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Impacts of changing sea-ice conditions on Arctic marine mammals

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Abstract Arctic sea ice has changed dramatically, especially during the last decade and continued declines in extent and thickness are expected for the decades to come. Some ice-associated marine mammals are already showing distribution shifts, compromised body condition and declines in production/abundance in response to sea-ice declines. In contrast, temperate marine mammal species are showing northward expansions of their ranges, which are likely to cause competitive pressure on some endemic Arctic species, as well as putting them at greater risk of predation, disease and parasite infections. The negative impacts observed to date within Arctic marine mammal populations are expected to continue and perhaps escalate over the coming decade, with continued declines in seasonal coverage of sea ice. This situation presents a significant risk to marine biodiversity among endemic Arctic marine mammals.

Keywords Climate change · Competition · Conservation · Extinction threat · Habitat deterioration · Management

Introduction

The Arctic has several unique physical characteristics that set it apart from mid-low latitude systems. Some of the most important defining characters include: strong seasonality in light, from complete winter darkness to continuous daylight in summer, cold overall temperatures with winter extremes, and the presence of extensive shelf seas around a deep central ocean basin. But perhaps the most defining character of Arctic marine systems for the last 5+ million years has been the presence of a "permanent cap" of ice, made up of multiyear ice (MYI) and first year ice (FYI) that forms annually and extends and retreats seasonally over vast ocean areas (see Polyak et al. 2010 for historical sea-ice patterns). Arctic sea ice constitutes a unique habitat which has become home to 11 marine mammal species that have evolved within or joined this environment over the millions of years of its existence (Table 1). This habitat is spatially extensive, has few surface predators and is virtually free of disease vectors. The major decline in sea ice that has taken place in the Arctic since 2000 has become an iconic climate change signal.

Sea ice in the Arctic has declined in terms of overall extent, thickness, proportion of MYI and seasonal duration. In the past decade, multiyear sea ice was reduced at three times the rate that had been the norm in the previous three decades (Maslanik et al. 2007). Springtime MYI extent was

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Table 1 Ice-associated marine mammals, their primary linkages to sea ice and their key sensitivity to changing sea-ice conditions

Species	Relationship to sea ice	Key sensitivity to changing sea-ice conditions
Pinnipeds		
Walrus	Walruses give birth and mate on sea ice and use it seasonally to reach bivalve beds too far from shore	Sea ice broadens the feeding distribution of this species markedly, which permits greater overall walrus abundances
Ringed seal	Ice-associated year round, requires stable ice for several months (with good snow cover) for raising pups, breeding and moulting as well as summer ice for resting, also dependent to some extent on ice-associated prey	Ice formation must occur in time to accumulate sufficient snow for the construction of lairs and must remain stable for several months to accommodate lactation (and breeding and moulting)
Bearded seal	Ice-associated year round, requires stable FYI pans late in spring for raising pups and moulting as well as summer ice for resting	Sea ice must be available over shallow water that has a rich benthic community (especially during the nursing period)
Ribbon seal	Breeds on pack ice	Pack ice must be available in late-winter/early spring for pupping in regions where food will subsequently be available for the weaned young
Spotted seal	Breeds on pack ice	
Harp seal	Breeds on pack ice	
Hooded seal	Breeds on heavy, large floes of pack ice late in the ice season	
Cetaceans		
Bowhead	Highly ice adapted, lives in the Arctic year round, usually in association with ice	The key ice related sensitivity for the ice adapted whales is likely how the sea-ice structures the ecosystem and influences prey availability
White whale (beluga)	Most populations live in association with sea ice much of the year	
Narwhal	Lives in association with sea ice much of the year and feeds intensively in pack-ice regions during the winter (on benthic fauna)	
Polar bear	Ice is the principle hunting platform and an important transportation corridor (especially for females with young cubs)	Shortened ice season means a longer period of fasting

the lowest on record in 2008 (in the QuikSCAT data record since 2000), representing a loss of 40% (Nghiem et al. 2007). Recent estimates of Arctic Ocean sea-ice thickness from satellite altimetry show a remarkable overall thinning of ~0.6 m in ice thickness between 2004 and 2008 (Kwok and Rothrock 2009), although the average thickness of the FYI in mid-winter (~2 m) has not exhibited a downward trend (Kwok et al. 2009). In combination, these changes have resulted in seasonal ice becoming the dominant Arctic sea-ice type, both in terms of area coverage and of volume. Most changes in sea-ice extents have been seasonally asymmetric (Grebmeier et al. 2010). That is, most Arctic warming has had an impact on late summer and autumn sea-ice extents. The extreme sea-ice retreats in 2007–2009 lengthened the open-water season in full in the Pacific Arctic by roughly 4 weeks (Grebmeier et al. 2010). Natural variability still has large impacts on year to year variability in springtime sea-ice extents. Maximum extents of sea ice in March/April in the Bering Sea have actually been at near records during the cold period of 2007–2010, following an extreme warm period of 2000–2005. However, a return to warmer conditions in the Bering Sea in the future is expected and this, combined with the emerging global warming trend, is expected to result in new extremes in ice reductions in the Pacific Arctic. The Barents Sea, lying about ten degrees of latitude further north than the Bering Sea, appears to be part of the overall central Arctic warming pattern (Overland 2009), exemplified by events such as the dramatic loss of sea ice during April 2010 in this region.

Expectations for the future are that summer sea ice will continue to decline, perhaps reaching a nearly sea-ice-free summer state by 2035 (Wang and Overland 2009). Even areas that are expected to retain late spring-time sea ice in most years during these next decades are likely to experience a doubling in the percentage of years with minimum sea-ice coverage. For the southern Chukchi Sea in June, this would increase the number of sea-ice-free years from 2 to 4 within a 10-year period. Such frequency changes in themselves are expected to have significant consequences for marine ecosystems in the Arctic.

These changes in sea ice are directly reducing the habitat available for ice-associated marine mammals that give birth on sea ice, hide from predators or inclement weather within ice fields or that eat ice-associated fish and invertebrate prey or other ice-associated marine mammals (e.g., Barber and Iacozza 2004; Kovacs and Lydersen 2008; Laidre et al. 2008a). Additionally, ice declines are causing changes to Arctic food webs that will have indirect effects on the quality or quantity of traditional lipid-rich zooplankton and fish prey available to High Arctic marine mammals (e.g., Grebmeier et al. 2006a, b). Although sea-ice losses will not be the only impact of global warming within the Arctic, the declines over the past 3 decades and the predicted, continued declines in sea ice (e.g., Wang and Overland 2009) are in themselves expected to have significant consequences for marine ecosystems in the Arctic, including their mammalian inhabitants.

The earliest warning signs of climate change in the Arctic gave rise to concern for the potential impacts on marine mammals of the region (Stirling and Derocher 1993; MacGarvin and Simmonds 1996; Tynan and DeMaster 1997; Moore 2000; Carmack and McLaughlin 2001; Kelly 2001) and particular concern has been raised for pagophilic ("ice-loving") species (e.g., ACIA 2005; Johnston et al. 2005; Laidre and Heide-Jørgensen 2005; Moore and Laidre 2006; Simmonds and Isaac 2007; Kovacs and Lydersen 2008; Laidre et al. 2008a; Moore and Huntington 2008). Loss of sea ice represents a reduction in available habitat for ice-associated marine mammals that is already affecting some species, and in the longer term, it is expected that foraging success, fertility rates, mortality rates, etc. will be impacted for additional populations and species of endemic Arctic marine mammals. Generally speaking, specialist feeders are likely to be more heavily impacted by changes in Arctic food webs that will accompany sea-ice losses compared with generalist feeders, and ice-breeders that require long periods of stable ice late in the spring season are likely to be impacted more rapidly than late winter ice-breeders that require ice for shorter periods of time (Kovacs and Lydersen 2008; Laidre et al. 2008a). But there will be significant regional variation in the severity and timing of impacts on ice-associated marine mammals, depending on actual sea-ice loss rates across the Arctic, local bathymetry conditions, community composition and other factors associated with climate change in a more general sense (e.g., water temperature impacts on prey populations). However, recent analyses of decadal patterns of sea ice and their influences on marine mammals suggest that changes that have taken place in recent years are likely to impact resident marine mammal populations at regional and hemispheric scales (Barber and Iacozza 2004).

The objectives of this paper are: (1) to provide a brief summary of the linkages between Arctic marine mammals and sea ice; (2) to report on documented changes observed to date in marine mammal populations related to changes in sea-ice conditions; (3) to make predictions for future changes to marine mammal populations in view of current scenarios for Arctic sea ice into the twenty-first century. Attribution of changes in the distribution and abundance of marine mammal populations to loss of sea ice is complicated by changes in hunting regimes on many Arctic marine mammal populations, both in the near and more distant past and by other changes taking place in the Arctic due to climate change. But sea-ice changes have already been dramatic, and assessing their impacts on marine mammals may serve as an early warning sign for future change among marine mammals in the North.

Arctic marine mammals and their association with sea ice

The largest of the Arctic pinnipeds, the walrus (*Odobenus rosmarus*), ranges across the circumpolar Arctic, but the species's distribution is disjunct and two subspecies are recognized, one in the Pacific (*O. r. divergens*) and the other in the Atlantic (*O. r. rosmarus*). The distribution of walruses is restricted by their narrow ecological niche. They depend on shallow water (≤100 m) with suitable bottom substrate to support high bivalve abundances, reliable open water over rich feeding areas, and haul-out platforms (ice or land) near feeding areas (Fay 1982). For much of the year, the preferred haul-out platform is sea ice (e.g., Freitas et al. 2009). Atlantic walruses of all ages and sexes use terrestrial haul outs in summer and autumn, and Pacific walrus males behave similarly. But females and calves of the Pacific subspecies remain in the Marginal Ice Zone (MIZ) during summer. There are probably in excess of 200,000 walruses worldwide, but many population assessments are out of date and in some areas are non-existent (e.g., Franz Josef Land, Pechora Sea, Laptev Sea). A key sea-ice-related sensitivity with walrus is that, at least seasonally, all populations use the MIZ as a platform to move over foraging areas that are too far from land-based haul-out sites to be energetically feasible sites for feeding. The use of the two seasonally different haul-out habitats, by at least segments of the population, broadens the feeding distribution markedly, which in turn permits greater overall walrus abundances.

The smallest of the Arctic seals, the ringed seal (*Pusa hispida*) is also a circumpolar species. The world-population of ringed seals probably numbers in the millions, but few areas have been systematically surveyed (Hammill 2009). This species is the only northern seal that can maintain breathing holes in thick sea ice and thus has the broadest distribution among the Arctic pinnipeds, ranging north to the Pole. Ringed seals are extremely dependent on sea ice, which is their exclusive breeding and haul-out platform. Typically, ringed seals prefer land-fast ice in fjords and along coastlines, with a reasonably thick and stable snow cover; but they can also live and breed in drifting pack ice [e.g., in the Barents Sea (Wiig et al. 1999), Davis Strait (Finley et al. 1983)]. Snow on the surface of the sea ice is essential for the construction of lairs (small caves above a breathing hole), in which the seals routinely rest during the winter months and also give birth in the early spring (e.g., Furgal et al. 1996). Ringed seals have the longest lactation period of any of the northern true seals (members of the family Phocidae), and need stable ice throughout the period of neonatal dependence in addition to good snow cover (Lydersen and Kovacs 1999). Ringed seal pups are only ca. 4 kg when born, so they depend on the lair environment to stay warm. The lair also provides protection against polar bears, Arctic foxes (*Alopex lagopus*) and other predators (Smith et al. 1991). Lack of snow build up on the ice in autumn or warm spring temperatures and rain can result in reproductive failure in this species (e.g., Smith and Harwood 2001; Stirling and Smith 2004). Ringed seals remain associated with ice throughout the year (Freitas et al. 2008a) and feed predominantly on ice-associated prey, which are particularly important to young ringed seals. Polar cod (*Boreogadus saida*), Arctic cod (*Arctogadus glacialis*) and large zooplankton species such as *Parathemisto libellula* make up most of the ringed seal's diet (e.g., Wathne et al. 2000; Labansen et al. 2007). A key sea-ice-related sensitivity for ringed seals is their reliance on a stable sea-ice platform with sufficient snow for lair construction and maintenance through winter and the spring nursing period.

Bearded seals (*Erignathus barbatus*) have a patchy distribution throughout the Arctic, occurring at low densities throughout their range. The global population of bearded seals has not been assessed, but probably numbers in the hundreds of thousands (Kovacs and Lydersen 2006). This species is largely solitary, though small groups can be seen on the ice during late spring and early summer, when they are breeding and then molting. Similar to walruses, bearded seals forage mainly on benthic organisms (Kovacs 2009a). Therefore, they reside in drifting pack ice over shallow water. They are largely coastal animals but can also be found in drifting pack ice far from shore in shallow areas such as the Bering and Barents Seas. Bearded seals avoid densely packed ice unless open-water leads are available. During winter, they concentrate near polynyas or in areas where leads are frequent, or they stay near ice edges. Bearded seals prefer shallow coastal environments with drifting sea ice that contain a rich bottom fauna to support their energy requirements.

Four other ice-associated seals live within Arctic and sub-Arctic pack-ice areas. These include harp seals (*Pagophilus groenlandicus*) and hooded seals (*Cystophora cristata*) in the North Atlantic region and spotted seals (*Phoca largha*) and ribbon seals (*Histriophoca fasciata*) in the Bering Sea, Chukchi Sea and Sea of Okhotsk. All of these species give birth to their young on pack ice and spend most of their lives associated with sea ice (Burns 2009; Kovacs 2009b; Lavigne 2009; Lowry and Boveng 2009). With the exception of the spotted seal, these species normally haul out only on ice. Spotted seals are relatively recently evolved from harbor seals and in summer can be seen hauled out on shore within harbor seal groups. The other three species can spend long periods pelagically in areas without ice, but are found in association with ice whenever it is available. All four of the Arctic pack-ice seals display broad diets, consuming a wide variety of small fish and invertebrate species. They favor lipid-rich schooling fishes such as polar cod, Arctic cod and capelin (*Mallotus villosus*). The largest species, the hooded seal, also eats larger prey such as Greenland halibut (*Reinhardtius hippoglossoides*) and deep-dwelling red fish (*Sebastes* spp.), and they share a diet of cephalopods with ribbon seals (Haug et al. 2007). All four species are sensitive to the availability of vast fields of pack ice in late winter/early spring when they give birth to their young and nurse them on the ice.

Three species of cetaceans are endemic to the Arctic, the narwhal (*Monodon monoceros*), the white whale (or beluga, *Delphinapterus leucas*) and the bowhead whale *(Balaena mysticetus)*. Beluga and bowhead whales a have a circumpolar distribution, while the narwhal occurs primarily in the North Atlantic Arctic (Heide-Jørgensen 2009; O'Corry-Crowe 2009; Rugh and Shelden 2009). The narwhal is the most specialized of the ice whales (Laidre et al. 2008a). It is typically found in waters north of 60°N latitude in the eastern Canadian High Arctic, offshore east and west Greenland, Svalbard and Franz Joseph Land. Narwhals over-winter in deep, ice-covered habitats along the continental slope and spend roughly two months in summer in ice-free shallow bays and fjords. In some areas these disjunct seasonal distributions are connected by annual migrations that can be up to 1,000 km and last about 2 months. Narwhals feed intensively from November to March in dense pack-ice habitat, which may be a key factor to their survival. In contrast, white whales occupy estuaries, continental shelf and slope-waters as well as deep ocean basins in conditions that range from open water to dense annual pack ice. Some belugas undertake long migrations between summering and wintering sites, while others remain in the same region year-round (e.g., Lydersen et al. 2001; Richard et al. 2001). Migratory belugas occur along the west and north coasts of Alaska, in the Canadian High Arctic and western Hudson Bay. Beluga populations that do not make long migrations often move short distances on a seasonal basis. The dependency of beluga and narwhal on sea ice is likely due to their prey being ice-associated (directly via living in association with sea ice or indirectly via receiving nutrients falling through the water column from sea ice); though both species can travel far from sea ice and some populations routinely spend many months in ice-free habitats (e.g., Cook Inlet beluga, West Greenland narwhal). Protection from killer whales might also play a role in their use of ice-covered waters. Additionally, the shelter offered from wave activity in ice-covered waters, particular during storms, may serve as an attractant. Bowhead whales are well adapted to sea ice, spending summers in the high Arctic and winters in sub-Arctic seas (Moore and Reeves 1993; Finley 2001); this species is the only baleen whale to reside in the North year-round. Bowheads often occupy polynyas during winter, but can move easily through extensive areas of nearly solid sea ice and break through ice up to 45 cm thick. Although strongly ice adapted, bowheads often feed in open water areas, especially in late summer and autumn, when sea ice can be hundreds of kilometers offshore (Moore 2000; Moore et al. 2010). As for beluga and narwhal, the key ice related sensitivity for bowhead whales is likely how the sea-ice structures the ecosystem, influences prey availability and offers protection from predators and rough seas.

Polar bears (*Ursus maritimus*) have a circumpolar Arctic distribution. Nineteen populations of polar bears are currently recognized, varying in size from a few hundred to a few thousand animals within a global population estimated to be between 20,000 and 25,000 animals (Aars et al. 2006). Polar bears are heavily dependent on sea ice for foraging and on ice corridors for transportation to and from denning areas, which are usually located on land along slopes near shore-lines where snowdrifts form (Stirling 2009). Female polar bears emerge from their dens in spring, following a fasting period of 4–5 months. They depend on immediate access to sea ice and a plentiful supply of ringed seals, particularly pups, at this time of year. Polar bears are scarce in the permanent MYI of the central Arctic Ocean as they prefer FYI that forms over shelf areas where seals, their primary prey, are most abundant (Molnar et al. 2010). Ringed seals are the dominant prey of polar bears, but bearded seals and other ice-associated seals, such as harp and hooded seals, are important regionally. Even walruses and the ice-associated cetaceans are consumed by polar bears in some areas (see Thiemann et al. 2008). Polar bears spend most of their lives on sea ice, travelling thousands of kilometers over the ice searching for mates and hunting seals each year.

Changes observed among marine mammals in the Arctic in response to changing sea ice

Biological impacts related to the decreases taking place in sea ice in the Arctic are expected to occur throughout Arctic food webs (e.g., Markham 1996; Hunt et al. 2002; Schumacher et al. 2003; Hassol 2004; Piepenburg 2005; Grebmeier et al. 2006a; Mueter and Litzow 2008; Wassmann 2008; Mueter et al. 2009). Changes observed to date among marine mammals, linked to sea-ice declines, are summarized below.

Among the highly mobile pinnipeds and cetaceans, alterations in distribution would be expected to be among the first responses observed due to changes in ice extent and seasonal availability. Vibe's (1967) analysis of the relationship between multi-decadal environmental fluctuations and marine mammal harvest success in West Greenland was one of the first studies that explored decadal-term patterns of distributions of Arctic marine mammals in relation to ice type and distribution. Vibe clearly showed the importance of availability of specific ice types in determining the distribution of marine mammals of the region. However, while northward expansions are possible for temperate species, such as gray whales (*Eschrichtius robustus*) in the Pacific sector (Moore et al. 2003; Stafford et al. 2007; Moore 2008), Arctic endemics have limited capacity for range shifts northward. But distributional changes are clearly taking place. A pupping herd of harp seals has been observed recently off west Greenland (Rosing-Asvid 2008) and vast herds of harp seals have been seen in recent years on the east coast of Svalbard during the period from January to March, times of year that they are not normally in this region (Norwegian Polar Institute Marine Mammal Sighting Data Base). The degree to which the pelagic ice-associated seals are capable of "relocation" of breeding areas is unknown. Tradition plays a significant social role in being in the right place at the right time for many ice-breeding species that disperse broadly outside the pupping/mating period.

In the Canadian High Arctic, killer whales (*Orcinus orca*) appear to be extending their season of Arctic habitation and expanding their range northward, at least in periods when ice conditions permit (e.g., Ferguson 2009; Higdon and Ferguson 2009). Early-season sightings of this species have occurred in recent years at very high latitudes in the Northeast Atlantic as well (e.g., early March at above 80°N, Norwegian Polar Institute Marine Mammal Sighting Data Base), though the lack of comparative historical data limits interpretations of these latter data. Anecdotal data also suggest that some typically temperate cetaceans are shifting their summer distributions northward into the Arctic. For example, sei whales (*Balaenoptera borealis*) and harbor porpoises (*Phocoena phocoena*) have been seen in Svalbard waters in recent years for the first time, and unusually high densities of fin (*Balaenoptera physalis*) and minke (*Balaenoptera acutorostrata*) whales have occurred in July and August along the shelf break west of Spitsbergen recently (Norwegian Polar Institute Marine Mammal Sighting Data Base). Blue whales (*Balaenoptera* *musculus*) are also being sighted with some regularity near Svalbard, though population increases, rather than range shifting due to changing ice conditions, might be the reason for the increased incidence of this species in this area. The expansion of these temperate species north for longer seasons has the potential to have some competitive stress on resident cetacean populations if their diets and spatial distributions become overlapping, and in the case of the killer whale potential for increased predation pressure.

However, it is important to note that in the only high Arctic cetacean for which there is reasonable time-series data—the Bering-Chukchi-Beaufort populations of bowhead whales—there has been no dramatic change in distribution or migratory timing. This population has in fact increased at a rate of 3% per year since the late 1970s (George et al. 2004). Additionally, calf counts and harvested whale body condition suggest that the reduced sea ice in the eastern Beaufort Sea has actually been improved conditions for this population (George et al. 2006; IWC 2010). Oceanographic modeling suggests that the extreme sea-ice retreats in the Pacific Arctic sector may favor upwelling of prey onto the Beaufort Sea shelf, which improves foraging opportunities for Bering-Chukchi-Beaufort bowheads, especially in late summer and autumn (Moore and Laidre 2006). Specifically, for whales feeding near Barrow, a wind-driven prey-trap model has been formulated to account for the large aggregations of bowheads feeding on euphausiids in the region (Ashjian et al. 2010; Moore et al. 2010).

Major declines in abundance or pup production have recently been documented for hooded seals in the Northeast Atlantic, harp seals in the White Sea and ringed seals in Hudson Bay, which have been attributed largely to climate change impacts on ice conditions (Ferguson et al. 2005; Chernook and Boltnev 2008; ICES 2008). Low ice years have also been correlated with low body condition indexes for female ringed seals and ovulation rates as low as 50% of the norm in extreme low ice years (Harwood et al. 2000). Ice-seals in other areas are also likely to be experiencing declines in reproductive success, and perhaps also condition, but lack of monitoring activities make it impossible to assess the current extent of change. For example, ringed seals on the west coast of Svalbard have not had sufficient ice for normal breeding to occur since 2005 (Kovacs and Lydersen, personal observations) and are likely in decline.

A growing body of data suggests that Pacific walruses are also showing negative impacts of sea-ice reductions (http://alaska.usgs.gov). Abandoned calves have been reported at sea (Cooper et al. 2006), which suggests that females with dependent young might be experiencing nutritional stress with their usual sea-ice resting platform retreating north of the continental shelf during summer, separating them from feeding areas. Mothers and calves are certainly spending more time on land (Kavry et al. 2008; also see Arnbom 2009), where stampede incidents have recently caused significant mortality of both adults and young animals (from hundreds to thousands of individuals) (e.g., Ovsyanikov et al. 2008; Fischbach et al. 2009). There are also suggestions that Pacific walruses may have shifted their diet toward eating more seals and fewer benthic invertebrates (Sheffield et al. 2001; Rausch et al. 2007). However, the magnitude of this dietary shift by walruses in the Pacific is difficult to assess (see Sheffield and Grebmeier 2009). Some walrus harvest data show that the proportion of females in the catch has increased while the relative proportions of pregnant females have declined and the age of first reproduction has shifted. These changes are suggested to be related to harvest management regimes and changing environmental conditions resulting in a distributional shift for females and slower rates of growth, perhaps due to food limitations caused by a shift from a benthic to a pelagic-dominated system (Garlich-Miller et al. 2006; Grebmeier et al. 2010). Atlantic walruses might be somewhat more resilient to changes in sea ice because they utilize more near-shore areas for feeding (Born 2005), but all walruses are dependent on benthic-pelagic coupling permitting rich benthic communities of bivalves, which are fed in part by vertical flux from ice-algae and MIZ algal blooms (Hobson et al. 1995; Grebmeier et al. 2006a, b; Tamelander et al. 2006).

Changes in harvest levels of several marine mammal species have been noted with respect to changing sea-ice conditions in the North Atlantic Arctic. For example, West Greenland harvests of harp seals have increased 100-fold for adults and tenfold for juveniles in the last 20 years; in the 1980s only some hundred adults were taken and less than 2,000 young animals. This has increased to in excess of 20,000 of each age group annually in the period 1995–2005 (Rosing-Asvid 2008). Harp seals are increasingly available in the area, and ice conditions permit increased access to the seals. Given the size of the stocks, this does not represent a specific management problem in this case. However, other increased catches might be more significant from a conservation point of view for stock viability. A doubling of narwhal catches by hunters in Siorapaluk, Greenland, has taken place since 2002 due to changed sea-ice conditions (Nielsen 2009). Sea ice is now more broken and hunters can now gain access to narwhal feeding areas that were previously inaccessible to them. This increased harvest has unknown implications because of a lack of information about the status of this stock, but is suspected to be having a negative influence on population status.

In one of the southernmost populations of polar bears, in western Hudson Bay, changes in the date of breakup of the sea ice were suspected to be having negative influences on body condition and reproductive output of polar bears in the early 1990s (Stirling et al. 1999; Derocher et al. 2004;

Stirling et al. 2004). By the late 1990s it was clear that early ice-break up and delayed freeze-up had resulted in a shorter sea-ice-season in the region which caused the bears to spend more time ashore, resulting in declining body condition, reproductive rates, survival, and population size (Stirling et al. 1999, 2004; Parks et al. 2006; Stirling and Parkinson 2006). Litter production rate and natality declines, as well as reductions in body length, have also been detected in Svalbard polar bears, which show a relationship to large-scale climate variation (Derocher 2005). However, in this region density-dependent factors cannot be ruled out as being part of the cause of these changes (see Aars et al. 2009). Reduced prey availability for polar bears due to changing ice conditions has been suggested for bears in East Greenland, where bears are now smaller than they were some decades ago; though contaminant increases may also play a role in these observations in this region (Pertoldi et al. 2009). Most recently, polar bears in the Beaufort Sea have exhibited reduced breeding rates, lower cub litter survival, reduced body size and reduced adult survivorship, which are correlated with an increasing duration of the ice-free period (Regehr et al. 2006, 2007, 2010; Rode et al. 2010). These conclusions follow earlier reports from this area of cannibalized and starved bears and suggestions that Beaufort Sea bears were periodically nutritionally stressed during the early part of this century because of increasing duration of the open water season and possible decreases in seal populations, or at least their accessibility to bears (Stirling et al. 2008).

Polar bear distribution has also shifted in the Alaskan Beaufort Sea in recent decades, with more bears seen along the coast and in open water, particularly in the early fall. These changes are thought to reflect a behavioural response by polar bears to changes in ice type and cover and the timing of ice formation and ablation (Gleason and Rode 2009). Polar bear denning locations have shifted in some regions in response to changing ice conditions, with fewer dens in MYI and more on shore (e.g., Fischbach et al. 2007). The tendency for bears to spend more time on land (e.g., Schliebe et al. 2008) increases the potential for human-bear interactions (e.g., Towns et al. 2009) and may give false impressions of regional densities (Stirling and Parkinson 2006). In more southerly areas such as Western and Southern Hudson Bay, it also puts bears at risk to new threats such as forest fires (Richardson et al. 2007).

Polar bears are capable of opportunistically altering their foraging behavior to take advantage of locally abundant prey, and to some degree compensate for a decline in a dominant prey species (Thiemann et al. 2008). Dietary shifts have been documented in the Hudson Bay polar bear population, with fewer ice-seals and more open-water seals in the diet of bears over the period from 1991–2007 (Mckinney et al. 2009), and an increased consumption of terrestrially-based food such as geese and their eggs, berries, etc. (Hobson et al. 2009; Rockwell and Gormezano 2009; Dyck and Kebreab 2009; Smith et al. 2010). But it seems unlikely that current population sizes of polar bears could be maintained on alternate dietary energy sources if the diet does not include significant quantities of marine mammals, which are normally accessed by bears from a sea-ice platform.

Predictions and research needs

By their very nature, predictions are speculative, but given the potential for major change in Arctic marine mammal populations due to sea-ice declines, it is important to prepare mitigation strategies and management plans with the best available models and expert predictions. The physical models that predict sea-ice extent still contain a lot of variability, but all of the models converge to predict a more or less rapid decline in September sea-ice extent during this century. Observations indicate that we are moving towards a seasonally ice-free Arctic more rapidly than both general circulation models and high-resolution coupled ocean-sea ice-atmosphere models have predicted. Current estimates suggest the Arctic may be free of multiyear sea ice somewhere during the period 2013–2035 (Wang and Overland 2009). Recent results by Barber et al. (2009) and Kwok et al. (2009) support the earlier part of this temporal range.

In marine ecosystems, responses to changes in physical forcings are neither direct nor linear and are therefore difficult to predict with confidence. Additionally, large interannual variability is a natural state in the Arctic marine ecosystem, which means that there are time-lags in discerning trends. Even basic, seemingly straightforward predictions, such as increased primary production in the Arctic when there is less ice cover to block sunlight, are not possible to predict with certainty. Overall, the system will almost certainly shift from light limitation to nutrient limitation, but actual production levels will exhibit strong regional variation and therefore are very difficult to predict (see Arrigo et al. 2008; Pabi et al. 2008 and Grebmeier et al. 2010 in combination, also see Walsh 2008). Storm activity, which is expected to increase, may also cause remaining sea ice to be more often broken-up and dissipated. Additionally, the impacts of changes in Arctic sea ice, which are the focus of this review, cannot be considered in isolation from other changes taking place in the Arctic in the broader context of global warming. Superimposed on sea-ice associated changes in light availability, stratification and mixing, timing of ice formation/melt/retreat, and the position of ice edge, other major changes such as increased riverine input, increased sea surface temperature, increased air temperatures, melting and receding glaciers, changes in precipitation and atmospheric forcings will all contribute to modify Arctic marine ecosystems and have impacts on marine mammal populations directly or indirectly via their prey or competitors/predators.

Ecosystem responses will vary regionally, depending on different regimes of oceanic and climatic forcings and in relation to variation in bathymetry and within the biological communities themselves, including advection patterns and in carbon-flow pathways (e.g., Moore and Huntington 2008). Based on variability observed in the past, both on interannual and decadal scales (e.g., Barber and Iacozza 2004), and with some background studies such as those reporting the impacts of cold and warm years in the Barents Sea (Orlova et al. 2002; Ingvaldsen and Gjøsæter 2008) and Bering Sea (Hunt et al. 2008), predictive scenarios for the more extreme conditions in the coming decades can be extrapolated with modest levels of certainty for species that are well studied.

Changes observed to date in marine mammal populations under diminished ice regimes strongly suggest that impacts will continue to intensify. Range shifts are already taking place and are expected to continue, which will alter population structure and genetic exchange rates (O'Corry-Crowe 2008). Population reductions of some ice-associated species have already been documented in the Atlantic Arctic sector and are expected to continue, perhaps at escalated rates. Compression of the ranges of endemic ice-associated species, as well as competition from temperate species moving north, are likely to result in increased competition for food. Food resources are also likely to be more dispersed both spatially and temporally in the future compared with the situation that has existed for a long time in the Arctic with extensive polynyas and a MIZ, which have both been temporally/spatially predictable (Stirling 1980, 1997; Kingsley et al. 1985; Heide-Jørgensen and Laidre 2004).

Pacific walruses are already spending more time at land-based haul outs; this increases the risk of polar bear predation in some areas. Additionally, if this trend continues they could deplete near-shore benthic resources, which would result in a lower carrying capacity for this species, even if benthic community health were otherwise unaltered. One area within the range of Atlantic walruses might actually be enhanced as a foraging area by changing ice conditions; thick ice over in eastern Greenland currently limits access by walruses to plentiful inshore bivalve banks to the short summer period. Less ice in this region would extend the foraging season in this area and permit more Atlantic walruses to occupy the region (Born 2005). But less extensive seasonal ice coverage throughout most of the Arctic is almost certain to have a long-term negative impact on benthic food resources that walruses of both subspecies depend upon, due to reductions in benthic biomass because of reduced sympagic-benthic coupling. Additionally, if walruses become more spatially restricted because of distance to suitable haul-out areas, abundances are likely to decline in most areas because of increased intraspecific competition for food (Kovacs and Lydersen 2008). Additionally, more open ice conditions in late winter and spring might make walruses more accessible to hunting. This is already a concern in Northwest Greenland, where walruses were historically inaccessible to hunters because of heavy ice, but are now increasingly available to hunters in small boats because of the open ice conditions (Born 2005). However, conversely in the northern Bering Sea, walrus hunting has been curtailed by the speed of the retreating sea ice in recent years (Metcalf and Robards 2008).

There are serious concerns for the future of the two circumpolar high Arctic, endemic phocid seals, the bearded seal and the ringed seal. These species are currently under consideration for listing by the United States under their Endangered Species Act, despite the fact that they currently number in hundreds of thousands, or millions, respectively. These species are heavily dependent on the availability of sea ice. Northward contraction of their range or a shift to breeding earlier in the season are possible responses to protracted periods of reproductive failure due to later ice formation and reduced sea-ice extent. But how flexible these species are in this regard remains to be seen. Arctic ringed seals are not known to use land as an alternate haul-out platform and the ability to do so would require a remarkable degree of behavioural plasticity, which has not been seen to date in this species in regions where ice reductions have been rapid and major (Kovacs and Lydersen 2008); although it must be noted that other ringed seal subspecies do use land as a summer haul-out platform, such as the ringed seals in the Baltic Sea (Härkonen et al. 1998). Energetics modeling suggests that ringed seals in Svalbard will no longer benefit from offshore summer migrations to the ice edge when the retraction of ice from the archipelago reaches distances of 600–700 km (Freitas et al. 2008b). Bearded seals might be somewhat more flexible in dealing with changing ice conditions than ringed seals. They are bigger and stronger at birth and they have some subcutaneous blubber when born, so they do not need lairs to cope with the cold (Lydersen and Kovacs 1999). Additionally, bearded seals do use land as a summer haul-out platform in some regions and they eat little if any ice-associated prey. So, this species might be able to survive ice-free summers.

The pack-ice seals do not require sea ice on a year-round basis. They are able to remain pelagic, without ice, for extended periods. But, similar to the other Arctic seals, they need an ice breeding platform and it is clear that some populations of these seals are already suffering from breeding habitat deterioration given the situation exhibited among Northeast Atlantic hooded seals and White Sea harp seals (e.g., Chernook and Boltnev 2008, ICES 2008, also see Johnston et al. 2005). Even in populations that are stable or increasing, such as harp seals breeding in the Gulf of St Lawrence, greater variability in ice conditions from year to year in the past decade, compared with earlier decades, is resulting in greater variability in pup survivorship (near zero survivorship in 2010, M.O. Hammill, pers. comm.). The Pacific pack-ice breeding species might be less impacted than those in the Atlantic region, given that the projections for ice conditions in the Bering Sea during late winter suggest that the pack ice in that region might continue to sustain ribbon and spotted seal breeding. But our current state of knowledge (and lack of monitoring) means that even major declines would likely not be detectable in ribbon or spotted seals.

Unlike Arctic pinnipeds that rely on sea ice as a platform, the relationship of cetaceans to sea ice rests principally on how ice structures trophic pathways (Bluhm and Gradinger 2008). Possible changes in benthic-pelagic coupling are expected to impact marine mammals that use benthic resources. The question is, of course, how will this impact Arctic species, including cetaceans? The answer lies within the ability of each species to adapt to changing food webs. In the case of narwhals, loss of pack ice in their wintertime benthic feeding habitat may be of particular concern. This factor contributed to their extreme sensitivity index to climate change when ranked among all Arctic marine mammals (Laidre et al. 2008a). Conversely, the flexibility in beluga diet may provide them with some resilience to changing prey resources. Similarly the generalist feeding habits of gray whales may give them an advantage over the largely planktivorous bowhead whale in a changing Arctic, although recent observations of bowheads feeding on euphausiids alongside gray whales suggests these whales may be capable of effective competition for this type of prey (Moore et al. 2010). Overall, the feeding ecology of Arctic cetaceans (e.g., generalist versus specialist feeders) and their capacity to adapt to new or different food resources will play a key role in their success in a changing environment.

Similar to other marine mammals, projections for the future with regard to cetaceans and sea-ice declines vary by region, with the greatest changes anticipated for the 'inflow' sectors of the Pacific and Atlantic Arctic where an additional 125 ice-free days are expected (Moore and Huntington 2008). While it is anticipated that these regions may become more productive, existing food webs may be significantly altered. All cetaceans rely on dense prey aggregations for efficient foraging, so the effect of sea-ice reduction on potential prey is a key link in forecasting impacts. Further, it has been surmised that sea ice also provides protection for Arctic cetaceans from predators (killer whales). Increased presence of the killer whales could have significant impacts on endemic Arctic whales (and seals) in an Arctic with less sea ice. Killer whales in the eastern Canadian Arctic seem to target cetaceans preferentially, with 90% of the registered prey being taken consisting of beluga, narwhal and bowhead, while the remainder was pinnipeds (Ferguson 2009). Reduced ice cover will also mean that the ice-associated cetaceans will not have this refuge from turbulent water during storm activity; this could indirectly increase energetic costs and possibly directly increase calf mortality. Thus, Arctic cetaceans face multiple challenges in that they will have to adapt to altered food webs, while potentially dealing with increased competition for prey with seasonally migrant species that remain in Arctic waters longer, and in some areas cope with increased levels of predation.

Large future reductions in most subpopulations of polar bears are expected, such that this species will be lost from many areas where it is common today (e.g., Wiig et al. 2008; Durner et al. 2009; Regehr et al. 2010). Habitat losses are expected to be greatest in the southern seas of the polar basin, especially the Chukchi and Barents seas, and least along the Arctic Ocean shores of Banks Island over to northern Greenland. Density and energetic effects are likely to become important as polar bears make increasingly long migrations from traditional winter ranges to remnant high-latitude summer sea ice. The impacts are likely to be sex- and age-specific and may ultimately preclude bears from seasonally returning to their traditional ranges (Amstrup et al. 2008; Thiemann et al. 2008; Durner et al. 2009). Expected abundance declines range from 30–70% in the next half century and, in the extreme, it is expected that the circumpolar population of polar bears will exist only as a few distinctly isolated populations within relatively few decades (e.g., IUCN 2008). The ensuing population subdivision is also expected to reduce gene flow among population clusters in the future (Crompton et al. 2008).

In addition to the direct impacts of habitat loss through loss of sea ice and the potential for increased competition and predation, marine mammals in the Arctic are likely to face increased disease and parasite risks (Harvell et al. 1999; Rausch et al. 2007; Van Bressem et al. 2009). For example, *Toxoplasma gondii* has shown marked increases in the last decade in ice-associated marine mammals in Svalbard (Jensen et al. 2010). Arctic marine mammals might also face increased risks from contaminants (AMAP 2003; MacDonald et al. 2005; Noyes et al. 2009). Additionally, it is highly likely that over the coming decades Arctic marine mammals will face increased impacts from human traffic and development in previously inaccessible, ice-covered areas (e.g., Kovacs and Lydersen 2008; Fuller et al. 2008; Ragen et al. 2008; AMSA 2009).

In combination, these various changes are likely to result in substantial distributional shifts and abundance reductions for many endemic Arctic marine mammal species. The behavioral plasticity that they will exhibit (or not) is impossible to predict with certainty. These species have never before been challenged by the extreme environmental changes occurring and predicted for Arctic sea-ice communities, and the rate at which change is occurring (extraordinarily fast) is particularly concerning. If species are fixed in traditional spatial and temporal cycles, and are unable to shift them within decadal time scales, some populations will be threatened with extirpation. In somewhat longer time frames, species extinctions can also be envisaged.

Despite observations to date being largely uncoordinated, fragmentary research efforts, they clearly indicate that broad-scale ecosystem alternations are occurring in both the Pacific Arctic and the Atlantic Arctic regions which are impacting marine mammal populations. Among ice-associated marine mammals, scant base-line data on even the most basic population parameters, such as population size, make tracking the effects of environmental shifts and extrapolating to future scenarios very challenging. Abundance is a basic metric for measuring impacts and "health" of mammalian populations. But the logistical difficulties in enumerating dispersed marine mammal populations make population surveys very expensive and hence infrequent, incomplete or simply non-existent. Despite these limitations and the financial and logistic challenges, comprehensive monitoring plans must be put in place for key ice-associated species. It is important that management systems have up-to-date information on all stocks, and the capacity to respond to changing conditions (Prowse et al. 2009). Failures in polar bear management systems to respond to population declines in a timely manner have resulted in severe overharvesting in Baffin Bay and Kane Basin, populations which are shared by Canada and Greenland (e.g., Taylor et al. 2008), and highlight the need for responsive management procedures for this and other species under the currently rapidly changing environmental conditions (also see Wiig et al. 1995; Clark et al. 2008; Dowsley and Wenzel 2008; Dowsley 2009). Precautionary harvest levels are in order for all ice-associated species given the predictions for the direction and magnitude of change expected in their sea-ice habitats.

Several international plans have been developed to monitor selected marine mammal species, but these plans remain unfinanced (e.g., Kovacs 2008; Laidre et al. 2008b; Simpkins et al. 2009; IWC 2010). Monitoring key populations of Arctic marine mammals as ecosystem sentinels can provide a window into a rapidly changing ecosystem and such monitoring should be put in place at an international level immediately (Moore 2005, 2008). In some areas of the Arctic, one means of monitoring is to form research partnerships with Arctic residents that rely on marine mammals for subsistence. These collaborations provide access for attachment of satellite transmitters to track animal movements and, via harvest monitoring, to investigate changes in diet, body condition and contaminant burdens concomitant with ecosystem variability (Metcalf and Robards 2008; Moore and Huntington 2008). Monitoring efforts over decadal time frames and across a range of spatial scales are fundamental to any effort to predict long-term ramifications of sea-ice loss to marine mammals (Grebmeier et al. 2010).

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