# QUANTIFYING THE SENSITIVITY OF ARCTIC MARINE MAMMALS TO CLIMATE-INDUCED HABITAT CHANGE

Kristin L. Laidre,[1,6] Ian Stirling,[2] Lloyd F. Lowry,[3] Øystein Wiig,[4] Mads Peter Heide-Jørgensen,[1] and Steven H. Ferguson[5]

[1]*Greenland Institute of Natural Resources, Box 570, 3900 Nuuk, Greenland*
[2]*Canadian Wildlife Service, Environment Canada, 5320 122 Street, Edmonton, Alberta T6H 3S5 Canada*
[3]*School of Fisheries and Ocean Sciences, University of Alaska, 73-4338 Paiaha Street, Kailua-Kona, Hawaii 96740 USA*
[4]*Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway*
[5]*Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba R3T 2N6 Canada*

*Abstract.* We review seven Arctic and four subarctic marine mammal species, their habitat requirements, and evidence for biological and demographic responses to climate change. We then describe a pan-Arctic quantitative index of species sensitivity to climate change based on population size, geographic range, habitat specificity, diet diversity, migration, site fidelity, sensitivity to changes in sea ice, sensitivity to changes in the trophic web, and maximum population growth potential ($R_{max}$). The index suggests three types of sensitivity based on: (1) narrowness of distribution and specialization in feeding, (2) seasonal dependence on ice, and (3) reliance on sea ice as a structure for access to prey and predator avoidance. Based on the index, the hooded seal, the polar bear, and the narwhal appear to be the three most sensitive Arctic marine mammal species, primarily due to reliance on sea ice and specialized feeding. The least sensitive species were the ringed seal and bearded seal, primarily due to large circumpolar distributions, large population sizes, and flexible habitat requirements. The index provides an objective framework for ranking species and focusing future research on the effects of climate change on Arctic marine mammals. Finally, we distinguish between highly sensitive species and good indicator species and discuss regional variation and species-specific ecology that confounds Arctic-wide generalization regarding the effects of climate change.

*Key words: Arctic; climate change; extinction risk; global warming; marine mammals; sea ice; sensitivity index.*

## INTRODUCTION

Since Darwin (1859), the environmental conditions to which organisms are exposed have been recognized as a defining influence on individual fitness and population success. The alteration of Arctic habitats as a consequence of climatic change, along with associated cascading effects on marine predators, is not a newly discovered phenomenon. Abrupt and radical climate changes have occurred several times over millennia including a dramatic 7°C temperature increase over 50 years that occurred in the North Atlantic approximately 7000 years ago (Dansgaard et al. 1989, 1993).

Vibe (1967) made the first quantitative observations of the impacts of climate change on the distribution and abundance of different types of sea ice and some of their consequences for Arctic marine mammals in the early

1900s. He noted that multi-decadal environmental fluctuations in West Greenland influenced the density and distribution of top predators, as documented largely through harvest and trade records because of the importance of these species to the economy and culture of the Greenlandic population. He summarized this perspective as follows: "The history of Greenland is the testimony of prosperity and poverty following each other in rapid succession. Oral as well as written records from the last centuries, and archaeological finds from the last four-five thousand years, unfold the same picture: The climatic fluctuations forced the sea mammals and sea birds of Greenland to look for new foraging grounds.... In all cases migration during changing climatic periods moved periodically towards Greenland and then away from Greenland again, leaving man starving behind" (Vibe 1967:13).

In recent decades, evidence for unidirectional climate warming through circumpolar reductions in sea ice and increased air and sea temperatures is substantial (Johannessen et al. 1999, Parkinson et al. 1999, Vinnikov et al. 1999, Morison et al. 2000, Wigley and Raper 2001, Comiso 2002, Parkinson and Cavalieri 2002), and recently studies have documented slowing of the North Atlantic meridional overturning circulation

by 30% over the last 50 years (Bryden et al. 2005) and predicted significant sea level rise (Overpeck et al. 2006). As "*K* strategists" Arctic marine mammals are adapted to a fluctuating environment and have a greater capacity to tolerate sudden interannual changes, thus have survived repeated periods of cooling or warming over evolutionary time (Harington 2008). However, long-term unidirectional changes, as opposed to large-scale interannual variation, present a particularly difficult challenge to the conservation of large polar marine mammals because such changes are likely to result in permanent habitat change, if not complete habitat loss, in some cases.

Habitat change or loss is critical when a species is highly specialized or dependent upon particular ecological conditions at specific times of the year. The life histories, behaviors, and feeding patterns of Arctic marine mammals are temporally tuned to specific ecological conditions in specific seasons. They are thus vulnerable to changes in climate that are sudden, unidirectional, or unusually large in magnitude. Identifying or quantifying habitat loss or change in Arctic marine environments, as well as understanding the significance of the manner in which the changes affect marine mammals, is complex. Habitat choice is not always well enough understood for some species or circumstances to facilitate quantification of selection, and key variables themselves may be in a state of flux. Habitat loss for pagophilic or sympagic species may include: (1) reduction in total habitat area (i.e., reduced ice cover), (2) habitat fragmentation (i.e., discontinuous pack ice), (3) habitat deterioration (i.e., thinner sea ice, increased rainfall, reduced primary production), and (4) unidirectional change in the timing of seasonal distribution and abundance of sea ice. All four types of degradation may affect the availability of resources and potentially increase mortality, reduce fertility, impact foraging success and fitness, or alter indirect mechanisms that include competition with invasive species, predation, and disease.

Species-specific responses to climate change are not likely to be consistent across the circumpolar Arctic. Species are regionally exposed to varying sets of environmental conditions in different parts of their range (Parkinson and Cavalieri 2002, Hanna and Cappelen 2003, Stern and Heide-Jørgensen 2003, ACIA 2005) and thus may demonstrate fairly plastic species-specific responses more complex than might be expected in a simple circumpolar assessment. Potential variation among subpopulations or stocks, given differences in regional environmental trends, often coupled with a shortage of critical biological information, makes pan-Arctic species-wide predictions difficult at best and often impossible (Tynan and DeMaster 1997).

The processes that drive changes in Arctic habitats are typically difficult to see or understand due to their dynamic nature, huge scale, limited accessibility (particularly in winter), and complexity. Changes can generally be divided into direct or indirect effects (Forchhammer and Post 2004). Direct effects are those that act on the animal itself. They are often manifested more immediately and often related to one organism on a single trophic level (e.g., year-to-year survival or failure to reproduce after a severe season) and thus tend to be the focus of short-term ecological studies. Indirect effects are more complex, acting on some element of the animal's environment or associated ecological community. They often involve several trophic levels and a temporal delay in response (i.e., climate impacts on ecosystem structure or top-down/bottom-up cascades).

This review focuses on the possible consequences of continued unidirectional warming trend on Arctic marine mammals, the primary feature of which is the loss of sea ice. Arctic marine mammals were classified into two broad categories: (1) those that occur north of the Arctic Circle for most of the year and depend on the Arctic ecosystem for all aspects of life and (2) selected subarctic species whose life histories include seasonal migration to and occupation of Arctic waters, yet do not depend on the Arctic ecosystem for some parts of the year. The core Arctic marine mammals considered here are the narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*), bowhead whale (*Balaena mysticetus*), ringed seal (*Phoca hispida*), bearded seal (*Erignathus barbatus*), walrus (*Odobenus rosmarus*), and polar bear (*Ursus maritimus*). The subarctic species selected for discussion are the spotted seal (*Phoca largha*), ribbon seal (*Phoca fasciata*), harp seal (*Pagophilus groenlandicus*), and hooded seal (*Cystophora cristata*).

The total range of most species covers a large suite of habitats and integrates seasonal, annual, and geographical variation. Based on available data on the biology and ecology of each Arctic marine mammal species, we have considered a "habitat" to be any area where resting, socializing, birthing and care of young, mating, avoiding predators, migration, and feeding occur. This paper presents a quantitative sensitivity index for Arctic and subarctic marine mammal species, which is built upon: (1) present-day habitat associations and (2) historical documentation of responses to habitat alteration. Development of the indices is preceded by brief overviews of Arctic marine mammal habitat features, species-specific natural history, and documented responses to past climate change relevant to the quantification of sensitivity.

## Arctic Marine Mammal Habitat

### Sea ice

A defining feature of the Arctic marine ecosystem is the formation and melting of sea ice. This primary physical habitat feature influences nearly all aspects of life for marine mammals in the Arctic. For animals that live in the ocean and breathe air, the physical structure of sea ice may act variably as a substrate or a barrier (Fay 1974). Arctic pinnipeds rely on the sea ice as a platform for hauling out, whelping, and molting, as well as for sub-ice foraging, while polar bears rely on

seasonal sea ice primarily as a platform for hunting (but also for most mating and some maternity denning). Fast ice is a barrier for cetaceans, excluding them from underlying marine areas they might otherwise access for feeding. For this group, ice generally reduces habitat availability even though Arctic cetaceans are well adapted for life in ice-covered waters, breaking through thin ice to breathe or breathing between floes and using ice for feeding or predator avoidance.

Annual sea ice cover has cascading indirect impacts on habitat. A phase lag between sea ice extent, break-up, and solar radiation constrains and controls the onset and pattern of primary production (Hansen et al. 2002, Smayda et al. 2004, Bluhm and Gradinger 2008), particularly in marginal ice zones where the ice edge retreats northward, exposing the waters to sunlight and creating conditions necessary for a primary production bloom fueled by the winter store of nutrients (Bluhm and Gradinger 2008). A production bloom thus slowly sweeps across the area previously covered with seasonal sea ice. This relatively slow, geographically widespread, and spatially variable transfer of production to the higher trophic levels of the food web is predominantly mediated by zooplankton (Pershing et al. 2004, Bluhm and Gradinger 2008), although in some regions of the Arctic production passes through the water column to the benthos (Hunt et al. 2002). These areas are critical seasonal habitat and support high concentrations of marine mammals.

Changes in sea ice regimes with global warming will impact this trophic coupling. The timing and extent of primary production are strongly related to the patterns of ice formation in autumn and spring recession, confounded by the mosaic of land/ice landscape. Extensive ice coverage cools the water column during the critical spring period when herbivorous zooplankton graze on phytoplankton. Reduced sea ice cover or minimal geographic coverage allow solar energy to warm and stratify the water column earlier, resulting in a premature phytoplankton bloom disrupting the connection between the phytoplankton and copepod grazers that ascend from depth at specific times of the year (Hansen et al. 2002, Hunt et al. 2002, Bluhm and Gradinger 2008).

The temporal scale over which such trophic decoupling occurs is important as rapid shifts in ice conditions may send cascading effects through the food web (Hansen et al. 2002). Predicting the degree of temporal change relative to different habitats in the Arctic is more complex than in temperate regions characterized by more consistent intra- and interannual variability (Ferguson and Messier 1996) and generally more resource allocation that facilitates a better ability to model and document changes.

### Polynyas

In some parts of the Arctic, polynyas (areas of open water surrounded by sea ice) form in the ice and last throughout the winter. Polynyas may vary in size from a few hundred meters across to hundreds of square kilometers. Some polynyas occur as unique events while others, known as reoccurring polynyas, develop at the same time and place each year, which allows marine mammals to seasonally depend upon them for feeding and/or safe overwintering (Stirling 1980, 1997, Heide-Jørgensen and Laidre 2004). Reoccurring polynyas result from persistent upwelling of deeper and warmer water, persistent unidirectional winds, tidal currents, or a combination of those factors (Stirling and Cleator 1981). Larger polynyas, such as the North Water Polynya, are capable of having a substantial positive influence on productivity (Odate et al. 2002, Ringuette et al. 2002, Tremblay et al. 2002), often rivaling that of the ice edge zone and consequently attracting large numbers of marine mammals to feed seasonally or overwinter. For example, a majority of the beluga population summering in northern Canada overwinters in the North Water (Richard et al. 1998a, b), the Northeast Water in East Greenland is an important wintering area for walrus (Born 2005), and the Saint Lawrence Island polynya in the Bering Sea hosts thousands of seals, walruses, bowhead whales, and belugas every winter (Simpkins et al. 2003). Smaller recurrent polynyas are also biologically important (Stirling 1997, Heide-Jørgensen and Laidre 2004).

### Non-ice habitat

Other important measures of marine habitat include oceanographic and topographic features largely independent of sea ice. The bathymetric structure of the sea floor can steer major currents on the shelf, slope, and basin and directly impact densities of zooplankton or forage fish. Bathymetry can also be a primary influence on where marine mammals forage. Shallow shelves constitute a large portion of the Arctic and tend to be areas where nutrients are more easily mixed in the water column, thus promoting phytoplankton production. Species vary in their preferred foraging depth; for example, narwhals target Greenland halibut (*Reinhardtius hippoglossoides*) at >1000 m (Laidre and Heide-Jørgensen 2005a) while Pacific walrus forage on bivalves usually at <100 m (Lowry and Frost 1981). Topographic features such as canyons, shelf breaks (including the continental shelf), ridges, and plateaus often attract or funnel prey into specific areas where they may be easily targeted by marine mammals (Moore 2000, Moore et al. 2000, Laidre et al. 2004c). Dynamic oceanographic features such as sea surface temperatures, chlorophyll *a* concentrations, eddies, gyres, or currents also influence densities of prey and are important in structuring Arctic habitat. Static habitat features (i.e., bathymetry, coastline substrate, and sea floor structure) are unlikely to be impacted by a warming climate beyond those effects of sea level rise on the coast, although the interactions of these features with other oceanographic or atmospheric processes (i.e., timing of production blooms, snow cover, precipitation) may be altered by changes in climate.
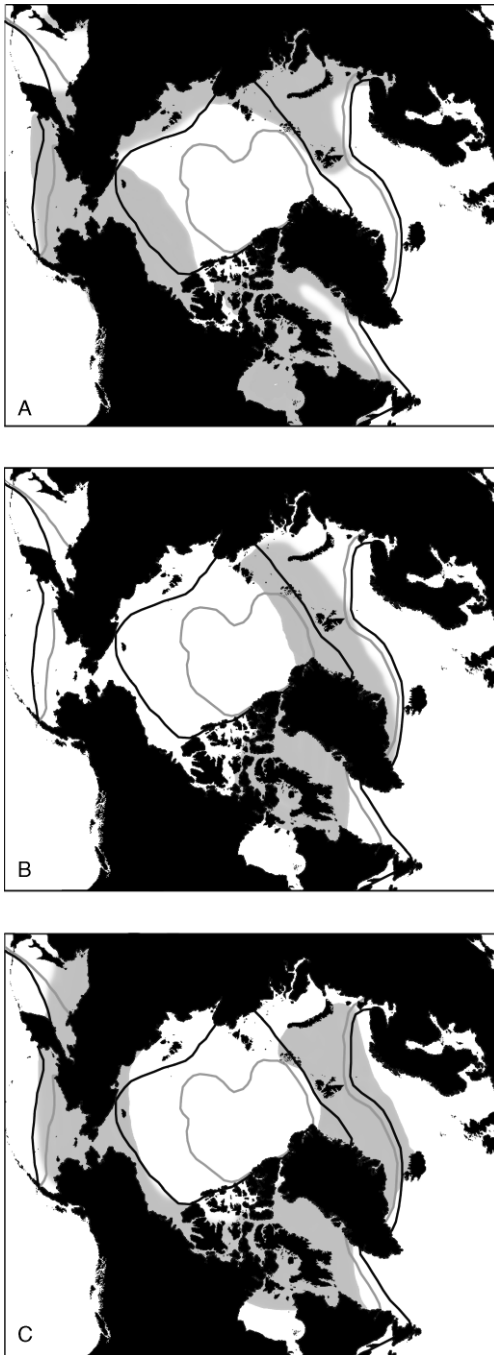
FIG. 1. Geographic range of Arctic cetaceans: (A) belugas, (B) narwhals, and (C) bowhead whales. Current and projected sea ice edges for March and September after Walsh (2008) are based on the Arctic Climate Impact Assessment (ACIA) five-model medians for 1980–2000 (current) and 2040–2060 (projected). Current sea ice is displayed with a solid black line, and projected sea ice edge is displayed with a solid gray line.

### SPECIES BIOLOGY AND HABITAT RELATIONSHIPS

#### Cetaceans

Three species of cetaceans occupy Arctic waters year round. The narwhal and beluga, medium-sized toothed whales, somewhat overlap in ecological niche, prey choice, and focal area use, whereas the bowhead whale, the only mysticete endemic to the Arctic, exploits the ecosystem in a very different way. The bowhead whale and the beluga have a circumpolar distribution, while the narwhal only occurs in the Atlantic sector of the Arctic (Fig. 1A–C).

*Beluga*.—Belugas, or white whales, occupy estuaries, continental shelf and slope waters, and deep ocean basins in conditions of open water, loose ice, and heavy pack ice (Fig. 1A). Satellite telemetry, genetic studies, and organochlorine analyses show belugas have strong matrilineally driven seasonal site fidelity to fjords and estuaries for summering and separate wintering grounds and are distributed in discrete populations around the Arctic (O'Corry-Crowe et al. 1997, 2002, Richard et al. 2001, de March et al. 2002, Innes et al. 2002, Palsbøll et al. 2002). Belugas generally prefer to overwinter in shallow or coastal areas, usually with light or highly moveable ice cover (Barber et al. 2001, Richard et al. 2001, Suydam et al. 2001, Heide-Jørgensen et al. 2003c; Table 1) and may occur as fully Arctic populations (Richard et al. 1998a, 2001, Suydam et al. 2001) or subarctic populations (Hobbs et al. 2005).

Some belugas undertake large-scale annual migrations between summering and wintering sites, while others remain in the same area year round, shifting offshore only when excluded from coastal habitat by fast ice formation (Hobbs et al. 2005). Large numbers of migratory belugas occur along the northwest and northern part of the Alaskan coast, in the Canadian High Arctic, and western Hudson Bay. At certain times of the year, those whales migrate thousands of kilometers, in some cases as far as 80° N into dense pack ice (Suydam et al. 2001) or thousands of kilometers into the North Water polynya or to the pack ice off West Greenland (Richard et al. 1998a, b, 2001, Heide-Jørgensen et al. 2003c). Nonmigratory belugas that generally make seasonal shifts in distribution of <100 km are found in Cook Inlet, Cumberland Sound, Svalbard, and the Gulf of St. Lawrence (Lydersen et al. 2001, Kingsley 2002, Hobbs et al. 2005).

Little is known about the movements and habitat use of belugas in the Russian sector of the Arctic other than that they occur in a continuum from the Laptev and Kara seas to the Severnaya Zemlya. Belugas that summer in the Russian section of the Chukchi Sea (Anadyr Gulf) and in the White Sea are of the nonmigratory form and only move offshore as far as necessary to find suitable ice conditions for wintering (R. C. Hobbs, *personal communication*; M. P. Heide-Jørgensen, *personal observation*).

While the general features of beluga whale habitat can be described for the relatively well-studied populations, the importance of those features is not well understood. For example, the summer occupation of nearshore/estuarine waters has been ascribed to feeding (Seaman et al. 1982), warm water providing a thermal advantage to

TABLE 1. Importance of physical and biotic Arctic habitat features for primary Arctic marine mammal species (X, used; XX, important; XXX, critical).

| Habitat | Beluga | Narwhal | Bowhead whale | Ringed seal | Bearded seal | Walrus | Polar bear | Harp seal | Hooded seal | Spotted seal | Ribbon seal |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Physical features** | | | | | | | | | | | |
| Shore-fast ice | | | | XXX | X | | XXX | | | | |
| Loose annual pack ice | XXX | X | X | XX | XX | XX | XX | XX | XX | XX | XXX |
| Dense annual pack ice | | XXX | XX | XX | XXX | XXX | XXX | XXX | XX | X | X |
| Multiyear pack ice | X | | | X | X | X | XX | | | | |
| Shear zones/leads | XX | XXX | XX | X | XX | X | XX | | | | |
| Polynyas | XXX | | XX | X | | XX | | | | | |
| Open water | XX | XX | XX | X | | XX | | XXX | XXX | XX | XX |
| Shallow water/ continental shelf | XXX | | XXX | X | XX | XXX | | XX | | XX | XX |
| Shelf break | XX | XXX | X | X | | | | X | XX | | X |
| Deep ocean basins | | XXX | | X | | | | | XXX | | X |
| Estuaries/lagoons/fjords | XXX | XXX | | X | | | | | | XXX | |
| Land haul-outs | | | | X | X | XXX | | | | XX | |
| Land denning areas | | | | | | | XXX | | | | |
| **Biotic features** | | | | | | | | | | | |
| Macroplankton/nekton | | | XXX | XX | | | | | | X | X |
| Macrobenthos | X | | XX | X | XXX | XXX | | X | | X | X |
| Midwater fish (polar/ Arctic cod) | XXX | X | | XXX | X | | | XXX | XX | XXX | XX |
| Benthic fish | X | XXX | | X | XX | | | | XXX | X | XX |
| Marine mammals as prey | | | | | | X | XXX | | | | |
| **Interactions** | | | | | | | | | | | |
| Pack ice × open water (ice edge) | XX | XX | XX | | | | | | | XX | XX |
| Pack ice × continental shelf | | | | X | XX | XX | | XXX | XX | XX | XX |
| Polynya × shallow water | XXX | | | | | X | | | | | |

neonates (Sergeant and Brodie 1969), and the presence of freshwater and coarse substrates facilitating skin shedding during molt (St. Aubin et al. 1990, Frost et al. 1993). The relative importance of each of those factors likely varies based on the environmental conditions (e.g., water temperatures and prey availability) specific to each of the summering areas (Frost and Lowry 1990*a*). Similarly, it is unclear why belugas sometimes move into deep, ice-covered waters. One potential reason would be to avoid killer whale predation (Frost et al. 1992). However, the movements into the ice appear excessive for what would be needed to avoid killer whales (Suydam et al. 2001) and actually could expose belugas to predation by polar bears (Lowry et al. 1987*a*) as well as increase the risk of entrapment in the ice. It is possible belugas move into ice-covered offshore regions for feeding, primarily on Arctic cod (*Boreogadus saida*), but few data are available to support this hypothesis. Similarly, the associations of belugas with features such as the continental shelf break (Moore 2000) may be related to oceanographic processes that produce good feeding conditions.

*Narwhal.*—Narwhals occur year-round north of 60° N in the eastern Canadian High Arctic and in waters around West and East Greenland, Svalbard, and Franz Joseph Land (Fig. 1B). The narwhal is the most specialized Arctic cetacean and the most restricted in distribution. In summer, narwhals spend approximately two months in High-Arctic ice-free shallow bays and fjords and overwinter in offshore, deep, ice-covered habitats along the continental slope (Heide-Jørgensen and Dietz 1995). These disjunct seasonal distributions are connected by extensive annual migrations (>1000 km) that last approximately two months (Koski and Davis 1994, Dietz et al. 2001, Heide-Jørgensen et al. 2002*a*, 2003*a*, Innes et al. 2002). In all areas of their occurrence, narwhals prefer deep or offshore waters and show a clear ecological partition with the nearshore shallow water beluga in regions where both occur. Calving occurs in spring, and very little feeding has been documented in summering areas (Laidre and Heide-Jørgensen 2005*a*), so the reason for coastal summer habitat choice is unclear. Narwhals from Canada and West Greenland have high site fidelity to the winter pack ice of Davis Strait and Baffin Bay in regions along the continental slope with high gradients in bottom temperatures, predictable open water (<5%), and relatively high densities of Greenland halibut (Laidre et al. 2004*a*). It is not known where narwhals from some summering areas (i.e., Hudson Bay, East Greenland, and Svalbard) occur in winter (Richard 1991). Sightings suggest that the Greenland Sea may be an important wintering area for narwhals from East Greenland and/or Svalbard (Gjertz 1991), and it has been speculated that some narwhals occupy Hudson Strait in winter (Richard 1991).

The wintering grounds may be the most critically important habitat for narwhals. Intense benthic feeding

behavior has been documented between November and March for narwhals from northern Canada and West Greenland (Laidre et al. 2003, Laidre and Heide-Jørgensen 2005a) and, in contrast to low feeding activity during the summer period, suggests a major portion of the annual energy intake is obtained in Baffin Bay in winter (Laidre et al. 2004a, Laidre and Heide-Jørgensen 2005a). This may also be true for the Greenland Sea, but has yet to be documented.

Narwhals are highly adapted to pack ice habitat where there is limited open water throughout the winter (Laidre et al. 2004b, Laidre and Heide-Jørgensen 2005b). No other cetacean species occupies such dense winter sea ice cover for such a long period of time.

*Bowhead whale.*—Bowhead whales summer in Arctic waters but migrate to subarctic seas to winter (Fig. 1C). The species is well adapted to ice-covered waters and can easily move through extensive areas of nearly solid sea ice cover (Ellison et al. 1987, George et al. 1989, Mate et al. 2000, Heide-Jørgensen et al. 2003b, 2006, Heide-Jørgensen and Laidre 2004). Bowhead whales often inhabit polynyas and the marginal ice zone in winter and early spring (Moore and Reeves 1993, Bogoslovskaya 2003). In the western Arctic, they select open water or light to moderate sea ice cover (10–70%) in summer and autumn (Moore et al. 2000). Currently, bowhead whales are divided into five populations that occupy Davis Strait–Baffin Bay, the Foxe Basin–Hudson Bay, the Bering–Chukchi–Beaufort seas, Svalbard, and the Sea of Okhotsk. Recent data on bowhead movements have confirmed their ability to travel substantial distances, which has brought previous conclusions about some population delineations into question (Heide-Jørgensen et al. 2006).

The bowhead whale is the Arctic's largest and most zooplankton-dependent predator. Their diet has been relatively well described for the Chukchi and Beaufort seas because stomach contents of subsistence-harvested whales are available for examination. Bowheads in this region eat mostly a variety of pelagic and epibenthic crustaceans (Lowry 1993, Lowry et al. 2004) and feed throughout the water column, including near or on the bottom. Copepods (primarily *Calanus* spp.) and euphausiids (*Thysanoessa* spp.) are the most important prey. Diets differ regionally and over time, suggesting whales' diet is related to seasonal availability of prey and that they locate prey concentrations that presumably result from oceanographic features such as upwelling and fronts. It is unknown whether bowhead whales feed offshore (beyond the range of shore-based whalers) or between late fall and early spring. Stable isotope studies suggest that a significant amount of feeding may occur in those areas and times for the Bering–Chukchi–Beaufort population (Lee et al. 2005). Although the spring migration of bowhead whales around the northwest and north coast of Alaska is well known (Mate et al. 2000, George et al. 2004), large-scale studies of bowhead movements with satellite tracking have only

been conducted in Canada and Greenland (Heide-Jørgensen et al. 2006; L. P. Dueck, M. P. Heide-Jørgensen, M. V. Jensen, L. D. Postma, and S. E. Cosens, *unpublished manuscript*).

### Arctic ice-associated pinnipeds

Arctic ice-associated pinnipeds with a circumpolar distribution include the ringed seal, the bearded seal, and the walrus. These species partition their use of sea ice habitats either through direct habitat selection or seasonal migrations coinciding with changing sea ice conditions (Burns 1970; Fig. 2A–C).

*Ringed seal.*—No other Arctic seal inhabits such a large geographic range or diversity of habitats as the ringed seal (Table 1, Fig. 2A). Although the primary breeding habitat of the ringed seal is the land-fast ice over the continental shelf along Arctic coasts, bays, and interisland channels (Smith and Hammill 1981), they may also be abundant and have pups in drifting pack ice both nearshore and offshore (Burns 1970, Finley et al. 1983, Smith 1987, Wiig et al. 1999, Lydersen et al. 2004). They are able to inhabit the fast ice between freeze-up and breakup because they can make and maintain breathing holes in thick ice by continuing to abrade the ice with the heavy claws of their foreflippers (McLaren 1958). In late spring, ringed seals give birth and nurse their pups in subnivean (under snow) lairs that they excavate above the breathing holes (Smith and Stirling 1975). While some pups are born on pack ice (Wiig et al. 1999), land-fast ice is thought to be the preferred pupping habitat because it is normally more stable throughout the pupping and nursing period (McLaren 1958, Burns 1970). Birth lairs for neonate pups are a key feature for this species, providing protection from predators and shelter for wet pups (Smith et al. 1991, Lydersen et al. 1992).

During the open-water season (between breakup in early summer to freeze-up in the fall) ringed seals remain pelagic (Smith 1987, Harwood and Stirling 1992). They occur at lower densities in multiyear ice of the High Arctic than in annual ice areas (Kingsley et al. 1985), probably because biological productivity is lower in the thicker ice and it is more difficult to maintain breathing holes in or between multiyear ice floes.

Ringed seal density patterns suggest that bathymetry, distance from the fast ice edge, and ice deformation have significant influences on distribution patterns (Smith and Stirling 1975, Lukin and Potelov 1978, Kingsley et al. 1985, Hammill and Smith 1989, Smith et al. 1991, Frost et al. 2004, Carlens et al. 2006, Krafft et al. 2006, 2007). Fewer data are available on distribution during the open-water season, though seals may concentrate at high densities, particularly in the autumn, in areas of high prey availability (Smith 1987, Harwood and Stirling 1992, Lydersen 1998). Healthy ringed seals rarely haul out on land, except in the Baltic Sea and Okhotsk Sea when they are ice-free during summer or in

freshwater lakes such as Lake Saimaa and Ladoga (Ognev 1935, Sipilä and Hyvärinen 2002).

In general, ringed seals are not thought to be migratory but several satellite tracking studies have demonstrated long-distance movements of adults and juveniles (Heide-Jørgensen et al. 1992b, Teilmann et al. 1999, Gjertz et al. 2000a, Born et al. 2004, Lydersen et al. 2004). The only consistent annual movement pattern that has been reported to date is the fall migration of young seals from the eastern Beaufort Sea and Amundsen Gulf, west across the north slope of Alaska to the Chukchi and Bering seas (Smith 1987; L. A. Harwood and T. G. Smith, *unpublished data*). It is not known whether these seals return in either the following spring or subsequent years.

Ringed seals feed under the ice or in the upper part of the water column (<50 m), although they are capable of diving to greater depths (>250 m; Teilmann et al. 1999). Their diet is diverse and varies seasonally and regionally, including large zooplankton, epibenthic and under-ice crustaceans, and pelagic and demersal fishes (Lowry et al. 1980a, Weslawski et al. 1994, Lydersen 1998, Siegstad et al. 1998, Wathne et al. 2000). Throughout the Arctic, ringed seals are heavily preyed upon by polar bears (Stirling and Archibald 1977, Smith 1980, Hammill and Smith 1991, Stirling and Øritsland 1995), and in some areas pups are also preyed upon by Arctic foxes (Smith 1976). Seals of all ages may occasionally be taken by walruses (Lowry and Fay 1984, Gjertz and Wiig 1992, Born et al. 1994).

*Bearded seal.*—Bearded seals are widely distributed throughout the circumpolar Arctic, mainly over the relatively shallower waters of the continental shelf and usually in association with moving ice or shore leads and polynyas (Burns 1970; Fig. 2B). Bearded seals occasionally occur in shore-fast ice, indicating that they have some ability to maintain breathing holes (Stirling and Smith 1977). They are thought to be mainly pelagic during the summer and fall, although they may remain in or near the sea ice year round. However, in the Okhotsk Sea and Hudson Bay they regularly haul out on land during ice-free summer months (Ognev 1935; V. Burkanov, *personal communication*; W. Bernhardt, *personal communication*). Although it is not known to be common, bearded seals (mostly juveniles) are regularly reported hauling out to molt on shore and sand bars near river mouths and some distance up rivers in some parts of southern Hudson Bay and the southern Beaufort Sea (I. Stirling and M. Obbard, *unpublished data*). Weaned pups also may haul out onshore in western Alaska (K. Frost, *personal communication*). In Svalbard, bearded seals give birth on small, first-year ice floes in the free-floating pack ice or on similarly sized white, glacial ice areas frozen into gray shore-fast ice (Kovacs et al. 1996, Andersen et al. 1999), and pups, which are highly mobile, are nursed for ~24 days (Lydersen and Kovacs 1999).
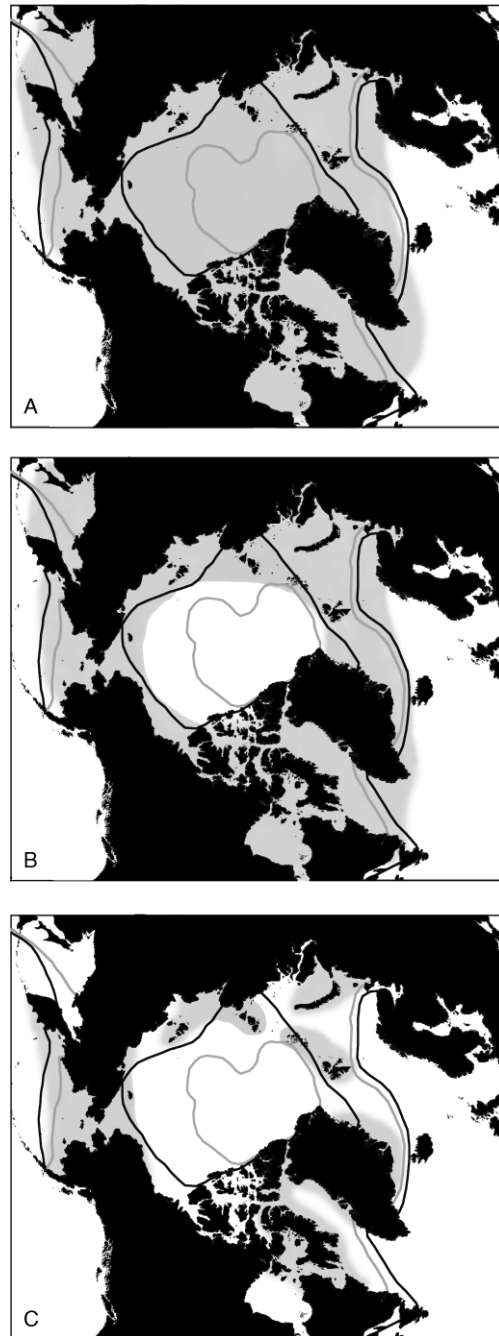


FIG. 2. Geographic range of Arctic pinnipeds: (A) ringed seals, (B) bearded seals, and (C) walrus. Current and projected sea ice edges for March and September after Walsh (2008) are based on the Arctic Climate Impact Assessment (ACIA) five-model medians for 1980–2000 (current) and 2040–2060 (projected). Current sea ice is displayed with a solid black line, and projected sea ice edge is displayed with a solid gray line.

There have been few studies that directly address bearded seal movements and diving (Krafft et al. 2000). Pups tagged in Svalbard dispersed offshore from their coastal birthing area after weaning, moving to Greenland and Jan Mayen (Gjertz et al. 2000b). Populations
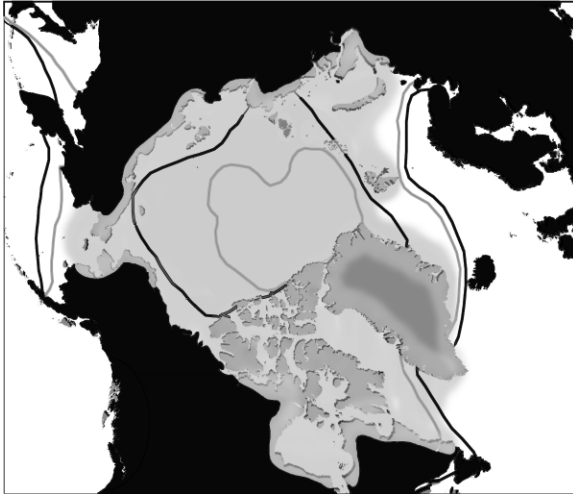
FIG. 3. Geographic range of polar bears. Current and projected sea ice edges for March and September after Walsh (2008) are based on the Arctic Climate Impact Assessment (ACIA) five-model medians for 1980–2000 (current) and 2040–2060 (projected). Current sea ice is displayed with a solid black line, and projected sea ice edge is displayed with a solid gray line.

appear to be mainly sedentary as evidenced by the development of strong regional vocal dialects in underwater vocalizations (Cleator et al. 1989). However, in the Bering and Chukchi seas, many bearded seals make well-defined seasonal movements to maintain association with ice year-round (Burns 1970).

Bearded seals, with their particularly sensitive whiskers, are predominantly benthic feeders and take shrimp, clams, crabs, other benthic invertebrates, and fishes (Lowry et al. 1980b, Antonelis et al. 1994, Hjelset et al. 1999). Less is known about their diet in deep, offshore areas. Bearded seals are preyed upon by polar bears (Stirling and Archibald 1977, Smith 1980, Derocher et al. 2002) and walruses (Lowry and Fay 1984).

*Walrus.*—The walrus has a discontinuous circumpolar distribution (Fig. 2C). Three subspecies are recognized: the Atlantic walrus (*Odobenus rosmarus rosmarus*), distributed from the eastern Canadian Arctic to the Kara Sea; the Laptev walrus (*Odobenus rosmarus laptevi*), distributed between the eastern part of the Kara Sea, the Laptev Sea, and the western part of the East Siberian Sea; and the Pacific walrus (*Odobenus rosmarus divergens*), distributed in the Pacific Arctic from Mys Shelagskyi in Siberia to Barter Island in Alaska and in the Bering Sea.

Walrus in the Pacific and Atlantic display sex-specific distribution and movement patterns. Females with young move to separate summering areas from those of males, although both sexes generally occupy the same areas in winter (Fay 1982, Wiig et al. 1996, Sease and Chapman 1998). Walruses use the same terrestrial haul-out sites and wintering areas from year to year (Born and Knutsen 1997, Born et al. 2005).

In the Pacific, nearly the entire population of walruses spends the winter in the Bering Sea, where they use ice floes for hauling out over the relatively shallow continental shelf. In the summer, adult males mostly haul out on more than 30 terrestrial sites along the Russian coast of the Bering Sea and Chukchi Sea and a few on the coast of Alaska (Estes and Gol'tsev 1984). These terrestrial haul-outs are presumed to be located in close proximity to areas suitable for feeding. As ice cover recedes in spring, juvenile and adult female walruses move northward with the ice into the Chukchi, east Siberian, and Beaufort seas (Fay 1982). The females and juveniles move southward in the fall to join the males in the Bering Sea ice.

In the Atlantic, walruses use both sea ice and terrestrial haul-outs as a hub for feeding excursions on shallow nearshore banks with substantial bivalve mollusk production (Born et al. 1994). In summer in the Atlantic, walruses of both sexes and all age classes often leave their ice-based haul-outs for terrestrial haul-outs, although many terrestrial haul-outs (especially in Greenland and Svalbard) have been abandoned because of excessive hunting pressure (Gjertz and Wiig 1994, Born et al. 1995). In East Greenland walrus are forced to leave terrestrial haul-outs and move offshore to winter in waters >100 m deep (Born 2005).

Walruses are specialized feeders and target benthic invertebrates, primarily mollusks, in shallow waters (Fay 1982, Gjertz and Wiig 1992, Born et al. 2003). Walruses are dependent upon suitable substrate (land or sea ice) close to foraging grounds for resting. They often overwinter in areas with polynyas that provide open water and access to benthic food resources (Vibe 1950, Fay 1982, Born et al. 1995, Stirling 1997). Walruses also occasionally prey on seals (Lowry and Fay 1984, Gjertz and Wiig 1992, Born et al. 1995), especially in deep water where they do not have access to the bottom to feed. Walruses breed aquatically from January through March in their wintering areas near polynyas or in areas of drifting pack ice (Fay 1982, Sjare and Stirling 1996).

*Polar bear.*—Polar bears are distributed throughout the ice-covered areas of the circumpolar Arctic (Fig. 3), especially in areas of annual ice cover over the continental shelf and the inter-island channels of various archipelagos. They are distributed in approximately 19 different populations (Bethke et al. 1996, Paetkau et al. 1999, Lunn et al. 2002, Mauritzen et al. 2002, Amstrup et al. 2004, Derocher 2005). Polar bears have annual movement patterns within individual home ranges. They demonstrate long-term fidelity to denning and spring feeding areas and are faithful to denning substrate (i.e., land vs. ice; Ramsay and Stirling 1990, Amstrup and Gardner 1994, Wiig 1995, Mauritzen et al. 2001). Most maternity denning takes place on land, although denning on land-fast ice and drifting multiyear ice has been documented in the Beaufort Sea (Lentfer 1975, Amstrup and Gardner 1994). Polar bears are dependent

upon the sea ice to reach traditional denning areas (Derocher et al. 2004).

Polar bears are primarily dependent upon sea ice as a platform for hunting. Sea ice also facilitates seasonal movements, mating, and, in some areas, maternal denning, even though these activities can all take place (to varying degrees) on land. Bears of all ages and sex classes may seek shelter in temporary dens in drifted snow on the ice at high latitudes for up to several weeks at a time to escape periods of intense cold or inclement weather or when seals may be less abundant or accessible (Messier et al. 1994, Ferguson et al. 2000a, b, Van de Velde et al. 2003).

Polar bears feed on ringed and bearded seals and occasionally take belugas, narwhals, walrus, harbor seals (*Phoca vitulina*), reindeer (*Rangifer tarandus*), and birds (Smith 1985, Calvert and Stirling 1990, Smith and Sjare 1990, Stirling and Øritsland 1995, Derocher et al. 2000). Bears in Davis Strait are thought to take substantial numbers of harp and hooded seals at the whelping and molting patches where those species are seasonally abundant and accessible (Iverson et al. 2006).

In the polar basin and adjacent areas, polar bears primarily hunt on the annual ice over the continental shelf but may move into multiyear ice in some areas. Thus, some bears remain on sea ice year-round. In more southerly areas (i.e., Hudson Bay, Foxe Basin, Baffin Bay/Davis Strait), the annual ice melts completely and all bears are forced to spend up to several months on land fasting until freeze-up allows them to return to the ice again (e.g., Stirling et al. 1999, Taylor et al. 2001, Stirling and Parkinson 2006).

On the basis of limited satellite tracking and data from mark–recapture studies, males are assumed to have similar-sized home ranges and movement patterns as females, though they may walk longer distances in search of mates during the breeding season (Amstrup et al. 2001). Polar bear home ranges are up to 600 000 km$^2$ but vary greatly between individuals (Garner et al. 1990, Wiig 1995, Born et al. 1997b, Ferguson et al. 1999, Amstrup et al. 2000, Mauritzen et al. 2001, Wiig et al. 2003). Large home ranges reflect the low densities of ringed seals, which are dispersed over very large areas. Bears inhabiting active offshore ice generally have larger home ranges than those on land-fast ice (Ferguson et al. 1999, 2000a, Amstrup et al. 2000, Mauritzen et al. 2001, 2002).

Polar bears of all age and sex classes, especially adult females with cubs, hunt newborn ringed seals and their mothers in subnivean lairs in spring. The most important feeding time for polar bears is right after the relatively naïve seal pups are weaned with peak fat stores of ~50% fat by wet mass (Stirling and McEwan 1975). Overall, bears live both in areas of high productivity (annual ice) and low productivity (multi-year ice) and with a variety of different potential prey species.

*Subarctic ice-associated seals*

Subarctic ice-associated seal species depend on sea ice only during parts of their life cycle, especially for parturition, molting, mating, and resting during spring. Unlike Arctic ice-associated seals, they do not occupy the Arctic ecosystem year-round and only seasonally rely on sea ice. Of these, the ribbon seal and spotted seal occur only in the Bering–Chukchi–Okhotsk seas region, and the harp seal and hooded seal occur only in the North Atlantic.

*Spotted seal.*—Spotted seals occur in the North Pacific and peripheral seas (i.e., the Japan Okhotsk, Bering, Chukchi, and Beaufort seas; Shaughnessy and Fay 1977; Fig. 4A). Spotted seals give birth to and care for their pups near the southern edge of seasonal pack ice (the "ice front"), which occurs over the relatively shallow continental shelf (Burns 1970). Some spotted seals move to coastal haul-outs along the Bering Sea coast as ice disappears or follow the retreating ice northward and use coastal haul-outs in the Chukchi and western Beaufort seas (Lowry et al. 1998). Haul-outs occur in predictable, traditional locations, many of which are in or near coastal lagoon systems and are characterized by low relief, sandy or fine-gravel substrate, and quick access to relatively deep-water channels. These characteristics may provide opportunities to escape from potential predators such as humans and bears (Frost et al. 1993). Spotted seals show considerable flexibility in the concentrations of sea ice they use (Lowry et al. 2000), yet appear most commonly near the sea ice edge and prefer relatively small ice floes (Simpkins et al. 2003). They move southward with advancing sea ice in October, and during the period from November to April, they use a broad band of sea ice extending up to 300 km north of the ice edge in the eastern Bering Sea. Virtually all seals remain on the continental shelf in water less than 200 m deep (Lowry et al. 2000). Mitochondrial DNA studies suggest phylogeographic partitioning among seals in the Sea of Japan, the western Okhotsk Sea, and the Bering–Chukchi seas and the existence of separate populations (G. M. O'Corry-Crowe, *unpublished data*).

In western Alaska during summer, spotted seals haul out for periods averaging about two days and then make long foraging trips (averaging about nine days) (Lowry et al. 1998). They have a diverse diet and exploit both the pelagic and benthic communities, feeding on fishes, shrimp, or other crustaceans and octopus with substantial regional differences (Bukhtiyarov et al. 1984, Burkanov 1989). Important prey species in the Bering Sea include walleye pollock (*Theragra chalcogramma*), capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), and Arctic cod. In the eastern part of the Okhotsk Sea during summer spotted seals feed extensively on salmon (*Oncorhynchus* spp.).

*Ribbon seal.*—Ribbon seals, like spotted seals, occur only in the North Pacific and peripheral seas (i.e., the Okhotsk, Bering, Chukchi, and Beaufort seas; Burns
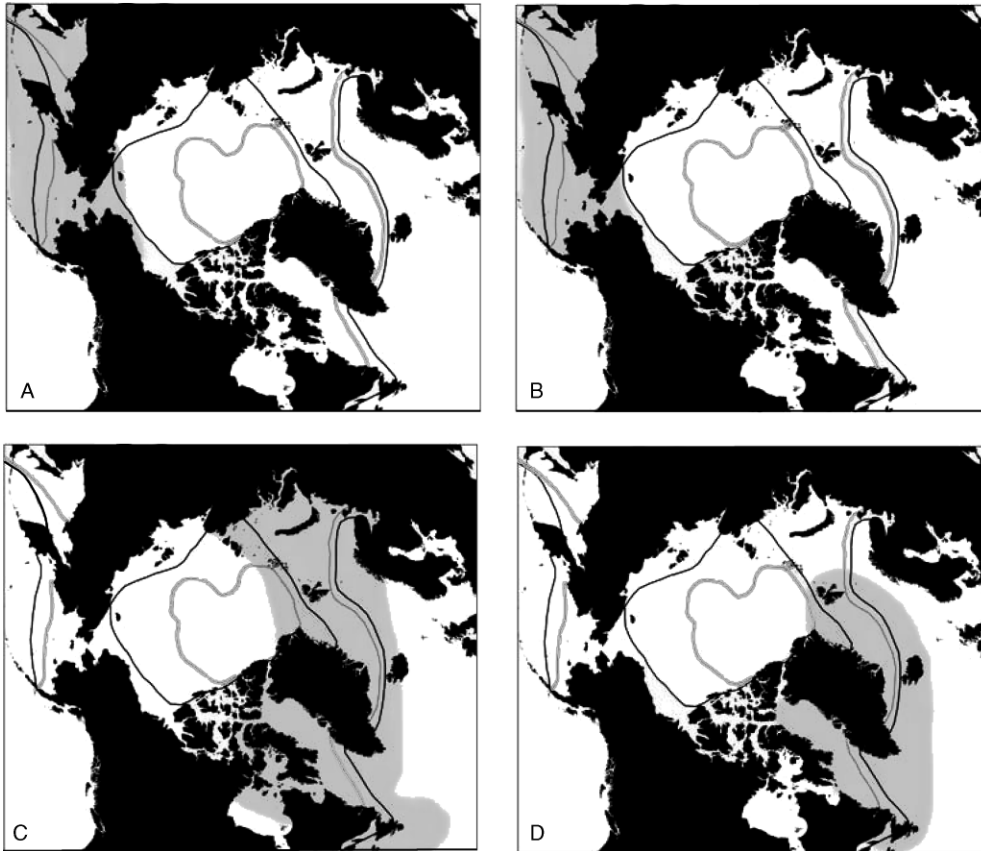
Fig. 4. Geographic range of subarctic pinnipeds: (A) spotted seals, (B) ribbon seals, (C) harp seals, and (D) hooded seals. Current and projected sea ice edges for March and September after Walsh (2008) are based on the Arctic Climate Impact Assessment (ACIA) five-model medians for 1980–2000 (current) and 2040–2060 (projected). Current sea ice is displayed with a solid black line, and projected sea ice edge is displayed with a solid gray line.

1981; Fig. 4B). There are no data on genetic population structure; however, considerable distance and the Kamchatka Peninsula separate ribbon seals in the Okhotsk Sea and those in the Bering Sea. Fedoseev (2002) indicates four pupping areas spread over a variety of sea ice conditions.

Ribbon seals use the marginal ice zone or ice front in late winter through spring where they give birth, care for pups, and molt (Burns 1970, 1981). There is little information on the specific characteristics of ice preferences other than general descriptions (Burns 1970, Simpkins et al. 2003). Some ribbon seals may remain in the same general region year-round (e.g., the Bering Sea and Okhotsk Sea; Burns 1981), while others may seasonally migrate into the Chukchi Sea and North Pacific Ocean (Kelly 1988). It is generally believed that, other than during the pupping/molting period, ribbon seals live a pelagic existence, as they are almost never seen hauled out on ice or land (Burns 1981).

In the Bering Sea, ribbon seals feed on many of the same species of fish and invertebrates as spotted seals (Frost and Lowry 1990b). In the Okhotsk Sea, juveniles feed on euphausiids and shrimp, whereas adults feed on

mostly pollock (Fedoseev 2002). However, when not over the continental shelf ribbon seals may feed in deeper waters and dive to deeper depths (Deguchi et al. 2004).

*Harp seal.*—Harp seals are distributed throughout the North Atlantic (Fig. 4C). Female harp seals have their pups in large high-density whelping patches, which is the basis for population delineation. Three populations are recognized: one that whelps off eastern Canada (Labrador and Newfoundland coasts and in the Gulf of St. Lawrence; Sergeant 1991), one that whelps off east Greenland in the West Ice, and one that whelps on sea ice in the White Sea. Genetic studies indicate significant reproductive isolation between trans-Atlantic breeding populations (Perry et al. 2000).

Whelping and lactation occur over a period of ~12 days and coincide with seasonal ice cover, just prior to breakup in the spring (Lavigne and Kovacs 1988). Mating takes place in the water at the same time and molting occurs on pack ice floes shortly thereafter. Thus harp seals are highly dependent upon access to stable ice floes at specific times of the year, albeit for relatively short periods. In summer and early fall, harp seals range

widely throughout the North Atlantic. They may move north into ice-free Arctic seas in Baffin Bay, West or East Greenland, the interisland channels of the Canadian High Arctic (Sergeant 1991), and west into northern Hudson Bay. They are also known to range widely into subarctic and temperate waters near the Faroe Islands and the Barents and Norwegian seas.

Throughout their range, harp seals tend to prefer waters over the continental shelf, often feeding at depths less than a few hundred meters. Their diet is varied and includes capelin, mysids, pandalus shrimp, and euphausids (Lydersen et al. 1991, Murie and Lavigne 1991, Sergeant 1991, Beck et al. 1993, Lawson et al. 1995, Hammill et al. 2005).

Deployment of satellite transmitters on harp seals show that they spend a considerable amount of time in ice-free Arctic waters and their distribution largely overlaps that of capelin. Harp seals in the Greenland Sea stay near the pack ice through June/July (Folkow et al. 2004) and then migrate into the Barents Sea, where they overlap with the population breeding in the White Sea. They return to the Denmark Strait in autumn, where they stay until breeding next spring.

In keeping with its wide range, the harp seal has broad habitat preferences. At some times of the year it is a completely open-water species that does not require sea ice or a haul-out platform. However, despite this flexibility, the species has a critical dependence on stable ice in specific locations for whelping and lactation.

*Hooded seal.*—Hooded seals have a similar range within the North Atlantic to the harp seal (Fig. 4D). Hooded seal populations are also defined in relation to their high-density whelping patches, which are located in the pack ice off the coast of Newfoundland, the Gulf of St. Lawrence, Davis Strait, and the Greenland Sea. There is no genetic or morphological stock discreteness between the different whelping herds (Wiig and Lie 1984, Sundt et al. 1994).

Hooded seals have a similar dependence on stable ice floes for parturition, as do harp seals. Hooded seal pups are born in late March in an advanced developmental stage and are weaned in approximately four days (Bowen et al. 1985) with no mother–pup bond, after which the pups are left alone to fast on the ice for up to several weeks. When they first enter the water to feed, they prey on krill and other invertebrates until they improve their swimming and diving skills sufficiently to be able to capture fish (Hammill and Stenson 2000, Kovacs 2002a). Females mate immediately after weaning pups and molt on pack ice afterwards in June (Lavigne and Kovacs 1988).

Hooded seals are widely distributed in the open-water season, predominantly in subarctic waters, although they occasionally occur along the European coast and the east coast of the United States (Lavigne and Kovacs 1988). They are deep divers and reach depths below 1000 m regularly when foraging for benthic prey such as Greenland halibut. They tend to remain farther offshore

and in deeper water than harp seals. Satellite tagging of hooded seals at the breeding and molting ground in the Greenland Sea revealed a significant amount of time spent in open water between Greenland, the Faeroe Islands, Norway, and Svalbard between molting in July and breeding in March (Folkow et al. 1996). Likely prey species include Greenland halibut, redfish (*Sebastes* spp.), Arctic cod, herring (*Clupea harengus*), squid, and blue whiting (*Micromesistius poutassou*) (Folkow and Blix 1999).

### DOCUMENTED IMPACTS OF CLIMATE CHANGE

Conclusively documented studies that confirm a direct relationship between ecological changes caused by climate warming and responses of individual species of Arctic marine mammals are essential for developing testable hypotheses about possible future impacts. Unfortunately, to date there are few quantified studies that clearly demonstrate such effects. Thus, in lieu of reiterating speculations on large-scale ecological consequences of global climate warming that have already been usefully summarized previously (e.g., Tynan and DeMaster 1997, Ainley et al. 2003, Derocher et al. 2004), we chose to highlight case studies in the scientific literature that have detected and quantified specific biological, physiological, or ecological effects of changing climate. We then use that information to develop an index of sensitivity to help design testable hypotheses.

#### Distribution

Species ranges are generally expected to shift northward with climate warming partly so that individuals can inhabit areas within their preferred metabolic temperature tolerances, but also because conditions at the southern limits of their previous distribution will no longer meet their ecological needs. This phenomenon has been documented for various terrestrial flora and fauna. Root et al. (2003) demonstrated a consistent temperature-related shift in distribution of plants, insects, and birds over the past 100 years in the direction expected based on known physiological constraints. Changes in the distribution of large mammals are often detected via investigations on long timescales (i.e., hundreds or thousands of years), far longer than the context of present-day ecological studies or monitoring programs (see Moore 2005). Obtaining this information also requires extensive and expensive surveys conducted over decades, thus few data are available from the past 50–100 years on smaller scale (both temporal and geographic) range changes with climate warming.

In the case of Arctic marine mammals, distributional shifts with climate variation have been documented in the past (Vibe 1967, Harington 2008). Dyke et al. (1996) used radiocarbon ages of subfossils to demonstrate that distribution of bowhead whales in the Canadian Arctic archipelago expanded and contracted abruptly several times over the last 10 500 years. Those fluctuations allow for a reconstruction of the postglacial sea ice history in

the area, where bowheads were forced out of habitat due to ice cover or allowed to expand their range into new habitat in the absence of ice cover. Evidence suggests Basque whalers harvested similar numbers of bowhead whales and right whales (*Eubalaena glacialis*) in the 16th century in the Strait of Belle Isle, a region far south of the present-day range of the bowhead whale, thus indicating a southward shift during the Little Ice Age (Cumbaa 1986, Rastogi et al. 2004; D. S. Weber, C. Gaines, R. L. Brownell, P. J. Clapham, L. N. Cooper, and H. C. Rosenbaum, *unpublished manuscript*). Furthermore, evidence that narwhals once occurred as far south as England during the Little Ice Age (observed in 1588; Hay and Mansfield 1989) and post-Pliocene fossils from Tertiary strata in England and Germany (Owen 1846, Collings 1933) indicate a substantial contraction of range with climate.

Polar bears ranged much further south during periods of climatic cooling. The oldest subfossil finding from the Palaearctic is probably an ulna found at Kew Bridge, London, dated to 40 000–50 000 yr before present (BP; Kurten 1964). Another find dated to ~22 000 yr BP was in Kjøpsvik, Nordland, northern Norway (Lauritzen et al. 1996). Ten finds of subfossil polar bears are known from southern Scandinavia, of which six have been dated to the period between 12 500 yr BP and 10 500 yr BP (Aaris-Sørensen and Petersen 1984, Blystad et al. 1984, Berglund et al. 1992), evidence that strongly suggests that the distribution of polar bears was influenced by climate variation during late Pleistocene and early Holocene and that they had a more southerly distribution than today.

The walrus was a part of the fauna in the North Sea during this period. Møhl (1985) reported on two skull fragments of walruses dated to ~24 400 and 30 900 yr BP. On the Atlantic coast of North America many records of walruses are available from late glacial and post-glacial time periods, making it possible to track the northward expansion of walruses as the sea ice retracted (Dyke et al. 1999). The northern limit for walruses was in the vicinity of Long Island, New York, after which it advanced to the Bay of Fundy by 12 700 yr BP, to southern Labrador by 11 000 yr BP, and to the central Canadian Arctic by 9700 yr BP. The southern distribution limit also retracted and was in the Bay of Fundy by 7000 yr BP. There are very few records of Pacific walrus from late glacial and early post-glacial time. The oldest find, from Vancouver Island, is ~70 000 yr old. Another was found in San Francisco harbor and dated to 27 200 yr BP (Dyke et al. 1999).

### Abundance

Very few species of marine mammals have been studied anywhere in the Arctic for long enough to allow an assessment of the possible effects of long-term environmental fluctuations, including climate warming, on population size and demographic parameters. Changes in population abundance in relation to changes in habitat have been best documented for Arctic pinnipeds and polar bears as their population levels are more easily monitored than are those of cetaceans. Stirling (2002) reviewed studies of large-scale declines in ringed seal and polar bear reproduction and survival of young in both the mid-1970s and mid-1980s in the southeastern Beaufort Sea. Reduced reproductive rates or lack of reproduction in ringed seals were associated with heavy overwinter sea ice conditions, late breakup, and probably reduced primary and secondary productivity (Smith and Stirling 1978, Stirling et al. 1982, Kingsley and Byers 1998) and demonstrated that environmental fluctuations were capable of having a significant influence on reproductive success.

Dense or complete ice cover may act as a barrier to cetaceans as they need to breathe at the surface (Lowry 2000). When sufficient open water is not available, large-scale mortality events may occur. Ice entrapments are best documented for belugas and narwhals, where sudden changes in weather conditions cause rapid freeze-up of leads and cracks, thus eliminating access to oxygen (Siegstad and Heide-Jørgensen 1994, Heide-Jørgensen et al. 2002b). Approximately 15 000 belugas move through the system of recurrent open-water leads and cracks in the North Water polynya in winter, situated at the entrance to Smith Sound between Northwest Greenland and the northeastern Canadian High Arctic (Vibe 1950, Finley and Renaud 1980, Reeves and Mitchell 1987, Richard et al. 1998b, 2001). Historically there are several examples of belugas being entrapped in the North Water pack ice and any long-term change in sea ice in this region (increasing ice concentrations or increasing variability in the pattern of ice breaking up and refreezing; Heide-Jørgensen and Laidre 2004) could increase the potential of sea ice entrapments and affect the abundance of beluga stocks.

A decline in the polar bear population of western Hudson Bay has also been linked to climate warming (Stirling et al. 1999, Stirling and Parkinson 2006, Regehr et al. 2007), particularly in the spring months of April through June (Gagnon and Gough 2005). The average date of breakup is now approximately three weeks earlier than it was 30 years ago (Stirling et al. 2004). Polar bears are coming ashore in spring in progressively poorer body condition and have to fast for at least four months during the ice-free period (eight months for pregnant females). The decline in reproduction and survival of young and very old bears, combined with continued harvesting at what are now unsustainable levels, has resulted in a reduction in population size (~22%) from 1200 bears in 1987 to ~935 in 2004 (Regehr et al. 2007).

### Movements and migrations

Typically, the distributions of large mammals do not vary greatly over the timescales at which ecologists usually study them. For many Arctic marine mammals, migration routes are not well understood and many

specific routes remain undescribed. Thus, evaluations of possible altered movement or migration patterns of most Arctic marine mammals are predominantly "educated guesses" at best, based on observations of past and current habitat preferences. There are no reports in the literature documenting changes in movements and migrations that can be linked to climate change. Several studies have documented migration patterns for narwhals (Dietz et al. 2001, Heide-Jørgensen et al. 2003*a*), belugas (Barber et al. 2001, Richard et al. 2001, Suydam et al. 2001), and bowheads (George et al. 2004, Heide-Jørgensen et al. 2006). These studies indicate animals use very similar routes each year. In these cases, migration may not be altered with changes in habitat given that matrilineal behavior learning apparently "locks" populations into traditional habitat use and reduces the ability to make adaptive adjustments to environmental change. The movements of ice seals, polar bear, and walrus are, to a large degree, facultative and only occur to the extent necessary for the species to remain in its preferred habitat. Thus changes in migrations routes or movement patterns of these species will likely not be detected until ecological conditions, particularly the distribution and abundance of ice, change significantly. To date, no climate-related changes in migration patterns have been documented.

### Demography

Several studies have demonstrated the demographic sensitivity of ringed seals to changes in sea ice conditions or habitat. In the mid-1960s, 1970s, and 1980s, reproductive failures in ringed seals in the Beaufort Sea and Amundsen Gulf were associated with severe ice conditions (Stirling and Archibald 1977, Smith and Stirling 1978, Stirling et al. 1982, Smith 1987, Kingsley and Byers 1998, Stirling 2002). It took approximately three years before reproduction and pup survival returned to normal, and immigration may have been partially responsible for the recovery in total numbers. These events, as well as the vulnerability of pups in subnivean lairs to warm weather or rain in spring (Stirling and Smith 2004), clearly demonstrate the sensitivity of ringed seals to changes in their sea ice habitat. More recent studies of ringed seals in western Hudson Bay have indicated reduced reproduction, pup survival, and recruitment of ringed seals possibly correlated with decreased snow depth, a general warming trend, and changes in the timing of breakup of sea ice (Ferguson et al. 2005, Stirling 2005).

In the early to mid-1980s, the natality of female polar bears in western Hudson Bay was the highest recorded for polar bears anywhere. In those years, up to 40% of the yearlings were successfully weaned at only 1.5 years of age instead of the normal 2.5 years and triplet litters were common (Ramsay and Stirling 1988). Through the late 1980s and the 1990s there was a steady decline in the proportion of cubs weaned as yearlings and almost no triplet litters. The survival of bears ≤4 years and ≥20 years of age were directly and significantly affected by breakup date (i.e., reduced survival in years with early breakup). Survival probabilities of bears 5–19 years old were unaffected (Regehr et al. 2007). In Svalbard, polar bear natality rate and litter production decreased between 1993 and 2002 (Derocher 2005) and were both correlated with the Arctic Oscillation. However, since the population may also be showing density-dependent responses, climate effects could not be discerned.

In recent years in the Beaufort Sea, the edge of the polar pack has retreated to much farther north in summer (Comiso 2002, Serreze et al. 2003, Walsh 2008), resulting in a wider expanse of open water between the ice and shore, later freeze-up, and increased difficulties for female polar bears seeking terrestrial denning sites. Again, 2005 was a record year for summer sea ice minima, suggesting continued increases in the distance between land and ice (Stroeve et al. 2005). In the Beaufort Sea, fewer maternity dens of polar bears have been recorded in the multiyear ice than on shore (Amstrup and Gardner 1994), but if the trend of retreating pack ice in summer continues, the proportion of females denning offshore might increase, depending on the availability and stability of suitable sea ice habitat.

Demographics of Arctic cetaceans are difficult to study as they are infrequently observed and rarely resighted. Therefore, few studies have documented links between cetacean demography and Arctic climate. It has been postulated that decreases in summer ice extent and resultant increases in open water may initially benefit whales via enhanced local production of prey, extension of the foraging period, or both (Moore and Laidre 2006; J. C. George, C. Nicholson, S. Drobot, and J. Maslanik, *unpublished manuscript*). Consistent growth of the western Arctic bowhead population at an annual rate of 3.4% for the period 1978–2001 (George et al. 2004) indicates positive demographic changes during a period of sea ice reduction. However, while the relationship could be considered a demographic cause and effect with respect to climate change, such an interpretation is confounded by the severely depleted state from which bowhead whales are recovering as a result of overharvesting.

### Body condition

Habitat loss may put additional physiological demands on animals. Not only may body condition be compromised, but individuals may be put at increased risk of disease and epizootics (Burek et al. 2008). In some cases, reduced body condition has been clearly linked with changes in sea ice.

A statistically significant relationship exists between date of sea ice breakup and the body condition of polar bears when they come ashore in western Hudson Bay (i.e., the earlier the breakup the poorer the condition of the bears; Stirling et al. 1999). Bears are forced off the ice onto land earlier in the summer and have a shorter

time to feed on the ice at the most important time of the year. This reduces fat stores, and the length of the period through which they are able to fast on their reserves decreases (Stirling et al. 1999, Derocher et al. 2004). In the 1980s the mean mass of pregnant female polar bears in autumn was 283 kg (Derocher et al. 1992), and no females below 189 kg were recorded with a cub in the following spring. Derocher and Stirling (1995) recorded a mean annual mass loss of 4.7 kg for pregnant females between 1980 and 1992. Assuming a linear trend in mass loss, the average females may be below the minimum required mass for successful reproduction within the next 20–30 years, assuming the climate continues to warm as projected by the Intergovernmental Panel on Climate Change (IPCC; Derocher et al. 2004, Stirling and Parkinson 2006). In Svalbard, Derocher (2005) detected a cyclic variation in body size of adult male and female polar bears that, between 1990 and 2002, correlated with the Arctic Oscillation.

Bowhead whale body condition has also been linked to patterns of sea ice loss (J. C. George, C. Nicholson, S. Drobot, and J. Maslanik, *unpublished manuscript*). Body condition of bowheads landed by Alaskan Eskimos between 1982 and 1999 was higher when average sea ice concentrations in summer feeding areas were lower. Local increases in primary production due to reduced sea ice cover in the eastern Beaufort Sea (improved feeding opportunities) have been hypothesized as the reason for improved body condition.

### Behavior and interspecific interactions

Marine mammals likely compete with one another on some level despite their different specializations (Lowry 2000). If the climate continues to warm, a continued reduction in sea ice will follow and likely result in the northward expansion of some presently subarctic species, with potential for increases in disease, predation, and competition for food.

Currently, several subarctic species move into the Arctic in summer to feed (e.g., humpback [*Megaptera novaeangliae*], fin [*Balaenoptera physalus*], minke [*Balaenoptera acutorostrata*], gray [*Eschrichtius robustus*], blue [*Balaenoptera musculus*], pilot [*Globicephala melas*], killer [*Orcinus orca*] whales, and harbor porpoises [*Phocoena phocoena*]), and some of these may start to arrive further north at progressively earlier dates and perhaps be in direct competition with those species that live year-round in the Arctic. For example, harp seals that pup in the eastern North Atlantic and migrate to the Barents Sea in summer have been documented moving in herds of >100 000 seals to coastal Norway or the North Sea during years when sea temperatures deviated below normal and/or years with low prey abundance (e.g., Wiig 1988, Øritsland 1990, Haug et al. 2006).

Coinciding with warming trends, there has been a well-documented influx of subarctic species that is shown in West Greenland hunting statistics. The prevalence of ringed seals decreased dramatically with a shift to a warmer climate beginning in the 1920s (Rosendal 1961, Teilmann and Kapel 1998), while Arctic cod and other ringed seal prey items receded northward and Atlantic cod from Iceland invaded the West Greenland coast (Jensen 1939). This resulted in harp seals replacing ringed seals as the largest proportion of the catch. This northward retraction of ringed seals may have resulted from both the change in sea ice habitat and the availability of their preferred prey species.

Stirling (2005) reported an increase in the number of harbor seals in the open water harvest by Inuit hunters in Arviat, on the western coast of Hudson Bay, possibly because of a trend toward greater amounts of open water. Similarly, Iverson et al. (2006) reported increasing proportions of harbor seals in the diet of polar bears in western Hudson Bay, based on analysis of fatty acid composition. Using data from archeological middens on the coast of Labrador and southeastern Baffin Island, Woolett et al. (2000) reported that the frequency of occurrence of ringed seals decreased and that of harbor seals increased during periods of light ice coverage.

In Alaska increased summer use of coastal habitats by polar bears has been reported in the southern Beaufort Sea population (Schliebe et al. 2005). A significant positive relationship was found between the distance from shore to the ice edge and the number of bears observed on the coast. The timing of fall freeze-up has been one to two months later during the last 10–15 years and the number of interactions with people has increased as bears have spent more time on land along the coast. The number of bears killed annually for safety reasons increased from approximately three in the early 1990s to ~10 between 1998 and 2004. In northeast Greenland (i.e., ~69° N to 76° N), the fraction of polar bears shot from a boat (as opposed to spring sled trips) increased from ~5% in 1983–1991 (Born 1995) to ~30% in 1994–1999 (Sandell 2001).

Most recently, observations of intraspecific predation and cannibalism in polar bears in the Beaufort Sea may reflect nutritional stress related to longer ice-free seasons (Armstrup et al. 2006). Also, C. Monnett and colleagues (C. Monnett, J. Gleason, and L. Rotterman, *unpublished data*) reported seeing several bears that had probably drowned while swimming in the open water between the coast and offshore pack ice during a strong storm. It was not known which direction the bears may have been swimming or what factors may have stimulated them to swim across the extensive open water present in September. Regardless, larger waves, resulting from a greater fetch of open water in recent years, makes polar bears more vulnerable to drowning if caught by storms while swimming in open water.

In 1998, the summer ice of the Chukchi Sea covered 25% less area than during the minimum for the previous 35 years. Kelly (2001) observed that during this time, a substantial proportion of the ice edge was north of the

continental shelf over water that was too deep for walruses to feed. Recent observations of walrus calves separated from their mothers during years with extensive retreat of seasonal ice cover also suggest walrus recruitment may be impacted by reduced amounts of ice over the continental shelf (Cooper et al. 2006). Furthermore, in years when unusually high numbers of walruses use the terrestrial haul-out of Wrangel Island, Russia, polar bear predation is high, especially on young of the year (Ovsyanikov 1996).

Killer whales have a large distribution that includes both subpolar and polar waters. In the Pacific sector, they are known to range into sea ice and prey upon Arctic species, including walruses, belugas, and ice-associated seals (Lowry et al. 1987b). George et al. (1994) found that 4–8% of harvested western Arctic bowheads showed scars indicative of killer whale attacks. Killer whales were the likely cause of a severe reduction in sea otters (*Enhydra lutris*) in the Aleutian Islands (Estes et al. 1998), and energy calculations show that they are capable of having a large predatory impact on marine mammal prey (Williams et al. 2004). The number of killer whale sightings in the eastern Canadian subarctic waters has doubled every 20 years since the 1920s, with observations shifting from Hudson Strait–Foxe Basin to Hudson Bay, suggesting greater dispersion within Arctic waters in the last 30 years (S. Ferguson, *unpublished data*). If killer whales respond to reduced Arctic ice cover by moving further north, it is possible that their predatory impact on other marine mammal populations will increase.

## QUANTIFYING THE SENSITIVITY OF ARCTIC MARINE MAMMALS

Although several speculative papers have provided an important stimulus to thinking about the manner in which future climate warming (as projected by the IPCC [ACIA 2005]) might affect Arctic marine mammals, we need to address what may happen in the future with individual species and ecologically interrelated species on a circumpolar scale. Thus, we have attempted to quantify, as objectively as possible, which ecological factors singly or in combination might have significant effects. Such an approach will provide an objective basis for assessing the relative vulnerability of Arctic marine mammals and facilitate identification of the most sensitive species, regions, and reasons for vulnerability. This in turn should aid development of testable hypotheses and goals for future research and monitoring studies, thus significantly increasing our ability to understand, and respond to if possible, ongoing processes.

A sensitivity index was constructed based on nine variables that likely have the greatest influence on the response and vulnerability of Arctic marine mammals to climate change. "Sensitivity" was operationally defined as the degree to which Arctic marine mammal species respond to perturbations or stresses (i.e., deviations of environmental conditions beyond the expected range in the previous century) induced by climate warming. The index primarily quantifies differential species sensitivity as measured by the change in environmental conditions on a circumpolar scale.

Each model variable was associated with specific quantitative ranking criteria evaluated on a three-point scale (with 1 being most sensitive and 3 being least sensitive). Ranks were evaluated independently by each author. We recognize that in this initial attempt to devise an objective index, all factors are treated as equally influential, when in reality it is likely that some factors will be more important than others and that the importance of each could vary significantly between species. However, in general, this approach sets the stage for more advanced quantification of the relative importance of each factor in the future as we document and understand more about individual climate effects on different species. Thus, in this index, the minimum value was 9 (highly sensitive in all categories) and the maximum value was 27 (least sensitive in all categories). The sum of the ranks in all categories resulted in an overall species-specific sensitivity ranking and facilitated comparisons between species. The evaluation and ranking of each species considered the species biology and ecology on a circumpolar perspective (i.e., across the entire range). Variables and criteria were as follows:

1) Population size: This variable refers to the current worldwide population size for each species. Species that are numerous should have more options for adapting or reestablishing themselves in local or new areas. A species with a population size <100 000 individuals was ranked as a 1, a species with a population size between 100 000 and 500 000 individuals was ranked as a 2, and a species with a population size >500 000 individuals was ranked as a 3. Uncertainty in population size was considered but in all cases the general magnitude of the population size was classifiable without error.

2) Breadth/extent of geographic range: This variable identifies the geographic distribution of each species within the circumpolar Arctic. Breadth of geographic range was considered important because widely distributed species should be less vulnerable than narrowly distributed species given regional deviations in the direction and magnitude of climate warming (see Schwartz et al. 2006). The Arctic was divided into eight equivalent octants along 45° longitude lines beginning at 0° W. If a species distribution occupied fewer than five octants it was ranked as a 1, if a species occupied five to seven octants it was ranked a 2, and if a species had a complete circumpolar distribution (occupied all eight octants) it was classified as a 3.

3) Habitat specificity: This variable describes the capacity of the species to use different habitats in the Arctic. It is considered important because habitat generalists are more buffered against climate change than habitat specialists given they can occupy a greater range of habitat types. Species were ranked based on

winter/spring habitat use, the season in which the most pronounced climate-warming effects are being detected. A comprehensive list of physical habitats (Table 1) was used to determine whether a species used each habitat. A species that used seven or fewer different types of physical habitats was ranked a 1, a species that used eight or nine physical habitats was ranked as a 2, and a species that used more than nine different physical habitats was ranked a 3. This classification involved unquantifiable subjectivity.

4) Diet diversity: This variable identified the diversity of diet. The diet diversity of a species is considered a fundamental variable because diet flexibility or ability to consume a variety of prey species should result in decreased sensitivity. A species was classified as a 1 if only one prey type comprised >20% of its diet, a species was classified as a 2 if two prey types each comprised >20% of its diet, and a species was classified as a 3 if three or more prey types each comprised >20% of its diet. Prey types were sometimes considered to be individual species (e.g., Arctic cod, Greenland halibut) but in other cases, out of necessity, were functional groups (e.g., copepods).

5) Migrations: This variable describes the extent and frequency of annual migrations. Migratory species are characterized as more vulnerable due to a specific temporal or seasonal reliance on a certain habitat. A species was ranked a 1 if the entire population undertook annual migrations >1000 km with defined routes and specific sites used throughout the year, a species was ranked a 2 if the population undertook smaller migrations or substantial seasonal shifts in distribution, and a species was ranked a 3 if the population remained in the same general region over the course of its annual cycle.

6) Individual site fidelity: This variable quantifies the degree of individual site fidelity. Site fidelity is considered important because heavy reliance on localities with predictable environmental conditions year after year increases vulnerability to changes in those conditions. A species was ranked a 1 if individuals used specific sites year after year throughout their life cycle, a species was ranked a 2 if it had fidelity to many different sites throughout the life cycle, and a species was ranked a 3 if it had periods of its life cycle completely lacking site fidelity. A "site" was considered to be a summering or wintering ground, haul-out area, or denning area that is localized or <25 000 km² in area.

7) Influences of changes in sea ice: This variable described the sensitivity of a species to direct changes in sea ice (as a physical structure). A species was considered highly sensitive and ranked a 1 if it was critically dependent upon sea ice to complete its life cycle or to feed, a species was ranked a 2 if changes in the physical structure of sea ice would moderately influence the life cycle or feeding success but in the absence of ice alternatives would be available, and a species was ranked a 3 if it was not dependent upon the physical structure of sea ice for its life cycle or feeding.

8) Influences of changes in the trophic web: This variable described the sensitivity of a species to changes in the trophic web (altered patterns of primary and secondary production) due to a warming ocean. This considered the influx of new or alternate prey species within the species range, together with the disappearance of current prey species, and classified the manner in which the carrying capacity of the species would be affected. A species was ranked a 1 if its carrying capacity would be reduced due to reduced food sources, a species was ranked a 2 if its carrying capacity would generally remain the same, and a species was ranked a 3 if changes in the trophic web would result in increased food sources and an increased carrying capacity. This was clearly a speculative classification based on available knowledge of food chain relationships and possible alterations during a warming climate.

9) Maximum rate of population increase ($R_{max}$): This variable quantifies a species' maximum population growth rate. Species with a high growth potential are more able to take advantage of good environmental conditions whenever they may occur and those with low growth potential, particularly mammals, tend to be more vulnerable to extinction. If a species had an $R_{max}$ ≤ 5% it was classified as a 1, if it had an $R_{max}$ between 6% and 10% it was classified as a 2, and if a species had an $R_{max}$ that was >10% it was classified as a 3. This classification was considered precise.

### Species Rankings and Index Results

Several of the variables included in the sensitivity model are known broadly to be important features controlling species vulnerability in a wide variety of habitats and ecosystems (Furness and Tasker 2000, IUCN 2001), including small population size, limited geographic distribution, specialized diet, low dispersal, and site fidelity. Factors included in the model that make the exercise specific to Arctic marine mammals include Arctic habitat choice (Table 1) and flexibility with respect to changes in sea ice regime and prey base.

Species sensitivity scores ranged from 12 to 25 and were spread well across the potential range of values (Table 2). The position of each species on this index was fairly robust to small changes in individual scores since the index ranges over 19 points, with species fairly evenly spread across this entire range of scores. Some factors were based on objective and published criteria (population sizes, $R_{max}$) while others were based on a more subjective expert assessment (influences of changes in sea ice or trophic web). Each factor received equal weight in computing the index, yet weighting could be applied to factors as further data become available on what features influence vulnerability to climate warming.

The three most sensitive species (scores ≤15) were the hooded seal, the narwhal, and the polar bear. Species

TABLE 2. A sensitivity index for Arctic marine mammals.

| Species | Population size[†] | Geographic distribution[‡] | Habitat specificity[§] | Diet diversity[‖] | Migration[¶] | Site fidelity[¶] | Sea ice changes | Trophic web changes | $R_{max}$[#] | SUM |
|---|---|---|---|---|---|---|---|---|---|---|
| **Arctic** | | | | | | | | | | |
| Beluga | 2 | 2 | 2 | 2 | 2 | 1 | 3 | 3 | 1 | 18 |
| Narwhal | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 2 | 1 | 12 |
| Bowhead | 1 | 2 | 2 | 2 | 1 | 2 | 3 | 2 | 1 | 16 |
| Ringed seal | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 3 | 3 | 25 |
| Bearded seal | 2 | 3 | 2 | 3 | 3 | 3 | 1 | 3 | 3 | 23 |
| Walrus | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 3 | 2 | 18 |
| Polar bear | 1 | 3 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 14 |
| **Subarctic** | | | | | | | | | | |
| Spotted seal | 2 | 1 | 3 | 3 | 2 | 2 | 1 | 2 | 3 | 19 |
| Ribbon seal | 2 | 1 | 3 | 2 | 2 | 3 | 1 | 2 | 3 | 19 |
| Harp seal | 3 | 1 | 3 | 3 | 1 | 1 | 1 | 3 | 3 | 19 |
| Hooded seal | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 3 | 15 |

*Notes:* The index was developed for nine variables on a three-point scale (1, highly sensitive; 3, least sensitive). Criteria for ranking are described in *Quantifying the sensitivity of Arctic marine mammals.*

† Ringed seal worldwide abundance is several millions (Frost and Lowry 1981, Reeves 1998). The world population of bearded seals is uncertain but has been estimated to be ~750 000 (Bychkov 1971, Burns 1981, Cleator 1996). Worldwide, harp seals number several millions of animals (International Council for the Exploration of the Sea/North Atlantic Fisheries Organization, *unpublished manuscript*), and total pup production at the turn of the century was estimated to be 1.4 million animals per year (Stenson et al. 2003, Haug et al. 2006). Total worldwide abundance of hooded seals is >400 000 animals in Atlantic Canada (Reeves and Ling 1981, Stenson et al. 1997, Michalsen 2004). Spotted seal worldwide abundance has been estimated to be 335 000–450 000 animals (Burns 1973), and Burns (1981) estimated the worldwide population of ribbon seal at 240 000 in the mid-1970s. The population size of Atlantic walruses is probably <20 000 (Born et al. 1994), with 2000 in the Barents Sea (Gjertz and Wiig 1995), several thousand in the Laptev (Belikov et al. 1998), and between 200 000 and 235 000 in the Pacific (Gilbert et al. 1992). The worldwide population size of polar bears is between 20 000 and 25 000 (Aars et al. 2006). Worldwide population size of narwhals is ~50 000 animals (Koski and Davis 1994, Innes et al. 2002). While good population estimates are available for some beluga populations, the abundance of others is virtually unknown, and beluga abundance worldwide is estimated to be at least 100 000 (Harwood et al. 1996, Boltunov and Belikov 2002, Innes et al. 2002). Bowheads number less than 20 000 animals worldwide (George et al. 2004; S. Cosens, L. Dueck, and P. Richard, *unpublished manuscript*).

‡ See Figs. 1–4. Species ranges are from Burns (1981), Rice (1998), Heide-Jørgensen (2002), Kovacs (2002*a*, *b*), Lavigne (2002), Miyazaki (2002), Reeves et al. (2002), and Born (2005). Current and projected sea ice edges are from Walsh (2008) based on Arctic Climate Impact Assessment five-model medians for 1980–2000 (current) and 2040–2060 (projected).

§ See Table 1 and *Species biology and habitat relationships.*

‖ Data sources: belugas (Seaman et al. 1982, Heide-Jørgensen and Teilmann 1994), narwhals (Laidre and Heide-Jørgensen 2005*a*), bowheads (Lowry 1993, Lowry et al. 2004), ringed seals (Lowry et al. 1980*a*, Lydersen 1998, Siegstad et al. 1998, Wathne et al. 2000), bearded seals (Lowry et al. 1980*b*, Antonelis et al. 1994, Hjelset et al. 1999), walrus (Fay 1982, Gjertz and Wiig 1992, Born et al. 2003), polar bears (Smith 1985, Calvert and Stirling 1990, Smith and Sjare 1990, Stirling and Øritsland 1995, Derocher et al. 2002), subarctic seals (Bukhtiyarov et al. 1984, Burkanov 1989, Frost and Lowry 1990*b*, Lydersen et al. 1991, Murie and Lavigne 1991, Sergeant 1991, Beck et al. 1993, Lowry et al. 1998, Folkow and Blix 1999, Deguchi et al. 2004, Hammill et al. 2005).

¶ Data sources: belugas (Richard et al. 1998*a*, 2001, Suydam et al. 2001, Hobbs et al. 2005), narwhals (Dietz et al. 2001, Heide-Jørgensen et al. 2003*a*), bowheads (Moore and Reeves 1993, Heide-Jørgensen et al. 2006), ringed seals (Smith 1987, Heide-Jørgensen et al. 1992*a*, Teilman et al. 1999, Gjertz et al. 2000*a*, Born et al. 2004, Lydersen et al. 2004; L. A. Harwood and T. G. Smith, *unpublished data*), bearded seals (Gjertz et al. 2000*b*, Krafft et al. 2000), walrus (Fay 1982, Gjertz et al. 1993, Gjertz and Wiig 1994, Born 2005), polar bears (Garner et al. 1990, Ramsay and Stirling 1990, Wiig 1995, Born et al. 1997*b*, Ferguson et al. 1999, Amstrup et al. 2000, Mauritzen et al. 2001, Wiig et al. 2003), subarctic pinnipeds (Kelly 1988, Sergeant 1991, Folkow et al. 1996, 2004; J. L. Bengtson, *unpublished data*). Also see *Documented impacts of climate change: Movements and migrations.*

# $R_{max}$ is estimated to be 4% per year for belugas and narwhals (Brodie 1971), ~3% for bowheads (George et al. 2004), 8% for walrus (Sease and Chapman 1988, Chivers 1999), and 5% or less for polar bears (Taylor et al. 2005). We assumed a pinniped maximum theoretical net productivity rate of 12% for ringed, bearded, harp, hooded, ribbon, and spotted seals (Wade and Angliss 1997, Reeves 1998).

that were moderately sensitive (scores from 16 to 20) were the bowhead whale, beluga, harp seal, spotted seal, ribbon seal, and walrus. The least sensitive species (scores > 20) were the ringed seal and bearded seal. The sensitivity index identified three types of sensitive Arctic species: narrowly distributed and specialized feeders (i.e., narwhal, walrus), seasonally ice-dependent species that use the marginal ice zone (i.e., hooded seal, harp seal), and species principally reliant on annual sea ice over the continental shelf and areas toward the southern

extent of the edge for foraging (i.e., polar bears). Species with circumpolar distributions, large population sizes, a varied diet, and flexible habitat requirements were in general less sensitive (i.e., ringed seals) than those that were more restricted in distribution, less abundant, or habitat specialists.

Parameters that contributed to high sensitivity for cetaceans were high site fidelity, migratory behavior, and low $R_{max}$. In the case of the narwhal, a high degree of specialization, small population size, and limited range

and diet resulted in greater sensitivity when compared to the beluga or bowhead whale. The widely distributed and relatively flexible beluga was the least sensitive cetacean with a score of 18. Cetaceans were the least sensitive to the influence of sea ice change.

All pinnipeds were sensitive to the influence of sea ice changes, with subarctic pinnipeds receiving higher overall ranks due to a limited geographic distribution, site fidelity, and migration. Polar bears and walrus were also highly sensitive to sea ice changes.

## DISCUSSION

Assessment of the relative vulnerability of different Arctic marine mammals to climate warming with a sensitivity index provides an objective way of ranking each species on a circumpolar scale. It is widely accepted that many, if not all, Arctic marine mammals will be affected by climate warming due to direct and indirect habitat alterations. In simple terms, the broad and rapid disappearance of the primary habitat feature, sea ice, on which nearly all species are reliant in some way, seems unlikely to result in positive ecological responses. The sensitivity index scores should not be considered indicative that some species are free from vulnerability. In particular, at this stage of development, our initial index does not include information on regional or local sensitivity of populations within the overall species.

Not all potentially influential variables are included in the sensitivity index. Items such as carrying capacity of the environment, uneven distribution of subpopulations (i.e., population fragmentation), dispersal potential, trends in populations (past, present, or projected), and vulnerable life history stages could prove more critical to species' sensitivity than we are able to project at this point. Variables were selected based on consensus of the most important features of climate alteration but may not be evaluated equally on a circumpolar scale. For example, the geographic distribution parameter rests on the equality of octants in terms of habitat quantity and quality, as well as whether such habitat in each octant will be equally likely to change with changes in climate. Conceptually, this index could be taken to the next level by estimating species vulnerability as the probability that a species will be exposed to individual stresses to which it may be sensitive. Even so, it remains highly difficult to define sensitivity on an Arctic-wide scale due to the large uncertainty in climate predictions and regional deviations in trends.

As developed in this paper, the index includes the implicit assumption that all measures of sensitivity are equal in significance. Thus, the implication is that most species would likely have to be sensitive to many effects before becoming truly vulnerable. In most cases, we suspect that generalization would be correct. However, vulnerability of some species, such as the ringed seal, may be much more influenced by a single type of change. For example, a trend toward unseasonable rain in spring, which could melt the subnivean birth lairs in

which pups are normally protected from cold and predators (e.g., Stirling and Smith 2004), could have a large negative impact on the survival of whole cohorts of pups in a large area. There may be other examples of species that, like ringed seals, are relatively insensitive to many factors but highly vulnerable to the effects of others.

### Sensitive species vs. indicator species

An important distinction should be made between "sensitive species" and "useful indicator" species. A species that ranks highly on this sensitivity index does not, by default, necessarily make it an ideal indicator species. Many of the most sensitive species are expensive, difficult, or impossible to monitor, and there is great logistic complexity in collecting data over long periods. Thus, sensitivity is just one factor that should be considered in designing monitoring programs. Furthermore, there is a risk that focusing monitoring on a highly vulnerable species, particularly one with a small population and relatively limited distribution, may provide results relevant to a local assessment, although not necessarily useful or informative from a circumpolar perspective.

In some cases, the sensitivity model suggests a species may not be most sensitive to climate change even when impacts have already been detected. An example is the ringed seal, in which the effect of its numerical abundance, wide distribution, and range of habitats all contribute to its lower sensitivity value, but that could be misleading. The combined effects of loss of snow cover for subnivean lairs, reduction of sea ice, and possible ecological regime shifts that affect prey species may be so great that size of regional populations could be reduced significantly, and possibly quickly, in some areas.

There is also the strong likelihood that we are simply unaware of equally or more important impacts occurring on populations of some species simply because of the logistic difficulty and expense of monitoring them. In addition, because the climate has been warming in some areas of the Arctic for at least 30–40 years, changes have already occurred so that with the exception of a very small number of baseline studies, there are few reference points against which to measure possible changes.

Alterations in sea ice are predicted to occur most rapidly in the southern regions along the marginal ice zone (Walsh 2008), therefore seasonally ice-dependent seals or polar bears using the southern extent of the ice edge may be the best short-term indicators of climate warming. The dependency of ice-breeding phocid seals on stable pack ice, at least until pups have weaned and completed their post-weaning fast and transition to pelagic feeding, is critical (Stirling 2005). Reduced total areas and stability of sea ice in whelping areas may cause neonatal mortality, changes in food availability for pups, and increased risk of epizootics due to crowding on whelping patches (Lavigne and Schmitz 1990, Heide-

Jørgensen et al. 1992a, Johnston et al. 2005, Burek et al. 2008). Polar bears will likely disappear from the southern portions of their present-day range and retreat to areas of the polar basin and adjacent interisland channels of Arctic archipelagos that retain suitable ice conditions.

### Regional contrasts: Pacific vs. Atlantic walrus

The sensitivity model evaluated each species on a circumpolar scale. In some cases, ranking species was difficult given the large range of behaviors and habitat preferences and ecological flexibility exhibited by stocks or populations. Species in some regions were considered highly sensitive to climate warming while the same species in another region appeared to be less vulnerable. This is reflected in the moderate sensitivity scores (~18–20) of these species (i.e., walrus and beluga; Table 2), and in some cases a pan-Arctic species consensus was difficult because of ecological differences in parts of their range.

The walrus exemplifies this situation. Seasonally, walrus haul out on ice, but in summer they will use both land and ice floes, if available. Ice likely provides several advantages, including free transportation with the current, a platform for whelping and nursing, and the ability to remain and rest over offshore feeding areas.

Atlantic walruses of both sexes and all age classes haul out together on land in several places, even when ice is present. Historically, some Atlantic walruses occurred in areas with little or unpredictable sea ice (e.g., Nova Scotia, northern Norway, and Iceland; Reeves 1978). Furthermore, the walrus, as a species, is clearly anatomically and behaviorally capable of surviving in areas with no ice, provided there are areas of continental shelf with sufficient benthic fauna within energetically feasible swimming range of a haul-out. Thus, because the critical factor is likely the proximity of the haul-out to adequate food resources at shallow depths, the upward limit to population size in a given area may not be related to the extent and availability of sea ice.

Reductions of summer sea ice coverage were considered to be more serious for walruses in the Pacific Ocean than in the Atlantic. The large Pacific walrus population is sustained by substantial benthic production on the shallow continental shelf of the northern Bering and Chukchi seas (Fay 1982, Grebmeier et al. 2006). In the recent past, this region was covered seasonally with sea ice that provided the walruses a platform from which they were able to access benthic resources throughout the entire area (Fay 1982). The normal pattern has been for many male Pacific walrus to remain in the Bering Sea in summer and use terrestrial haul-outs to rest between feeding forays, while most of the females, juveniles, and calves follow the receding ice into the Chukchi Sea. Prior to the recent period of climatic warming, when the sea ice reached its annual summer minimum, the southern edge was typically still on (or near) the continental shelf

so that walruses could continue to feed over much of the Chukchi Sea from ice haul-outs. With recent climate warming, however, the summer ice edge now recedes far into the Arctic Ocean, hundreds of kilometers north of the shelf break (Comiso 2002, Walsh 2008). This poses a particular problem for adult female walruses that are nursing young calves that presumably would be disadvantaged by swimming long distances in the open sea (Cooper et al. 2006). Unlike males, female Pacific walruses seem to avoid hauling out on land, perhaps because when they do so their calves are vulnerable to crushing in the large dense herds (Fay and Kelly 1980), and they may be preyed upon by polar bears (Ovsya-nikov 1996) and perhaps brown bears (*Ursus arctos*). Furthermore, walrus calves are dependent upon maternal care for approximately two years before they can forage completely on their own and are therefore ill-adapted to lack (or rapid retreat) of seasonal ice cover (Cooper et al. 2006).

Reduced seasonal sea ice cover in the Bering Sea will also affect walrus feeding, though how that might develop is less clear at present. Adult males have long used terrestrial haul-outs on both sides of the Bering Sea during summer (Fay 1982) from which they range seaward to feed (Jay and Hills 2005), and that behavior will likely continue independent of changes in sea ice. Historically however, all sex/age classes have used ice haul-outs during fall, winter, and spring for up to five months (Fay 1982). Projections indicate that sea ice in the Bering Sea will become much less extensive in the coming years (Walsh 2008), making it more difficult for walruses to access all of the shallow areas where feeding has occurred in the past.

Overall, with less seasonal ice coverage throughout their historic range, Pacific walrus will have difficulty exploiting as large an area for feeding as they could when more ice was available. In addition, the productivity of walrus prey populations is likely to be directly impacted by warming of their environment (Grebmeier et al. 2006). Thus, we predict that the Pacific walrus population will be (in fact probably already is being) significantly impacted by climate warming, with the impact on females being especially significant because they require both sufficient access to food resources and safe places to rest and care for their young.

In the Atlantic, however, the present walrus population is much smaller relative to its historical maximum due to reductions by harvest (Born et al. 1997a), and it appears to be more coastal in habitat preference, in part probably because of a narrower continental shelf over much of its range compared to the huge offshore shelf area of the Bering and Chukchi seas. Variably sized mixed groups of all age and sex classes make regular seasonal use of terrestrial haul-outs and sometimes use land for resting even when sea ice is available. Over the short term at least, reductions in sea ice in this region are not considered to be as threatening to the survival of Atlantic walruses, which may be partly because of their

lower numbers relative to the assumed availability and biomass of benthic resources (Born et al. 1997a). Nearly all potential and productive feeding areas in the Atlantic are closer to terrestrial haul-outs than in the Pacific, and fast ice (especially in severe ice years) has generally been assumed to be the factor seasonally excluding walrus from feeding areas in the Atlantic. It has been postulated that the warming climate and reduction in sea ice may increase both foraging area availability and primary production in the nearshore shelf areas, stimulating benthic productivity and feeding opportunities for walruses (Born 2005, 2006).

Lastly, in this context we note that until walruses were eliminated by overharvest, the distribution of Atlantic walrus in Canada extended south to Sable Island, Nova Scotia (Mansfield 1959, Reeves 1978, Dyke et al. 1999). Miller (1997) concluded that between 12 800 and 2900 yr BP walruses occurred in the Bay of Fundy in water temperatures of 12°–15°C, and walruses in Northumberland Sound in the 17th century inhabited waters with summer temperature of up to 18°C. Ray (1960) stated that walruses frequented the Orkney Islands through the mid-16th century and concluded that both Sable Island and Orkney Islands lay within the normal range of the species in historic time. Thus, while it is not possible to predict how walrus will fare with climate warming throughout their range, it is possible that their responses will be different in the Pacific and Atlantic sectors. It would be useful to conduct sensitivity analyses for regional populations of walruses, and perhaps other species such as belugas, in relation to climatic trends predicted for those areas.

### Contrasts within the ice-breeding seals

Two fundamentally different nursing strategies are exhibited by ice-breeding phocid seals (Lydersen and Kovacs 1999) and are important when trying to predict the consequences of significant reductions in the availability of sea ice at critical times in their respective life histories. Harp and hooded seals form dense congregations in pupping areas and have very short lactation periods, during which a large amount of energy is transferred from mothers to pups through extremely energy-rich milk. Mothers store all the energy they require for the nursing period during offshore feeding and generally do not feed during lactation. In contrast, bearded and ringed seals pup at low densities over large areas, and females lactate longer and provide milk that is less energy-rich. Mothers feed during lactation, and, as the pups mature, they slowly learn to swim and feed by following the females into the water. In the case of the bearded seal, pups are also highly mobile so females can easily move between alternative sites. Although far more restricted in geographic distribution and not well studied, spotted seals and ribbon seals appear to be more similar to ringed and bearded seals in terms of their densities in breeding areas and time taken to wean their pups.

Thus, we suggest that an initial reduction in the amount and stability of pack ice in pupping habitat will be more deleterious for harp and hooded seals than bearded or ringed seals. Recently weaned seal pups of all ice-breeding species require a period of largely undetermined duration during which the sea ice remains stable so they can rest upon it and possibly hunt epontic species beneath it. This period must be long enough to survive the period through which they fast and learn to hunt independently, even if they have sufficient fat stores at the time of weaning (Stirling 2005). The stability of ice floes in the marginal ice zone is likely especially important for harp and hooded seal pups that whelp in large numbers at high density and with a high degree of fidelity to traditional and critical whelping locations. Harp and hooded seal pups wean in 10 and 4 days, respectively, which is essential because even the normal potential for rapid degradation and loss of sea ice in early spring requires that they become independent quickly. Thus, there could be significant negative effects on the survival of harp and hooded seals if the marginal ice becomes less stable and breakup occurs progressively earlier as a result of climate warming.

Increasing instability of annual ice would likely have a negative impact on the successful weaning of ringed seal pups given that early breakup increases the possibility of separation of pups from their mothers and that adult females must feed during the six-week lactation period. Ringed seals may have some potential to adapt their behavior to local changes in ice conditions or even the loss of ice in some circumstances, given their small size, low energy requirements, and ability to make use of low snow cover areas. However, the effects of predators will influence the success of such facultative responses once snow and/or ice cover declines below minimums. Some ringed seal terrestrial habitat use occurs in the Baltic Sea (Härkönen et al. 1998) and freshwater lakes of Finland (Sipilä and Hyvärinen 2002). In the Baltic Sea and Bothnian Bay, ringed seals may whelp directly onto the sea ice or make birth lairs in deep drifts along the shore because the sea ice often does not form suitable drifted pressure ridges. It is difficult to say whether ringed seals in other parts of the Arctic, where terrestrial predators are still abundant, would broadly adopt any of these behavioral traits. However, even if they could adapt to using terrestrial habitat to some degree, it seems likely that such habitat could facilitate the survival of a small proportion of the present-day population of ringed seals in the Arctic marine ecosystem.

The current density of ringed seals in the central Arctic Basin is low, although it is possible this region might be able to support a larger population if marine productivity is enhanced through reduced sea ice coverage and multiyear ice is replaced by thinner annual ice (which would allow the passage of more light to stimulate photosynthesis). Even so, the Arctic basin is characterized by deep, highly stratified water where primary productivity is lower than it is in adjacent areas

over the continental shelf. Furthermore, there is considerable overlap in the diet of ringed seals with other species, such as bowhead whales, belugas, and other seals, so it is presently unclear the manner in which whatever resources might be present would be shared.

## CONCLUSION

The ability to develop effective conservation measures for most Arctic marine species in relation to climate warming has been hampered by insufficient data on polar amplification of warming trends, incomplete information on Arctic species distributions and life history traits, and nonuniform or region-specific patterns (Ragen et al. 2008). Overall, the basic biology of Arctic marine mammal species is reasonably well known. However for most species, at least some information on population size, trends, and vital parameters is missing, generally because they tend to be difficult and expensive to monitor. Consequently, demographic and geographic changes will be difficult to detect and to measure and, even more so, to attribute to climate change.

Whatever the effects of habitat change on Arctic marine mammals may be, the situation must still be considered in relation to other potential threats to these resources. Two anthropogenic factors capable of having a significant effect on the status of the Arctic marine mammals are hunting and pollution. In some parts of the Arctic (i.e., especially the North Atlantic sector) hunting is evidently the most serious threat at present (Hovelsrud et al. 2008). Historically several populations have been depleted by overexploitation from which they have not yet recovered (e.g., bowhead whales in the Northeast Atlantic), and alterations in habitat are unlikely to improve their current status. Other populations are currently harvested beyond sustainable levels (e.g., belugas, narwhals, walrus, and polar bears in West Greenland; Alvarez-Flores and Heide-Jørgensen 2004, Wiig 2005, Witting and Born 2005, Stirling and Parkinson 2006) and identification of possible effects of future climatic warming may be confounded by the continued depletion level of these populations. Moreover, for those populations currently being exploited at some level, it may be impossible (with the current ability to assess population size and trend) to accurately detect and describe some of the more subtle consequences of climate warming given that the effects can only be estimated with reasonable accuracy for a few species (e.g., ringed seals and polar bears) and that the magnitude of the uncertainty surrounding the effects of the simultaneous harvest will be large. Although it remains difficult to accurately factor in the consequences of climate warming on assessments of population sizes and trends for most species of Arctic marine mammals, it remains critical to do so because the available evidence suggests alterations to Arctic sea ice and species ecology will be significant, assuming the climate continues to warm as predicted by the IPCC.

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