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Declining Extent of Open-water Refugia for Top Predators in Baffin Bay and Adjacent Waters

Global climate change is expected to severely impact Arctic ecosystems, yet predictions of impacts are complicated by region-specific patterns and nonuniform trends. Twentyfour open-water overwintering areas (or "microhabitats") were identified to be of particular importance for eight seabird and marine mammal species in the eastern Canadian High Arctic and Baffin Bay. Localized trends in the available fraction of open-water were examined in March during 1979–2001, derived from approximate sea ice concentrations from satellite-based microwave telemetry. Declines in the fraction of open-water were identified at microhabitats in Baffin Bay, Davis Strait, coastal West Greenland, and Lancaster Sound. Increases in open-water were observed in Hudson Bay, Hudson Strait, and Foxe Basin. The biological importance of each microhabitat was examined based on species distribution and abundance. Potential consequences of reduced open-water for top marine predators include impacts on foraging efficiency and oxygen and prey availability.

INTRODUCTION

The waters adjacent to the Arctic Ocean are generally perceived as barren and inaccessible, completely covered in sea ice and darkness during winter months. However, in this white stretch of frozen Arctic sea, winter refugia or "microhabitats" exist for millions of air-breathing marine animals. The refugia range widely in size, existing as cracks or leads only a few hundred meters long to hundreds of kilometers of vast open-water. They remain ice-free during even the coldest period of winter and are generally surrounded by solid sea ice. These areas can be annually recurrent 'polynyas' (the Russian word for 'open-water area surrounded by ice') driven by upwelling or wind, variable shore leads and cracks, or tidal- and wind-driven openings in the consolidated pack ice (1). These microhabitats occur predictably in the same locations year after year, despite the variety of ways in which they are physically generated and maintained. The geographical and temporal predictability permits numerous Arctic seabirds and marine mammals to utilize open-water during winter when survival in the sea ice is most critical. Large-scale upwelling events occur along the ice edge, driven by the absence of ice, providing early availability of light for photosynthesis (2). Consequently, the high levels of production found in many of these open-water habitats are used by predators seeking to benefit from high densities of zooplankton and associated fish abundance.

Species utilizing open-water winter refugia include cetaceans, pinnipeds, seabirds and polar bears (*Ursus maritimus*). Their winter habitat preferences are diverse and unique to their species-specific requirements for survival and reproductive success. One of the largest Arctic winter refugia, the North Water, is utilized by approximately 13 000 belugas or white whales (*Delphinapterus leucas*) (who undertake a northbound migration to this locality from Lancaster Sound in the fall) during winter and spring, thousands of narwhals (*Monodon monoceros*), and 30 million breeding pairs of little auks (*Alle alle*) (3–6). In other areas, alternate and smaller open-water localities of great importance are situated over shallow banks, such as Store Hellefiske Bank in West Greenland. This region contains vast benthic resources utilized by species with limited diving abilities like king eiders (*Somateria spectabilis*), common eiders (*Somateria mollissima*), and walrus (*Odobenus rosmarus*) (7–10). Hundreds of thousands of thick-billed murres (*Uria lomvia*) from Canada, Greenland, Iceland, Svalbard, and eastern Russia overwinter in smaller regions along the productive coastal open-water area in West Greenland (7–9). Other microhabitats occur in offshore areas of Baffin Bay and Davis Strait, where leads and cracks in the ice over deep waters serve as the primary wintering grounds for narwhals utilizing benthic fish and squid resources (11, 12).

Global warming, predicted with considerable certainty (13), is assumed to severely impact sea ice formation in the Arctic. The extent of sea ice has declined in the past 20 years, at a rate of about 3% per decade in the Northern Hemisphere (14). However, this trend is not uniform throughout the Arctic and several regional deviations from the general warming pattern have been observed. For example, the length of the sea ice season and the concentrations of sea ice have increased in the past two decades in the Baffin Bay and Davis Strait (14–16). Passive microwave telemetry and mapping of sea ice distribution over the past 5 decades demonstrate a significant increase in sea ice amounting to about 600 km^2 or 1.3% per decade in Baffin Bay (17). The causes of the cooling trend in Baffin Bay are uncertain but are likely due to simultaneous changes in the thermohaline circulation (causing changes in the relatively warm northward flowing West Greenland current), the North Atlantic Oscillation, and the formation of the sea ice bridge in Smith Sound (17, 18). In Hudson Bay and Foxe Basin a non significant sea ice extent decrease of 1.8% per decade was observed between 1979–1996 (14). However, the length of the sea ice season declined in northwestern Hudson Bay and increased in central Hudson Bay and in Foxe Basin (16, 18).

There have been scattered attempts to study the biological importance of winter refugia in the Arctic. Most have focused only on the larger polynyas (e.g. the North Water or the Northeast Water in East Greenland (19)). Generally, the importance of the smaller high Arctic microhabitats has not been well understood or studied because of obvious logistic problems with field research in dark, cold, and ice covered regions. Due to the importance of open-water pack ice refugia for marine mammals and seabirds, it is critical to identify the changes in these microhabitats and develop predictions of how changes will alter the trophic web or biological resources. Baffin Bay and the eastern Canadian High Arctic have a complex coastline, an influx of warm Atlantic water along the West Greenland coast, and a restricted opening to the polar basin through Robeson Channel, which results in numerous microhabitats in the region. In addition, the abundance of animals overwintering in the dense pack ice in this region is large, making it important for examination of

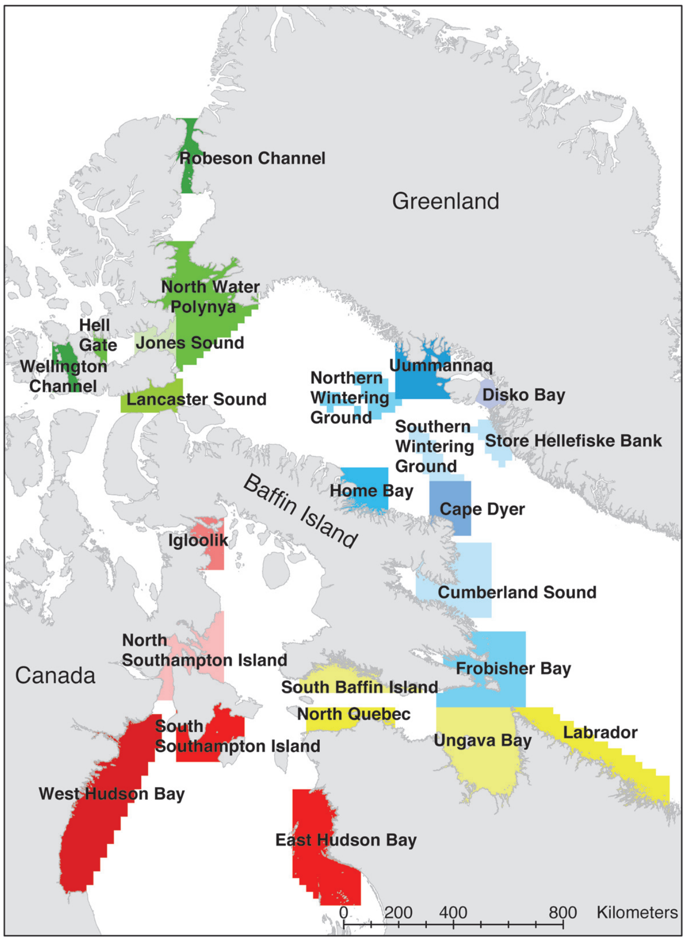

Figure 1. Map of selected microhabitats examined for trends in the fraction of open-water (regions with less than 85% sea ice on 15 March for more than two years within the study period). Regions are indicated by shades or colors; Foxe Basin and Hudson Bay microhabitats are in red, Hudson Strait microhabitats are in yellow, Baffin Bay-Davis Strait microhabitats are in blue, and Northern Baffin Bay and Lancaster Sound microhabitats are in green.

trends in sea ice conditions. In this study, changes in the fraction of open-water in 24 pack ice microhabitats were examined over a 23-year time series using remotely-sensed microwave sea ice data. Observed trends were related to the relative importance of each wintering microhabitat for eight marine indicator species and potential impacts on winter success and survival were examined.

MATERIAL AND METHODS

Selection of Localities and Dates

The overall study area was chosen to encompass the year-round range of selected birds and marine mammals, including Baffin Bay, Davis Strait, Hudson Strait, northern Hudson Bay, Foxe Basin, Lancaster Sound, and Robeson Channel (Fig. 1). Specific microhabitats were selected based on visual investigation of the sea ice time series on 15 March each year (Fig. 2). Recurrent open-water areas were identified and delineated, where 85% or less sea ice was found on 15 March for more than two years within the study period. Some additional areas were selected based on the literature, where specific areas have been documented to harbor wintering populations of marine mammals and seabirds.

SSMR/SSMI Methods

Sea ice concentration data were obtained from passive microwave telemetry available in two datasets from the National Snow and Ice Data Center (NSIDC). The Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR) dataset extending from 1979 through 1987 and the Defense Meteorological Satellite Programs Special Sensor Microwave/Imager dataset covering the period from 1987 through 2001 were used. Sea ice concentration was derived using the Bootstrap algorithm following Comiso (20), where daily sea ice concentrations for the Northern Hemisphere were mapped to a polar stereographic projection (true at 70°N) at a 25 km resolution. Sea ice data obtained from the NSIDC were converted from raw binary to ASCII format using a program written in Compaq Visual Fortran 90 and imported into a geographic information system (ESRI ArcINFO 8.3) as raster grids. The center of each cell received the estimate of average sea ice concentration in that 625 km^2 (a constant approximation for pixel areas) area and pixels were consistently classified as land or sea ice across all years. A March composite was created as the product of the vertical spatial and temporal average ice concentration for each cell for all days in March each year and used to calculate the fraction (or percentage) of open-water.

The fraction of open-water, the 'ice-free' portion of each microhabitat, (F) was modeled as:

$$F = \left(\sum_{i=1}^{h} (PC^*(1-(IC/100)) \right) / MHA$$

where i indexes the lowest sea ice concentration in the microhabitat to h, the highest sea ice concentration, IC is specific sea ice concentration calculated in full integer units and recorded as a percent, PC is pixel count for each specific sea ice concentration, and MHA is the microhabitat area in number of pixels. Trends in the fraction of open-water were examined for each microhabitat between 1979–2001. Open-water localities smaller than 7 pixels were not examined because the sea ice data were not of sufficient resolution to describe the ice formation at those localities. Several microhabitats were, however, composed of a mosaic of many smaller areas.

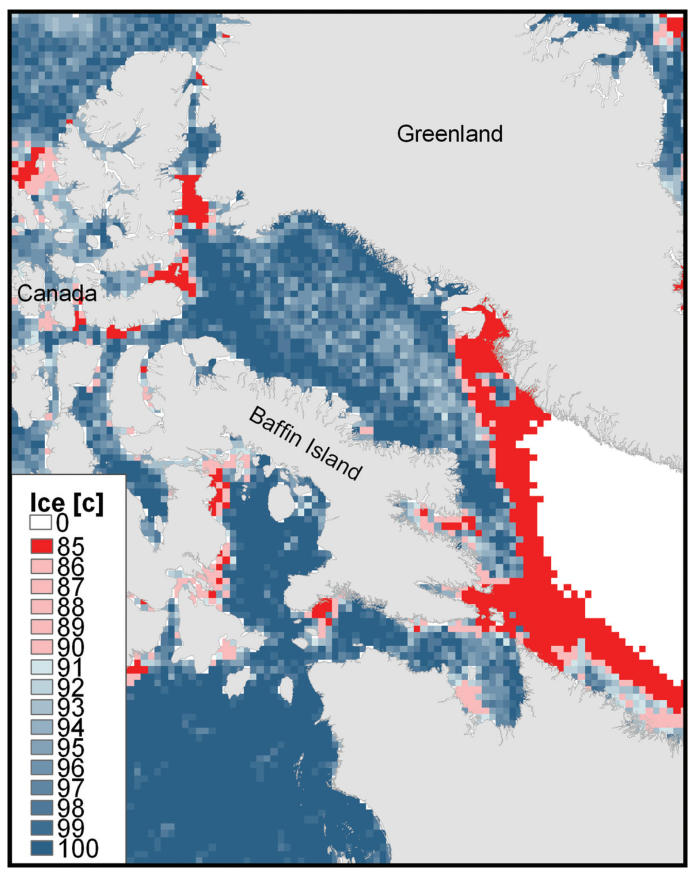

Figure 2. Example of SSMI/SSMR sea ice concentration readings from 14 March 1986. Red regions are 85% sea ice concentration or less and pixels are approximated at 25 km^2.

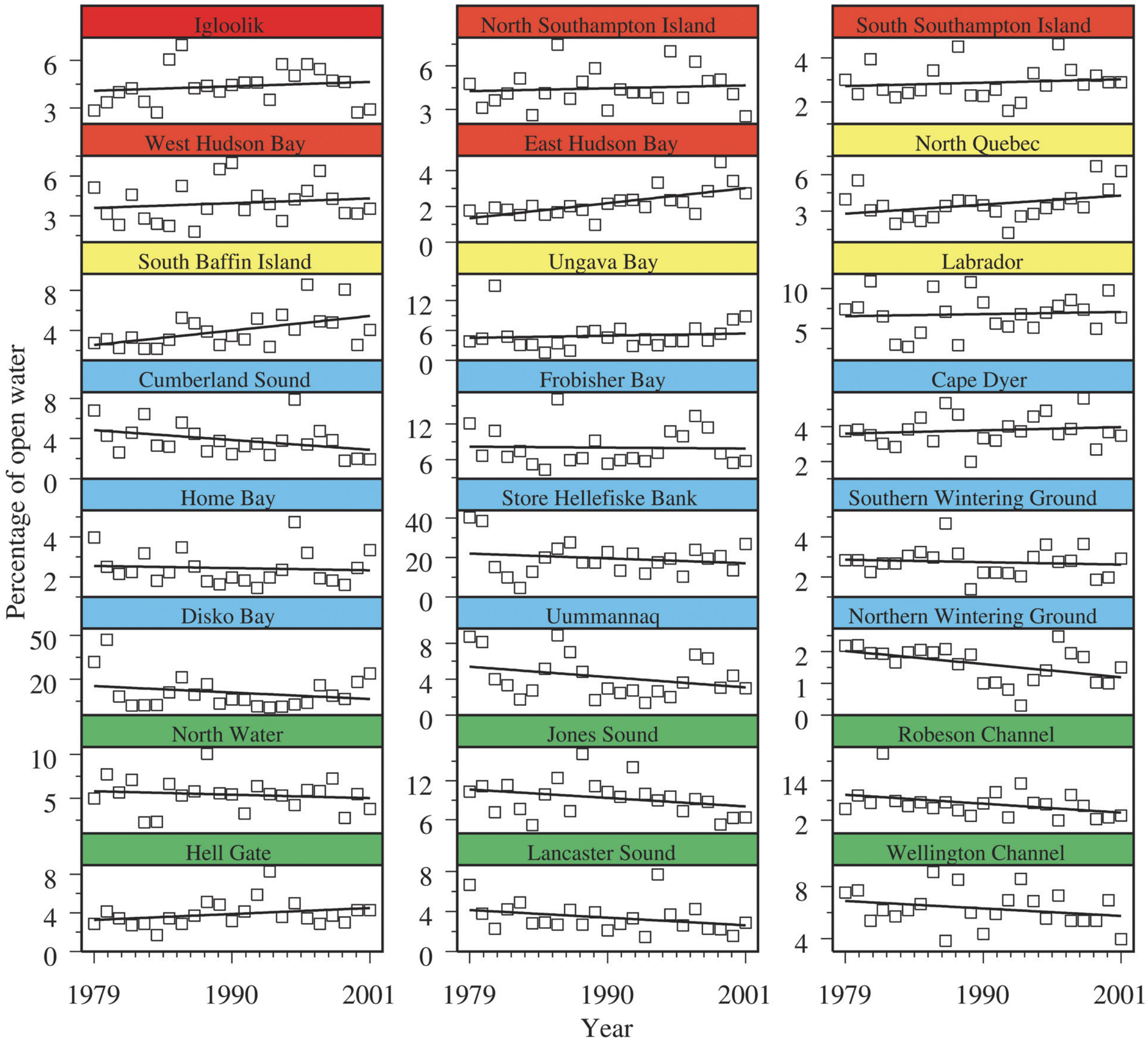

Figure 3. Trends in the fraction of open-water at 24 microhabitats in Canada and West Greenland. Regions are indicated by colors (following Fig. 1) where Foxe Basin and Hudson Bay microhabitats are in red, Hudson Strait microhabitats are in yellow, Baffin Bay-Davis Strait microhabitats are in blue, and Northern Baffin Bay and Lancaster Sound microhabitats are in green.

Statistical Analyses of the Extent of Open Water

Least square linear regressions were fit through the time series of the proportion of open-water in March at each microhabitat. The probability of each trend was assessed from the marginal posterior distribution of the Bayesian regression of the fraction of open-water over time. This method was chosen to provide a specific probability for the observed trends rather than a standard significance level.

Biological Importance of Microhabitats

The biological importance of each pack ice microhabitat was determined based on the occurrence and abundance of eight High Arctic indicator species: the walrus, the bowhead whale (*Balaena mysticetus*), the narwhal, the beluga, the king eider, the common eider, the little auk, and the thick-billed murre. These species were chosen because of their specific dependence on open-water localities during winter. Other Arctic species such as the black guillemot (*Cepphus grylle*), gull species (Laridae), Northern fulmar (*Fulmarus glacialis*), bearded seal (*Erignathus barbatus*), ringed seal (*Phoca hispida*), and polar bear were not included either because little is known about their occurrence (e.g. gulls and bearded seals) or because they are found virtually at all the open-water localities (e.g. black guillemot) or in the coastal fast ice (e.g. ringed seals and polar bears). Basic information on distribution, abundance, and habitat use was compiled from existing literature and used to document the dependence on open-water areas during winter and potential effects of changes in open-water on success and survival.

RESULTS

Trends in Open Water

Within the overall study area, six large regions were identified and examined: Foxe Basin, Hudson Bay, Hudson Strait, Baffin Bay-Davis Strait, northern Baffin Bay, and Lancaster Sound. Within these six regions, 24 specific pack ice microhabitats were identified based on open-water in March (Table 1, Fig. 1). Regionally, Foxe Basin, Hudson Bay, and Hudson Strait showed increasing trends in the fraction of open-water and the trend at all microhabitats combined ranged from 0.2 to 0.7% per decade. Regions of Baffin Bay-Davis Strait, northern Baffin Bay, and Lancaster Sound showed overall decreasing trends in the fraction of available open-water in March. The trend in all microhabitats combined in Baffin Bay-Davis Strait and northern Baffin Bay was -1% per decade and the trend in Lancaster Sound microhabitats was -0.6% per decade.

The two pack ice microhabitats in Foxe Basin (North Southampton Island and Igloolik) were equivalent to an area of approximately 50 000 km². These two microhabitats showed slight increasing trends in the proportion of open-water between 1979–2001 (Table 1). Approximately 200 000 km² were examined in the Hudson Bay region and trends in the fraction of open-water in the three microhabitats were also slightly increasing. In the region of Hudson Strait, four localities were examined, approximately 200 000 km², and increasing trends in the fraction of open-water were detected in all four (Fig. 3 and Table 1).

In the region of Baffin Bay-Davis Strait (total area of 280 000 km^2), eight out of nine microhabitats demonstrated declines in available open-water. Decreasing trends ranged widely, from -0.01 in Frobisher Bay to -0.40% per year in Disko Bay. Four of these eight had high probabilities of a negative trend > 0,86 (Cumberland Sound, Disko Bay, Uummannaq, and the Northern Wintering Ground, Table 1) and four other localities (Home Bay, Store Hellefiske Bank, Frobisher Bay) also had moderately high probabilities of a decline (> 0.56). Only the locality of Cape Dyer in central Baffin Bay showed a trend for increasing open water (0.02% yr^{-1}) (Fig. 3, Table 1).

In the northern Baffin Bay region, three of four microhabitats (110 000 km^2) had high probabilities of a negative slope (> 0.73) and only Hell Gate had an increasing proportion of open-water with a low probability (0.1) that the trend is actually negative. The small size of Hell Gate (only 7 pixels) and substantial amount of land surrounding the microhabitat probably affected the results. Finally, both the microhabitat of Lancaster Sound and Wellington Channel (in the Lancaster Sound region) (30 000 km^2) demonstrated declines in open-water (- 0.05 to - 0.07% yr^{-1}) with probabilities > 0.88.

Arctic Species Diversity and Abundance

Of the eight selected species of Arctic birds and marine mammals, abundance and diversity supported conclusions on the most important wintering regions within the study area. In the case of marine mammals, important microhabitats included South Baffin Island (in the region of Hudson Strait), Cumberland Sound and offshore, the North Water, Store Hellefiske Bank, and Disko Bay (Table 1). In the case of seabirds, important winter microhabitats included Store Hellefiske Bank, the North Water, Lancaster Sound, and Jones Sound (Table 1). As expected, there was considerable overlap of important areas for seabirds and marine mammals.

Walrus

Walrus make seasonal movements from coastal areas to offshore wintering grounds where open-water can be predictably found in the pack ice. Walrus depend on shallow water banks with open-water (< 80 m), where they can access benthic prey and oxygen. Data on numbers of walruses distributed across the 24 pack ice microhabitats were based on counts made during summer surveys at haul-out sites. The location of wintering preferences is unknown for most of these summering aggregations, as the stock delineation of walrus in West Greenland and eastern Canadian Arctic is incomplete. Due to this, correct allocation of the already sparse information to the wintering localities was uncertain. Two major winter aggregations of walrus are known for certain: those within the microhabitats of Store Hellefiske Bank and the North Water. Of these, only Store Hellefiske Bank has been systematically surveyed for walrus abundance in winter (10). The North Water is probably supplied by animals that summer in the Canadian High Arctic or in Kane Basin. Due to the large proportion of walrus that are not accounted for at the two winter microhabitats, the data indicate that many animals must use other unidentified open-water areas (e.g. Foxe Basin, Hudson Bay and Hudson Strait, especially the areas around North and South Southampton Island) during winter (Table 1).

Table 1. Important microhabitats used by wintering sea birds and marine mammals. Slope of regression for annual trends (1979–2001) in the percentage point (fraction) of open-water are reported with probabilities of slopes being negative. Estimated winter and spring abundance of selected marine mammals and birds are indicated based on past surveys reported in the literature. Within each region the microhabitat names refer to the map in Figure 1. The term 'some' refers to the presence of the species however in unknown numbers.

Region	Microhabitats	# of pixels	Area (km^2)	Trend	Probability of slope < 0	Walrus	Bowhead whale	Narwhal	Beluga	King eider	Common eider	Little auk	Thick billed murre
Foxe Basin	Igloolik	25	15 625	0.03	0.25	0	0	0	0	0	0	0	0
	North Southampton Island	55	34 375	0.02	0.33	5500	0	0	0	0	0	0	0
Hudson Bay	South Southampton Island	47	29 375	0.01	0.28	3000	0	0	0	0	0	0	0
	West Hudson Bay	170	106 250	0.03	0.24	0	0	0	0	0	0	0	0
	East Hudson Bay	113	70 625	0.08	0.00	500	< 100	0	> 1000	some	12 000	0	0
Hudson Strait	North Quebec	37	23 125	0.07	0.05	0	< 100	2000	> 25 000	0	some	some	some
	South Baffin Island	52	32 500	0.13	0.01	3000	> 100			some	some	some	0
	Ungava Bay	129	80 625	0.04	0.33	< 100	some	0	some	0	some	0	some
	Labrador	93	58 125	0.02	0.38	< 1000	some	0	some	0	some	0	some
Baffin Bay-Davis Strait	Cumberland Sound and offshore	83	51 875	-0.09	0.96	< 1000	< 100	> 1000	1000	some	some	some	0
	Frobisher Bay and offshore	109	68 125	-0.01	0.56	< 1000	< 100	> 1000	< 1000	some	some	some	some
	Cape Dyer	41	25 625	0.02	0.27	< 1000	< 100	> 1000	0	0	0	0	some
	Home Bay	40	25 000	-0.01	0.64	< 1000	0	> 1000	0	0	0	0	0
	Store Hellefiske Bank	25	15 625	-0.13	0.67	< 1000	250	< 1000	8000	> 100 000	> 100 000	> 10 000 000	> 100 000
	Disko Bay	20	12 400	-0.40	0.86	0		3000		0	some	some	some
	Southern Wintering Ground	37	23 125	-0.02	0.26	0	0	5000	0	0	0	0	0
	Uummannaq	52	32 500	-0.11	0.92	0	0	some	0	0	0	some	some
	Northern Wintering Ground	40	25 000	-0.04	1.00	0	0	45 000	0	0	0	0	0
Northern Baffin Bay	North Water	129	80 625	-0.04	0.73	< 3000	< 100	< 1000	13 000	0	some	> 50 000 000	> 100 000
	Jones Sound	20	12 500	-0.12	0.92	< 1000	0	0	some	0	some	> 10 000 000	> 100 000
	Robeson Channel	19	11 875	-0.25	0.97	0	0	0	0	0	0	0	0
	Hell Gate	7	4375	0.06	0.10	< 1000	0	0	0	0	0	0	0
Lancaster Sound	Lancaster Sound	32	20 000	-0.07	0.93	< 1000	0	0	0	some	some	> 10 000 000	> 100 000
	Wellington Channel	17	10 625	-0.05	0.88	< 1000	0	0	0	some	some	0	some
References						10	4, 45, 46	24, 25, 47, 48, 49	46, 49, 50	8, 29, 51	7, 8, 29, 51	6, 51	7, 8, 41, 51

Bowhead Whale

In winter, bowhead whales are generally found in association with dense pack ice or at the ice edge. During spring migration periods, bowheads have been observed penetrating severe pack ice in Baffin Bay and apparently have the ability to break breathing holes (21, 22). The low abundance of bowheads in Baffin Bay is a result of past exploitation, however, there are recent indications of an increase in population size (23). The most important wintering microhabitats for bowhead whales are in West Greenland (Store Hellefiske Bank and Disko Bay) and in the region of Hudson Strait in Canada. Bowheads may also be found in low numbers in winter in the North Water, off Cape Dyer, and off Cumberland Sound. The two microhabitats in West Greenland display declining trends in open-water, however, in Canada the trends in the region of Hudson Strait are increasing (Table 1). In spring, bowheads are dependent on opportunities for feeding on zooplankton blooms in Disko Bay, the North Water, northern Foxe Basin and Lancaster Sound.

Narwhal

Narwhals are the most abundant cetaceans in Baffin Bay, with an estimated abundance exceeding 50 000 (24). Narwhals depend heavily on open-water for their winter survival and build up of fat deposits. Narwhals winter in the regions of Hudson Strait and Baffin Bay-Davis Strait, as well as Disko Bay. Narwhals wintering in Hudson Strait in smaller numbers however are assumed to belong to the Northern Hudson Bay summer population (25). The largest abundance of narwhals is found in the offshore areas of Baffin Bay and Davis Strait, and within this region, two offshore microhabitats have been identified (the Northern and Southern Wintering Ground) (11). The narwhal population in Baffin Bay is presumed to be separate from that in Foxe Basin and within Baffin Bay, several subpopulations occur each with high site fidelity to separate wintering grounds (11). There is sufficient evidence to detect a clear decline in the amount of open-water in several narwhal wintering microhabitats, including the Northern Wintering Ground, Southern Wintering Ground, Disko Bay, Store Hellefiske Bank, North Water, and Cumberland Sound and adjacent offshore areas (Table 1). The increase in the extent of open-water at some localities in Hudson Strait, where narwhals from Foxe Basin are believed to winter, indicates that different subpopulations experience different sea ice trends.

Beluga

Arctic belugas have been found in most types of sea ice but appear to prefer loose pack and avoid longer stays in dense ice. Discrete stocks of belugas are found across Arctic Canada and in West Greenland, all of which have specific wintering grounds. The 20 000 belugas summering in the Canadian High Arctic (near Somerset Island) (24) move out of the area in fall to either the North Water (where the largest abundance overwinters) or the coast of West Greenland (in the microhabitats of Disko Bay and Store Hellefiske Bank) (3). A fourth microhabitat is occupied by a resident population of belugas in Cumberland Sound, which moves offshore with forming fast ice for the winter. All four of these microhabitats show a declining trend in the extent of open-water. Other distinct beluga stocks occupy eastern and western Hudson Bay in summer numbering up to 25 000 animals (26). The exact area where these whales overwinter is unknown, however, there are increasing trends in open-water in Hudson Strait where a large majority likely is found.

The King and Common Eider

King eiders breed in northern Canada and North Greenland. Nearly the entire population from eastern Canada and Greenland winters in the dense pack ice on Store Hellefiske Bank, West Greenland (> 100 000 pairs, Table 1) (27, 28). In this area king eiders can find ideal feeding opportunities during winter on the shallow banks, as they can dive to the bottom and take mussels. Common eiders also breed in West Greenland and Canada, however, this species is more coastal in its distribution and occurrence during winter (7). In eastern Hudson Bay, a sedentary population of common eiders also winters in the shallow open-water areas (29). A large proportion of common eiders from the Canadian Arctic and Northwest Greenland winter in the coastal areas of West Greenland and Store Hellefiske Bank (8). Here, they similarly utilize shallow coastal open-water areas for feeding.

Little auks at bird cliffs in Northwest Greenland. Photo: M.P. Heide-Jørgensen.

The Little Auk

The wintering areas for little auks extend from Davis Strait to Newfoundland. Many birds are found along the West Greenland coast, especially on Store Hellefiske Bank. It is likely that both little auks from North Greenland and Svalbard winter in southwest Greenland waters, however, the total number of little auks wintering in southwest Greenland is unknown (9). The little auk is planktivorous and is highly dependent on primary and secondary production in their feeding areas. In spring, little auks move north to breed in colonies in Northwest Greenland in the North Water and adjacent waters. When the birds arrive at breeding sites in early May, they feed in the offshore open-water in the North Water utilizing the rich abundance of copepods (primarily *Calanus hyperboreus* and *C. glacialis*) (5, 30). Recent surveys have estimated the population to number at least 33 000 000 breeding pairs in the North Water during this time (6). The ice-free areas of the North Water and Lancaster Sound are declining and less water is available for the little auks in May.

The Thick-billed Murre

In winter, large numbers of thick-billed murres move to West Greenland from areas as far as Svalbard, East Greenland, East Baffin, the Canadian High Arctic, Iceland, and eastern Russia (8). Later in spring, these birds return from their wintering grounds in southwest Greenland to their breeding grounds where they require open-water for feeding. Thick-billed murres breed at bird cliffs in Northwest Greenland, along the east coast of Baffin Island, in Hudson Strait and in the Canadian High Arctic. In these areas they are dependent on open-water with high productivity close to the colonies.

DISCUSSION

Regional increasing trends in sea ice coverage in Baffin Bay and Davis Strait (resulting in declining open-water) were as high as 7.5% per decade between 1979–1999 (14, 16, 18, 31, 32) and comparable significant increases have been detected back to 1953 (17). Similar trends in sea ice have also been detected locally along the West Greenland coast, with slightly lower increases of 2.8% per decade ($p < 0.07$) (17). Until now, regional trends have not been detected on microhabitat scales and little has been done to investigate the effect on aggregations or sub-populations of marine predators dependent on these localized areas. Several species rely heavily on open-water during winter periods, which is often critical to their survival or survival of their offspring. With respect to resource management of Arctic marine predators, it is necessary to incorporate understanding of the impacts of climate change on habitats into decisions for resource use.

Open-water wintering areas smaller than 25 km^2 were not examined in this study because the coarse resolution of the sea ice data prevented localized trend detection. It is likely that marine mammals and seabirds also use very small open-water areas during winter (e.g. shore leads < 1 km in width). The extent to which they rely on these areas is unknown and most likely, these species utilize larger or more predictable areas most frequently. It is reasonable to assume that the 24 microhabitats examined here represent the majority of the intensively utilized wintering areas in the Canadian High Arctic and West Greenland. It is also likely that the smaller areas, not examined here but adjacent to larger localities, have similar trends in the proportion of open-water and that these trends may be inferred from their larger neighboring localities.

In this study, contrasting trends in the fraction of open-water were observed. The eastern Canadian High Arctic microhabitats generally showed an increase in open-water, whereas microhabitats in Baffin Bay-Davis Strait showed decreasing open-water. Although trends varied across regions in this study, the 'biologically' most important wintering areas were found in regions with increasing sea ice, with the exception of Hudson Strait. This increase has both obvious direct effects on oxygen access as well as indirect effects on marine productivity. It is, however, important to note that top marine predator vulnerability may not merely lie in the gradual reduction of open-water, as it must be assumed that the animals have some ability to adapt to long-term changes in their environment. What may be more important is the increasing sea ice coverage in combination with environmental variability, which leads to an increased frequency of periodic complete freeze-over. This can result in catastrophic mortalities that can affect population trajectories. For example, in Disko Bay, less than 5% open-water was observed on 89% of the days (n = 124) in March between 1992–1995, and during this period, 15% of these days had complete freeze-over of Disko Bay (< 0.1% open-water).

Vulnerability of Marine Mammals

Failure to maintain access to oxygen has been documented to cause immediate mortality in Arctic cetaceans (33, 34). Narwhals and belugas are not capable of breaking breathing holes in the ice and are occasionally found trapped in large numbers. Marine mammals are more capable of tolerating longer periods with nutritional stress than seabirds as they have thick blubber layers, which can be used as a reserve during periods with little forage. Despite this, density dependent effects of nutritional stress on reproduction and survival for marine mammals cannot be discarded regardless of their relative resilience (e.g. 35, 36). Seabirds, in contrast, have an active strategy for avoiding nutritional stress due to a much higher mobility, easily travelling several hundred km a day in search of favorable feeding areas.

The walrus is the only one of the four marine mammal species examined here that is truly capable of breaking thick ice for access to air (37). Walrus are often found in small leads or open-water created by tidal movements around icebergs. There are no reports of fatal ice entrapments of walruses and they are clearly well adapted to life in the sea ice, flexible in their selection of foraging sites and prey. Walruses do depend heavily on shallow banks for feeding on bivalves but are reported to occasionally take seals over deeper water (38, 39). The walrus may be less vulnerable to reduced open-water space in the pack ice than the other marine mammal species.

Bowhead whales travel long distances over short time periods and have less firm migratory patterns than observed for belugas and narwhals. Furthermore, bowhead whales often travel alone and are widely dispersed during both summer and winter, so only a small fraction of the population will, at any given time, be susceptible to ice entrapments. Although bowhead whales can break thick new ice, they are also occasionally trapped in sea ice together with either narwhals or belugas. Bowhead whales depend on access to zooplankton, and changes in marine productivity may either have nutritional effects or cause changes in movement patterns. The timing and composition of the zooplankton blooms, related to extension and residency of sea ice, is critical for optimal feeding opportunities for bowhead whales.

Bowhead whale and belugas at an ice entrapment in Lancaster Sound in May 1999. Photo: M. Ramsay.

Narwhals utilize leads and cracks for access to air in dense ice and are occasionally found in ice entrapments in the thousands. Narwhals feed heavily on the wintering grounds and are dependent on access to open-water for breathing between deep foraging dives. The large numbers of narwhals on the Northern Wintering Ground are assumed to be geographically isolated from those on the Southern Wintering Ground. Due to their strong site fidelity, the narwhal aggregations must be considered functionally separate units, highly sensitive to any further increase in pack ice, as they inhabit areas with the least amount of open-water. On the wintering grounds, the fraction of open-water can be as low as 0.5–2.0% at the end of March. The regional decrease of open-water of 1.0% per decade detected in Baffin Bay will clearly impact this species.

In Baffin Bay, belugas overwinter in the four microhabitats with the largest fractions of open-water: the North Water, Jones Sound, Disko Bay, and Store Hellefiske Bank. These microhabitats all show declining trends in open-water with high probabilities of slopes less than zero. Like narwhals, belugas are occasionally trapped in sea ice in large numbers, especially in Disko Bay and Jones Sound (33–35). Belugas also winter offshore in Cumberland Sound, where they may face reduced amount of open-water at the wintering site. The belugas wintering in West Hudson Bay and Hudson Strait do not appear to be at risk of ice entrapments as open water is increasing in their wintering areas.

Vulnerability of Seabirds

The vulnerability of Arctic seabirds diverges from marine mammals in that reduced open-water generally only limits access to prey. Common eiders, little auks, and thick-billed murres have, however, been reported to occasionally succumb in ice entrapments (29, 40). Seabirds have high metabolic rates and require dependable year-round access to rich prey resources for survival, reproduction, and chick rearing. Several species of seabirds rely heavily on the open-water areas in the Arctic for overwintering and feeding during critical periods determining success for their breeding cycle. Reduced marine production may have immediate effects on seabirds as their fat deposits cannot sustain them through a season with intensive nutritional stress. Seabirds wintering in West Greenland appear to rely heavily on a few specific localities, one of which is Store Hellefiske Bank. This locality is important because access to shallow water is available in winter, when most coastal shallow areas are covered with fast ice.

Store Hellefiske Bank is particularly important for king and common eiders, which must reach benthic prey at depths < 50 m and < 20 m, respectively (7, 8). The declining trend in open-water on Store Hellefiske Bank may significantly inhibit successful benthic foraging for these species. Even though the total amount of the open-water on Store Hellefiske Bank is still large (> 10%), the area shows a strong decline in the amount of open-water and some critical feeding grounds for the sea ducks may be disappearing. Further reduction of the open-water will force the eiders to move south, to areas with deeper water and less available prey. Store Hellefiske Bank is also host for several species of alcids during winter and spring migration. These alcids differ from sea ducks in that they rely on pelagic prey and can take advantage of deeper open-water further south in Davis Strait if sea ice continues to increase on Store Hellefiske Bank.

Other important regions for seabirds are northern and southern Baffin Bay and Hudson Strait, used for intensive feeding in spring by the little auk and the thick-billed murre during the early stages of the breeding cycle. In spring, the North Water, Jones Sound, and Lancaster Sound are completely surrounded by pack ice when the birds arrive at the bird cliffs, which are strategically located close to the productive open-water areas. Increased distance from colonies to open-water will impact the energetic costs. Further, a reduction of open-water with a subsequent reduction in productivity will affect the feeding success of the millions of little auks and hundreds of thousands of thick-billed murres that rely on these resources for successful breeding. Failure to breed due to extended sea ice cover has been reported for little auks and thick-billed murres (41).

Marine Productivity

The timing and extent of primary production is strongly related to the patterns of ice formation. Extensive and prolonged ice coverage cools the water column during the critical spring period when herbivorous zooplankton graze on phytoplankton (42). Late ice break up of sea ice may delay phytoplankton production and may disrupt the connection between the phytoplankton and copepod grazers that ascend from depth at specific times of the year (43, 44). A cold upper layer of the water column would slow the production of copepods and make the surface waters less productive. Species such as little auks and bowhead whales, which rely on predictable copepod resources during spring in the open-water areas, will be affected by extended ice coverage during this critical feeding period. Fish species like polar cod (*Boreogadus saida*), Arctic cod (*Arctogadus glacialis*), capelin (*Mallotus villosus*), and the larvae of Greenland halibut (*Reinhardtius hippoglossoides*) are also dependent on the spring production of zooplankton. A negative influence from poor production on these forage fish species will ultimately affect top predators such as the thick-billed murre, beluga, and narwhal. If the timing of the coupling between phytoplankton and zooplankton is disrupted by sea ice, changes in the benthos are also to be expected. Phytoplankton that is not consumed by zooplankton will ultimately sink to the bottom and contribute positively to benthic production. This may benefit benthic feeders such as walrus and eiders if they have access to the feeding grounds.

CONCLUSION

Among the pan-Arctic responses to climate change, Baffin Bay and Davis Strait are regions that uniquely deviate from warming patterns and decreasing sea ice. This creates an opportunity for comparing and contrasting effects of climate change on top predators. Here, two types of vulnerability have been identified relative to increasing sea ice: *i)* the direct physical impact of sea ice as a barrier for air-breathing foraging animals; and *ii)* the cascading effects of changes in marine productivity.

Generally the cetaceans are the most vulnerable to a reduction in available open-water, because they urgently require oxygen after dives that cannot exceed 25 minutes. Horizontal displacement within the pack ice is limited to *i)* their maximum swimming speeds (approximately 2 m sec^{-1}); *ii)* available leads and cracks; and *iii)* their ability to detect alternative open-water areas. The frequency of occurrence and fate of whales in ice entrapments outside the inhabited coastal areas of West Greenland and Arctic Canada may even go undetected. Little is known about the ability of cetaceans to react to decreased marine production.

Given the severity of the detected trends in increasing sea ice coverage at important wintering areas, it remains pertinent to focus research efforts on the fate of the eight indicator species examined here. Future studies should specifically address questions related to changes in phenology of migration, alterations in focal areas of importance, signs of nutritional stress, and effects on survival and reproduction for top predators utilizing the Arctic ecosystem during periods of extensive sea ice coverage. Finally, harvest management of top predators must account for the additional risk introduced by reduction in carrying capacity caused by increased sea ice coverage, which may naturally adjust populations downward in response to environmental change.

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