

Observations and Predictions of Arctic Climatic Change: Potential Effects on Marine Mammals

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ABSTRACT. Recent analyses have revealed trends over the past 20–30 years of decreasing sea ice extent in the Arctic Ocean coincident with warming trends. Such trends may be indicative of the polar amplification of warming predicted for the next several decades in response to increasing atmospheric CO₂. We have summarized these predictions and nonuniform patterns of arctic climate change in order to address their potential effects on marine mammals. Since recent trends in sea ice extent are nonuniform, the direct and indirect effects on marine mammals are expected to vary geographically. Changes in the extent and concentration of sea ice may alter the seasonal distributions, geographic ranges, patterns of migration, nutritional status, reproductive success, and ultimately the abundance and stock structure of some species. Ice-associated seals, which rely on suitable ice substrate for resting, pupping, and molting, may be especially vulnerable to such changes. As recent decreases in ice coverage have been more extensive in the Siberian Arctic (60°E–180°E) than in the Beaufort Sea and western sectors, we speculate that marine mammal populations in the Siberian Arctic may be among the first to experience climate-induced geographic shifts or altered reproductive capacity due to persistent changes in ice extent. Alteration in the extent and productivity of ice-edge systems may affect the density and distribution of important ice-associated prey of marine mammals, such as arctic cod *Boreogadus saida* and sympagic (“with ice”) amphipods. Present climate models, however, are insufficient to predict regional ice dynamics, winds, mesoscale features, and mechanisms of nutrient resupply, which must be known to predict productivity and trophic response. Therefore, it is critical that mesoscale process-oriented studies identify the biophysical coupling required to maintain suitable prey availability and ice-associated habitat for marine mammals on regional arctic scales. Only an integrated ecosystems approach can address the complexity of factors determining productivity and cascading trophic dynamics in a warmer Arctic. This approach, integrated with monitoring of key indicator species (e.g., bowhead whale, ringed seal, and beluga), should be a high priority.

Key words: Arctic Ocean, climate change, sea ice extent, global warming, marginal ice edge zone, bowhead whale, *Balaena mysticetus*, ice-associated seals, ringed seal, *Phoca hispida*, beluga, *Delphinapterus leucas*

RÉSUMÉ. Des analyses récentes ont fait apparaître des tendances, au cours des 20 à 30 dernières années, à la diminution de l'étendue des glaces de mer dans l'océan Arctique qui coïncident avec des tendances au réchauffement. Ces tendances pourraient être symptomatiques de l'amplification polaire du réchauffement prédit pour les prochaines décennies suite à la hausse de CO₂ dans l'atmosphère. Cet article offre un résumé de ces prédictions et des schémas non uniformes de changement climatique dans l'Arctique, en vue d'examiner leurs retombées potentielles sur les mammifères marins. Vu que les tendances récentes de l'étendue des glaces de mer ne sont pas uniformes, les retombées directes et indirectes sur les mammifères marins devraient varier sur le plan géographique. Des changements dans l'étendue et la concentration de la glace de mer peuvent modifier les distributions saisonnières, les aires géographiques, les schémas de migration, l'état nutritionnel, le succès de la reproduction, et, en fin de compte, l'abondance et la structure de la population de certaines espèces. Les phoques associés à la glace, qui dépendent d'un support glaciaire pour le repos, la mise bas et la mue, seraient particulièrement affectés par de tels changements. Vu que les diminutions récentes de couverture de glace ont été plus importantes dans l'Arctique sibérien (de 60° E. à 180° E.) que dans la mer de Beaufort et les secteurs occidentaux, on pense que les populations de mammifères marins dans l'Arctique sibérien pourraient être les premières à faire l'expérience de variations géographiques dues au climat ou d'une modification de leur capacité de reproduction causée par des changements chroniques dans l'étendue de glace. Une modification de l'étendue et de la productivité des systèmes de la marge glaciaire pourrait affecter la densité et la distribution de proies associées à la glace importantes pour les mammifères marins, comme la morue arctique *Boreogadus saida* et les amphipodes vivant en contact avec la glace. Les modèles climatologiques actuels ne sont toutefois pas en mesure de prédire les dynamiques régionales de la glace, les vents, les caractéristiques à mésoéchelle ainsi que les mécanismes de réapprovisionnement en éléments nutritifs, tous éléments que l'on doit connaître pour pouvoir prédire la productivité et la réponse trophique. Il est par conséquent critique que des études à mésoéchelle axées sur les processus identifient les interactions du milieu naturel nécessaires pour maintenir, à des échelles arctiques régionales, une disponibilité de proies et un habitat associé à la glace appropriés aux mammifères marins. Seule une approche intégrée des écosystèmes peut envisager la complexité des facteurs déterminant la productivité et les dynamiques

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trophiques qui en résultent dans un Arctique plus tempéré. Cette approche, intégrée avec la surveillance d'espèces indicateurs clés (p. ex., la baleine boréale, le phoque annelé et le bélouga), devrait constituer une haute priorité.

Mots clés: océan Arctique, changement climatique, étendue de la glace de mer, réchauffement de la planète, zone de la marge glaciaire, *Balaena mysticetus*, phoques associés à la glace, phoque annelé, *Phoca hispida*, bélouga, *Delphinapterus leucas*

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INTRODUCTION

This paper reviews our current state of knowledge of model predictions for arctic climate change and trends of increased warming and decreased ice extent in the Arctic Ocean over the past 30 years. We also speculate on the impact of anticipated climate change on several species of marine mammals and recommend using data about changes in their distributions and life history parameters to corroborate the existence of arctic climate change. Despite the observed trend of arctic climate (increased warming and decreased ice extent), the patterns of change in the Arctic Ocean and subpolar seas are nonuniform (Parkinson, 1992) and highly complex, with interannual and decadal scale oscillations (Mysak et al., 1990). In view of climate model predictions and recently observed trends in arctic climate, monitoring of certain aspects of the physical environment (e.g., sea ice extent) and the seasonal distribution of indicator species (e.g., bowhead whale [*Balaena mysticetus*], ringed seal [*Phoca hispida*], and beluga [*Delphinapterus leucas*]) should be a high priority.

The Arctic Ocean and adjacent seas strongly influence global climate (Arctic System Science Workshop Steering Committee, 1990). Variations in sea ice extent are involved in complex high-latitude and global feedback processes (Barry et al., 1993). In addition, arctic sea ice is considered to be a sensitive indicator of climatic conditions, and variations in sea ice are generally consistent with air temperature anomalies (Chapman and Walsh, 1993; Maslanik et al., 1996). All general circulation models (GCMs) predict an amplification of warming at high latitudes over the next several decades in response to increasing atmospheric CO₂ (Manabe et al., 1992; IPCC, 1996a, b). The polar amplification of warming is attributable to complex snow-sea-ice albedo feedbacks at high latitudes. For example, a retreat of the ice margin allows the ocean to store more heat in summer and slows down the growth of sea ice from fall to winter (Manabe et al., 1992); further, altering the snow-ice albedo not only produces regional changes, but can significantly increase tropical sea surface temperature (Meehl and Washington, 1990).

Recent analyses show trends of decreasing arctic sea ice extent (Maslanik et al., 1996), coincident with warming trends (Martin et al., 1997), for the past 20 to 30 years. However, climatic trends in the Arctic are nonuniform, and longitudinal differences occur (Parkinson, 1992; Martin et al., 1997). Given these predictions and observations of arctic climatic change, we advise precautionary approaches to high-latitude ecosystems management until specific responses of arctic species to complex regional air-sea ice dynamics, ocean circulation, and production have been determined.

The sea ice of the Arctic Ocean varies annually in areal extent by a factor of two, from a minimum in September to a maximum in March (Parkinson et al., 1987). Low air temperatures vary from -30°C during winter to near freezing in summer (Barry et al., 1993). The formation of ice requires a near-freezing, low-salinity surface layer, which is often well-mixed to 50 m and originates primarily from continental runoff and Bering Strait inflow (Aagaard and Carmack, 1989; Barry et al., 1993). Below the surface layer is a more saline layer with temperatures above 0°C. This warmer layer originates from inflow of the North Atlantic Current into the Norwegian Sea. The presence of a strong halocline (vertical gradient in salinity) retards mixing and contributes to the stability of the water column; accordingly, the vertical density structure of the Arctic Ocean is determined by salinity.

The sea ice cover is generally kept in motion by winds and surface currents (Thorndike and Colony, 1982). The mean annual drift of the pack ice consists of a clockwise (anticyclonic) circulation in the Beaufort Sea of the Canadian Basin, often referred to as the "Beaufort Gyre," and the Transpolar Drift Stream. Sea ice moves across the pole away from the Siberian coast and eventually exits through Fram Strait, between Greenland and Svalbard (Fig. 1). The major freshwater discharge, occurring as ice through Fram Strait, is second only to the Amazon, and is twice as large as the combined discharge from the four largest rivers in North America (Aagaard and Carmack, 1989). Ice and meltwater exiting Fram Strait move southward along the east coast of Greenland in the East Greenland Current. The introduction of sufficient freshwater to the Greenland, Iceland, and Norwegian Seas can prevent convective overturn even in the case of substantial surface cooling (Aagaard and Carmack, 1989) and hence suppress deep water formation in the northern North Atlantic. Therefore, any changes in the extent, formation, circulation, or outflow of arctic sea ice are expected to have pronounced effects on the climate and circulation of the subpolar seas. The maintenance of the thermohaline circulation of the North Atlantic is very sensitive to the net freshwater outflow from the Arctic Ocean. Changes in the extent and thickness of arctic sea ice influence global climate by: 1) altering the surface albedo and radiative balance; and 2) affecting the thermohaline circulation of the North Atlantic.

CHANGES IN AIR AND SEA SURFACE TEMPERATURE

General circulation models (GCMs) predict a polar amplification of greenhouse gas-induced warming due to complex temperature-albedo and temperature-water vapor feedbacks

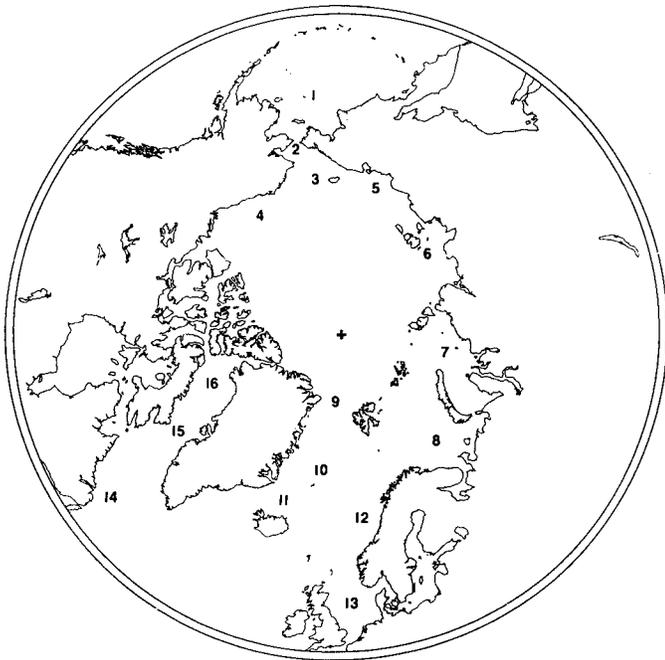


FIG. 1. The Arctic Ocean and subpolar seas: Bering Sea (1); Bering Strait (2); Chukchi Sea (3); Beaufort Sea (4); East Siberian Sea (5); Laptev Sea (6); Kara Sea (7); Barents Sea (8); Fram Strait (9); Greenland Sea (10); Iceland Sea (11); Norwegian Sea (12); North Sea (13); Labrador Sea (14); Davis Strait (15); and Baffin Bay (16).

resulting from the retreat of sea ice and snow (Chapman and Walsh, 1993; IPCC, 1996a, b). At the present rate of increase of 1% CO₂ per year, surface air temperatures are predicted to warm by 4–5°C over the Arctic and northern seas by the middle of the next century (Manabe et al., 1991). Polar warming is projected to be nonuniform, with some longitudinal dependences; however, all global circulation models indicate a polar amplification. Over the past three decades, air temperature data, collected 2 m above the ice surface from North Pole drifting ice stations, show a significant warming trend during May and June (1°C per decade in May, Martin et al., 1997). Although trends observed at ice stations for other seasons are not statistically significant, they are consistent with the temperature trends observed at land stations. Distinct warming trends north of 40°N have occurred during winter and spring for the period 1961–90; the greatest warming in the Northern Hemisphere occurred over subpolar land in Alaska, northwestern Canada, the North Atlantic marginal ice zone, and northern Eurasia (Walsh and Chapman, 1990; Chapman and Walsh, 1993). Little warming of air temperature is evident over southern Greenland and western subpolar North Atlantic (Chapman and Walsh, 1993).

After 60–80 years of a 1% per year increase in CO₂, GCMs predict a reduction of arctic sea ice, a reduction of surface albedo, and consequently an increased surface absorption of solar energy (Manabe et al., 1992). Increased thermal expansion of the oceans and melting of ice are expected to increase the global mean sea level by 15–95 cm by the year 2100 (IPCC, 1996b). At a rate of increase of CO₂ of 1% per year, arctic zonal-mean sea surface temperatures at 80°N are

expected to warm by 0.5–1.0°C by the middle of the next century (Fig. 6 of Manabe et al., 1992). Accordingly, the increased heat storage in the ocean slows down the growth of sea ice from fall to winter. Sea surface temperature should increase less in the Arctic and in the Atlantic Ocean south of Greenland than at lower latitudes because of the heat involved in melting or freezing arctic sea ice and the potential for deep vertical mixing, respectively (Manabe et al., 1991). Greater warming in subpolar regions is predicted: northern North Pacific, +2°C; Greenland Sea, North Sea, Norwegian Sea and Barents Sea, +2°C; Iceland Sea, +1–2°C; Labrador Sea and Davis Strait, +1°C (Manabe et al., 1991). However, complex arctic processes, occurring on spatial and temporal scales not well represented in the global models, could alter the amount of warming, particularly in the northern North Atlantic and adjacent seas. For example, increased fluxes of freshwater into the northern seas of the North Atlantic could cap the surface layer, reduce deep vertical mixing and formation of North Atlantic Deep Water, and substantially reduce the thermohaline circulation in the North Atlantic (Broecker et al., 1985; Broecker, 1987).

CHANGES IN SALINITY

Increased precipitation and consequent continental runoff are predicted for high latitudes in response to increasing CO₂. After 60–80 years of an atmospheric increase of 1% CO₂ per year, precipitation rates of 0.5–1.0 m per year are predicted for the Arctic and subpolar seas (Manabe et al., 1992). Increased freshwater runoff from continents may increase ice extent in some regions. Increased freshwater drainage from the Mackenzie River into the Beaufort Sea not only increases regional ice extent, but contributes to remote ice anomalies, via increased export of ice through Fram Strait into the Greenland Sea, and results in large increases in ice in the Greenland Sea 2–3 years after large runoffs (Mysak et al., 1990). Fluctuations of precipitation in the Mackenzie Basin have been significantly correlated with variations of North Pacific storm tracks (Bjornsson et al., 1995). Such studies verify the complexity of interaction between atmospheric pressure systems and ice dynamics. Further, the “Great Salinity Anomaly” (GSA) of 1968–82, an advective freshening of the surface layer in the subpolar North Atlantic (Dickson et al., 1988), appears to have caused large sea ice anomalies in the Greenland Sea, and later in the Labrador Sea (Mysak and Manak, 1989). The GSA may be related to variations in ice discharge from Fram Strait (Aagaard and Carmack, 1989). This climatic event adversely affected the recruitment of a number of deep-water fish stocks in the northern North Atlantic (Mertz and Myers, 1994). The GSA has been viewed as a smaller version of the halocline catastrophe scenario, proposed by Broecker et al. (1985), in which freshwater runoff from continental deglaciation may have shut down the thermohaline circulation of the North Atlantic during glacial periods (Aagaard and Carmack, 1989). Conversely, a decrease in freshwater runoff to the Arctic

Ocean might reduce stratification, increase the upward flux of heat from the warm sub-surface Atlantic layer, and diminish ice extent and thickness.

The complexities of arctic atmospheric-sea ice dynamics are not well modeled in GCMs. Models do not incorporate interannual and decadal fluctuations in regional ice extent (Mysak et al., 1990; Barry et al., 1993). However, ice formation is dependent on the presence of a low-salinity layer, and models do project changes in salinity for high latitudes. Models predict a decrease of salinity north of 45°N of more than 1.0 psu (practical salinity unit) in the upper 200–300 m of the water column (Manabe et al., 1991). The decrease in salinity is due to an excess of precipitation over evaporation at high latitudes. The predicted reduction of surface salinity should make the thermohaline circulation of the North Atlantic weaker and shallower (Manabe et al., 1991). In addition, a reduction or cessation of the thermohaline circulation in the North Atlantic is expected to reduce the northward transport of heat to higher latitudes via contributions of the warmer, saline water from the North Atlantic Current to the Irminger and Norwegian Currents. The cessation or reduction of the thermohaline circulation could therefore cause northern Atlantic subpolar seas to cool rather than warm.

SEA LEVEL PRESSURE

Significant changes in sea level pressure in the central Arctic have occurred in the past decade. Walsh et al. (1996) show that the period 1988–94 was characterized by seven consecutive years of negative sea level pressure anomalies. The length of this period of decrease in arctic pressures is unprecedented over the past 45 years (1950–94). Further, the sea level pressure anomalies for the central Arctic during this period are larger than anywhere else in the Northern Hemisphere. Large ice-extent anomalies have been linked to a high frequency of cyclone activity (closed low-pressure systems) over the central Arctic Ocean (Serreze et al., 1995; Maslanik et al., 1996). Increased cyclone activity north of Siberia places the East Siberian Sea in the warm sector of the cyclones, contributing to recent ice reductions. Since it is the sea level pressure distribution and resultant winds that are largely responsible for the movement of sea ice, any significant changes in sea level pressure are expected to affect not only the distribution of arctic ice, but the export of ice through Fram Strait and effects on subpolar seas as well.

CHANGES IN ARCTIC SEA ICE EXTENT

Global circulation models predict substantial decreases in both coverage and thickness of arctic sea ice in response to greenhouse gas-induced warming (Manabe et al., 1992). The greatest decrease in ice extent and thickness should occur in summer. The IPCC (1996) projects that the Northwest Passage and Northern Sea Route of Russia will likely open for routine shipping as a consequence of sea ice

reduction. Although sea ice in the actual climate system may not be as sensitive to greenhouse warming as GCMs suggest (Walsh, 1995), trends of warming air temperatures over subpolar land areas and decreased ice extent in the Arctic have already been reported (Chapman and Walsh, 1993; Maslanik et al., 1996). Concomitant with the observed spring warming trend is an observed decrease in summer sea ice extent. Since 1978, microwave remote-sensing data have provided a record of sea ice concentration, from which ice extent is derived. An ice loss rate of 9% per decade has been reported for the period 1961–90 from July to September, with the greatest decrease occurring in the 1990s (Chapman and Walsh, 1993). From 1961–75 to 1976–90, 15-year mean surface air temperatures increased and sea ice extent decreased in the region 55°–75°N, except in the North Atlantic subarctic (40°W–40°E) where sea ice extent has decreased despite a cooling trend (Chapman and Walsh, 1993). From 1979 to 1986, the ice season shortened in the eastern hemisphere of the polar ice cover, particularly in the Barents Sea and the Kara Sea, and lengthened in much of the western hemisphere of the polar ice cover, particularly in Davis Strait, the Labrador Sea, and the Beaufort Sea (Parkinson, 1992). Therefore, reductions of arctic ice extent are nonuniform and depend regionally on several complex factors: freshwater discharge from rivers, salinity anomalies, strength and location of atmospheric pressure systems, and resultant wind direction. For example, in the Bering Sea, the interannual variation in sea ice cover is linked to a teleconnection between El Niño-Southern Oscillation Events (ENSO) and the winter position of the Aleutian Low (Niebauer and Day, 1989).

Overall, since 1979 there has been a negative trend in arctic summer ice coverage, with nearly continuous below-normal ice extent since 1990 (Maslanik et al., 1996). The greatest reduction of sea ice has occurred in the Siberian sector of the Arctic Ocean (60°E to 180°E). By August of 1990, arctic ice area had decreased by 21%, almost entirely because of ice-free conditions along Siberia (Serreze et al., 1995). Further, over the period from 1987 to 1994 the rate of decrease in the extent of arctic sea ice accelerated (Johannessen et al., 1995). Similarly, Maslanik et al. (1996) report a 9% reduction in the perennial ice pack in 1990–95 compared with 1979–89. Chapman and Walsh (1993) suggested that a succession of new ice minima in the early 1990s could signal the most climatically significant feature of recent sea ice variations. Therefore, the discovery since 1990 of three extreme minima of sea ice extent is portentous; ice extent in September of 1990, 1993, and 1995 was 13%, 9%, and 12% below normal, respectively (Maslanik et al., 1996).

Given these reductions in ice extent, with potential implications for Arctic and subpolar ecosystems and human activity within them, it is important to consider whether such changes are indicative of longer-term greenhouse gas-induced global warming, or are within the range of natural interannual and decadal climatic variability in the Arctic. Although seasonal and geographical changes of air temperature and

sea ice coverage over the past several decades are consistent with greenhouse experiments performed by GCMs (Chapman and Walsh, 1993), it is premature to rule out the possibility that observed trends represent normal variability within the system. Given the complex linkages between sea ice and polar climate, and the inability of GCMs to adequately simulate the subtle changes in atmospheric pressure patterns and ice extent on regional scales, it is important to continue monitoring the observed trends and the response of the ecosystem in the finely balanced arctic system.

PRESENT MONITORING OF THE PHYSICAL ENVIRONMENT

The maintenance of climate monitoring in the Arctic is essential to the validation of predictions from GCMs. The history of temperature measurements in the Arctic extends back to Nansen's 1893–96 expedition of the *Fram*. Shipboard temperature measurements made every 6 hours revealed the strong seasonal cycle of arctic air temperature: close to 0°C in summer and -30° to -40°C in winter (Nansen, 1902). Modern climatic data are derived largely from drifting buoys, satellites, and land-based stations. Records of arctic temperature include data sets at the Climate Research Unit of the University of East Anglia (Jones, 1994); and 6-hourly air temperatures collected 2 m above the ice surface from North Pole drifting ice stations (Martin et al., 1997). Monthly sea surface temperatures (SST) are available from the Comprehensive Ocean-Atmosphere Data Set as 2° latitude × 2° longitude gridded data from 1854 to the present (Woodruff et al., 1987); however, the data coverage is uneven in time and space, and fewer records exist for polar regions than for tropical and subtropical oceans (i.e., north of 70°N the total number of SST records available for a given 10° grid varies from 100 to 50,000 records). Since January 1979, the most accurate analyses of daily surface pressures and temperatures for the central Arctic have been compiled by the Polar Science Center at the University of Washington; these analyses rely on a network of 10–20 arctic buoys.

Sources of sea ice data available from remote sensing include Scanning Multichannel Microwave Radiometer (SMMR) data from November 1978 to August 1987 and Special Sensor Microwave/Imager (SSM/I) from July 1987 to the present. There are time series of sea ice clearing dates for some coastal regions of subpolar seas, such as the Labrador coast (Newell, 1996). In addition, weekly southern ice limit charts can be obtained from the U.S. Navy-National Oceanic and Atmospheric Administration Joint Ice Center. Russian North Pole ice stations were maintained continuously from 1954 to 1991; however, in recent years most ice stations have closed for lack of available funding (S. Martin, pers. comm. 1996). Such losses occur at a critical time, when synoptic coverage of both the western and eastern Arctic and the subpolar seas is crucial to the ongoing validation of general circulation model predictions.

Continued monitoring of the flow between subpolar seas and the Arctic Ocean is necessary to distinguish between large interannual variability and longer-term trends. Calculated wind speeds have been used to generate a time series of annual mean transport through the Bering Strait from 1946 to 1982 (Coachman and Aagaard, 1988). More recently, a mooring program has provided direct estimates of volume transport and measurements of water properties in the Bering Strait from 1990 to 1994 (Roach et al., 1995). When combined, these time series provide a 50-year history of the exchange between the Arctic and the Pacific Oceans. Seasonal and interannual variability are high in both transport and water properties (Roach et al., 1995). From 1946 to 1994, the largest transport, which occurred during the first 9 months of 1994, was nearly 50% greater than the long-term mean. Only continuous monitoring will reveal whether this recent increase is part of a longer-term trend.

POTENTIAL EFFECTS ON MARINE MAMMALS

In this section, we summarize the potential effects of climatic change on arctic marine mammals and provide examples of their use as indicator species. Direct effects of climate change on arctic marine mammals include the loss of ice-associated habitat. Indirect effects include regional or seasonal shifts in prey availability, which can affect nutritional status, reproductive success, and geographic range, and alterations in the timing or patterns of migrations, which may produce changes in species distributions and stock structure.

Ice as an Important Substrate for Pinnipeds and Polar Bears

In a warmer Arctic, pinnipeds and polar bears may be directly affected by changes in the availability of suitable ice-associated habitat. Ice-associated seals may be particularly vulnerable to changes in the extent or concentration of arctic ice because they depend on pack-ice habitat for pupping, foraging, moulting, and resting (DeMaster and Davis, 1995). Ringed seals (*Phoca hispida*) and polar bears (*Ursus maritimus*), which prey on them, are the only marine mammals that regularly occupy extensive landfast coastal sea ice (Smith et al., 1991). Ringed seals require snow cover in which to construct subnivean birth lairs on the fast ice. This species depends on the stability of ice for the successful rearing of its young (Burns et al., 1981). Although stable fast ice is critical for successful pupping of most populations of ringed seals (Finley and Renaud, 1980; Burns et al., 1981), at least one population in Baffin Bay is associated with the pack ice (Finley et al., 1983). These seals are smaller and have a different diet from those seals associated with fast ice. This suggests at least some degree of plasticity in this species to adapt to different ice environments. In contrast, bearded seals (*Erignathus barbatus*) prefer relatively shallow water (depth < 150 m) with thin, shifting ice and leads kept open by strong currents (Burns, 1981; Burns et al., 1981; Kingsley and

Stirling, 1991). In winter, both bearded seals and walrus (*Odobenus rosmarus*) require regions of thin or broken ice cover over suitably shallow depths to forage on benthic invertebrates (Finley and Renaud, 1980; Burns et al., 1981). The annual distribution of walrus is strongly coupled with the extent and concentration of arctic ice (Vibe, 1967). Walrus overwinter in areas of the pack ice where the ice is thin enough that they can break it with their heads to maintain breathing holes (Stirling et al., 1981), yet thick enough to support their weight (Burns et al., 1981). In this season, walrus are highly clumped in regions in and adjacent to polynyas and ice divergence. Therefore, the distributions, densities, and foraging success of these arctic pinnipeds are delicately poised with respect to the maintenance of suitable sea ice conditions, and consequently, these species may be sensitive indicators of climate change.

Polar bears require ice as a solid substrate on which to hunt for ringed seals (Stirling and Derocher, 1993; Stirling et al., 1993). The distributions of polar bears are probably a function of the distribution of ice conditions that allow them to travel and hunt most efficiently (Burns et al., 1981). Significant differences in usage patterns of sea ice habitat have been shown by bears of different sexes and age classes (Stirling et al., 1993). For example, in the spring, females with cubs of the year show a strong preference for fast ice with drifts, whereas adult males, lone adult females, and females with two-year old cubs occur more frequently in floe-edge habitat, where the highest densities of ringed seals are found. Consequently, changes in the extent and type of ice cover are also expected to affect the distributions and foraging success of polar bears. The onset of decline in the production of ringed seals, and consequently of polar bears, has been linked with the severity of ice conditions. In 1974 and 1975, a major decline of ringed and bearded seals in the eastern Beaufort Sea followed a winter of heavily compacted sea ice, which lacked the usual formation of leads parallel to the coast (Stirling et al., 1977). Similarly, a decline in ringed seal density in the southeastern Beaufort Sea from 1982 to 1985 was coincident with heavy ice conditions and less open water, particularly in late summer of 1985 (Harwood and Stirling, 1992). Although the causative mechanisms were unclear, Harwood and Stirling (1992) suggested that a reduction in regional productivity may have contributed to the poorer nutritional condition of ringed seals and bearded seals. Such observations indicate the need for more process-oriented studies that examine the effects of altered ice coverage, stratification, and convection on regional productivity and prey availability. Stirling and Derocher (1993) expect that the first impacts of climatic warming on polar bears will occur at the southern limits of the bears' distribution, such as in James and Hudson Bays. In these regions, polar bears already fast for approximately four months during the summer when the ice melts. Prolonging the ice-free season could increase their nutritional stress. Therefore, monitoring the movements, population status, and condition of polar bears and ringed seals in Hudson Bay could verify the effects of persistent climate change in the region.

Linkages between Ice and Cetaceans

The benefits of ice to arctic cetaceans may relate more to the linkage between prey availability and ice rather than to their direct needs of ice habitat per se. Off northern Alaska, the summer habitats of three species of arctic cetaceans differ in the percentage of sea ice cover: bowhead whales (*Balaena mysticetus*) are associated with moderate ice cover (44–60%); gray whales (*Eschrichtius robustus*) with low ice cover (less than 5%); and belugas (*Delphinapterus leucas*) with moderate to high ice cover (54–66%) (Moore and DeMaster, in press). Although seasonal shifts in the association of bowheads and belugas with ice cover have been observed (Moore and DeMaster, in press), the degree of plasticity within species and between stocks to adapt to longer-term changes in sea ice extent and prey availability is less well known. Although bowhead whales are considered ice-adapted, with a disjunct circumpolar distribution, it is uncertain whether this species can adjust well to ice-free waters. Interannual variability in seasonal distributions of bowheads in the Beaufort and Chukchi Seas may be influenced by ice cover and feeding opportunities (Moore and Reeves, 1993). In Alaskan waters, bowhead whales feed primarily on crustacean zooplankton, especially large copepods (such as *Calanus glacialis* and *C. hyperboreus*) and euphausiids (Lowry, 1993). It follows that the ability of bowheads to find suitable and reliable concentrations of zooplankton in a warmer Arctic will determine their movements and redistribution. It has been suggested that the demise of the Thule culture 500 years ago was related to the climate-induced absence of bowhead whales along the rim of the Canadian Basin, due to a decrease in open-water habitat during summer (McGhee, 1984; Aagaard and Carmack, 1994).

The narwhal (*Monodon monoceros*) is a strictly arctic species (Vibe, 1967), whereas the beluga (*D. leucas*) is an arctic and subarctic species rarely found south of 45°N (Reeves, 1990). Both species are strongly associated with ice (Burns et al., 1981), and are known to forage at ice edges and ice cracks (Bradstreet, 1982; Finley and Gibb, 1982; Bradstreet et al., 1986; Crawford and Jorgenson, 1990). As noted for arctic pinnipeds, because of their susceptibility to changes in ice conditions, the distributions and life history parameters for these cetacean species should be valuable indicators of climate change in the Arctic.

Given these uncertainties in cetacean response to climate-induced perturbations, and additional concerns over small population size, range restrictions, life history characteristics, and removals by Native subsistence hunters, the International Whaling Commission (IWC) considers the following arctic species or populations to be potentially more vulnerable than other species of cetaceans: Eastern Arctic bowhead whale (*B. mysticetus*); Okhotsk Sea bowhead whale (*B. mysticetus*); all stocks of beluga whale (*D. leucas*); and all stocks of narwhal (*M. monoceros*) (IWC, 1997). For these same reasons, it is likely that these species will be valuable indicators of persistent change in the arctic environment.

Importance of the Ice Edge and Sea Ice Community to Marine Mammals

Any discussion of the effects of climate change on arctic marine mammals needs to include an examination of the impact of climate on the comparative productivity of ice edges versus open water, and the importance of these habitats to arctic cod (*Boreogadus saida*). The secondary production associated with the sympagic (meaning “with ice,” Whitaker, 1977) community provides a critical linkage between primary productivity in the Arctic and marine mammals. The migrations of belugas, narwhals, and harp seals (*Phoca groenlandica*) are all linked to the vernal production of ice algae and ice-edge productivity. These species migrate long distances, leaving wintering grounds further south to inhabit the Canadian archipelago during the open-water season (Davis et al., 1980). Feeding aggregations of these three species in the Canadian High Arctic occur primarily in nearshore areas, where dense schools of arctic cod concentrate in late summer (Bradstreet et al., 1986). Belugas, narwhals, and harp seals often congregate at the ice edge and have been observed to dive repeatedly under the ice, presumably to feed (Bradstreet, 1982; Lydersen et al., 1991). However, coastal feeding aggregations may occur in open water, as well as beneath or near ice.

The arctic cod is a pivotal species in the arctic food web, as evidenced by its importance as a prey item to belugas, narwhals, harp seals, ringed seals, bearded seals, and hooded seals (*Cystophora cristata*) (Davis et al., 1980; Bradstreet, 1982; Bradstreet et al., 1986; Ainley and DeMaster, 1990; Borokin, 1990; Finley et al., 1990a; Welch et al., 1992; Crawford and Jorgenson, 1993). In arctic regions, no other prey items compare with arctic cod in abundance and energetic value (Finley et al., 1990a). The distribution and diet of arctic cod vary with ice conditions (Frost and Lowry, 1984; Crawford and Jorgenson, 1993) and large numbers of fish can occur locally, especially in areas of marginal ice zones (Andriashev, 1970). Therefore, the trophic cascade upon which arctic marine mammals depend is ultimately driven by the complex interactions between ice, light penetration, nutrient supply, and productivity.

In spring, ice algae form a thin, dense layer (ca. 1 cm), dominated by pennate diatoms, on the underside of the ice at the ice-seawater interface (Horner, 1976; Alexander, 1981; Alexander and Chapman, 1981; Cota et al., 1987; Cota and Horne, 1989). Nutrients are supplied to ice algae in a pulsed fashion by tidally dominated vertical mixing (Cota and Horne, 1989). Measurements in the Lancaster Sound region suggest that ice algae fix only 10% of the total primary production (Welch et al., 1992). Other studies, however, have concluded that at specific times and regions, ice algal productivity can exceed water column production (Smith et al., 1988; Wheeler et al., 1996). Regardless of the relative contributions of ice algae versus water column production to total productivity, it is well recognized that ice algae play an important role in sustaining the secondary production that supports marine mammals in the High Arctic.

Dense algal mats support a sympagic community that includes the crustaceans and cryopelagic fishes upon which marine mammals feed. For example, the pelagic amphipod *Parathemisto libellula* and the arctic cod are both major components of the sympagic community, and are also the two dominant prey species of the Northeast Atlantic population of harp seals (*Phoca groenlandica*), which migrate long distances in the Barents Sea to feed at ice edges (Lydersen et al., 1991). Harp seals of the Northwest Atlantic population also undertake long migrations (approximately 8000 km round trip) to feed intensively on arctic cod in northern Baffin Bay and the eastern Canadian archipelago (Finley et al., 1990a). In the eastern Canadian Arctic, ringed seals inhabiting the pack ice of Baffin Bay also feed extensively on *P. libellula*, whereas coastal seals associated with fast ice along northeast Baffin Island depend on arctic cod throughout the year (Finley et al., 1983).

Cryopelagic fishes such as arctic cod (*B. saida*) are especially adapted to feed under the ice where they rely on crustaceans associated with the ice undersurface and the adjacent water column (Lønne and Gulliksen, 1989), primarily amphipods (i.e., *Onisimus* spp., *Apherusa glacialis*, and *Parathemisto libellula*) and copepods (i.e., *Calanus glacialis* and *C. finmarchicus*) (Alexander, 1981; Dunbar, 1981; Bradstreet et al., 1986; Lønne and Gulliksen, 1989; Crawford and Jorgenson, 1993). Further, the placement and orientation of the mouth of arctic cod suggests an adaptation to under-ice feeding (Dunbar, 1981). In Admiralty Inlet (Northwest Territories, Canada), hydroacoustic surveys of fish recorded the highest densities immediately below landfast sea ice (Crawford and Jorgenson, 1990). The distributions of fish, presumably arctic cod, were associated with layers of zooplankton. Belugas and narwhals are known to congregate at ice edges and dive under the ice (Bradstreet, 1982; Crawford and Jorgenson, 1990), presumably to feed on arctic cod. Marine mammals likely find denser schools of arctic cod in nearshore regions, where the fish aggregate in late summer (Welch et al., 1992; Hobson and Welch, 1992; Welch et al., 1993). Behaviors of arctic cod that lead to the formation of large aggregations are probably quite crucial to the foraging of higher vertebrates. Otherwise, as noted by Welch et al. (1992:351), “It is difficult to imagine such large whale concentrations finding maintenance rations in the form of dispersed arctic cod....” It is also difficult to predict how arctic cod may be redistributed in a warmer Arctic. However, since their life history is closely linked to sea ice, we speculate that regional changes in the extent of sea ice may lead to redistributions of arctic cod, and consequently to redistributions and altered migrational patterns of marine mammals.

In the present arctic system, the development of the ice algal mat is followed approximately six weeks later by a bloom of phytoplankton in the water column (Gosselin et al., 1985). With spring warming and ice melt, algal cells are sloughed off into the surrounding water column, where the increased stratification helps initiate a seasonal bloom of phytoplankton. North of the oceanic Polar Front in the Barents Sea, blooms form a 20–50 km wide belt off the ice edge,

which progresses northward and generates a restricted zone of high productivity (Sakshaug et al., 1994). The most intense production at the ice edge occurs just as the ice is breaking up (Niebauer et al., 1981). In the Bering Sea, the bloom can extend away from the ice edge to a distance of 50–80 km (Niebauer et al., 1981). On the Bering Sea shelf, the spring ice edge bloom accounts for a significant proportion of the annual primary production, and climatic fluctuations may control the nutrient supply at the ice edge (Niebauer et al., 1981). In this region, the duration of high photosynthesis is limited to several weeks, likely because of silicon depletion and nitrogen deficiency (Alexander, 1981). Such severe nutrient depletion is commonly observed at ice-edge regions (Harrison and Cota, 1991). However, during colder years in the Bering Sea, when the ice extends to the shelf edge, there is greater nutrient resupply through shelf-edge eddies and tidal mixing, and consequently a longer spring bloom (Niebauer et al., 1981). Conversely, in warmer years, when the ice does not extend as far south, nutrient supply is reduced, and spring production on the shelf is diminished. Therefore, even the potential for a longer growing season and enhanced primary productivity in open-water regions of a warmer Arctic will depend on the existence of mechanisms that can resupply nutrients to the mixed layer at ice edges or in ice-free regions.

In the High Arctic, primary production in the water column decreases toward the pole, while production by ice algae increases, and in some regions (Makarov and Amundsen basins) algal production in the ice is about twice that in the water column (Wheeler et al., 1996). It has been suggested that planktonic production in the Arctic Ocean appears to be insufficient to support large herbivorous populations, whereas ice-associated production is sufficiently concentrated to support a specialized ecosystem (Dunbar, 1981). It is therefore not certain that more open water in the Arctic can be equated with increased productivity and an unaltered ecosystem. For example, over the eastern Bering Sea shelf there is little production after the spring ice-edge bloom (Alexander, 1995). As Dunbar (1981:38) has observed, “There seems, however, to be something more involved here than the simple disappearance of ice and the illumination of the open water....it is at the ice edge, rather than away from the ice, that the greatest activity takes place.”

In the High Arctic, the base of the food chain consists of ice algae rather than phytoplankton (Alexander, 1995). Many species of copepods (*Calanus glacialis*, *Pseudocalanus* spp., *Oithona similis*) reproduce under the ice before the phytoplankton bloom and feed on sedimenting ice algae (Drolet et al., 1991). Large *Calanus*, together with amphipods, constitute the bulk of the diet of arctic cod (Bradstreet et al., 1986). In turn, the larvae of arctic cod (*B. saida*) depend on the production of ice algae to support the productivity cycles of copepods, which supply the copepod eggs and nauplii upon which fish larvae feed (Drolet et al., 1991). Therefore, the timing of the phytoplankton bloom, driven by the breakup and melting of ice, is critical to the immediate success of first-feeding larvae of arctic cod. Consequently, the level of

recruitment of arctic cod can affect the foraging success and nutritional condition of marine mammals years later. Regional decreases in the recruitment of arctic cod larvae, due to a loss of critical ice-edge habitat or alteration in the seasonal timing of spring blooms, would be expected to adversely affect marine mammals. Similarly, the level of recruitment of capelin (*Mallotus villosus*), an important food species of harp seals and minke whales in the Barents Sea (Sakshaug et al., 1994) and of belugas in Hudson Bay (Richard, 1993), is also expected to affect the foraging success and distributions of these species. For example, a significant decline in the harp seal population in the Barents Sea followed a collapse of the capelin stock in the late 1980s (Sakshaug et al., 1994). During this period of “cold” years and reduced productivity in the Barents Sea (Sakshaug, 1997), large numbers of harp seals invaded coastal areas of northern Norway (Haug et al., 1991). These events were closely related to a reduction of the influx of Atlantic water to the Barents Sea and, ultimately, to the strength and position of atmospheric pressure systems in the North Atlantic (Sakshaug, 1997). This example illustrates the complex linkages between climate, basin-scale circulations, and the consequent effects on the productivity and trophic dynamics of pelagic arctic ecosystems.

One of the central questions regarding climate change and the effects on arctic marine mammals is whether a reduction of sea ice will increase productivity in a way that maintains suitable densities of important prey species, such as arctic cod. Given the coupling between the ice-edge habitat and the prey of many species of arctic marine mammals, we speculate that a sufficient reduction in the extent of the ice edge, and its associated community, may have deleterious consequences for marine mammals that have evolved with these unique systems. Marginal ice-edge zones along seasonally retreating ice can be highly productive systems (Smith and Nelson, 1985) that provide reliable availability of prey along important migratory routes for arctic seabirds and mammals (Ainley and DeMaster, 1990). Therefore, in addition to the potential adverse effects to ice-associated seals from direct loss of habitat, or to polar bears from loss of access to prey, there is the additional concern that species which rely on the ice-edge community for foraging, such as belugas, narwhals, and harp seals, could be adversely affected by a reduction in the areal extent and latitudinal shift of ice-edge habitat. Given that in recent years the greatest decreases in ice extent have occurred in the Laptev and East Siberian Seas (Maslanik et al., 1996), it follows that these regions may provide the first indications that marine mammal populations are experiencing climate-induced geographic shifts or altered reproductive capacity.

Polynyas also appear to play a critical role in the survival of many marine mammal populations in the Arctic (Stirling et al., 1981; Stirling, 1997). For example, polar bears find suitable hunting habitat at polynyas, such as the Northeast Water polynya off Greenland, because ringed seals are accessible and available on the fast ice and on the pack ice adjacent to the polynya (Born et al., 1997). However, predictions of the occurrence, location, and productivity of polynyas in a warmer

Arctic are unavailable. One aspect of a warmer Arctic may be that species or stocks previously dependent on polynyas for hauling or resting habitat (e.g., ice seals) may become less dependent, while polar bears, adapted to take advantage of predictable aggregations of prey, may be disadvantaged by a reduction in seasonally concentrated prey. Another aspect of warming and increased ice melt is the potential for greater stratification of the water column and decreased nutrient resupply. In the Northeast Water polynya, nitrate limitation of phytoplankton growth was found to be greater late in summer when thermal stratification was strongest (Smith et al., 1997), suggesting that increased stratification accompanying ice melt may restrict nutrient resupply. As a first step, coupled biophysical models of polynyas and ice-edge regions are needed in order to evolve predictive capabilities for a warmer Arctic.

At present, it is difficult to predict the particular areas in which marine mammal species will be most affected by climate change. This is because mesoscale features, such as frontal zones and eddies, which are associated with enhanced productivity and are important to arctic apex predators, are not well resolved by the present spatial resolution of general circulation models. These features and processes often sustain local production through the pulsed resupply of nutrients (i.e., upwelling, frontal zone circulations, tidal mixing, and eddies). In order to develop regional predictions, specific smaller-scale coupled air-sea-ice submodels of circulation and production are needed. Results from these first regional models of production, linked to ice extent, ice transport, stratification, and nutrient resupply, can then serve as a starting point for evaluating the impact of a warmer Arctic on marine mammals.

In addition to the linkages between the sympagic community and marine mammals feeding near ice edges, there is a linkage between ice algal production and benthic communities. Ice algae that are ungrazed and sediment to the bottom provide a flux of carbon to the benthic community, upon which bearded seals, walruses, and gray whales depend. Along the Bering Sea shelf, a significant portion of the organic carbon fixed at the ice edge may be contributed to the benthos (Alexander, 1981). Zooplankton grazing of phytoplankton accounts for less than 2% of the daily phytoplankton production in the ice-edge zone over the middle shelf of the Eastern Bering Sea (Coyle and Cooney, 1988). In addition, high production in the "Green Belt" at the Bering Sea shelf-edge (Springer et al., 1996), and in Bering Shelf-Anadyr Water, sediments as high-quality organic carbon, which supports high benthic biomass in the northern Bering and Chukchi Seas (Grebmeier et al., 1988). This sedimentation of carbon on shallow arctic shelves is critical to the benthic foraging success of walruses, bearded seals, and gray whales in these regions. Therefore, the quality and quantity of detritus available to the benthic community affect the species composition of apex consumers in shallow arctic seas. We speculate that climate-induced regional changes in the flux of carbon from ice or water-column production to the benthos could affect the distribution and reproductive

success of gray whales, walruses, and bearded seals. In addition, the proximity of the ice edge to shallow-shelf habitat suitable for benthic foraging is seasonally critical to some ice-associated pinnipeds that must rely on sea ice as a platform for resting, pupping, and molting. Arctic warming may move the summer position of the ice edge to deeper water, thus changing this relationship. The effects of such changes on ice seal populations could be substantial.

Migrations and Movements of Marine Mammals Relative to the Annual Ice Cycle

Because marine mammal migrations are closely linked to the seasonal cycle of sea ice, shifts in the timing or pattern of onset or breakup of seasonal ice might affect the distributions of these animals (Bradstreet, 1982). In the Bering Sea, bowhead whales, walruses, belugas, ringed seals, and bearded seals stay with the ice edge as it annually advances and retreats (Goering and McRoy, 1974). Reductions in the southern extent of seasonal sea ice could displace southern ranges of these species northward. Interannual changes in the onset and severity of seasonal sea ice may also affect the length of feeding seasons, timing of migrations, fecundity, and survivorship of marine mammal species. For example, sighting data of gray whale calves during the northbound migration suggest that higher calf counts are associated with years of delayed onset of seasonal ice in the Chukchi Sea (W. Perryman, pers. comm. 1997). During years of earlier onset of ice, pregnant females must leave feeding grounds sooner, having less time to nourish the developing fetus and store the fat necessary to support lactation during their stay in the Mexican lagoons and the long trip back to Alaskan waters. Therefore, for species like the gray whale, for which sea ice acts as a barrier to benthic foraging, a warmer Arctic may be beneficial. Conversely, for those species that are dependent on prey whose abundance is positively correlated with sea ice extent, a warmer Arctic may be unfavorable.

Another region where ice conditions have been linked to altered timing and pattern of cetacean migrations is in Baffin Bay and Davis Strait. Vibe (1967) provides a comprehensive review of the history of cetacean and pinniped movements off Greenland relative to climatic conditions. In northwestern Greenland, the narwhal departs early in cold winters. Conversely, with rising temperature and increased inflow of Atlantic water into Davis Strait, narwhals move further north in Baffin Bay and are more abundant at Upernavik and Thule. This movement of whales further north is linked to the advance of drift ice in Davis Strait. In years when the Atlantic climate advances far north in Davis Strait along the coast of West Greenland, narwhals stay at higher latitude and for a longer period during fall and winter. The southern boundary of the distribution of this species is closely connected to ice conditions and circulation.

Periods with great advances of drift ice also affect the movements of ringed seals, harp seals, and hooded seals in Baffin Bay and Davis Strait. During periods of heavy drift-ice advance, populations of ringed seals along the east coast of

Greenland head southward round to the west coast, whereas harp seals along the central coast of West Greenland move further north (Vibe, 1967). Both the harp seal and hooded seal are migratory seals, with a northern distribution in summer and a southern distribution in winter (Vibe, 1967). The range and relative abundance of hooded seals may also be influenced by changes in ice cover and climate (Rasmussen, 1960; Vibe, 1967). This species whelps on the pack ice in three main breeding areas: “West Ice” near Jan Mayen Island (east of Greenland), the “Front” off Newfoundland and in the Gulf of St. Lawrence, and in Davis Strait (Kovacs and Lavigne, 1986; Hammill, 1993). Periods of large influxes, or pulses, of East Greenland ice into the southern Davis Strait (1870–1910) appear to have coincided with larger numbers of hooded seals along West Greenland (Vibe, 1967). Conversely, during “melting stages” (after 1910), the number of hooded seals along West Greenland declined simultaneously with decreases of East Greenland ice in Davis Strait. Therefore, changes in the arrival and amount of drift ice in Davis Strait can cause serious ecological consequences (Vibe, 1967). From 1979 to 1986, the sea ice season lengthened in Davis Strait and the Labrador Sea, but shortened off the east coast of Greenland and in the Canadian Arctic Archipelago (Parkinson, 1992). Such regional variation in sea ice season, and species-specific variations in distribution relative to ice conditions, illustrate the difficulty in making geographically broad predictions of marine mammal response. Further, present global coupled models typically treat sea ice as a motionless thermodynamic slab and do not include sea ice dynamics, such as the advection of sea ice from the Arctic into the Greenland and Norwegian Seas (IPCC, 1996a). However, on the basis of historical analyses (Vibe, 1967), we speculate that large fluxes of drift ice through Fram Strait and along the coasts of Greenland could restrict narwhals and belugas to higher latitudes in Baffin Bay. Heavy drift ice could also shift populations of East Greenland ringed seals to regions where winter ice remains sufficiently solid, move harp seals further north or west in Baffin Bay, and increase the abundance of hooded seals off West Greenland.

Two specific regions of particular interest for monitoring the response of marine mammals to environmental change are the Northwest Passage and the Russian Northern Sea Route. The predicted opening of the Northwest Passage and the Russian Northern Sea Route for up to 100 days a year is expected to increase human activity in these regions (IPCC, 1996b). Substantial reductions in summer ice cover in the Siberian Arctic have already been observed (Maslanik et al., 1996). Associated concerns include the potential for an increased burden of pollutants entering the arctic environment and an increased incidence of epizootics; the effects of increased ship traffic, exploration, industrial activities, fisheries, and associated noise; and the synergistic effects of these factors and climate-induced shifts in the ecosystem on marine mammal populations (IWC, 1997). The Lancaster Sound region is the eastern part of the Northwest Passage and serves as an important summering habitat and migratory corridor for belugas and narwhals. This region and the

southern portion of the North Water polynya of northern Baffin Bay are among the richest areas for marine mammals and birds in the Canadian Arctic (Stirling, 1997). Large polynyas, such as the North Water, and edges of the polar pack, “particularly where they are over the continental shelf, are vital to the overall biological productivity of polar oceans and to all trophic levels of the associated ecosystems” (Stirling, 1997:18). For these reasons, comparative process-oriented studies, which can examine and monitor changes in the structure and function of these systems, will be of critical importance over the decades of predicted arctic warming.

Such seasonal changes in ice extent and human activity in the Arctic may lead to redistributions of arctic whales and seals and possibly confound our current understanding of stock structure by changing existing patterns of gene flow. For example, the migrational patterns of belugas between wintering grounds, where breeding is thought to occur, and summering grounds, where whales feed and moult, help to maintain geographically separate stocks. The permanent pack ice of the central Canadian Arctic may also help to separate western from eastern stocks of belugas (Sergeant and Brodie, 1975), although extralimital sightings do occur (Stewart and Burt, 1994). Populations of belugas in the Mackenzie Delta (Beaufort Sea) and Arviat (West Hudson Bay) regions have been genetically separate for an estimated 3900 years (Buchanan et al., 1995). Such separate stock structure among belugas helps to maintain maximum genetic diversity across the Arctic. It is unknown how migrations and selection of wintering and summering grounds may shift in a warmer Arctic. At present, the eastern Canadian stock of belugas arrives in the High Arctic in late June and early July and migrates westward through Lancaster Sound to summering areas in the Canadian Arctic Archipelago. From the opposite direction, in the southern Beaufort Sea, male belugas have been tracked as far northward and eastward as Viscount Melville Sound in the summer (A. Martin, pers. comm. 1996), returning to the Bering Sea during the winter.

Therefore, we speculate that a lengthening in the open-water season in the Canadian Arctic Archipelago might alter the timing and geographical patterns of seasonal migrations as well as the time spent in select summering or wintering grounds. Sufficient changes in beluga behavior may promote genetic exchange between stocks.

Linkages between Changes in the Freshwater Budget and Marine Mammals

Predicted increased rates of precipitation in the Arctic and subpolar seas (Manabe et al., 1992; IPCC, 1996b) could have a variety of effects on marine mammals. Ringed seals rely on both the duration of the ice cover and the total precipitation to create sufficient snow depth for the building of subnivean lairs (Smith et al., 1991). In this case, while increased snowfall could be beneficial for the construction of lairs, especially on smoother ice with few pressure ridges or ice hummocks, a reduction in the amount and extent of fast-ice habitat could be detrimental. Increased precipitation, and consequently

increased freshwater runoff from continents, may also affect the biomass of ice algae, prey availability, ice formation, and the load of pollutants in the Arctic. In situ incubation experiments of ice algae in southeastern Hudson Bay suggest that low salinity limits the growth of ice algae (Legendre et al., 1992). Thus, increased freshwater flux from rivers may reduce the growth of microalgae at the ice-water interface. Climate-induced increases in freshwater discharge in spring could also impair local feeding conditions for marine fish larvae, and consequently affect marine mammal foraging. For example, the foraging success of first-feeding arctic cod (*B. saida*) larvae is adversely affected by large freshwater plumes, in which larvae avoid the freshwater surface layer and do not feed (Gilbert et al., 1992). Within the Great Whale River plume in Hudson Bay, light attenuation caused by a turbid surface layer also reduces the foraging efficiency of first-feeding arctic cod larvae and sand lance *Ammodytes* sp. larvae (Ponton and Fortier, 1992). Another consequence of increased river discharge is the enhanced formation of ice. Increases in freshwater discharge from the Mackenzie River drainage basin can increase regional ice extent in the Beaufort Sea (Mysak et al., 1990). Heavy ice conditions in the eastern Beaufort Sea appear to be associated with declines in ringed seal densities (Stirling et al., 1977; Harwood and Stirling, 1992). Therefore, the monitoring of river runoff and the consequent effects on regional ice dynamics, productivity, larval recruitment, and marine mammal populations should be integral components of arctic climate change programs.

Another consequence of climatic warming and increased precipitation at high latitudes is the potential for larger introductions of river-borne pollutants into arctic marine ecosystems. There is already evidence that pollutants are accumulating in the Arctic and that marine mammals, as long-lived apex consumers with high lipid content, have a high potential for long-term accumulation of contaminants (Alexander, 1995). Contaminants can also be assimilated through the sympagic food web, by the fallout of airborne pollutants on sea ice (Alexander, 1995). Some existing programs have begun to consider the contamination present at various trophic levels in the Arctic (e.g., the international Arctic Monitoring and Assessment Programme [AMAP]). Programs which monitor the flux and bioaccumulation of pollutants in arctic systems should be integrated with climate change programs examining and modeling oceanic and atmospheric circulation.

A further consequence of arctic warming and the potential for increased human activity in polar regions is the introduction of additional noise to the environment. Richardson (1995) has reviewed the documented disturbance reactions of arctic marine mammals to anthropogenic noise. For example, some ringed seals and polar bears are sensitive to wintertime, on-ice seismic techniques and may abandon areas. Also, belugas have been reported to swim rapidly away from ships and icebreakers approaching within 35–50 km; narwhals, however, show less overt panic reaction to approaching ships, although their underwater vocalizations temporarily cease (Finley et al., 1990b). Finally, underwater noise from

drill sites and seismic survey vessels can elicit avoidance behaviors in migrating bowhead whales (Richardson, 1995). However, the long-term effects of the disturbance on these populations are unknown.

In summary, given the potential for increased human activity in the Arctic, concomitant with climate-driven alterations of shelf/basin circulation, ice conditions, and ecosystem structure and function, it is critical that regional process-oriented studies and integrated monitoring of key species become major components of arctic research. The development of long-term oceanic and biological time series in the Arctic is essential to document and interpret the effects of climatic variability and global warming on the ecosystem. Finally, managers of marine resources in the Arctic should be aware of present observations and predictions of climate change; further, they should develop risk-averse management strategies that take into account possible adverse impacts of arctic climate change on the ecosystem. For example, where populations are managed on the basis of a series of index counts from trend sites, a warming Arctic could result in redistributions of animals that would reflect emigration or immigration, rather than underlying changes in the actual size of the population. To mitigate such problems, managers will require additional information about both climate-induced alteration of habitat and movements of animals. Remote sensing and satellite telemetry, coupled with ongoing improvements in the spatial resolution and geographic specificity of climate models and process-oriented submodels, should be very helpful technologies. Another caution concerns the stock structure of arctic populations. Currently recognized discrete breeding units may not adequately define stock structure in a warmer Arctic. Therefore, given our limited predictive capacity, gene flow and movements of many species should be studied well into the next century.

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