The migratory behaviour of narwhals (*Monodon monoceros*)

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Abstract: Sixteen female narwhals (*Monodon monoceros*) were tracked by satellite in 2000 and 2001 from their summering ground near Somerset Island in the Canadian High Arctic to their wintering ground in central Baffin Bay. The wintering ground location was spatially discrete from another narwhal wintering ground in southern Baffin Bay. Area extent of the summering ground was approximately 9464 km^2 and area extent of the wintering ground was 25 846 km^2. Two of the narwhals were tracked for more than 12 consecutive months. These whales used three focal areas between their spring and autumn migration: a coastal area in the open-water season in August in the Canadian High Arctic, a wintering area from November through April in the consolidated pack ice of Baffin Bay, and an early summer area in front of the receding fast ice edge in Lancaster Sound. The whales showed remarkable site fidelity to summering grounds and had specific migratory routes that followed sea ice formation and recession.

Résumé : Seize narvals femelles (*Monodon monoceros*) ont été suivis par satellite en 2000 et 2001 de leur territoire d'été près de l'île Somerset dans le haut-arctique canadien vers leur territoire d'hiver dans le centre de la baie de Baffin. Le territoire d'hiver est séparé dans l'espace d'un autre territoire d'hiver de narvals dans le sud de la baie de Baffin. Le territoire d'été couvre environ 9464 km^2 et celui d'hiver 25 846 km^2. Deux des narvals ont pu être suivis pendant plus de 12 mois consécutifs. Les narvals utilisent trois régions principales entre leurs migrations de printemps et d'automne : une région côtière durant la saison d'eau libre en août dans le haut-arctique canadien, un territoire d'hiver de novembre à la fin d'avril dans les glaces dérivantes consolidées dans la baie de Baffin, ainsi qu'une région d'été au large de la banquise côtière en récession dans le détroit de Lancaster. Les narvals montrent une fidélité remarquable à leurs territoires d'été et ils ont des voies de migration spécifiques qui suivent la formation et le retrait de la glace de mer.

[Traduit par la Rédaction]

Introduction

The narwhal (*Monodon monoceros*) is an ice-associated cetacean that inhabits Arctic waters bordering Canada and Greenland. In the Baffin Bay region, the narwhal is one of the most abundant cetaceans, numbering at least 50 000 whales (Koski and Davis 1994; Innes et al. 2002). In summer months, narwhals congregate in fjords and bays in the High Arctic of Canada and Greenland. During winter, they are more broadly distributed in the pack ice of Baffin Bay and northern Davis Strait (Koski and Davis 1994). Several separate subpopulations are believed to exist in Baffin Bay and adjacent waters (Dietz et al. 2001).

Narwhals are an important part of the Inuit subsistence hunt in both Canada and Greenland, and harvest management requires information on stock delineation that is related to migratory patterns, relationships between summering and wintering grounds, and plasticity of movement patterns. Narwhals are winter inhabitants of waters covered by severe amounts of consolidated pack ice. Because of their need to surface, narwhals are vulnerable to ice entrapment events caused by restricted access to open water or changes in buildup of heavy pack ice. Narwhals are also known to be a predator of the Greenland halibut (*Reinhardtius hippoglossoides*) in Baffin Bay during winter, and movement patterns allow for the assessment of competitive interactions with a developing fishery on offshore halibut stocks.

Narwhals are among the most difficult cetaceans to study because of their fidelity to remote offshore Arctic regions, inaccessible to humans in winter because of darkness and pack ice. Until now, satellite tracking studies have provided information on the movements of narwhals, and other cetaceans, only for portions of a 12-month cycle (Dietz and Heide- Jørgensen 1995; Dietz et al. 2001; Heide-Jørgensen

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Table 1. List of 16 female narwhals (*Monodon monoceros*) instrumented in August 2000 and 2001 at Creswell Bay, Somerset Island, Canada.

PTT ID No.	Year	Date in August	Length (cm)	Fluke width (cm)	Type of transmitter	Date of last positions	Duration (days)
7927	2000	14	390	95	SCC-3	22 November 2000	100
7928	2000	14	370	100	SCC-3	25 October 2000	103
7929	2000	23	405	84	SPOT1	18 October 2001	421
7932	2000	24	406	94	SPOT1	9 September 2001	381
20683	2000	16	390	101	ST-16	1 November 2000	77
20688	2000	17	402	98.5	ST-16	15 December 2000	120
20689	2000	17	397	90	ST-16	1 December 2000	106
20690	2000	17	398	90	ST-16	16 November 2000	91
20691	2000	19	400	92	ST-16	3 September 2000	15
7927	2001	7	420	—	SPOT2	25 December 2001	138
7928	2001	8	389	—	SPOT2	25 August 2001	17
20167	2001	9	390	88	SPOT2	25 December 2001	138
20683	2001	12	394	90	SPOT2	25 September 2001	44
20690	2001	9	410	100	SPOT2	5 November 2001	88
20696	2001	12	387	97	SPOT2	25 August 2001	13
21793	2001	12	370	88	SPOT2	25 October 2001	74

et al. 2002*a*). Owing to short transmitter or attachment longevity, these past tracking studies failed to determine if the narwhal was indeed, by strict definition, a migratory species (i.e., moving between specific summer and winter localities).

Satellite tracking is one of few options for gaining insight into the winter behaviour of narwhals in offshore areas. Recently, the miniaturisation of satellite-linked radio transmitters has provided new opportunities for unveiling information on narwhal migratory routes. The technique can be used to address important questions about stock delineation, migratory patterns, and site fidelity. Narwhal stocks or subpopulations are identified based on spatial isolation in summer aggregation areas (or grounds) as well as on evidence of genetic isolation (Palsbøll et al. 1997). The capture locality for this study, Creswell Bay on Somerset Island, was chosen to sample the behaviour of perhaps the largest summer aggregation of narwhals worldwide (about 45 000 narwhals are found in summer; Innes et al. 2002), a locality where movements of narwhals had not previously been studied.

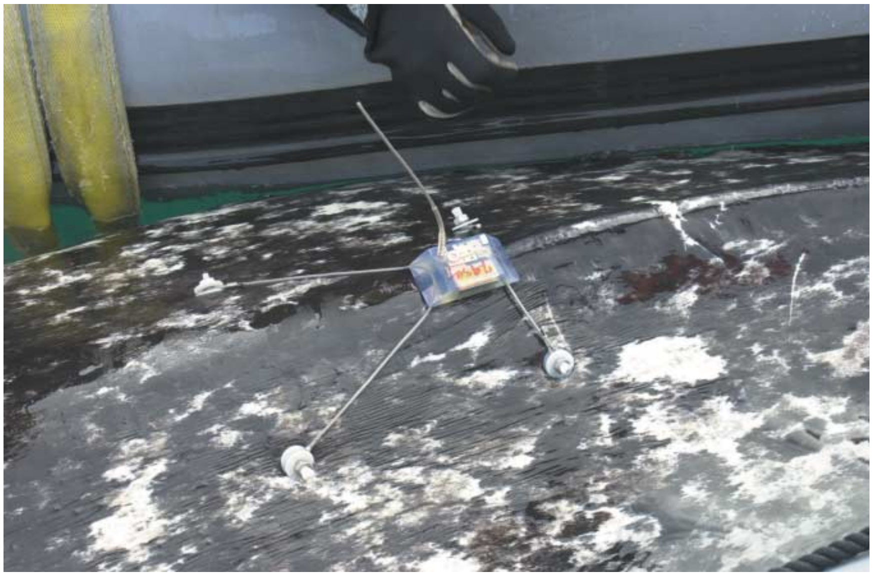
Methods

Narwhals were captured in set nets at their summering ground at Creswell Bay, Somerset Island, Canada (72°45′N, 94°5′W), in August 2000 and 2001 using methods described in Dietz et al. (2001). The whales were instrumented with satellite-linked radiotransmitters mounted on the dorsal ridge using three 6- or 8-mm nylon pins (in 2000) or 6-mm titanium rods (in 2001). The transmitters were attached to the pins by 0.5- to 2-mm plastic-coated stainless steel or Monel wires secured and cut to restrict the movements of the tags. The handling procedure lasted approximately 30 min and was conducted with the whales held in the net between two inflatables. No obvious reaction to being instrumented was observed, and only short-term (<0.5 h) changes in dive behaviour were detected after tagging operations (see Laidre et al. 2002).

A total of nine female narwhals were instrumented in 2000 (Table 1). Five whales were instrumented with ST-16 (300 g in air, 120 mm × 50 mm × 40 mm; Telonics Inc., Mesa, Ariz.) and two whales with SSC-3 (500 g in air, 173 mm × 97 mm × 41 mm; Seimac Inc., Dartmouth, N.S.) satellite transmitter packages programmed and cast in epoxy by Wildlife Computers, Redmond, Wash., U.S.A. In addition, two whales were equipped with small satellite transmitter packages (Fig. 1) (SPOT1 tags, 115 g in air, 86 mm × 52 mm × 19 mm; Wildlife Computers). These tags were programmed to be active for 24 h every 21 days to preserve battery power. Geographic positions (precision <1 km) were acquired approximately every day from the other seven tags. In 2001, seven females were instrumented with SPOT2 tags (115 g in air, 86 mm × 52 mm × 19 mm; Wildlife Computers) that were programmed to provide geographic positions on the 5th, 15th, and 25th day of each month.

Data from the transmitters were collected via the ARGOS system (Service Argos 1989; Harris et al. 1990). Distance (straight-line distance between sequential positions of good quality) and movement paths were calculated using only good-quality positions (LC-1–LC-3, error of <1 km) using ArcView GIS (Environmental Systems Research Institute, Inc., Redlands, Calif.). The digital coastline and bathymetric data were obtained from the international bathymetric chart of the Arctic Ocean (http://www.ngdc.noaa.gov/mgg/bathymetry/arctic/arctic.html). Area usages on the summering and wintering grounds were estimated as the 95%, 75%, and 50% fixed-kernel range estimates using the Animal Movement and Spatial Analyst extensions in ArcView (Hoodge and Eichenlaub 1997). Autocorrelation bias was removed by calculating an average daily position from all locations on a given day, which was then used to calculate range estimates. Because sample sizes affect the degree of accuracy of kernel estimates, sample sizes and dates were the same when home ranges were compared between whales. Range estimates were calculated with daily positions received from whales tagged in 2000 because of a larger sample size. The positions received from whales tracked in 2001 (10-day sampling rate) were compared with

Fig. 1. Small position-only satellite transmitter (SPOT1) used for tracking female narwhals (*Monodon monoceros*). The instrument was attached using four Monel wires and two nylon rods, which were anchored through the blubber and skin of the dorsal ridge of the whale. The transmitter used a standard frequency of 401.625 MHz, and a saltwater switch triggered the transmissions 0.2 s after the switch emerged from the water.



the range estimates for comparable temporal periods from whales tagged in 2000.

Results

The 16 whales captured in 2000–2001 provided good-quality positions for 13–421 days (Table 1). The longest tag duration for whales tagged in 2000 with SPOT1 transmitters was approximately 14 months, where the last positions received for the two whales were on 9 September and 18 October 2001. The longest tag duration for whales tagged in 2001 with SPOT2 transmitters was approximately 5 months, where the last positions were received on 25 December. The patterns of summer movements, timing of migration, and arrival on the wintering ground were almost identical for whales tracked in both years.

Summer movements

All 16 whales remained within <200 km of the tagging site in August. Whales occupied both the east and west sides of Somerset Island. They reached the west side by moving south along the east coast of Somerset Island and passing through Bellot Strait into Peel Sound, west of Somerset Island (Fig. 2). Of those moving through Bellot Strait, two were tagged in 2000 and three in 2001. Kernel range estimates were calculated for seven of the whales tagged in 2000 and were used to estimate the common area usage on the summering ground between 19 and 31 August. The 95% kernel was approximately 9464 km^2 (SD = 4718). Of the positions received from the whales tagged in 2001 with a 10-day sampling rate, 91% of average locations on 15 and 25 August fell within the boundary of the 95% kernel range estimate defined by the 2000 data (Fig. 2).

Autumn movements

Even as late as mid-September, most whales were still located <200 km from their tagging site. However, during this time, whales were more dispersed in the north–south direction on either side of Somerset Island, with some whales moving into Barrow Strait and western Lancaster Sound. In mid to late September, most whales began to migrate into western Lancaster Sound (Figs. 2 and 3). The eastward migration out of Lancaster Sound started in early October with most whales moving close to the southern shore of Devon Island. The pattern of movement out of the summering ground was relatively consistent between years, with the major difference being whether whales moved through Bellot Strait and north through Peel Sound (n = 5) or moved north along the east side of Somerset Island, bypassing Bellot Strait and Peel Sound. One individual tagged in 2000 remained in Peel Sound approximately 3 weeks longer than the rest of the tagged whales, moving south into Franklin Strait, reaching Pasley Bay (70°40′N, 96°00′W) in early October. It headed north and crossed Barrow Strait to Cornwallis Island on 20 October. From there, it headed east along the south coast of Devon Island, crossed Lancaster Sound again on 25 October, continuing east along the southern shore of the sound, and exited the sound north of Bylot Island on 29 October. All other whales exited Lancaster Sound before 15 October.

Winter movements

About 3 weeks (early November) after exiting Lancaster Sound, the whales crossed northern Baffin Bay and reached an area where they remained relatively stationary. The whale with delayed departure from Lancaster Sound moved south along Baffin Island before it crossed the deep portion of Baffin Bay and arrived in the same area used by the other whales on 23 November. This area, centred at 72°N, 60°W, was the location of the wintering ground, as whales made only localized movements in this area through March. The common 95% kernel range estimate on the wintering ground in 2000 (for the three tags that were still transmitting) was approximately 25 846 km^2 (Fig. 2). When daily average locations from the whales tagged in 2001 were compared with the 2000 range estimate, approximately 83% of daily average locations fell within the boundary of the 95% kernel range estimate from 2000.

Besides the similarity in the spatial location of the wintering ground used by narwhals tagged in 2000 and 2001, the timing of individual narwhal movements and arrival on the wintering ground was also similar in both years. The timing of passage across Baffin Bay in 2001 was remarkably close to that of whales tagged in 2000 (ranging from 15 to 100 km away from each other), suggesting a strict coordination between individuals. All four tags that lasted until late November 2001 were located together north of Bylot Island on 15 October and also located together west of the 2000-m depth contour in Baffin Bay on 25 October (Fig. 3). By 5 November, the whales had arrived, together, within the 95% kernel range estimate of the wintering ground for the whales from 2000. This consistent migratory timing between individuals was also evident for most of the whales in 2000, suggesting that this narwhal subpopulation has a regular annual pattern of migration.

Spring movements

The two tags with exceptional longevity provided the first movements ever recorded of the narwhal spring migration north back towards the summering grounds. In early April, the two whales with small position-only transmitters (SPOT1) returned towards Lancaster Sound (Fig. 4). They stayed at or near the sea ice edge in the eastern part of Lancaster Sound for approximately 6 weeks, from late May until early July (Fig. 5). Once these two whales entered Lancaster Sound, they moved quickly back to the summering ground near Somerset Island from which they had originated the previous summer. They returned to the west side of Somerset Island within the 95% kernel range area estimated from their positions on the summering ground 1 year earlier. Contact was lost with the tags on 9 September and 18 October of the second year, when the two whales were either in Peel Sound or in Baffin Bay heading towards their wintering ground.

Discussion

This is the first time a cetacean has been tracked over a complete migratory cycle and the first time a satellite tag has remained on the dorsal ridge of a whale for more than 6 months. Previous satellite tracking studies of narwhals monitored whale movements out of the summering grounds in the fall and, in some cases, all the way to the wintering grounds in Baffin Bay (Dietz and Heide-Jørgensen 1995; Dietz et al. 2001; Heide-Jørgensen et al. 2002*a*). Long-term tracking of narwhals both provides an opportunity for examining the relationship between different subpopulations across the entire winter duration and allows for observation of localized movements within inaccessible offshore areas of the high Arctic, which can ultimately be related to potential vulnerability to changing ice conditions.

The study documents only female behaviour. In 2001, three adult males were captured and instrumented at Creswell Bay, but either the transmitters or the instrumentations failed and no data were obtained. Previous studies from three other subpopulations have, however, clearly shown that male and female narwhals tagged and tracked from other localities had similar migratory schedules and winter destinations (Dietz and Heide-Jørgensen 1995; Dietz et al. 2001; Heide-Jørgensen et al. 2002*a*). Additionally, males and females were frequently seen moving together in Creswell Bay, and pods of both sexes were observed regularly. There is nothing to suggest that male migratory behaviour would differ from female behaviour for this subpopulation.

The whales in this study are a sample of the subpopulation that occupies the area around Somerset Island in summer, which has been estimated to number approximately 45 358 narwhals (95% confidence interval = 23 397 – 87 932) (Innes et al. 2002). Clearly, only a small sample of this population was tracked in this study and it cannot be ruled out that a larger sample size could reveal more diverse migratory patterns and wider dispersal in the winter and summer aggregation grounds. However, the migration pattern demonstrated in this study seems to be relatively consistent between years and individuals; whales followed a similar timing and had similar destinations. Also, the emerging pattern is consistent with what is known about narwhal movements from visual observations from the late 1970s (cf. Koski and Davis 1994).

The narwhals used three focal areas: a coastal area in the open-water season in August, a wintering ground from November through April covered with consolidated pack ice, and a spring ground from May through July in front of the receding fast ice edge. The whales followed specific routes during the migration between focal areas and maintained a migratory schedule that followed the succession of sea ice conditions. The return to the summering ground of their capture demonstrates a high degree of site fidelity. Narwhals may have some mechanisms to adapt to long-term changes in ice regimes; however, owing to their high degree of site fidelity to summering and wintering grounds, they are vulnerable to rapid changes in ice conditions.

Observations from late May or mid-June 2001 by Inuit hunters of two narwhals with tags on their backs observed at the ice edge near Elwin Inlet (73°25′N, 83°42′W) may have been of the two whales tracked for an extended period in this study (K. Ditz, Department of Fisheries and Oceans, personal communication). The whales made extensive movements within the eastern open-water basin of Lancaster Sound in May and June and were apparently restricted by the fast ice edge in Lancaster Sound, which lasted through June (Fig. 5). It appeared that the sea ice edge acted as a physical barrier, preventing the whales from moving farther west into Lancaster Sound (Fig. 5) (http://www.natice.noaa.gov). The sightings reported by the Inuit hunters could have been the instrumented whales travelling along the ice edge off Elwin Inlet.

On their return migration to the summering grounds, the two narwhals did not visit areas where narwhals from other stocks occur during summer. Therefore, it is likely that whales from different summering grounds are functionally isolated. This functional isolation is supported by previous satellite tracking studies as well as genetic evidence, where frequencies of narwhal haplotypes differ markedly between close geographic areas, suggesting a high degree of isolation of summering subpopulations and site fidelity to summer and autumn feeding grounds (Palsbøll et al. 1997). Narwhals from two other summering grounds (Melville Bay in West

Fig. 2. Area usage and tracklines of 14 narwhals tagged in Creswell Bay, Somerset Island, Canada (see red arrow) on 7–19 August 2000 and 2001. The area usage (estimated as the 95%, 75%, and 50% fixed-kernel home range) was calculated for the period 19–31 August 2000 and tracklines of the good-quality positions are shown on a monthly basis for the periods with data. The average 95% area usage for the seven whales in August 2000 was 9464 km^2 (SD = 4718). Individual range estimates for the seven whales varied from 7 663 to 16 428 km^2 in August. The 95% winter range was approximately 25 846 km^2 for three whales. Only positions rated LC-1 or better were included, and for each day, only the best position is shown.

Fig. 3. Winter kernel ranges (95% white region, 75% grey region, and 50% black region) estimated from data collected from whales tagged in Creswell Bay in August 2000. Tracklines and dates (10/15, 15 October; 10/25, 25 October) are shown for the daily average position of four whales instrumented in Creswell Bay in 2001. Note that the timing of migration towards the home range and location of wintering positions were obtained from the 2001 data. Approximately 83% of daily average positions from 2001 fell within the 2000 home range.

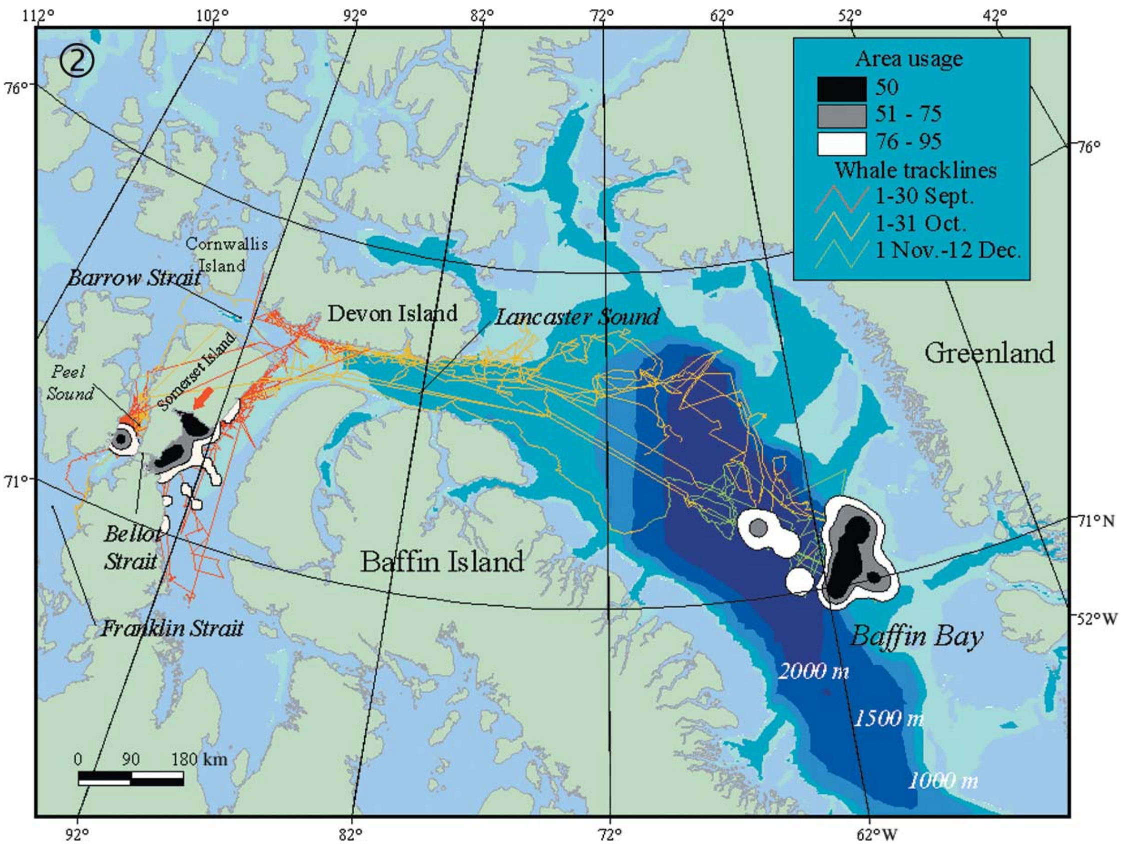
Greenland and Eclipse Sound in Canada) have previously been tracked to a wintering ground farther south of that used by the whales in this study (Dietz et al. 2001; Heide-Jørgensen et al. 2002*a*). There was no spatial overlap between the winter distributions of whales in the two wintering areas, and at least for the two long-term tags, there were no indications of exchange between the two areas (Heide-Jørgensen et al. 2002*a*). This indicates that narwhals maintain several subpopulations on both summering and wintering grounds in Baffin Bay, with little to no exchange between wintering grounds identified for other stocks. The high degree of site fidelity demonstrated by the return to the previous year's summering ground and the observed subpopulation structure (from both genetic haplotype frequencies and satellite tracking studies) may have important implications regarding the resilience of narwhals to environmental perturbations.

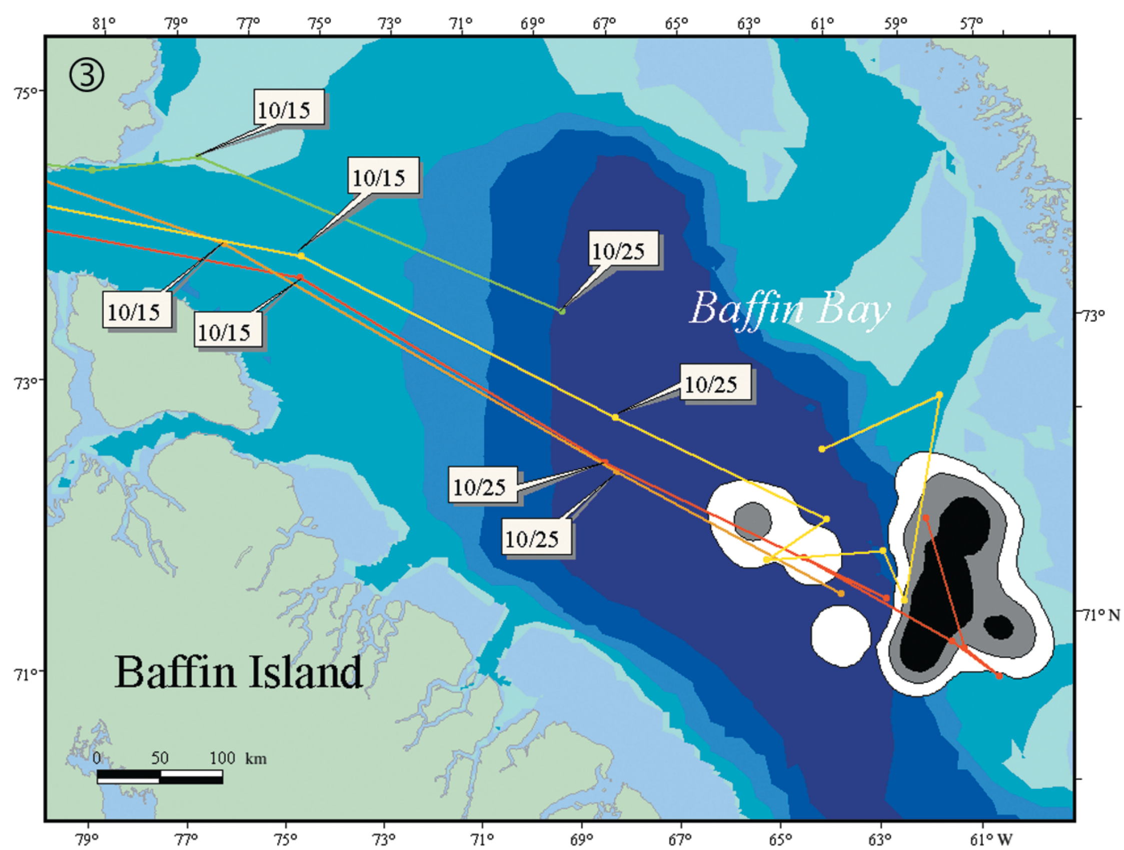
No other whale species venture as far into the dense sea ice in winter as the narwhal. Baffin Bay has a predictable annual formation of consolidated pack ice in winter (Parkinson et al. 1999), and satellite images confirm the extensive sea ice coverage in this area in March 2001 (http://www.natice.noaa.gov). While on the wintering ground, the animals showed relatively little horizontal activity. Previously, localized behaviour of narwhals on their wintering grounds had only been partially demonstrated by the track of one narwhal tagged in August 1999 and tracked through March 2000 (Heide-Jørgensen et al. 2002*a*). Narwhals appear to be restricted by aerobic dive limits of <24 min and vertical speeds of maximum 2.1 m/s (Heide-Jørgensen and Dietz 1995). This means that their maximum range of horizontal travel under the ice using aerobic metabolism is about 3 km, or half that distance if the animal must return to the same opening from which it departed. When narwhals dive close to the bottom of the central Baffin Bay (>1000 m) (Heide-Jørgensen and Dietz 1995; Heide-Jørgensen et al. 2002*a*), their foraging range in the horizontal plane must be even more restricted. Narwhals occur in large densities on the wintering grounds (Koski and Davis 1994; Heide-Jørgensen et al. 2002*a*), but little is known about their feeding habits in these areas, although they are likely feeding close to the bottom on Greenland halibut (Laidre et al. 2003). Some degree of horizontal dispersal on the ice-covered wintering ground is necessary to adjust to closing leads in the pack ice and to avoid local depletion of prey resources.

After arrival at their wintering ground, the whales undertook local movements within a specific area for up to 6 months during the continuous buildup of consolidated pack ice, intersected only with occasional cracks and small leads. Even though narwhals can push holes through new ice, they are not capable of breaking the often metre-thick pack ice in Baffin Bay (Siegstad and Heide-Jørgensen 1994). They are therefore totally dependent on access to leads and cracks in the ice to breathe. Failure to find open water or maintain holes in rapidly forming ice can be lethal to narwhals. This is evident from frequent ice entrapments in both Canada and Greenland (e.g., Siegstad and Heide-Jørgensen 1994; Heide-Jørgensen et al. 2002*b*) and supports the potential vulnerability of narwhals to increasing ice in their wintering areas, despite their pagophilic tendencies.

Evidently, narwhals follow a regular migratory schedule; they leave their well-defined summering grounds at a specific time (prior to ice formation) and move in certain "corridors" towards their wintering grounds (cf. Dietz et al. 2001; Heide-Jørgensen et al. 2002*a*) and arrive predictably on wintering grounds, where they make localized movements for 6 months. They migrate considerable distances between relatively small area ranges on summering and wintering grounds. The extreme similarity in movements and timing observed for the two adult female whales suggests kinship or strong social bonds between individuals, with implications for genetic sampling studies of this species.

It has been suggested that narwhals are among the most vulnerable marine mammals relative to changes in Arctic sea ice induced by global warming (Tynan and DeMaster 1997). This is supported by the results presented here, where whales depend on specific wintering areas with sufficient open leads and cracks and adequate prey resources. These requirements make them vulnerable to changes in ice regimes. Global warming, predicted with considerable certainty (Wigley and Raper 2001), will likely affect ice formation in the Arctic seas. Generally, the extent of sea ice in the northern hemisphere has decreased in the past 20 years at a rate of about 3% per decade (Parkinson et al. 1999). However, in Baffin Bay, a reverse trend has been observed. The length of the sea ice season and the extent of sea ice have increased in the past two decades in Baffin Bay (Parkinson 1995, 2000*a*; Parkinson et al. 1999). Passive microwave readings and historical mapping of sea ice distribution over the past five decades have confirmed this, demonstrating a significant increase amounting to about 600 km^2 or 1.3% per decade (Stern and Heide-Jørgensen 2003). The causes of this reverse trend in Baffin Bay are uncertain but are likely due to


②
Area usage
50
51 - 75
76 - 95
Whale tracklines
1-30 Sept.
1-31 Oct.
1 Nov.-12 Dec.
Cornwallis Island
Barrow Strait
Devon Island
Lancaster Sound
Greenland
Peel Sound
Somerset Island
Bellot Strait
Baffin Island
Franklin Strait
Baffin Bay
2000 m
1500 m
1000 m
0 90 180 km


③
10/15
10/15
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Baffin Bay
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Fig. 4. Fourteen-month movement paths collected from two narwhals (body length 405 and 406 cm) captured and tagged in Creswell Bay (see red arrow) on 23 and 24 August 2000 (ID Nos. 7929 and 7932). Stars represent positions in August–October 2001. The minimum distances travelled between the positions for 12 months were 3724 km for ID No. 7929 and 3471 km for ID No. 7932.

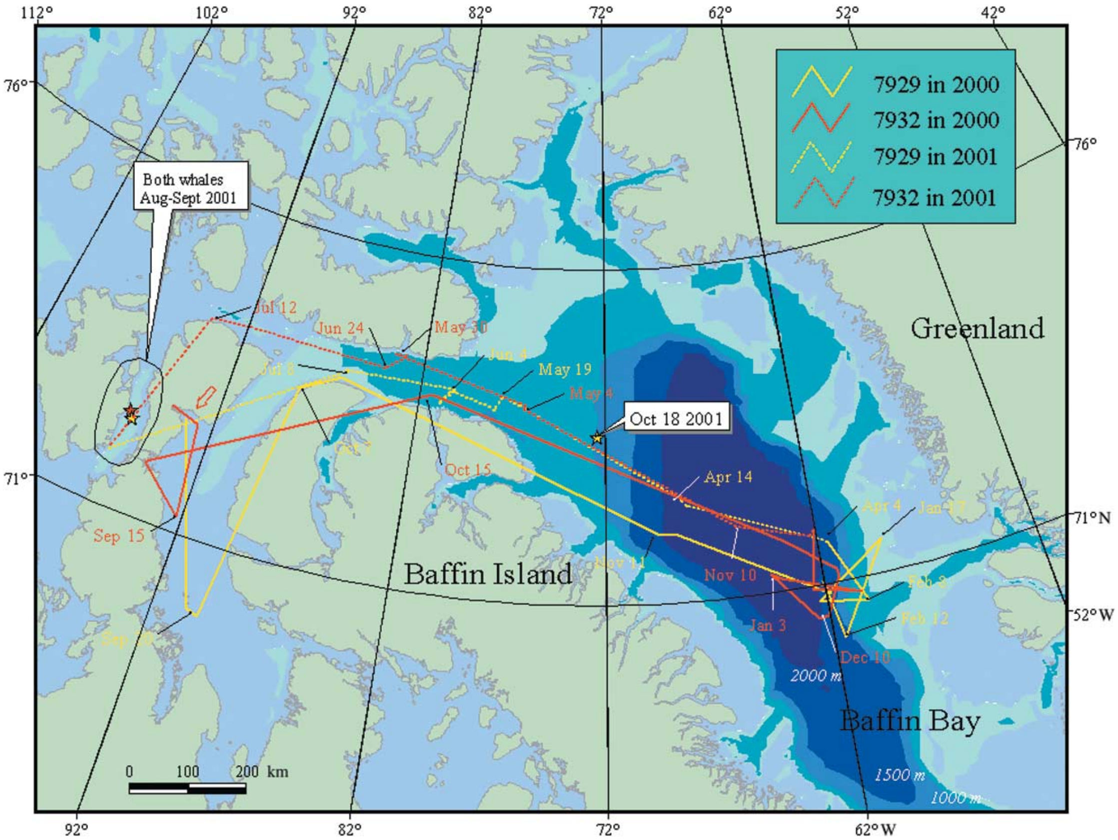
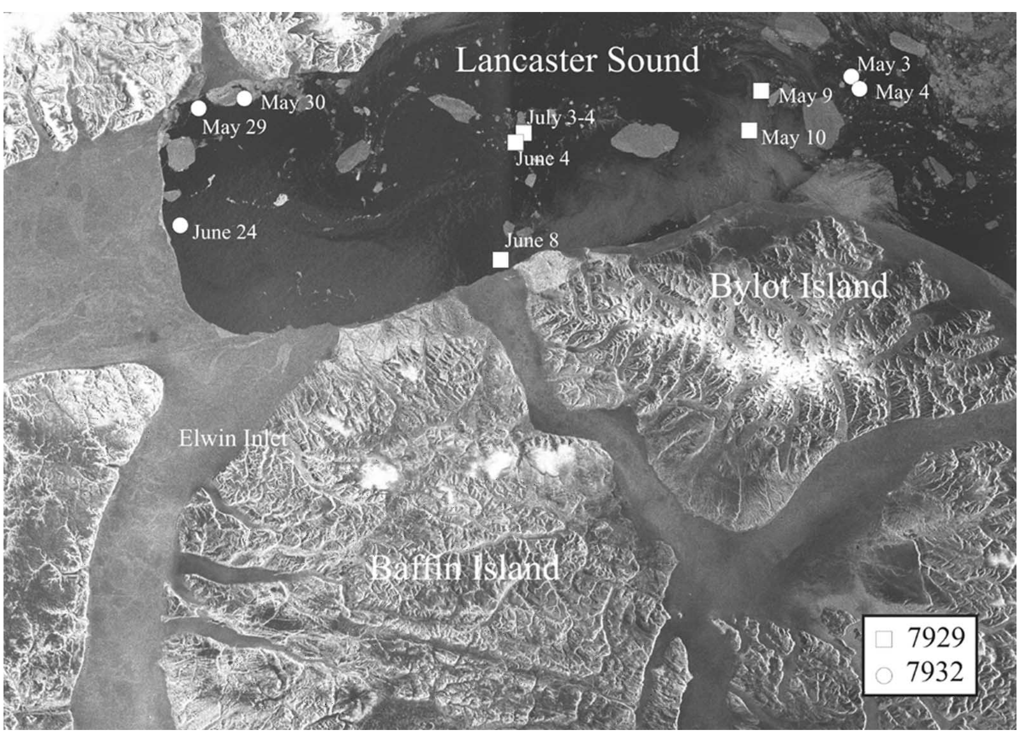


Fig. 5. Ice edge location in Lancaster Sound on 14 June 2001. The synthetic aperture radar satellite image (Scene ID M0264437; Radarsat International, Richmond, B.C.) shows the ice edge relative to the positions of the two narwals tagged in Creswell Bay (in 2000) in spring 2001.



simultaneous changes in the Gulf Current and the North Atlantic Oscillation (Parkinson 2000*b*; Stern and Heide-Jørgensen 2003).

This study has demonstrated that narwhals have high site fidelity to certain migratory routes and specific focal areas across their annual cycle. At least 50 000 narwhals winter in leads and cracks in the dense pack ice in Baffin Bay (Koski and Davis 1994; Innes et al. 2002). In combination with increasing sea ice, it must be feared that narwhals, owing to their restricted habitat preference, high site fidelity, low genetic diversity, and dependence on open water during their 6-month stay on the winter feeding grounds, have limited options for alternative strategies relative to changes in their habitat in Baffin Bay.

Acknowledgements

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References

Dietz, R., and Heide-Jørgensen, M.P. 1995. Movements and swimming speed of narwhals (*Monodon monoceros*) instrumented with satellite transmitters in Melville Bay, Northwest Greenland. Can. J. Zool. **73**: 2106–2119.

Dietz, R., Heide-Jørgensen, M.P., Richard, P.R., and Acquarone, M. 2001. Summer and fall movements of narwhals (*Monodon monoceros*) from Northeastern Baffin Island towards northern Davis Strait. Arctic, **54**: 244–261.

Harris, R.B., Fancy, S.G, Douglas, D.C., Garner, G.W., Amstrup, S.C., McCabe, T.R., and Pank, L.F. 1990. Tracking wildlife by satellite: current systems and performance. U.S. Fish Wildl. Serv. Fish Wildl. Tech. Rep. **30**: 1–52.

Heide-Jørgensen, M.P., and Dietz, R. 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behaviour in Baffin Bay. Can. J. Zool. **73**: 2120–2132.

Heide-Jørgensen, M.P., Dietz, R., Laidre, K., and Richard, P. 2002*a*. Autumn movements, home range and winter density of narwhals (*Monodon monoceros*) from Tremblay Sound, Baffin Island. Polar Biol. **25**: 331–341.

Heide-Jørgensen, M.P., Richard, P., Ramsay, M., and Akeeagok, S. 2002*b*. Three recent ice entrapments of Arctic cetaceans in West Greenland and the eastern Canadian High Arctic. NAMMCO Sci. Publ. **4**: 143–148.

Innes, S., Heide-Jørgensen, M.P., Laake, J.L., Laidre, K.L., Cleator, H.J., Richard, P.R., and Stewart, R.E.A. 2002. Surveys of belugas and narwhals in the Canadian high Arctic in 1996. NAMMCO Sci. Publ. **4**: 147–190.

Koski, W.R., and Davis, R.A. 1994. Distribution and numbers of narwhals (*Monodon monoceros*) in Baffin Bay and Davis Strait. Medd. Groenl. Biosci. **39**: 15–40.

Laidre, K.L., Heide-Jørgensen, M.P., and Dietz, R. 2002. Diving behaviour of narwhals (*Monodon monoceros*) at two coastal localities in the Canadian Arctic. Can. J. Zool. **80**: 624–635.

Laidre, K.L., Heide-Jørgensen, M.P., Dietz, R., Hobbs, R.C., and Jørgensen, O.A. 2003. Deep-diving by narwhals, *Monodon monoceros*: differences in foraging behavior between wintering areas? Mar. Ecol. Prog. Ser. In press.

Palsbøll, P.J., Heide-Jørgensen, M.P., and 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 Bellinghausen Sea. Ann. Glaciol. **21**: 348–352.

Parkinson, C.L. 2000*a*.Variability of Arctic sea ice: the view from space, an 18-year record. Arctic, **53**: 341–358.

Parkinson, C.L. 2000*b*. Recent trend reversals in Arctic Sea ice extents: possible connections to the North Atlantic oscillation. Polar Geogr. **24**: 1–12.

Parkinson, C., Cavalieri, D., Gloersen, D., Zwally, J., and Comiso, J. 1999. Arctic sea ice extents, areas, and trends, 1978–1996. J. Geophys. Res. Oceans, **104**: 20 837 – 20 856.

Porsild, M. 1918. On ‘Savssat’: a crowding of arctic animals at holes in the sea ice. Geogr. Rev. **6**: 215–228.

Richard, P., Weaver, P., Dueck, L., and Barber, D. 1994. Distribution and numbers of Canadian High Arctic narwhals (*Monodon monoceros*) in August 1984. Medd. Groenl. Biosci. **39**: 41–50.

Service Argos. 1989. Service Argos Inc. guide to ARGOS system, September 1989. CLS ARGOS, Toulouse, France.

Siegstad, H., and Heide-Jørgensen, M.P. 1994. Ice entrapments of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in Greenland. Medd. Groenl. Biosci. **39**: 151–160.

Stern, H.L., and Heide-Jørgensen, M.P. 2003. Trends and variability of sea ice in Baffin Bay and Davis Strait, 1953–2001. Polar Res. **22**: 11–18.

Tynan, C.T., and DeMaster, D.P. 1997. Observations and predictions of Arctic climate change: potential effects on marine mammals. Arctic, **50**: 308–322.

Wigley, T.M.L., and Raper, S.C.B. 2001. Interpretation of high projections for global-mean warming. Science (Wash., D.C.), **293**: 451–454.