

## Homing Behaviour in an Atlantic Walrus (*Odobenus rosmarus rosmarus*)

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### Abstract

An adult Atlantic walrus (*Odobenus rosmarus rosmarus*) male (31 years old in 2001) tracked by use of satellite telemetry in NE Greenland during four seasons (1989, 1990/1991, 2000/2001, 2001) revealed a remarkably high perennial tendency of homing and consistency of migration pattern. During all four inshore summering periods (August to September), the animal used only one terrestrial haul-out from which it made excursions to the same general shallow water area (i.e., likely clam beds) in western Dove Bay (ca. 76° to 77° N). In different years, the size of the inshore foraging area varied between 48 and 86 km<sup>2</sup> in August, and between 136 and 385 km<sup>2</sup> in September. The inshore foraging period lasted ca. 69 days in 1989 and 1990, but ca. 86 days in 2000 (no data for 2001). During fall 1989, 1990/1991 and 2000/2001, the walrus followed the same migration route in the Greenland Sea north to the wintering grounds in the Northeast Water polynya (ca. 79° to 81° N). Apparently, this movement pattern was relatively independent of annual variations in ice and temperature regimes. Offshore in the Greenland Sea–Fram Strait area, the walrus occurred mainly in areas with dense ice cover (> 90%). During both the inshore summer and offshore winter, the animal dived to at least 250 m (maximum depth limit of the transmitter). The tracking of this walrus, whose activity pattern was typical of male walruses in the region, shows that this stenophagous species is a creature of habit with a highly stereotypic movement pattern which apparently is influenced by the location of predictable feeding, wintering, and mating areas.

**Key Words:** Walrus, *Odobenus rosmarus rosmarus*, East Greenland, satellite telemetry, migration, tracking, homing, diving

### Introduction

Homing behaviour involves a migratory movement that brings an animal back to its previously occupied home range (Papi, 1992). Several species of marine mammals perform seasonal migrations and show a clear tendency of homing. Often, there is a regular annual migration between wintering areas and summering areas—or between mating areas and feeding areas (reviews in Dingle, 1996; Papi, 1992; Stevick et al., 2002).

Resources in the marine environment tend to have a patchy distribution. This and the relative predictability of encountering critical resources in particular areas are important features that influence patterns of movement and homing. Species of marine mammals that have evolved on separate breeding and feeding grounds must navigate over great distances from one season to the next (Stevick et al., 2002).

Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeast Greenland constitute a separate population (Andersen et al., 1998; Born et al., 2001) numbering about 1,000 individuals (Born et al., 1997). The majority of females and young of both sexes occur year-round in the Northeast Water (NEW) polynya at Nordostrundingen (Figure 1) where the adult males join them (Born & Knutsen, 1992; Born et al., 1997) during the mating season of November to April (Born, 2001, 2003). During early summer, the males migrate from their northern and offshore wintering grounds to inshore foraging areas (e.g., Dove Bay) that become accessible when the solid land-fast ice breaks up, usually occurring during the second half of July (Born & Knutsen, 1992; Born et al., 1997).

Although walruses make regular seasonal migrations (e.g., Born et al., 1995; Fay, 1982; Wiig et al., 1996), little is known about long-term individual movements.

In this paper, we report the movements of a male Atlantic walrus tracked by use of satellite telemetry in NE Greenland during two periods, nine years apart (1989 and 1990/1991; 2000/2001 and 2001). To our knowledge, this is the first time that an individual marine mammal has been tracked with satellite telemetry over such a long time interval. The purpose of this article is to reveal the great extent to which walrus are “creatures of habit.”

## Materials and Methods

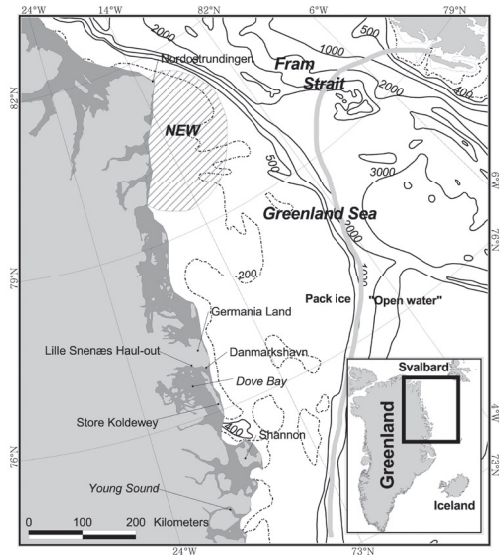
### Field Work and Satellite Transmitters

In connection with studies of walrus movement and energetics, several adult male walrus were equipped with satellite transmitters at their terrestrial haul-out, Lille Snenæs (LSN) (76° 52' N, 19° 38' W; Figure 1) in NE Greenland during August in 1989 and 1990 ( $n = 12$ ; Born & Knutsen, 1992, 1997) and 2000 and 2001 ( $n = 10$ ; Acquarone, 2004; this study). One individual (ID code: “N”) was handled during all four years (Table 1).

During handling in August 2000 (i.e., 10 years after the previous handling in 1990), N was recognized by his physical appearance (i.e., size, scarring pattern, tusk size, and healed circular holes in the hind flippers). The identification was tested in the fall of 2000 by comparing the DNA profile in a skin biopsy with previously established profiles from 1989. For that comparison, eight nuclear DNA microsatellite markers were used following the methods in Andersen et al. (1998). A 100% match confirmed the visual identification (L. W. Andersen, Danish Environmental Research Institute, Silkeborg/Kalø, Denmark, in litt., 2004).

Each year, a satellite transmitter was attached to one of N’s tusks. Three different types of transmitters were used (Table 1). The ST-3 transmitters were manufactured by Telonics (Mesa, Arizona, USA), whereas the other transmitters were made by Wildlife Computers (Redmond, Washington, USA).

All the transmitters provided data on location, but their protocols for sampling sensor data (e.g., haul-out time and dive activity) differed somewhat. For the ST-3 transmitters, information on haul-out activity was inferred from the activity of the saltwater switch and the temperature sensor (Born & Knutsen, 1997). Only the SCC3 transmitter collected dive data (maximum depth range was 250 m with a resolution of 2 m). For this unit, information on haul-out and at-sea time was collected via “timelines” (TIM), following methods in Born et al. (2002). Three types of dive data were considered from this transmitter: (1) daily maximum dive depth (MDD), (2) number of dives



**Figure 1.** Map of the areas in Northeast Greenland where an adult male Atlantic walrus was tracked using satellite telemetry during 1989, 1990, 1991, 2000, and 2001. The distribution of the land-fast ice in East Greenland is shown (dark grey). This ice is usually absent between late July and early October. The approximate extension of the Northeast Water (NEW) polynya and the approximate winter location of the edge of the pack ice in the Greenland Sea–Fram Strait area (thick grey line) are indicated. Bathymetry (in meters) was extracted from Anonymous (1997).

per day, and (3) time spent at different depth intervals (TAD = Time At Depth). Haul-out times were subtracted from the dive data prior to analysis of diving activity following Born et al. (2002).

*ArcView Version 3.0a* was used to map movements. For analyses, we used all locations of all quality classes (for definition of quality classes, see Harris et al., 1990) after having run the location data through the *PC-SASARGOS-filter Version 5.0* (D. Douglas, USGS, Alaska Science Center, P.O. Box 240009, Douglas, AK 99824, USA).

The movements of N in 1989 and 1990/1991 reported by Born & Knutsen (1992) are included in this study.

The approximate extension of N’s inshore feeding grounds in August and September was mapped using all “at-sea” locations. Total area of the inshore feeding ground was calculated from the minimum convex polygon using the *ArcView* extension *Animal Movement Version 2.04* (Hooge et al., 1999) and *Spatial Analyst Version 1.1* (ESRI, 380 New York Street, Redlands, CA 92373-8100, USA, info@esri.com, www.esri.com).

Walrus N died on 21 August 2001 during a second anaesthesia that season (Acquarone, 2004).

His total body mass (TBM) was measured post-mortem using the methods described in Knutsen & Born (1994) and Acquarone (2004). For the other years, estimates of TBM were obtained from a relationship between weighed TBM and age (Born et al., 2003).

The age of N was estimated in 2001 from reading the number of incremental layers in the cementum of unstained and undecalcified ca. 200  $\mu\text{m}$  thick longitudinal sections of lower molars following Mansfield (1958).

#### *Activity in Relation to Temperature, Ice Cover, and Bathymetry*

We wondered whether the timing of N's departure from the inshore foraging area was related to annual differences in air temperature and time of formation of fast ice in Dove Bay.

Temperatures measured at the Danmarkshavn meteorological station (76° 49' N, 18° 36' W; Figure 1) at the northern shore of Dove Bay were obtained from Cappelen (2004) and the Goddard Institute for Space Studies ([www.giss.nasa.gov/data/update/gistemp/station\\_data/](http://www.giss.nasa.gov/data/update/gistemp/station_data/)).

The offshore movements of N were described in relation to ice cover and bathymetry. One location was extracted per day and associated with the percent of ice cover and water depth at that site. If several good locations (i.e., quality class: 1-3) were available for a particular day, the most accurate was selected. In 1989, 20 offshore locations collected between 16 October and 29 November were available for analysis. A total of 20 and 36 locations from the periods 14 October 1990–27 March 1991 and 31 October 2000–24 January 2001, respectively, could be associated with ice cover and bathymetry. Hence, a total of 76 "location-ice-depth" data entries were available from all years; 56 of these were from the two winter seasons (1990/1991 and 2000/2001).

Daily ice concentration data were derived from multifrequency passive microwave observations by the Defence Meteorological Satellite Program's (DMSP) Special Sensor Microwave/Imager (SSM/I) using the Comiso Bootstrap ice

concentration algorithm (Comiso, 1986). Ice concentrations were estimated for 25 x 25 km grid cells around each location.

Area of ice cover ( $\text{km}^2$ ) in Dove Bay was inferred from the 25 x 25 km grid. Two grid cells covering the northern part of the bay (centered at 76° 36' N, 20° 12' W and at 76° 37' N, 19° 19' W) and one cell covering the entrance to the bay (at 76° 06' N, 19° 17' W) were used. All grid cells contained some fraction of land, but since this was the same in all years, no attempt was made to correct for inclusion of land.

To determine N's movements offshore in relation to bathymetry, one location per day (see "Temperature and Ice Cover") was associated with water depth at that particular site. The bathymetry of the East Greenland continental shelf is not well charted, but we attempted to estimate depths from bathymetric maps (Crane & Solheim, 1995) and navigational charts 2000 and 2300 (Kort-og Matrikelstyrelsen, National Survey and Cadastre, Denmark). For analyses, depths were organized into six intervals (m): 0-100, 101-200, 201-300, 301-400, 401-500, and 501-1,000.

We cannot entirely exclude the possibility that our activities at LSN during August influenced the natural haul-out behaviour of the walrus; however, N's haul-out activity in September, when there was no human disturbance in the area, can be described for 1989 and 2000 (due to system failure in 1990, sensor data were not received after early September).

The NEW polynya (cf. Schneider & Budéus, 1997) was defined as the area bounded by 79° 30' N to 81° 45' N and 5° to 20° W. The walrus was determined to be "offshore" and, hence, no longer in inshore areas when locations were south and east of the strait between the island of Store Koldewey and the mainland coast (Figure 1).

#### *Statistical Methods*

Z- and  $\chi^2$ -tests for difference in proportions of time (i.e., hauled out versus in water) followed Zar (1996).  $\chi^2$ -tests were used to analyze differences among years in water depth intervals while

**Table 1.** Year and date of instrumentation and satellite transmitter type used for tracking an adult male walrus during four seasons in Northeast Greenland, 1989-2001; the duration of contact (i.e., until reception of the last sensor data) and the age and estimated total body mass of the animal are also shown.

ID code	Year and day of instrumentation in August	Transmitter type	Power output (Watt)	Date of last message	No. of days active	Walrus age (years)	Total body mass (kg)
4345	1989 12	ST-3	1	30 November 1989	111	19	1,070
4349	1990 8	ST-3	1	2 April 1991	238	20	1,100
4347	2000 18	SCC3	1	4 March 2001	199	30	1,590
11271	2001 6	SPOT-2	0.5	21 August 2001	16	31	1,629

the walrus was offshore. A Student's *t*-test (using equal variance) was used to evaluate differences in MDD when N was inshore versus offshore. One-way ANOVA followed by Tukey post-hoc tests were performed on arc-sin and square-root transformed ice data to test for differences among fall seasons (i.e., the period from when the animal moved offshore and 30 November in 1989, 1990, and 2000) and years when N was tracked during winter (1990/1991 and 2000/2001) in ice cover (% cover). Calculations were made using SAS® (PC-Version 8). All tests at alpha = 0.05.

## Results

### Walrus N

In 2001, the study animal was 31 years old (i.e., in his 32nd year of life; birth usually occurs in late May/early June; Born, 2001) and had a TBM of ca. 1,629 kg (Table 1). Hence, when first tracked in 1989, N was 19 years old and, therefore, sexually and physically mature during the entire study (for age at sexual and physical maturity, see Born, 2003; Fay, 1982).

### Temperature and Ice Cover

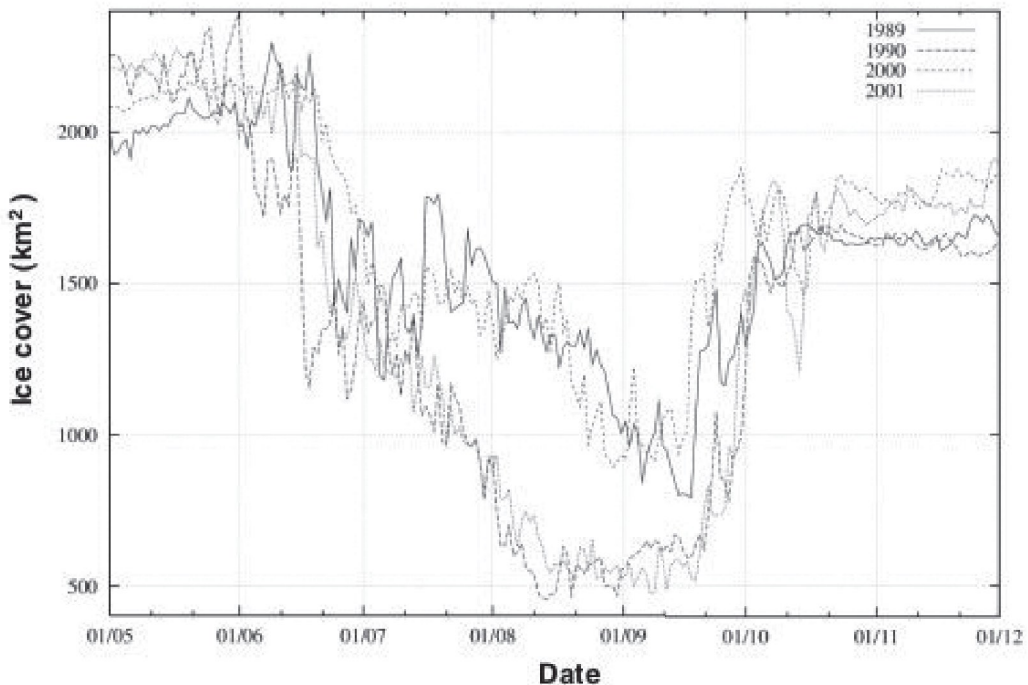
Cracks and leads in the fast ice in Dove Bay allow walruses to move from offshore wintering areas in

the Greenland Sea–Fram Strait region to the Lille Snææs haul-out (Figure 1) during the latter half of July and early August. Break-up of the fast ice usually occurs earliest along the northern shores of Dove Bay due to fluvial discharge from a nearby river (Born, pers. obs.), which may explain why the haul-out is situated there.

Generally, 1989 resembled 2000 because in both years temperatures were comparatively low and ice prevailed in Dove Bay during the open water season, whereas in 1990 and 2001, it was warmer and there was less ice.

August and September, when N was inshore in Dove Bay, was mild in 1990 compared with 1989 and 2000 (August–September mean air temp., °C: 1989 = -2.3; 1990 = 1.6; 2000 = -2.5). In contrast to this pattern, the mean temperature in October (i.e., the time of migration from inshore to offshore areas) was relatively mild in 2000 (mean temp., °C: 1989 = -15.6; 1990 = -14.6; 2000 = -13.3). In 2001, when N did not transmit after 21 August, it also was relatively mild (mean temp., °C: August–September = 2.2; October = -10.9).

In 1989 and 2000, the time of the ice break-up and the amount of dissolved fast ice remaining in Dove Bay were similar. During these years, more ice prevailed during the open-water season than during the other two years (Figure 2). In 1989 and 2000,



**Figure 2.** Development during summer and fall of the ice cover in Dove Bay (NE Greenland) during 1989, 1990, 2000, and 2001

many floes of dissolved ice remained in northern Dove Bay during the open-water season, whereas in 1990 the area was devoid of ice from 4 August until the formation of new ice (Born & Knutsen, 1992; this study). Formation of fast ice began about mid-September in 1989 and 2000 and about two weeks later in 1990 and 2001 (Figure 2).

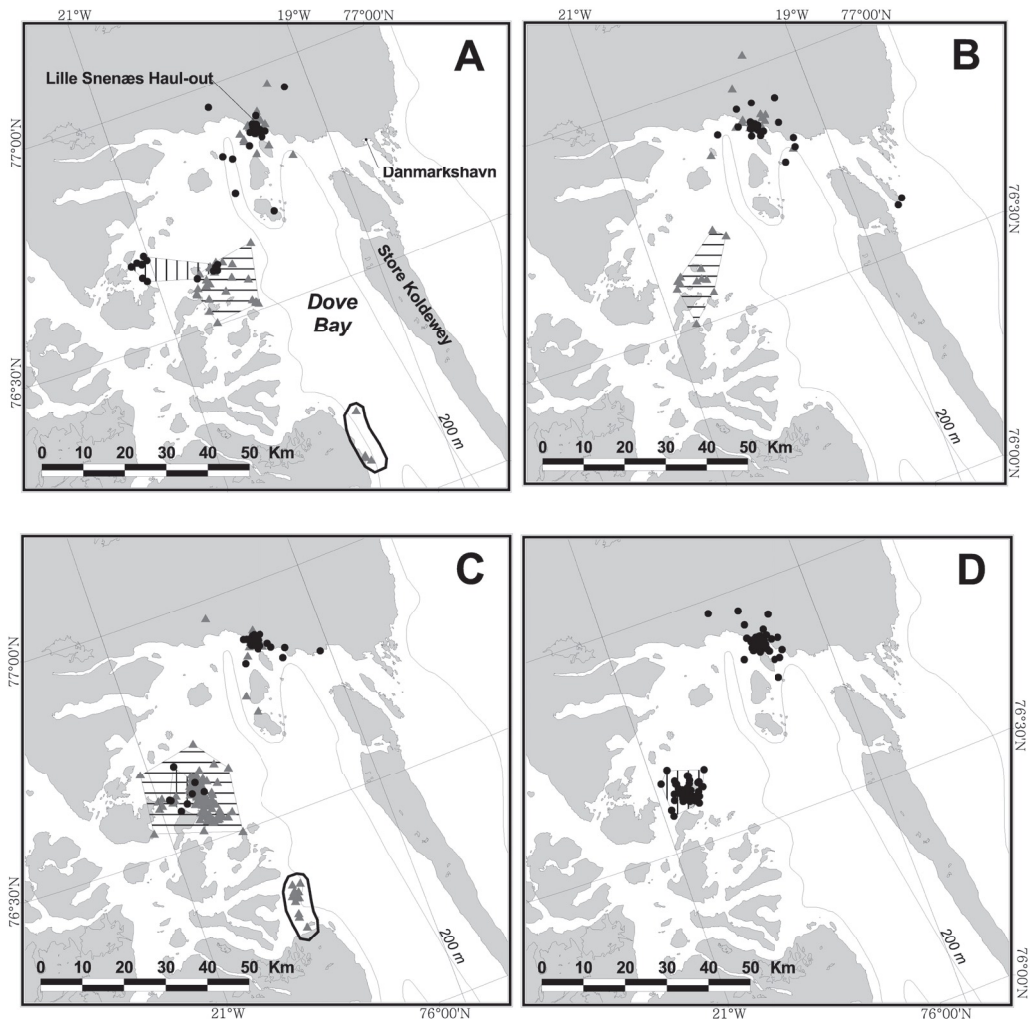
#### Movements

Dates of N's first appearance at the haul-out were remarkably similar during all years, except during 2000 (day in August; 1989: 9; 1990: 8; 2001: 6), indicating a high degree of consistency in his movement from the wintering to the summering

ground. In 2000, N was not observed at LSN until 17 August.

While inshore at Dove Bay, N used the same foraging grounds during all four seasons. Between periods of rest at the LSN haul-out, N mainly moved to a distance of up to ca. 50 km from LSN to western Dove Bay presumably to forage in areas where water depths are < 100 m (Figure 3A-D). In August, the area visited by N in western Dove Bay was roughly 48-86 km<sup>2</sup>, whereas it apparently was two to four times larger in September (Table 2).

Inferred from when the last good-quality locations (i.e., locations class 1-3; cf. Harris et al., 1990) were received from the haul-out, N used the



**Figure 3.** Location and approximate extension of foraging areas of an adult male walrus in Dove Bay during August (dots) and September (triangles) in four different years (A: 1989, B: 1990, C: 2000, and D: 2001); the encircled locations (A, C) were not included in the calculation of size of foraging areas because they were received when the walrus was en route offshore (i.e., 29-30 September).

**Table 2.** Approximate size of inshore foraging areas used in August and September by an adult male walrus during four seasons in NE Greenland

Year	Size of foraging area (km <sup>2</sup> )			
	August	<i>n</i>	September	<i>n</i>
1989	85.9	17	184.7	28
1990	*	*	136.1	12
2000	48.2	8	385.1	112
2001	84.3	61	**	**

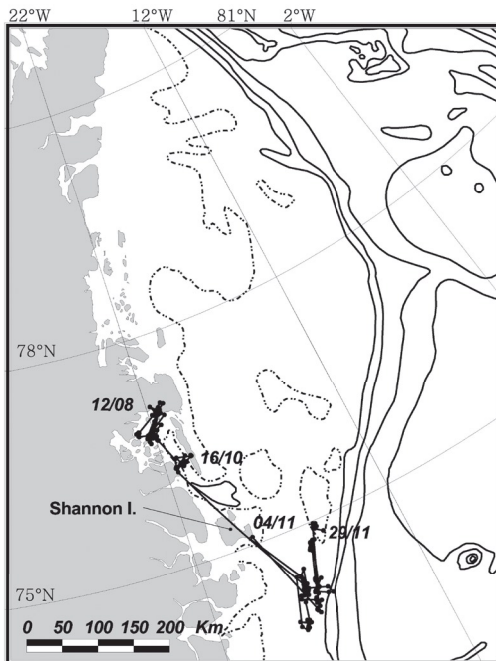
\* Too few at-sea locations for calculation

\*\* The animal died on 21 August 2001.

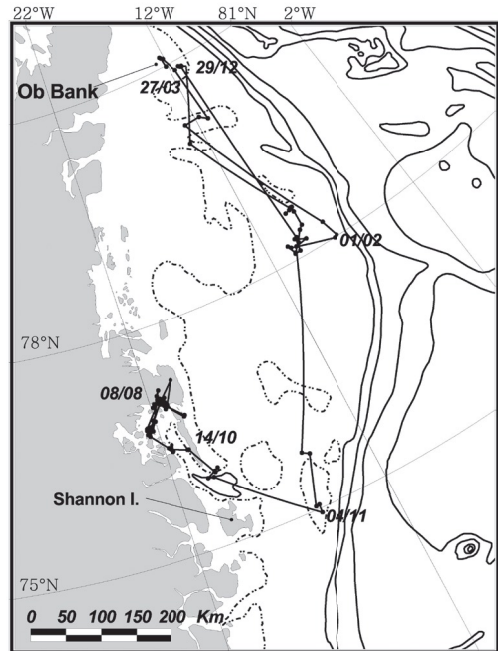
LSN until September or early October (1989: 19 September; 1990: 5 October; 2000: 10 September; 2001: no data). Likely, at this time of year the fast ice off the haul-out becomes too thick for the walruses to break through (i.e.,  $\geq$  ca. 20 cm; Fay, 1982).

In all three years, the walrus moved south in Dove Bay after his last visit to the haul-out and then left the inshore area through the strait between the mainland coast and the island of Store Koldewey (Figures 4, 5, & 6).

In 1989, after leaving the coastal areas around 16–17 October 1989, N spent most of the time until transmission stopped at the edge of the



**Figure 4.** Movements of an adult male Atlantic walrus tracked in NE Greenland using satellite telemetry between 12 August and 29 November 1989

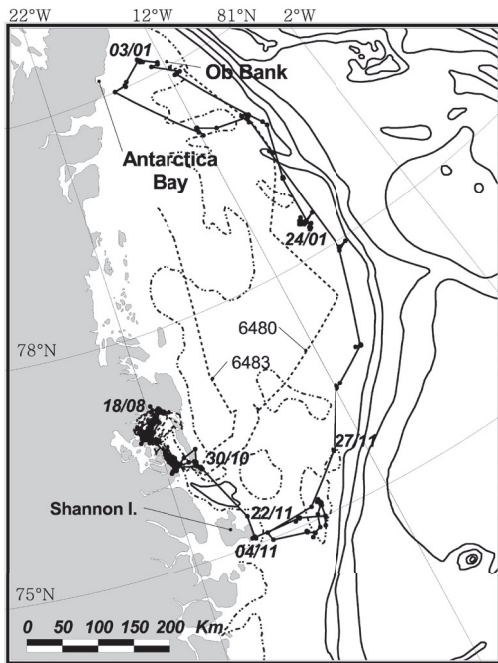


**Figure 5.** Movements of an adult male Atlantic walrus tracked in NE Greenland using satellite telemetry between 8 August 1990 and 27 March 1991

continental shelf, about 100 km off the Greenland mainland. On 2–4 November, a visit was made to Shannon Island—a known shallow-water walrus foraging area (Born et al., 1997)—and on 26 October and 17 November, locations were received from a bank east of Shannon Island (i.e.,  $< 200$  m depths). Apparently, N initiated a northward movement on 20 November, but contact was lost on 29 November 1989 when he was at  $74^{\circ} 53' N$ ,  $14^{\circ} 36' W$  (Figure 4).

In 1990, N moved offshore around 14 October, visited a bank east of Shannon Island ( $< 200$  m) on 4 November, and then commenced his migration north on 13 November. The locations show that N was in the NEW polynya area between 20 and 29 December. By 1 January 1991, N had moved a little to the south, but then remained in the NEW from 19 February until the last location was received on 27 March at  $80^{\circ} 41' N$ ,  $09^{\circ} 18' W$  (Figure 5). While in the NEW, N visited the Ob Bank.

In 2000, N left the inshore area on 30 October. Apart from this later departure, the fall migration route was surprisingly similar to that in 1989 and 1990. After visiting the Shannon Island area on 4–6 November, N moved north along the edge of the continental shelf to the NEW area on 27 November. The periods 15 December–6 January and 11–14 January were spent in the NEW where



**Figure 6.** Movements of an adult male Atlantic walrus tracked in NE Greenland using satellite telemetry between 18 August 2000 and 24 January 2001; the movements during fall 2001 of two other adult male walruses (6480, 6483) are also shown.

locations were received from shallow areas: Antarctica Bay and the Ob Bank. Transmissions stopped on 24 January 2001 at  $78^{\circ} 12' N$ ,  $6^{\circ} 56' W$  (Figure 6).

Between 6 and 21 August 2001, N visited the southwestern parts of Dove Bay (Figure 3D). No offshore movements were recorded subsequently.

Hence, in 1989 and 1990 the inshore period (i.e., from first appearance at LSN until migration offshore) lasted 69 and 68 days, respectively, whereas in 2000 it lasted 86 days. Furthermore, in contrast to the situation in 1989 and 1990, the northward movement of N in 2000 occurred one to two weeks later.

During northward migrations, N moved against the East Greenland Current at an average speed of 4.0 km/h (SD = 4.0, range: 0.5–11.1 km/h,  $n = 15$ ) during 13 November–20 December 1990, and 5.1 km/h (SD = 9.2, range: 0.3–15.5 km/h,  $n = 30$ ) during 27 November–15 December 2000.

During all fall and winter periods, the offshore locations received from N were in areas with dense ice cover. The ice cover in areas from which locations were received during the fall did not differ among years ( $F = 1.142$ ,  $DF = 2, 37$ ,  $p = 0.33$ ), and during this period of the year, N occurred in areas with 93.1% ice cover (SD = 4.4,  $n = 40$ ); however,

during the winter of 2000/2001, locations came from areas with significantly denser ice (mean = 97.4%, SD = 3.6,  $n = 20$ ) than during the winter of 1990/1991 (mean: 90.9%, SD = 4.7,  $n = 16$ ) ( $F = 7.500$ ,  $DF = 1, 34$ ,  $p = 0.01$ ).

We found no relationship between ice cover and water depth in areas where N occurred offshore ( $r^2 = 0.002$ ,  $z = 0.374$ ,  $n = 76$ ).

#### Haul-Out and Diving Activity

In September, when N was inshore, he hauled out for 22.5% of the time in 1989 and 35.9% in 2000 (Table 3). These proportions of haul-out time did not differ statistically ( $z = 1.11$ ,  $p > 0.05$ ). Nor was there a statistically significant difference between these two years in the percent of total haul-out time spent on ice (1989: 46.7%; 2000: 57.9%;  $z = 0.52$ ,  $p > 0.05$ ) or on land (1989: 53.3%; 2000: 42.1%).

After moving offshore, N continued to haul out for 13.4 to 30.3% of the time, with the lowest haul-out activity in December 2000 (Table 3). During the fall months (October–November), there was no difference in the proportion of time spent hauled out between 1989 and 2000 ( $z$ -tests;  $p > 0.05$ ).

Although the amount of haul-out time differed among months in 2000/2001—being highest in September and lowest in December—this difference was not statistically significant ( $\chi^2 = 8.85$ ,  $DF = 4$ ,  $p > 0.05$ ).

While in Dove Bay in August and September 2000, the walrus spent from approximately 50% to 65% of his at-sea time at depths of 6 to 42 m (Table 4) (i.e., at depths where walruses typically forage; Gjertz et al., 2001; Jay et al., 2001). After September, however, the fraction of time spent at greater depths increased markedly. In November and December, 2.5 to 8.9% of the time was spent at depths greater than 90 m (Table 4). This tendency to dive deeper during winter also was reflected in the number of dives to different depths (not shown) and in the daily records of maximum dive depth, MDD (Figure 7). While inshore in 2000,

**Table 3.** Percentage of time hauled out, by month, of an adult male walrus in NE Greenland in 1989 and 2000

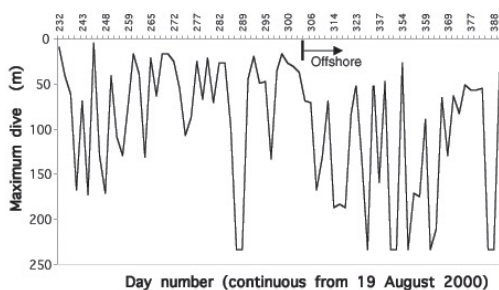
Month	1989		2000		2001	
	% time hauled out	No. days monitored	% time hauled out	No. days monitored	% time hauled out	No. days monitored
September	22.5	29	35.9	27	-	-
October	24.1	28	18.7	23	-	-
November	30.3	27	18.8	21	-	-
December	-	-	-	-	13.4	22
January	-	-	-	-	19.2	15

**Table 4.** Percentage of time spent at different depths by an adult male walrus during August-December 2000 and January 2001

Month	% of time spent at different depths					Days monitored	No. of 6-h time blocks
	0-6 m	6-18 m	>18-42 m	>42-90 m	>90-250 m		
August	47.5	47.1	3.3	1.4	0.8	12	30
September	33.6	60.3	4.9	0.9	0.4	27	81
October	33.7	44.7	20.1	1.5	0.01	16	42
November	38.2	40.4	13.4	5.6	2.5	26	61
December	22.8	45.7	6.5	16.2	8.9	25	68
January	35.7	38.9	5.3	19.7	0.4	24	55

N's MDD averaged 70.7 m (SD = 59.1, range: 6-234 m,  $n = 43$ ), whereas offshore the MDD averaged 129.0 m (SD = 73.7, range: 28-234 m,  $n = 35$ ), which was significantly deeper ( $t = 3.88$ , DF = 76,  $p < 0.001$ ).

N showed a tendency to exploit areas with similar water depths during the two winter seasons (1990/1991 and 2000/2001) when he was tracked offshore (1989 is not included because of premature transmission failure on 29 November). The distributions of "daily location per bathymetrical intervals" (see "Materials and Methods") did not differ significantly between 1990/1991 and 2000/2001 ( $\chi^2 = 7.23$ ; DF = 5,  $p = 0.20$ ) and, therefore, data from the two periods were combined. For the majority of time, N occurred in areas with relatively deep water. Of a total of 56 winter locations, 73.2% were in areas with 100-500 m depths (the remainder were in areas with 501-1,000 m depths). None of the locations were in areas with depths of < 50 m. It must be kept in mind, however, that detailed bathymetry in the East Greenland area is not available.



**Figure 7.** Daily maximum depths (m) of an adult male walrus in NE Greenland between 19 August 2000 (= day 232) and 31 January 2001 (day 396); the walrus left the inshore areas in Dove Bay and moved into the Greenland Sea on 30 October 2000 (day 304). The satellite-linked dive-recorder recorded dives to ca. 250 m.

## Discussion

Areas of high marine mammal density may shift temporally in response to changes in the abundance of prey. Hence, marine mammals that feed on non-sessile prey (e.g., crustaceans, fish, and squid) may change their distribution according to shifts in prey distribution and abundance (e.g., Tollit et al., 1997; Weinreich et al., 1997). Generally, Arctic seals (e.g., ringed seals, *Phoca hispida*, and harp seals, *Pagophilus groenlandicus*; Frost & Lowry, 1981; Ronald & Healey, 1981) have broad food preferences and, therefore, exhibit a relatively high degree of plasticity in their choice of foraging habitats. In contrast, walrus are stenophagous and depend almost entirely on access to shallow banks with clams and other benthic invertebrates and on wintering areas that are not covered with solid ice that is thicker than ca. 20 cm (Fay, 1982; Vibe, 1950). Consequently, walrus are conservative in their choice of areas of occupancy during periods of the year that are critical to them (e.g., summer feeding, wintering, and mating areas). Our study confirmed this. During all years, animal N returned to the same haul-out site and used the same foraging grounds each summer. Furthermore, his migration path during three falls was almost identical, and apparently he wintered in the NEW polynya each year.

This study described the activity of only one walrus; however, the behaviour of the study animal appeared typical of that of other male walrus in the Dove Bay area. During the inshore period of all four seasons, the walrus that were tracked from LSN with satellite tags moved to western Dove Bay to forage (Acquarone, 2004; Born & Knutsen, 1992, 1997). Furthermore, in 1990, when four satellite tags functioned after mid-October, these four walrus all moved north to the NEW area during the fall (Born & Knutsen, 1992). In 2000, only N's tag functioned after mid-October, whereas in 2001, two animals whose radios transmitted during the fall both moved north from the Dove Bay area; one stopped transmitting at 79° 34' N and one at 80° 45' N (Figure 6).



Returning to specific sites where prey has been abundant in the past may be a useful foraging strategy (Stevick et al., 2002). Such a strategy has been described in humpback whales, *Megaptera novaeangliae* (e.g., Clapham et al., 1993) and grey seals, *Halichoerus grypus*, for example (McConnell et al., 1999). Both the location of clam beds and the sea ice cover influence migration routes and areas of occupancy by walruses in NE Greenland. In NE Greenland, shallow banks (< 100 m depth) where walruses can feed during summer are limited in extent and are found inshore or near-shore in relatively few areas around 74° N and 77° N. These banks are covered with solid ice for nine to ten months of the year (Born et al., 1997). Walruses access inshore feeding areas only when the solid ice breaks up during summer, and they have to leave during fall when fast ice covers these areas. Walrus feeding banks also are found in the NEW polynya area, an important wintering area (Born & Knutsen, 1992; Born et al., 1997). Walruses also have been observed during the winter in other small polynyas in NE Greenland and in the shear zone between fast ice and pack ice along the East Greenland coast (Born et al., 1997). Obviously, limited access to food and wintering areas in NE Greenland means that the walruses in this region must adhere to a movement pattern that is tightly synchronized with ice break-up and ice formation. We suggest that it is not only in NE Greenland that walruses show a high degree of fidelity to predictable foraging and mating grounds but that, given their basic life history, this is likely also true in other parts of their range. For example, a male walrus tagged in the North Water polynya in Smith Sound (NW Greenland) in August 1989 was shot in May 1991 about 70 km from the tagging site (Born, 1991). Also, in the Canadian High Arctic, individual walruses have shown perennial fidelity to certain wintering areas (Sjare, 1993).

Sexual segregation in migratory movement is observed in several pinniped species (review in Stevick et al., 2002). The foraging range also can differ between sexes (probably at least partly influenced by body size), for example, in harbor seals, *Phoca vitulina* (Thompson et al., 1998). In East Greenland, the majority of females and young remain in the NEW area year-round while the males migrate south to inshore feeding grounds during summer (Born et al., 1997). Similarly, in the Svalbard-Franz Joseph Land walrus population (cf. Andersen et al., 1998), the females stay at Franz Joseph Land and at the eastern parts of the Svalbard Archipelago, whereas males tend to migrate from Franz Joseph Land to the western and southwestern parts of Svalbard (Wiig et al., 1996). In contrast, female Pacific walruses (*O. rosmarus divergens*) with young are the most

strongly migratory during summer (i.e., they migrate north), whereas many adult males stay close to the traditional haul-outs further south in Bristol Bay (Fay, 1982).

Walrus N moved a straightline distance of about 550 km between his wintering and summering grounds. Traveling long distances between feeding and mating areas is also known in Pacific walruses (Fay, 1982) and in several other pinniped species, for example, the northern elephant seal, *Mirounga angustirostris* (Le Boeuf et al., 2000). Adult male walruses are typically 1.5-2 times heavier than females (Fay, 1982; Knutsen & Born, 1994). Hence, if males feed in different areas from females during summer, this could have the effect of reducing intraspecific competition for food. A similar pattern was observed in the highly sexually dimorphic northern elephant seal (e.g., Stewart & DeLong, 1993).

In winter, Pacific walruses concentrate in areas where the ice is thinnest or most dispersed (Fay, 1982). In contrast, the present study indicated that during winter, Atlantic walruses in NE Greenland can cope with even very dense pack ice; however, it is presumably advantageous to walruses in this area that the ice conditions at their major wintering grounds in the NEW are less dense than in the surrounding areas, and therefore they choose to winter there.

Walruses usually occur in areas where the water is < 80-100 m deep (Fay, 1982; Vibe, 1950); however, N dived to at least ca. 250 m (the limit of the transmitters' ability to record dive depth) and probably deeper. Apparently, there is no suitable invertebrate walrus food at such depths in NE Greenland (Piepenburg, 1988; Piepenburg & Schmid, 1996). Several species of seals (e.g., ringed seals, *Phoca hispida*) are taken by walruses, and consumption of seals could play a significant role in the diet (Lowry & Fay 1984). It is certain that seals are actively killed and consumed, rather than being eaten only as carrion (Fay et al., 1990). Walruses are known to also eat ringed seals in NE Greenland (Born et al., 1997). Facultative feeding on seals during winter may explain why walruses occurred for prolonged periods of time offshore in areas with relatively deep water as revealed by satellite telemetry (Born & Knutsen, 1992). On one occasion at LSN in August 2000, the faeces of N consisted of pieces of seal skin (likely ringed seal) thereby confirming that this animal was a "seal eater" (Born & Acquarone, unpub. data).

N left inshore feeding areas and initiated his northward movement later in 2000 than in the other years. Conditions in 2000 seemed to differ from those in the other years in that October was warmer (i.e., thick and dense ice likely developed later). We speculate that this later ice formation

may have allowed N and other walrus to feed longer at their inshore clam beds.

In conclusion, Walrus N, considered representative of a group of male walrus in NE Greenland, showed a surprisingly high degree of site tenacity, consistency in migration, and homing behaviour over a 13-year period (judging by observations made during four field seasons). Overall, this animal's behaviour was influenced little by annual differences in ice formation and temperature.

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