively small ranges throughout the year, dividing their time between resting ashore and foraging at sea for some days at a time. They exhibit quite flexible diets and extraordinary flexibility in terms of breeding habitat. They are the only pinniped that breeds on pack-ice, land-fast ice and at terrestrial colonies. Given their flexible dietary habits, and that fact that grey seals currently seem to be extending their range and increasing in abundance, this species seals might be expected to increase in the coming decades, at least in populations where their numbers are not controlled through management regimes.

Conclusions

Northward range expansions have limited geographic scope for endemic arctic marine mammals, leaving them vulnerable to the effects climate change produces within their current ranges. Global climate change will affect the marine environment in many ways including increased water temperature, a rise in sea level, changes to salinity, CO_2 concentrations, pH, rainfall patterns and other factors such as freshwater inputs, storm frequency, wind speed and hence wave conditions, sea ice cover and climate patterns generally as well as potential changes in large scale ocean circulation patterns. Many of these changes will not have direct effects on arctic marine mammals, which are large, highly mobile homeotherms that cope well with significant amounts of variation in their environments and have physiological capacities that are unlikely to be challenged directly by these sorts of changes. But, predicted reductions in sea ice are likely to have direct impacts by reducing or eliminating the current breeding habitat of many arctic pinnipeds and shifting the location and timing of productivity in arctic shelf seas. Changes in ocean circulation patterns could cause shifts in the locations of fronts and the overall productivity of whole regions. These large scale changes are likely to have impacts on the distribution and abundance of marine mammals. These high trophic predators often forage at ocean fronts and other areas where upwelling stimulates high productivity. Combinations of the other climate induced changes are likely to have indirect effects on marine mammals, mediated through impacts on their prey. Fish and marine invertebrates are sensitive to temperature shifts, which can alter growth and survivorship, particularly of juvenile stages and cause shifts in interspecific competitive advantages[82–84]. Some changes of this sort have already been noted; the northeastern North Atlantic copepod assemblages have changed with a northward extension of warm-water species and a decrease in the number of cold-water species, reflecting regional increases in sea surface temperatures[41,85,86]. Less-lipid-rich, temperate, species replacing lipid-rich arctic species can be problematic for arctic marine mammals that depend on rapid accumulation of energy to restore blubber stores during the short season of productivity at high latitudes. Any negative impacts on polar cod abundance will undoubtedly have quite immediate impacts on many populations of arctic marine mammals. In turn, changes in abundance of the marine mammal top predators are certain to have cascading effects through the arctic ecosystem.

Physical changes in the arctic marine environment are also likely to enact further change via alterations to human activity patterns. Ice-free expanses in the Arctic will encourage increased shipping and development that are likely to affect the abundance and distribution patterns of some species within the arctic marine mammal community and increase the risk of oil spills, chemical, acoustic and other pollution[11]. These effects will be additive to: the habitat reductions via changes to the sea ice; changes to the forage base, with less lipid-rich species dominating the community; increased competition from temperate species expansions northward; increased predation rates from killer whales and perhaps also sharks and increased disease and parasite risks.

Full-time, ice-associated, resident species of marine mammals in the Arctic are likely to be significantly negatively impacted throughout most or all of their ranges. Some species will likely surprise us with adaptive flexibility not yet considered possible, but others will not. The degree to which fidelity to natal birth places, haulout locations and migratory rates is fixed in the various populations will be a major determinant of how they will adjust to altered environmental conditions. Additionally, their ability, or lack thereof, to prey shift will undoubtedly play a role in their future abundance. Of course, high levels of production with some geographical concentration of potential food resources will be essential if these large mammals are going to occur at levels near today's abundance levels in the Arctic of the future. Precise predictions of the impacts of climate change for individual species at the global level are not possible, and all exercises (including this one) in predicting possible scenarios are based on subjective assessments of what constitute the most sensitive components of the environment (biotic and abiotic) of individual species. But, population extinctions and perhaps even species extinctions are not beyond the range of possibility in the marine mammal community of the Northeast Atlantic Arctic in the coming decades.

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