

Arctic sea ice trends and narwhal vulnerability

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Abstract

Conservation measures related to global climate change require that species vulnerability be incorporated into population risk models, especially for those that are highly susceptible to rapid or extreme changes due to specialized adaptation. In the case of Arctic cetaceans, effects of climate change on habitat and prey availability have been subject to intense speculation. Climate perturbations may have significant impacts on the fitness and success of this group, yet measuring these parameters for conservation purposes is complicated by remote and offshore preferences. The narwhal (*Monodon monoceros*) in Baffin Bay occupies a habitat where reversed (increasing) regional sea ice trends have been detected over 50 years. We used a combination of long-term narwhal satellite tracking data and remotely sensed sea ice concentrations to detect localized habitat trends and examine potential vulnerability. Spatial and temporal variability in the fraction of open water were examined on two narwhal wintering grounds between November and April, 1978–2001 using approximate sea ice concentrations derived from microwave SSMR/SSMI passive brightness temperatures. Less than 3% open water was available to narwhals between 15 January and 15 April, and reached minima of 0.5% open water at the end of March (125 km² out of a 25,000 km² area). Decreasing trends in the fraction of open water, together with increasing trends in interannual variability, were detected on both wintering grounds, significantly in northern Baffin Bay (–0.04% per year, SE 0.02). The limited number of leads and cracks available to narwhals during the winter, in combination with localized decreasing trends in open water and high site fidelity, suggests vulnerability to changes in Arctic sea ice conditions. Increasing risk of ice entrapments, many of which may go undetected in remote offshore areas, should be incorporated into population risk assessments as this may exceed the natural response capacity of the species.

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1. Introduction

Significant physical and biological shifts have recently been reported for polar environments and are attributed to pervasive alterations in the global climate (Murphy and King, 1997; Morison et al., 2000; Wigley and Raper, 2001; Parmesan and Yohe, 2003; Root et al., 2003). In the past 25 years, the hemispheric extent of annual sea ice in the Arctic has decreased by 3% per decade, with perennial sea ice decreasing at 9% per decade (Johannessen et al., 1999; Vinnikov et al., 1999; Parkinson et al.,

1999; Parkinson and Cavalieri, 2002; Comiso, 2002). Combined with these sea ice trends are reports of changing salinity, warmer air and water temperatures (Morison et al., 2000; Wigley and Raper, 2001), shifts in thermohaline circulation (Morison et al., 2000; Mysak, 2001), and reorganization of marine zooplankton communities (Beaugrand et al., 2002), all of which leave growing scientific consensus that the Arctic climate is undergoing considerable change.

There are numerous hypotheses about how global climate change will impact top Arctic predators. Arctic marine predator movement patterns and life history can generally be linked to the cyclical nature of sea ice. Consequently, many studies predict nutritional stress due to redistribution of prey, changes in survivorship or fecundity, and shifts in migrations due to changing ice patterns. Conservation measures focused on population

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response have been hampered by insufficient data on polar amplification of warming trends, incomplete information on Arctic species distributions and life history traits, and non-uniform or region-specific patterns. A unifying feature of nearly all of these studies is that they focus on responses to warming trends and concurrent increasing temperatures or decreasing sea ice in areas such as Alaska (USA) and Hudson Bay (Canada) (Stirling and Derocher, 1993; Stirling, 1997; Tynan and DeMaster, 1997).

Although due attention has been given to the hemispheric warming trends, recent work indicates that patterns of climate-induced change must be examined on regional scales. Studies in the Canadian high Arctic, Baffin Bay, and West Greenland report findings that are markedly different from the overall trends of sea ice reduction. Since 1970, the climate in West Greenland has cooled, reflected in both oceanographic and biological conditions (Hanna and Cappelen, 2003). Contrary to a reduction of sea ice, Baffin Bay and Davis Strait display strong significant increasing trends in ice concentrations and extent, as high as 7.5% per decade between 1979 and 1996, with comparable increases detected back to 1953 (Parkinson et al., 1999; Deser et al., 2000; Parkinson, 2000a,b; Parkinson and Cavalieri, 2002; Stern and Heide-Jørgensen, 2003). Predictions for the future suggest similar trends, where climate models projecting sea ice trends over the next 50 years note Baffin Bay is one of the few areas with increased sea ice concentrations and sea ice thickness (Sewall and Sloan, 2004).

Few data exist to determine the effects of increasing sea ice concentration on Arctic cetaceans, as they occupy inaccessible habitats for most of the year and are not easily observed without the use of remote telemetry. Among the cetaceans that inhabit the Baffin Bay pack ice, the narwhal is perhaps the most conspicuous and offers a unique opportunity for examining effects of climate-induced sea ice trends. By far, the largest numbers of narwhals worldwide are found in Baffin Bay. They make extensive annual migrations from high Arctic summering grounds to low Arctic wintering grounds, where approximately 50,000 whales overwinter in the dense pack ice between November and April (Koski and Davis, 1994; Innes et al., 2002; Heide-Jørgensen et al., 2002a, 2003a). Narwhals arrive predictably on the wintering grounds between the end of October and 10 November (Dietz and Heide-Jørgensen, 1995; Heide-Jørgensen et al., 2002a, 2003a). To date, satellite tracking studies show that three sub-populations utilize two spatially distinct wintering grounds between which no overlap or exchange occurs (Heide-Jørgensen et al., 2003a). On these wintering grounds narwhals make highly localized movements and available data indicate different foraging strategies between different sub-populations (Laidre et al., 2003; Laidre

et al., 2004a). The wintering grounds are critically important for narwhal energy intake and overall fitness. Intense feeding behavior has been documented during the 6-month period of residency (Laidre et al., 2003), and in contrast to low feeding activity during the summer period, suggests a major portion of the annual energy intake for narwhals is obtained in Baffin Bay in winter (Laidre, 2003; Laidre et al., 2004b,c).

Narwhals require leads and cracks in the ice to breathe and cannot maintain open breathing holes. There have been no direct observations of narwhal mortality in the pack-ice in central Baffin Bay, as the area is hundreds of kilometers from shore and rarely visited by humans. There are, however, numerous reports of large-scale mortality events of narwhals in coastal pack-ice, where sudden changes in weather conditions cause rapid freeze up of leads and cracks eliminating access to oxygen (Siegstad and Heide-Jørgensen, 1994; Heide-Jørgensen et al., 2002b). Due to this documented vulnerability, reductions in the availability of open water in the Baffin Bay pack ice may have deleterious consequences for these uniquely adapted marine mammals.

In light of overall increasing sea ice in Baffin Bay and in terms of incorporating climate change vulnerability into population risk assessment, it is necessary to examine local trends in the fraction of open water on narwhal wintering grounds. The objectives of this study were to examine interannual and intraannual trends in the ice concentrations and fraction of open water on narwhal wintering grounds using a 23-year time series of satellite-derived ice conditions between 1978 and 2001. Information on sub-population specific area use was used to determine if region-wide trends in sea ice reported for Baffin Bay and North Davis Strait could be detected at the narwhal winter habitats. This information was coupled with known anthropogenic impacts and conservation measures discussed.

2. Materials and methods

2.1. Sea ice

Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC) in Boulder, Colorado for all available days between 26 October 1978 and 9 September 2001. The data set included passive brightness temperatures from both the scanning multichannel microwave radiometer (SSMR, every second day between 1978 and 1987) and the special sensor microwave imager (SSM/I, daily on several satellites since 1987). The sharp contrast in microwave emissions between the sea ice and the open water, together with the relative absence of atmospheric interferences from the microwave signal, allowed for the calculation of the sea ice edge and the

approximate sea ice concentrations within the ice pack. Sea ice concentration (1% resolution) was derived using the Bootstrap algorithm following Comiso (1995), 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 and daily data were imported to a geographic information system (GIS, ESRI ArcINFO 8.3) as raster grids, where the center of each cell received the estimate of average sea ice concentration in that 625 km² area. Daily ice grids were clipped to a predefined study area of interest (Fig. 1), which included the full spatial extent of both the northern and southern narwhal sub-population wintering grounds.

2.2. Narwhal wintering grounds

Spatial delineation of wintering grounds for each sub-population was based on 95% kernel probability area estimates derived from the satellite tracking geographic data where 40 narwhals were tracked by satellite from each sub-population site for 2–3 consecutive years (Heide-Jørgensen et al., 2002a, 2003a). Polygon home

range estimates were converted into a raster data format and used as a spatial mask to extract sea ice data for these regions on a daily basis. The sub-population of narwhals from Somerset Island, Canada occupies the northern wintering ground (NWG) in central Baffin Bay. This area was estimated to be 25,486 km², or approximately 40 pixels. The sub-populations from Melville Bay, West Greenland and Eclipse Sound, Canada occupy the southern wintering ground (SWG), an area estimated as 23,125 km², or 37 pixels.

2.3. Spatial and temporal analysis

A sample dataset was created by selecting the daily grids of the first and 15th day of each month (November through April) of each year of the time series for only those cells defining the home range of both sub-populations. When necessary (due to missing data) the second or 16th days of each month were used as substitutes. The fraction of open water and total area of open water (km²) on each wintering ground (variables describing ‘ice-free’ area within the ice pack) were calculated for each of the 12 observations within the time series. The fraction of open water on the wintering ground (F) was modeled as

$$F = \left(\sum_{i=1}^h (PC_i \times (1 - (IC_i/100))) \right) / WGA,$$

where i is the lowest sea ice concentration on the wintering ground for a given time t and h is 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 WGA is the wintering ground area in number of pixels. The area of open water (A) for a given time step was then $PA \times F \times WGA$, where PA is pixel area (625 km²).

Maximum ice concentration was found to most frequently occur in the month of March for both wintering grounds. A monthly mean time series for March (referred to as the March composite) was created for each year to explore the variation in the maximum ice concentration over time. The March composite was a product of the vertical spatial and temporal average ice concentration for each cell for all days in March. A 5-year moving average of the variance of the residuals between 1978 and 2001 was calculated for the March composite to elucidate interannual variability in the minimum amount of open water on the wintering grounds. Trends in sea ice were calculated as the slope of a line of best fit to each time series using a standard least squares procedure. The significance of the slope was estimated based on a standard F test. Autocorrelation in the time series was calculated out to 5-year lags for each observation point to examine interannual correlation.

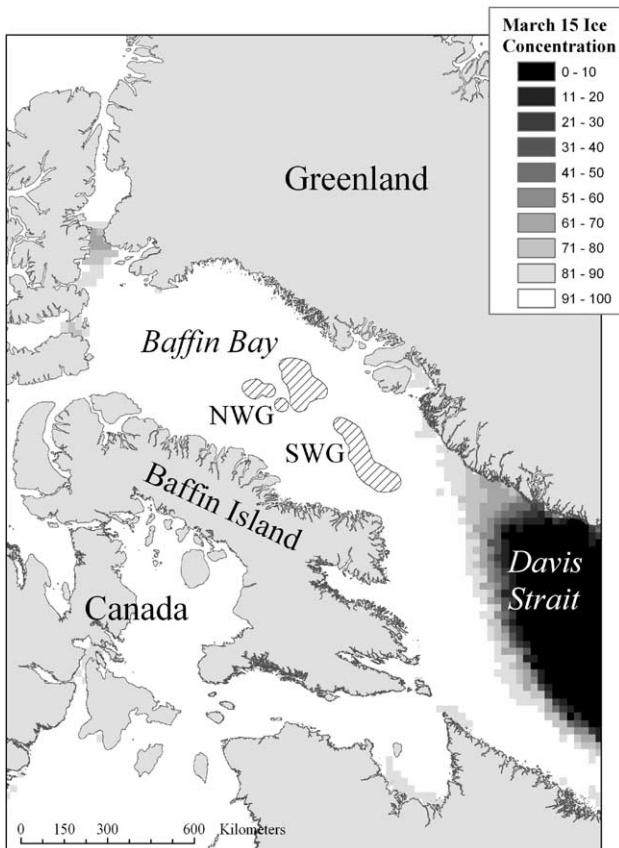


Fig. 1. Map of study region showing example of March 15 sea ice cover (taken from 2000) and the locations of the northern wintering ground (NWG) and southern wintering ground (SWG) (hatched regions within the white area of 91–100% sea ice). Pixels were 25 × 25 km².

3. Results

3.1. Intraannual variability

The range of sea ice concentrations and the fraction of open water varied widely between November and April on both wintering grounds. When whales arrived on the wintering grounds, average ice concentrations ranged between 29% (SD 20) and 69% (SD 26), with typically >60% of the wintering ground being ice-free. The most rapid growth of sea ice and the greatest variability occurred during the early months of the narwhal residency period (November and December). After 15 January, mean ice concentrations were between 95% and 98% on both wintering grounds (mean 97, SD 2) (Fig. 2), although the range in sea ice concentrations on the SWG (33–100%) was much larger than on the NWG (92–100%). The range of sea ice concentrations during this time, however, typically reached lower minima on the SWG (50%) than the NWG (92%).

The available open water declined rapidly between 1 November and 15 December. Freeze-up was faster on the NWG, where on any given date there were generally higher concentrations of sea ice and less open water. The rapid decline in open water slowed as 1 January approached, and by 15 January less than 5% open water was present on both wintering grounds (Fig. 3). The fraction of open water continued to slowly decline

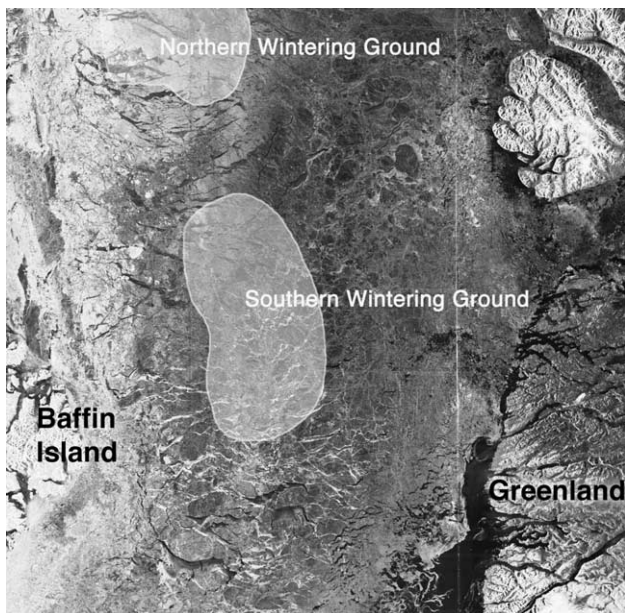


Fig. 2. RADARSAT satellite image of high-resolution (30 m) sea ice concentration in Baffin Bay on 17 February 1999. The dark areas are open water and white or gray areas are sea ice. Note the location of the two narwhal wintering grounds and minimal leads and cracks available in the area during this month, close to the peak freeze-up period. The northern wintering ground is not shown in entirety because it was not completely covered by the path of the satellite.

through February and conditions reached a minima of 0.5% open water on the NWG at the end of March (on average 132 km² out of a 25,000 km²) and 1.9% open water on the SWG at the same time (438 km² out of 23,125 km²).

The SWG consistently contained a 2–3 times larger fraction of open water than the NWG, on average 450–650 km² between 15 January and 15 April (Fig. 3). There was no evidence of an increase in open water availability on 15 April on either wintering ground, the time when whales initiate the spring migration north back to their summering grounds. All trends in fraction of open water on the NWG between 15 February and 15 April suggested decreasing open water, and those on 15 February and 15 March ($F_{1,21} = 5.83$, $p < 0.001$) were significant at the 99% confidence level. No significant trends were found on the SWG for any observation period.

3.2. Interannual variation

There was high year-to-year variability in the 22-year time series in both wintering grounds even though values for the fraction of open water remained below 5% during winter. Autocorrelation indices, examined out to 5-year lags, did not suggest temporal correlation for any given observation in either wintering ground. Autocorrelation coefficients for a 1-year lag ranged from 0.07 to 0.4 and beyond one year, no clear patterns emerged. Open water availability was at its lowest in the winters of 1986–87, 1992–93, 1996–97 and 2001, with cyclical changes most pronounced on the NWG and during the early period of residency between November and December. The cyclical pattern of open water variability followed region-wide Baffin Bay cyclical patterns reported in previous studies.

3.3. Changes in maximum area of open water

The area of open water calculated for the March composite ranged from 75 to 619 km² and from 319 to 1081 km² in the NWG and SWG, respectively. Linear models fit to monthly March average produced a significant decreasing trend in the fraction of open water on the NWG with a slope of -0.04% per year (SE 0.02) ($p = 0.02$, $r^2 = 0.22$) and a decreasing non-significant trend on the SWG with a slope of -0.01% per year (SE 0.02) (Figs. 4 and 5). There was a strong increasing significant trend (0.03% per year, SE 0.006) in the variance of the 5-year running average of the residuals for average conditions in March ($p < 0.001$) in the NWG (Fig. 4). In the SWG, the trend in variance of the residuals was also increasing, however, was not significant (Fig. 5). The amount of open water on the NWG measured for the March composite varied across one year by over a factor of 2.

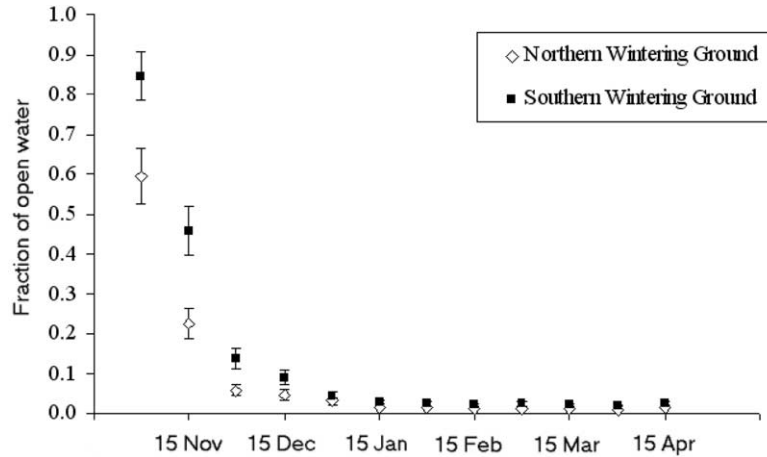


Fig. 3. Average fraction of water (\pm SE) on the wintering grounds in two-week intervals between November 1 and April 15, 1978–2001. Note the higher availability of open water on the southern wintering ground in all weeks.

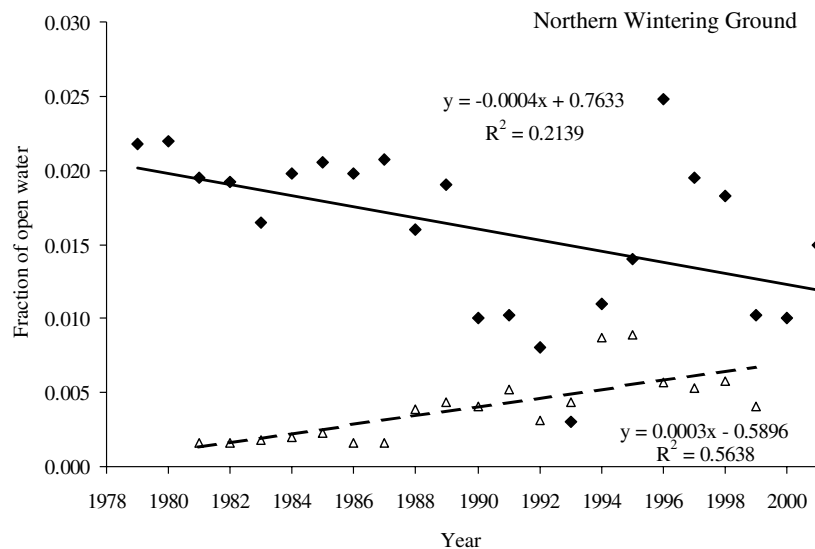


Fig. 4. Trend in the average fraction of open water on the northern wintering ground based on annual estimates of average March sea ice concentrations (solid symbols represent measure of the fraction available each year with solid trend line). A 5-year running average of the variance of the residuals shows an increasing trend (open symbols and dashed line). Both trends were highly significant at or above the 95% confidence level.

4. Discussion

Satellite tracking studies show narwhals arrive on the wintering grounds no later than 10 November (Heide-Jørgensen et al., 2002a, 2003a). The results from this analysis suggest that obstruction by sea ice does not influence when or where whales terminate their migration, as the wintering grounds are >60% open water when whales arrive and begin localized movements. Apparently, whales use alternative cues to locate the wintering grounds and do not cease their migration due to barriers created by ice. This is intriguing relative to patterns of narwhal site fidelity, as whales return to the same regions in central Baffin Bay year after year, where identifying landmarks are not available (Heide-Jørgen-

sen and Dietz, 1995, Heide-Jørgensen et al., 2002a, 2003a). This also has important implications for timing and pace of freeze-up around the wintering ground in December.

The extreme minimal amount of open water availability during March indicates narwhals are highly adapted to successful existence in pack ice. No other cetacean has been demonstrated to occupy such dense winter sea ice cover for such a long period of time. The fraction of open water available to whales between 1 February and 15 April was no more than 5% on both wintering grounds. Despite this restriction, narwhals manage to make relatively large daily movements during this time, up to 40 km per day in some months (Heide-Jørgensen et al., 2002a). Fractal dimensions of move-

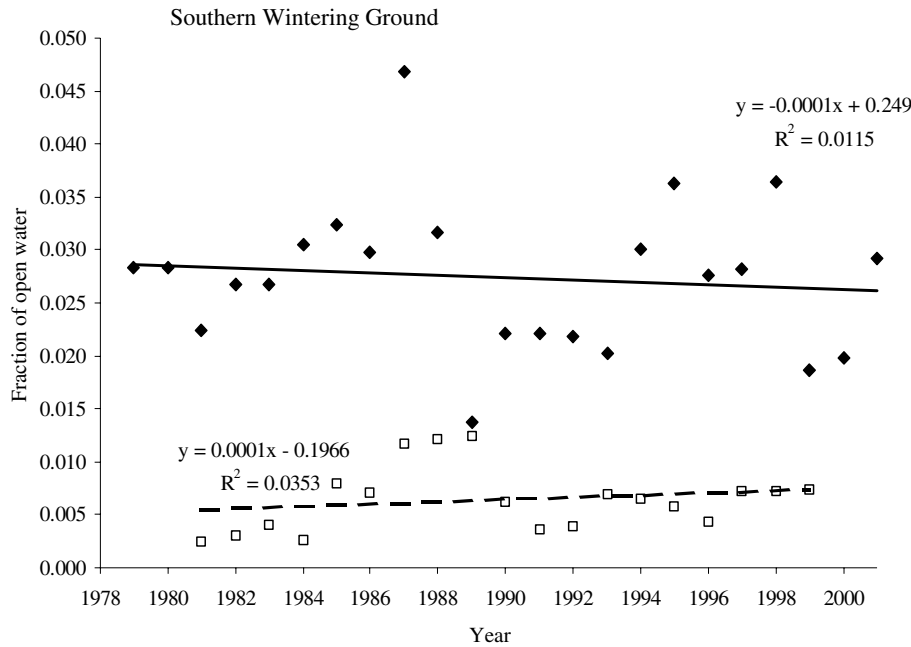


Fig. 5. Trend in the average fraction of open water on the southern winterring ground based on annual estimates of the average March sea ice concentrations (solid symbols represent measure of the fraction each year with solid trend line). A 5-year running average of the variance of the residuals shows a slight increasing trend (open symbols and dashed line), however, neither trend was significant.

ment illustrate whales on the NWG have more convoluted and tight movements (higher fractal dimensions) than whales on the SWG, which make more linear movements (lower fractal dimensions) (Laidre et al., 2004a). These movements appear to reflect sea ice conditions in the two areas where on the SWG narwhals have greater freedom to make linear movements with more open water access or must move larger distances to keep up with shifting leads and cracks. Whales on the NWG, alternatively, face more restrictive or constant sea ice conditions and must remain localized, excluded from longer-distance movements.

Local decreasing trends in the fraction of open water were detected on both narwhal winterring grounds in Baffin Bay. Although trends were similar on the SWG, they were not detected with the same strength as on the NWG, significant at the 95% level or higher. The non-significant trend on the SWG may be caused by its closer proximity to the pack ice edge or large open water areas in Davis Strait. The evidence of declining open water in March suggests winter pack ice, characterized by few leads and cracks available for access to air, results in a severe habitat constraint on narwhals and one that may negatively impact populations. Over the 23-year time series, the cyclical nature of the availability of open water on the winterring grounds followed cyclical patterns observed in region-wide Baffin Bay (Parkinson, 1995; Parkinson et al., 1999; Stern and Heide-Jørgensen, 2003). Consequently, it appears that large-scale trends detected for Baffin Bay and Davis Strait may be good

indicators of trends in localized and restricted narwhal habitats.

Often spatial resolution must be sacrificed for the sake of temporal continuity in remotely sensed data series. Infrequently, a daily estimate of 0% open water on the winterring grounds occurred and this is clearly an artifact of low spatial resolution. It is likely that in some years, open areas on the winterring grounds are so negligible that they cannot be detected by the SSMR/SSM/I sensors. The error estimated by the NSIDC for ice concentration ranges from 5% to 10% and spatially averaging pixels for the March composite examination of open water trends generally reduced the impact of the error in the estimates. Data required to fully assess the size of small patches of open water, how often leads and cracks open or close, and habitat patch size constraints for narwhals are generally lacking.

There are great uncertainties in cetacean response to climate-induced perturbations. Cetacean occurrence is generally negatively correlated with dense or complete ice cover due to the need to breathe at the surface. In the case of a species with high site fidelity such as the narwhal, increasing ice may be lethal if open water accessibility declines beyond the threshold which can be tolerated. Increasing sea ice may also affect prey availability, as the timing of primary and secondary production blooms occurs in concert with cetacean seasonal feeding patterns. Furthermore, altered migration timing (Johnson et al., 1981), shift in seasonal distributions (Moore, 2000; Moore et al., 2000), and changes in the

timing of life history events (Perryman et al., 2002) may also occur.

The three-year-round occupants of Arctic waters: the narwhal, beluga (*Delphinapterus leucas*), and bowhead whale (*Balaena mysticetus*) are listed as vulnerable to climate-induced perturbations by the International Whaling Commission (IWC, 1997). The beluga whale has been found in a range of ice types (Moore, 2000; Suydam et al., 2001), but usually avoids dense pack ice (Barber et al., 2001) by wintering in open water polynyas or loose ice (Richard et al., 2001; Heide-Jørgensen et al., 2003b). Bowhead whales prefer floe edge habitat and are nevertheless capable of breaking holes through several feet of ice. Knowledge about bowhead whale distribution and movement plasticity indicates that their dependence on open water is not entirely critical to survival (Moore et al., 2000; Heide-Jørgensen et al., 2003c). Lacking the ability to break holes in the ice and preferring dense pack ice for 50% of the year, narwhals are likely most vulnerable to changes in open water availability. This has been demonstrated by ice entrapment events where hundreds of narwhals died during rapid sea ice formation caused by sudden cold periods (Siegstad and Heide-Jørgensen, 1994; Heide-Jørgensen et al., 2002b).

The increasing trends in variability, in concert with the decreasing trends in the fraction of open water, provide an insight into the wide-ranging conditions experienced by narwhals on their wintering grounds. An optimal strategy for narwhals to persist in increasing winter sea ice cover would be to decrease site fidelity and move south to more open areas. With increasing inter-annual variability in the period with maximum ice cover, it is not clear whether whales receive the necessary stimuli to adjust their behavior and habitat use. Further, these altered habitat selections may need to be as early as December, before the whales are enclosed by expanses of dense pack ice.

Narwhals feed intensively on their wintering grounds (Laidre et al., 2003) and a major portion of their annual food intake is obtained in these areas (Laidre and Heide-Jørgensen, in press). Narwhals primarily take Greenland halibut (*Reinhardtius hippoglossoides*) although the diet also includes other species. During winter narwhals are highly restricted in the horizontal range of their movements and food intake must occur over a limited geographic range. Reduction in available open water at the surface (from which whales depart for benthic foraging) will likely have large implications for the area that narwhals can exploit on the bottom, potentially reducing the narwhal carrying capacity on the wintering grounds. Offshore Greenland halibut fishery operations were recently initiated in central Baffin Bay (Treble and Bowering, 2002). The fishery is conducted during the open water period but in the precise geographic areas where narwhals spend the winter (Laidre et al., 2004b). A reduced Greenland halibut abundance due to a

commercial fishery, together with increased restriction on winter dispersal, will likely influence narwhal foraging success.

Narwhals are hunted in Greenland and the Canadian high Arctic. Presently, there are few restrictions on the harvest and only recently have quotas been established based on estimates of harvest sustainability (NAMMCO, 2001). With increasing hunting effort due to larger human populations and improved technology, it will be necessary to enforce more restricted harvest regulations based on population size and sustainable yield estimates (Heide-Jørgensen, 2004). Climate change, trends in Baffin Bay pack ice, and narwhal site fidelity are extrinsic factors that must be considered in any conservation strategy. Reduced narwhal abundance due to increased pack-ice mortality or nutritional deficiency is difficult to detect due to the low level of precision obtained during intensive narwhal population surveys (Koski and Davis, 1994; Innes et al., 2002; Heide-Jørgensen, 2004). These trends call for more directed winter studies, including surveys, monitoring programs, and tagging work investigating winter activity patterns and mobility. Estimates of sustainable levels of exploitation should also include the risks of sudden large-scale mortalities on the wintering grounds.

Narwhals appeared sometime during the late Pliocene (Kellogg, 1928) and have apparently survived periods of environmental variability and glaciation. Thus, some flexibility with respect to pack ice and habitat selection must have allowed the species to survive. It is interesting to note that the narwhal has one of the lowest measures of genetic diversity of all marine mammals (Palsbøll et al., 1997). This suggests the species experienced at least one previous population bottleneck. This species does not display the propensity for altering behavior in any other situation, as narwhals repeatedly use the same migratory corridors and summering localities despite intense Inuit hunts and return to the same areas despite the occurrence of ice entrapments. Other than direct harvest, other extrinsic factors contributing to narwhal population stability include food availability on the wintering grounds during increasing offshore fishing activities, and winter access to specific feeding during a time of reduced habitat availability due to climate change. With the evidence of changes in sea ice conditions that could impact foraging, prey availability, and of utmost importance, access to the surface to breathe, it is unclear how narwhal sub-populations will fare in light of changes in the high Arctic.

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References

- Barber, D.G., Szuk, E., Richard, P.R., 2001. Examination of beluga-habitat relationships through the use of telemetry and a Geographic Information System. *Arctic* 54, 305–316.
- Baugrand, G., Ried, P.C., Ibanez, F., Alistair Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic copepod biodiversity and climate. *Science* 296, 1692–1694.
- Comiso, J.C., 2002. A rapidly declining perennial sea ice cover in the Arctic. *Geophysical Research Letters* 29, 17.1–17.4.
- Comiso, J.C., 1995. SSMI concentration using the bootstrap algorithm. NASA Report 1380.
- Deser, C., Walsh, J.E., Timlin, M.S., 2000. Arctic sea ice variability in the context of recent atmospheric circulation trends. *Journal of Climatology* 13, 617–633.
- Dietz, R., Heide-Jørgensen, M.P., 1995. Movements and swimming speed of narwhals (*Monodon monoceros*) instrumented with satellite transmitters in Melville Bay, Northwest Greenland. *Canadian Journal of Zoology* 73, 2106–2119.
- Hanna, E., Cappelen, J., 2003. Recent cooling in coastal southern Greenland and relation with the North Atlantic Oscillation. *Geophysical Research Letters* 30, 32.1–32.3.
- Heide-Jørgensen, M.P., 2004. Aerial digital photographic surveys of narwhals, *Monodon monoceros*, in Northwest Greenland. *Marine Mammal Science* 20, 246–261.
- Heide-Jørgensen, M.P., Dietz, R., 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behaviour in Baffin Bay. *Canadian Journal of Zoology* 73, 2120–2132.
- Heide-Jørgensen, M.P., Dietz, R., Laidre, K., Richard, P., 2002a. Autumn movements, home range and winter density of narwhals (*Monodon monoceros*) from Tremblay Sound, Baffin Island. *Polar Biology* 25, 331–341.
- Heide-Jørgensen, M.P., Richard, P., Ramsay, M., Akeagok, S., 2002b. In: Three Recent Ice Entrapments of Arctic Cetaceans in West Greenland and the Eastern Canadian High Arctic, vol. 4. NAMMCO Scientific Publications. pp. 143–148.
- Heide-Jørgensen, M.P., Dietz, R., Laidre, K.L., Richard, P., Orr, J., Schmidt, H.C., 2003a. The migratory habits of narwhals. *Canadian Journal of Zoology* 81, 1298–1305.
- Heide-Jørgensen, M.P., Richard, P., Dietz, R., Laidre, K.L., Orr, J., Schmidt, H.C., 2003b. An estimate of the fraction of belugas (*Delphinapterus leucas*) in the Canadian High Arctic that winter in West Greenland. *Polar Biology* 26, 318–326.
- Heide-Jørgensen, M.P., Laidre, K.L., Wiig, O., Jensen, M.V., Dueck, L., Maiers, L., Schmidt, H.C., Hobbs, R.C., 2003c. From Greenland to Canada in two weeks: movements of bowhead whales, *Balaena mysticetus*, in Baffin Bay. *Arctic* 56, 21–31.
- Innes, S., Heide-Jørgensen, M.P., Laake, J.L., Laidre, K.L., Cleator, H.J., Richard, P.R., Stewart, R.E.A., 2002. In: Surveys of Belugas and Narwhals in the Canadian High Arctic in 1996, vol. 4. NAMMCO Scientific Publications. pp. 147–190.
- IWC (International Whaling Commission), 1997. Report of the IWC workshop on climate change and cetaceans. Report of the International Whaling Commission 47, 291–320.
- Johannessen, O.A., Shalina, E.V., Wiles, M.W., 1999. Satellite evidence for an Arctic sea ice cover in transformation. *Science* 286, 1937–1939.
- Johnson, J.J., Braham, H.W., Krogman, B.D., Marquette, W.M., Sonntag, R.M., Rugh, D.J., 1981. Bowhead whale research: June 1979 to June 1980. Report to the International Whaling Commission 31, 461–475. SC/32/PS10.
- Kellogg, R., 1928. The history of whales – their adaptation to life in the water. *Quarterly Review of Biology* 3, 29–76.
- Koski, W.R., Davis, R.A., 1994. Distribution and numbers of narwhals (*Monodon monoceros*) in Baffin Bay and Davis Strait. *Meddelelser om Grønland, Bioscience* 39, 15–40.
- Laidre, K.L., 2003. Space use patterns of narwhals (*Monodon monoceros*) in the high Arctic. Ph.D. Thesis, University of Washington, Seattle, USA.
- Laidre, K.L., Heide-Jørgensen, M.P., Dietz, R., Hobbs, R.C., Jørgensen, O.A., 2003. Deep-diving by narwhals, *Monodon monoceros*: differences in foraging behavior between wintering areas? *Marine Ecology Progress Series* 261, 269–281.
- Laidre, K.L., Heide-Jørgensen, M.P., Logsdon, M.L., Hobbs, R.C., Dietz, R., VanBlaricom, G.R., 2004a. Fractal analysis of narwhal space use patterns. *Zoology* 107, 3–11.
- Laidre, K.L., Heide-Jørgensen, M.P., Jørgensen, O.A., Treble, M.A., 2004b. Deep ocean predation by a high Arctic cetacean. *ICES Journal of Marine Science* 61 (3), 430–440.
- Laidre, K.L., Heide-Jørgensen, M.P., Logsdon, M.L., Hobbs, R.C., Heagerty, P., Dietz, R., Jørgensen, O.A., Treble, M.A., 2004c. Seasonal narwhal habitat associations in the high Arctic. *Marine Biology*, in press.
- Laidre, K.L., Heide-Jørgensen, M.P., in press. Winter feeding intensity of narwhals (*Monodon monoceros*). *Marine Mammal Science*.
- Morison, J., Aagaard, K., Steele, M., 2000. Recent environmental changes in the Arctic: a review. *Arctic* 53, 359–371.
- Moore, S.E., 2000. Variability of cetacean distribution and habitat selection in the Alaskan Arctic, Autumn 1982–91. *Arctic* 53, 448–460.
- Moore, S.E., DeMaster, D.P., Dayton, P.K., 2000. Cetacean habitat selection in the Alaskan Arctic during summer and autumn. *Arctic* 53, 432–447.
- Murphy, E., King, J., 1997. Icy message from the Antarctic. *Nature* 389, 20–21.
- Mysak, L.A., 2001. Patterns of Arctic circulation. *Science* 293, 1269–1270.
- North Atlantic Marine Mammal Commission, 2001. NAMMCO Annual Reports 2000. North Atlantic Marine Mammal Commission, Tromsø, Norway. 359pp.
- Palsbøll, P.J., Heide-Jørgensen, M.P., Dietz, R., 1997. Population structure and seasonal movements of narwhals, *Monodon monoceros*, determined from mtDNA analysis. *Heredity* 78, 284–292.
- Parkinson, C.L., 1995. Recent sea-ice advances in Baffin Bay/Davis Strait and retreats in the Bellinghousen Sea. *Annals of Glaciology* 21, 348–352.
- Parkinson, C.L., 2000a. Variability of Arctic sea ice: the view from space, and 18-year record. *Arctic* 53, 341–358.
- Parkinson, C.L., 2000b. Recent trend reversals in Arctic Sea ice extents: possible connections to the North Atlantic oscillation. *Polar Geography* 24, 1–12.
- Parkinson, C.L., Cavalieri, D.J., 2002. A 21-year record of Arctic sea-ice extents and their regional, seasonal and monthly variability and trends. *Annals of Glaciology* 34, 441–446.
- Parkinson, C., Cavalieri, D., Gloersen, D., Zwally, J., Comiso, J., 1999. Arctic sea ice extents, areas, and trends, 1978–1996. *Journal of Geophysical Research/Oceans* 104, 20837–20856.

- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 42, 37–42.
- Perryman, W.L., Donahue, M.A., Perkins, P.C., Riley, S.B., 2002. Gray whale calf production 1994–2000: are observed fluctuations related to changes in seasonal ice cover? *Marine Mammal Science* 18, 121–144.
- Richard, P.R., Heide-Jørgensen, M.P., Orr, J., Dietz, R., Smith, T.G., 2001. Summer and autumn movements and habitat use by beluga in the Canadian High Arctic and adjacent areas. *Arctic* 54, 207–222.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 42, 57–60.
- Sewall, J.O., Sloan, L.C., 2004. Disappearing Arctic sea ice reduces available water in the American west. *Geophysical Research Letters* 31, L06209.
- Siegstad, H., Heide-Jørgensen, M.P., 1994. Ice entrapments of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in Greenland. *Meddeleser om Grønland Bioscience* 39, 151–160.
- Stirling, I., 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. *Journal of Marine Systems* 10, 9–21.
- Stirling, I., Derocher, A.E., 1993. Possible impacts of climatic warming on polar bears. *Arctic* 46, 240–245.
- Stern, H.L., Heide-Jørgensen, M.P., 2003. Trends and variability of sea ice in Baffin Bay and Davis Strait, 1953–2001. *Polar Research* 22, 11–18.
- Suydam, R.S., Llowry, L.F., Frost, K.J., O’Corry-Crowe, G.M., Pikok, D., 2001. Satellite tracking of eastern Chukchi Sea beluga whales into the Arctic Ocean. *Arctic* 54, 237–243.
- Treble, M.A., Bowering, R., 2002. The Greenland halibut (*Reinhardtius hippoglossoides*) fishery in NAFO Division 0A. Northwest Atlantic Fisheries Organization SCR Doc. 02/46. 10 pp.
- Tynan, C.T., DeMaster, D.P., 1997. Observations and predictions of Arctic climate change: potential effects on marine mammals. *Arctic* 50, 308–322.
- Vinnikov, K.Y., Robock, A., Stouffer, R.J., Walsh, J.E., Parkinson, C.L., Cavalieri, D., Mitchell, J.F.B., Garrett, D., Zakharov, V.F., 1999. Global warming and Northern Hemisphere sea ice extent. *Science* 286, 1934–1937.
- Wigley, T.M.L., Raper, S.C.B., 2001. Interpretations of high projections for global-mean warming. *Science* 293, 451–454.