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Summer and Fall Movements of Narwhals (*Monodon monoceros*) from Northeastern Baffin Island towards Northern Davis Strait

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ABSTRACT. Ten narwhals (*Monodon monoceros*) were instrumented with satellite-linked radio transmitters in Tremblay Sound in August 1997 (N = 5) and August 1998 (N = 5). All whales stayed in the waters around Bylot Island until the end of September. On the basis of these animals and others tagged previously (total N = 24), it is believed that the Bylot Island summering population has limited or no contact with other summering populations in Canada or Greenland. Four whales were monitored during their southward movement along the east coast of Baffin Island. Three of them travelled close to the shore, visiting several fjords and bays, during September and October. The fourth whale started the southward migration at the same time as the other three, but it returned to the area east of Pond Inlet and made two trips northeast of Bylot Island. It headed south on 21 October 1998. South of Royal Society Fiord, it travelled offshore along the continental slope (1000 to 1500 m), probably because of ice formation in inshore areas. This narwhal and another male tagged in 1997 moved east toward the northern parts of the Davis Strait, reaching an area midway between Canada and Greenland in early November. Their winter movements were monitored until 30 January. The same wintering area in northern Davis Strait was previously documented for two male narwhals tracked from Melville Bay, NW Greenland, in 1993 and 1994. The whales showed a preference for deep areas, including deep fjords and the continental slope, where depths ranged between 500 and 1500 m. Even deeper areas, where maximum daily dives exceeded 1000 m, were also visited occasionally.

Key words: narwhal, *Monodon monoceros*, High Arctic, satellite telemetry, movements, migration, population, stock identity

RÉSUMÉ. On a équipé 10 narvals (*Monodon monoceros*) d'émetteurs radioélectriques en liaison avec un satellite dans le détroit de Tremblay en août 1997 (N = 5) et en août 1998 (N = 5). Toutes les baleines sont restées dans les eaux entourant l'île Bylot jusqu'à fin septembre. En considérant ces animaux et d'autres équipés précédemment (N total = 24), on pense que la population estivale de l'île Bylot n'a que peu, sinon pas de contact avec d'autres populations estivales du Canada ou du Groenland. Quatre baleines ont fait l'objet d'un suivi au cours de leur déplacement vers le sud le long de la côte est de l'île de Baffin. Durant les mois de septembre et d'octobre, trois d'entre elles longeaient la côte de près, effectuant des pauses dans divers fjords et baies. La quatrième a commencé sa migration vers le sud en même temps que les trois autres, mais elle est retournée dans la zone à l'est de Pond Inlet et s'est rendue par deux fois au nord-est de l'île Bylot. Elle a mis le cap vers le sud le 21 octobre 1998. Au sud du fjord Royal Society, elle s'est dirigée vers le large et a longé la pente continentale (à environ 1000 à 1500 m du rivage), probablement en raison de la formation de glace dans la zone côtière. Ce narval ainsi qu'un autre mâle équipé en 1997 se déplaçaient en direction de l'est vers la partie nord du détroit de Davis, atteignant début novembre une zone située à mi-chemin entre le Canada et le Groenland. En hiver, leurs déplacements ont été suivis jusqu'au 30 janvier. La même zone d'hivernage dans le nord du détroit de Davis a déjà été rapportée pour deux narvals mâles suivis en 1993 et 1994 depuis la baie Melville, au N.-O. du Groenland. Les baleines affichaient une préférence pour des zones profondes, y compris des fjords encaissés et la pente continentale, où la profondeur allait de 500 à 1500 m. De temps à autre, les baleines se rendaient aussi dans des zones encore plus profondes, où les plongées maximales quotidiennes dépassaient les 1000 m.

Mots clés: narval, *Monodon monoceros,* Extrême-Arctique, télémesure par satellite, déplacements, migration, population, identité des stocks

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INTRODUCTION

The narwhal (*Monodon monoceros*) occurs in inshore areas of northeastern Canada and Greenland during the open-water season, from July through September (Born et al., 1994; Dietz et al., 1994; Kingsley et al., 1994; Richard et al., 1994). By the time the Arctic fjords and bays freeze over in autumn, narwhals are leaving these areas. They apparently make long-distance movements between summering and wintering grounds (Dietz and Heide-Jørgensen, 1995). During winter and early spring (8–10 months), narwhals frequent areas covered with dense offshore pack ice (Koski and Davis, 1994). Although gross patterns of seasonal migration have been inferred from whaling records and various observational studies (e.g., Born et al., 1994; Koski and Davis, 1994; Richard et al., 1994), little is known about genetic exchange and movements of individual narwhals between summer and winter areas. Although a study of the population structure based on mtDNA revealed low nucleotide diversity, a significant level of heterogeneity was detected between a number of combinations of three West Greenlandic sampling areas and a combined group from eastern Canada and northwestern Greenland (Palsbøll et al., 1997). However, the sample size from Canada was too small (N = 29) to support conclusive analyses of population structures there.

Narwhals are hunted in both Canada and Greenland. Knowledge about stock discreteness is important for managing this exploitation. Other human activities such as shipping, commercial fishing, and development of nonrenewable resources (e.g., offshore oil and gas) may also have impacts on the feeding ecology and migrations of narwhal populations.

The remoteness and inaccessibility of areas inhabited by narwhals make these animals difficult to study in the field using traditional methods. Recent advances in satellite tracking have made it possible to monitor the movements of narwhals (Martin et al., 1994; Dietz and Heide-Jørgensen, 1995; Heide-Jørgensen and Dietz, 1995).

The objectives of the present study were to 1) assess site tenacity in coastal areas where narwhals congregate during the open-water season; 2) identify critical habitats, migration routes, and wintering grounds; and 3) examine the exchange among whales from different open-water aggregations.

MATERIALS AND METHODS

Study Area

The whales were all tagged off the Alpha River delta in Tremblay Sound (72˚21.382′N, 81˚05.951′W). Tremblay Sound is a narrow (down to 1.5 km wide) fjord about 45 km long with maximum depths of up to 275 m. The fjord is bordered with high (500 m or more) steep-sided mountains of the Lancaster Plateau (Sempels, 1982). The shores of Tremblay Sound are hence mainly steep-sided cliffs, but also promontories of low bluffs or raised beaches with shores of sand and gravel (Sempels, 1982). This fjord is a well-described narwhal habitat, and whales have previously been successfully captured and tagged there (Kingsley, 1993; Kingsley et al., 1994; Martin et al., 1994).

According to Inuit hunters camped in Tremblay Sound, the fast ice left the fjord in the middle of July 1998, and the first narwhals were seen on 28 July (J. Mucktar, pers. comm. 1998). No ice was present in the vicinity of the Alpha River during the tagging period (5 to 30 August) in either 1997 or 1998. Similar ice-free conditions were experienced in 1989 and 1991, whereas the fjord was packed with ice in 1993 and 1999 (Kingsley, 1993; Dietz and Heide-Jørgensen, pers. observation 1999).

In 1997, no hunting activities were observed close to the Alpha River, but a few boats travelled the sound, and two groups of hunters camped in Tremblay Sound during our stay. In addition to the narwhals, two bowhead whales (*Balaena mysticetus*), several ringed seals (*Phoca hispida*) and Greenland sharks (*Omnicephalus maximus*) were observed in the sound that year. Again in 1998, few boats were observed in the fjord. No bowheads were observed in 1998, but ringed seals, pods of harp seals (*Phoca groenlandica*), and Greenland sharks were observed in addition to the narwhals that year.

Capturing and Handling of the Whales

Five narwhals were caught in nets at the Alpha River delta between 8 and 24 August 1997 and tagged with satellite-linked transmitters. In 1998, five narwhals were likewise tagged at the same spot between 14 and 25 August. As in previous studies, the whales were captured in nets set close to the surface and perpendicular to the shoreline. The nets used in 1997 were deep, dark green and 5 m deep, with 20 × 20 cm mesh. Those used in 1998 were black and 10 m deep, with 40 × 40 cm mesh. The 1998 nets proved to be more effective, as almost no whales avoided them or became aware of their presence before entanglement.Three sections of net, each 50 m long, were kept afloat by white buoys. The nets were anchored at one end to a large stone on the beach and attached at the other end to a 200 L oil drum filled with stones, which served as an anchor in the water. The nets were kept under daily constant surveillance, and the presence of narwhals in the fjord was also monitored. Immediately after a whale became entangled, two inflatable boats were paddled or pulled towards the captured animal. Use of outboard engines was avoided as far as possible to minimize acoustic stress on the whales. The nets and narwhals were pulled to the surface to ensure that the animals could breathe and position them for the tagging operation. Oars (2.5 m) were placed between the boats through the nets to secure the animals during handling and to keep the boats separated. Ropes and transport belts were placed around the chest, tail, and tusk to secure the animal while the transmitters

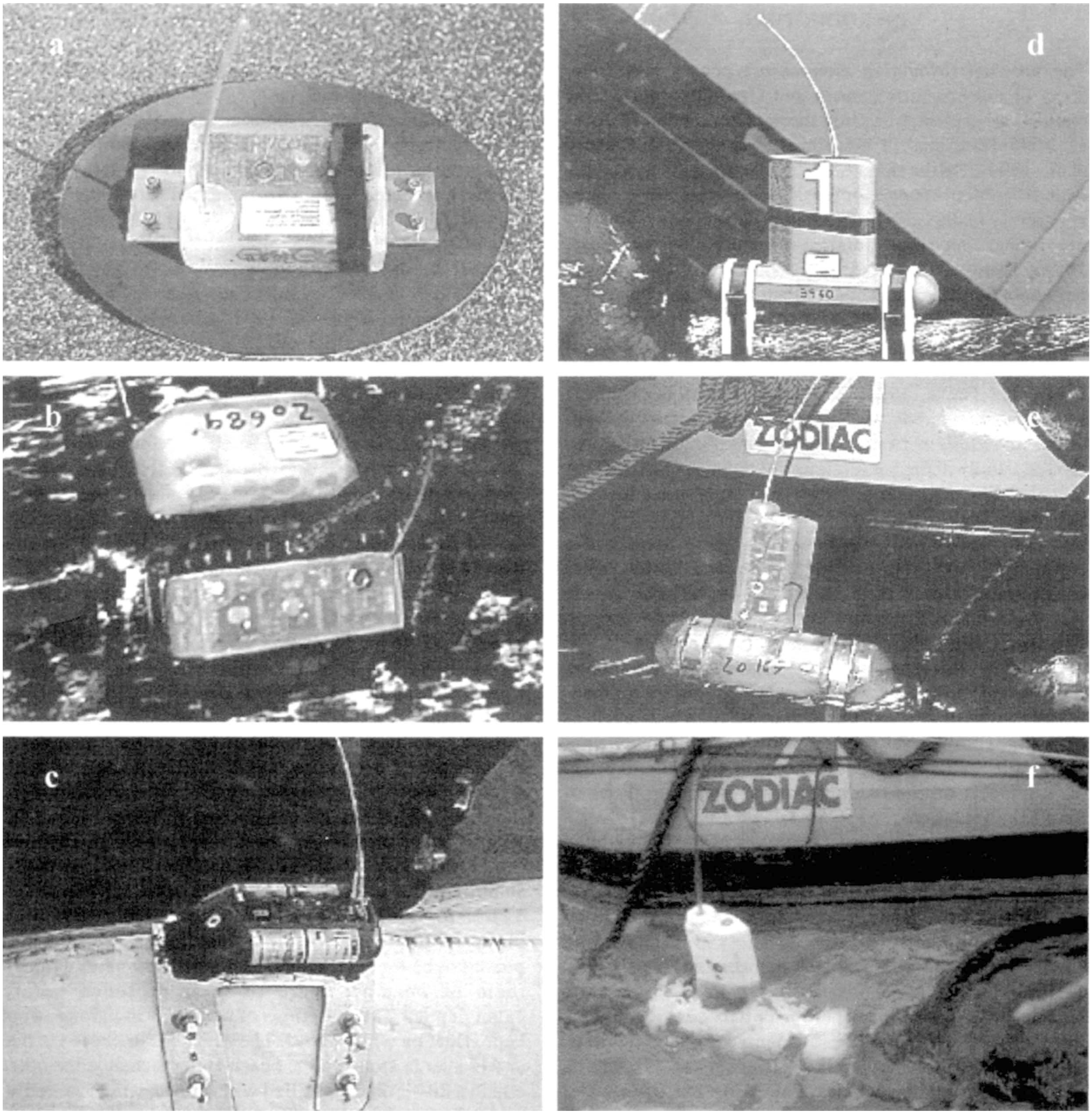

FIG. 1. Three first generations of narwhal (and beluga) backpack satellite transmitters (a–c) and three tusk transmitter generations (d–f).

were attached. After instrumentation, the nets were removed from the animals. Finally, the transport belts were detached at one end and the whales were released.

Instrumenting the Whales

Four whales, one female and one small male with a 40 cm tusk (external) in 1997 and two adult females in 1998, were instrumented with backpack transmitters that were pinned through the dorsal ridge. These transmitters had a power output of 0.5 W (ST-6, Telonics, Mesa, Arizona) and were programmed and cast in epoxy by Wildlife Computers (Woodinville, Washington). Three of the transmitters (#20682, #20691, and #20692) were of the second generation, each with two housings measuring 3 × 4.5 × 14 cm, one covering the battery package and the other the ST-6 transmitter (see Fig. 1a-c). The unit weighed approximately 950 g in air and 150 g in water. The saddle, 20 cm long and 24 cm wide, was made of a rubber material 5 mm thick (Ureol® polyurethane, composed of type XB 5073-1 and 6414 B in the proportion 100:18). Each transmitter, powered by four lithium C cells (3.5 V), was capable of 54 000 transmissions at 0˚C. The third female (#20696) was instrumented with a fourth-generation transmitter with a single housing (3 × 4.5 × 14 cm) covering both the ST-10 transmitter and the battery package (four 3.5 V lithium C cells). This unit also weighed approximately 950 g in air and 150 g in water. The transmitter was glued to a saddle made of 1.5 mm thick belt material (Fig. 1c). The saddle was 20 cm long, with a belt in each end extending 15 cm to each side. Each belt was 5 cm wide and pre-punched with a row of holes. Excess belt material beyond the selected holes was cut off to minimize drag during swimming. The saddle was secured to the animal with two 8 mm pins of flexible polyethylene (PEHD 1000) held in place by washers and nuts. The ends of the pins were cut to a length of 1 cm and compressed with pliers to prevent the nuts from loosening.

Six male narwhals with tusks measuring between 0.6 and 2.1 m (external length) were fitted with 0.5 W satellite-linked UHF transmitters (ST-6, Telonics, Mesa, Arizona), also manufactured by Wildlife Computers (Redmond, Washington) (Fig. 1d-f). The housings of the second- and third-generation transmitters both measured 8 (3.5) × 21 (6.5) × 27 (8) cm (width × height × length; max (min) measures) and weighed approximately 1 kg in air and about 400 g in water. We deployed four second-generation transmitters with a pressure transducer maximum of 1000 m (cast in transparent epoxy) and two third-generation transmitters with a pressure transducer maximum of 1500 m (cast in yellow epoxy; see Fig. 1e-f). The transmitter housings were hydrodynamically designed to minimize both water resistance and reflection of sonar signals. These transmitters were powered by eight lithium C cells (expected capacity of 180 000 transmissions at 0˚C).

The housing units were attached to the tusks by two 316-type stainless steel bands that were 19 mm wide (Band-it, Houdaille, Denver, Colorado). The tusk is assumed to rotate towards the left as it grows (e.g., Thompson, 1963; Kingsley and Ramsay, 1988); therefore, the transmitters were tilted slightly to the right side of the animal, so that the antennae would remain in an upright position for a longer time. None of the transmitters were duty-cycled. In 1997, a daily maximum of 500 transmissions was programmed to save battery power, but as this limit was seldom reached, no such upper limit was programmed in 1998. A saltwater switch triggered transmissions 0.2 s after the switch emerged from the water. The minimum time between transmissions (repetition rate) of the transmitters was 45 s. Each transmission contained 14 bytes of information. A status message was relayed every 15th transmission with information on sum of transmissions as well as the battery voltage. Data from the transmitters were relayed via the ARGOS DCLS system (Service Argos Inc., 1989; Harris et al., 1990).

Signal Monitoring in the Field

Before deploying the transmitters, we tested them in the field using a local uplink receiver (Telonics: TSUR-B Argos Uplink Receiver). The uplink receiver was connected to a PC to log and monitor signals within the fjord, evaluate whale behaviour after release, and determine how long the animals stayed in Tremblay Sound after the tagging. The uplinks also kept the team updated on the presence of whales nearby.

Maps

Only good-quality positions of Class 1 to 3 were used for the drawing of the maps. The Argos system predicts the accuracy of the best quality, Class 3, to be 150 m or less from the animal's real position for 68% of the locations The corresponding predictions are 350 m or less for Class 2 and 1 km or less for Class 1. Studies on seals have shown that the distances between predicted and observed positions are on average two to three times higher than ARGOS predicts. (e.g., Stewart et al., 1989; McConnell et al., 1992; Goulet et al., 1999). These positions were used to map the routes taken by 6 of the 10 tagged narwhals that had 24 or more "good" positions.

Maps were produced with ArcView GIS system for Windows NT by ESRI, using digital coastline and bathymetry derived from the GEBCO Digital Atlas (GEBCO 97 edition). Place names mentioned in the text and figures were extracted from Canadian Hydrographic Service nautical charts.

We included data from two of nine narwhals tagged in Greenland in 1993 and 1994 (Dietz and Heide-Jørgensen, 1995) to illustrate the common wintering area and the timing and rate of the southward migration.

RESULTS

Bylot Island Fjord Complex as a Summering Area

Table 1 gives information on the dates of capture, sex, and size of the 10 narwhals equipped with satellite-linked transmitters off the Alpha River delta during 8–24 August 1997 and 14–25 August 1998.

During the summer period of both years (10 August–22 September), the whales stayed within the Bylot Island area, including Tremblay Sound, Milne Inlet, Eclipse Sound, Navy Board Inlet, Oliver Sound, and Pond Inlet (see also Fig. 2 and Table 2). Only one position was obtained from Navy Board Inlet, suggesting limited use of this part of the fjord complex. No positions were obtained from Lancaster Sound or the more western summering areas of Admiralty Inlet and Prince Regent Inlet.

No good-quality positions were obtained from Tremblay Sound (or Milne Inlet) in 1997 even though the animals stayed for a considerable time (up to 12 hours after the

TABLE 1. Information on ten narwhals instrumented with satellite-linked transmitters.

Tag #	Type[1]	Date	Sex	Length (cm)	Tusk length (cm)
1997:					
20682	B	August 8	Female	400	–
3963	T	August 19	Male	375	83
20691	B	August 21	Male	306	40
3964	T	August 21	Male	370	63
6335	T	August 24	Male	440	137
1998:					
3960	T	August 14	Male	400+	148
20692	B	August 19	Female	380	–
20162	T	August 21	Male	475	190
3961	T	August 25	Male	500	210
20696	B	August 25	Female	380	–

[1] B = Backpack transmitter; T = Tusk transmitter.

tagging) in Tremblay Sound, as monitored in the field by a local uplink receiver (Fig. 3a, b). In contrast with the 1997 results, the 1998 tagging produced good-quality positions from both Tremblay Sound and Milne Inlet (including its offshoot, Koluktoo Bay) (Fig. 4a-d), indicating a connection between the whales that frequent these fjords. In both 1997 and 1998, the whales showed a preference for deep areas (500 to 750 m) in Eclipse Sound and Pond Inlet, whereas few or no positions were obtained from Navy Board Inlet and the narrow fjords east of Milne Inlet. The whales may have avoided some of these areas because they lack deep water (e.g., Assumption Harbour and Ragged Island Sound, both less than 170 m deep). However, even fjords with intermediate depths (up to 430 m) were not visited (e.g., Eskimo Inlet, White Bay, and Paquet Bay), and no visits were recorded in the rather deep Tay Sound (up to 640 m). Of the two fjords for which we have no information on depth (Oliver Sound and Stevenson Inlet), only Oliver Sound was visited, and that was only once by one animal (see Table 2).

Eastern Baffin Island and the Autumn Migration

In 1997, only one narwhal was monitored on its southward migration, whereas in 1998 three whales were tracked as they moved south along the east coast of Baffin Island (Fig. 5). In both years, the whales left the Bylot Island area between 20 and 29 September (Figs. 3b, 4b-d).

Narwhal #6335 was tracked for 76 days in 1997, over more than 4026 km (Figs. 3b, 6, 7). While moving south along the east coast of Baffin Island, this whale visited a number of fjords (Table 3). It showed a preference for deep areas at the mouths of Royal Society Fiord (400–550 m; north of Bergesen Island), Clark Fiord (500–700 m), and Sam Ford Fiord (550–660 m), as well as for the continental slope (500–1000 m) east of Home Bay and Kangeeak Point, all of which are deeper than the shallow (< 200 m) banks on the continental shelf (Figs. 3b and 6). Narwhal #6335 also clearly avoided the shallow (down to 14 m) Hecla and Griper Bank on its way south. It is uncertain whether it visited other fjords (e.g., Clyde Inlet), but the lack of positions and the rapidity of the southward migration suggest that it would have had little time for such visits. This animal travelled as far south as Broughton Island, and then moved northeast towards the deep southern part of Baffin Bay. It was tracked to the continental slope, where it transmitted the last position on 7 November at around 69˚N, 59˚W, in the very same area that had been frequented by two male narwhals from Melville Bay in early December of 1993 and 1994 (Dietz and Heide-Jørgensen, 1995). The last position of #6335 was only 3.5 km from the closest position of the narwhals tagged in Melville Bay.

Narwhal #20696, tagged in 1998, was the only female tracked on its southward migration. It covered more than 2742 km over the 49 days of tracking (Figs. 4b and 6). This female left the Bylot Island area on 28 September, one week later than the two males tracked the same autumn. Moving southward along the east coast of Baffin Island, female #20696 visited five of the nine fjords frequented by all four narwhals tracked along this route. When we lost contact with the transmitter on 13 October, the female had reached 69˚N, 66˚W east of Home Bay.

The two male narwhals tracked southward in 1998 (#20162 and #3961) left Bylot Island on the same date (20 September) and migrated from Coutts Inlet along Baffin Island, visiting deep fjords, e.g., Buchan Through (500–700 m), Buchan Gulf (200–800 m), and Royal Society Fiord (Figs. 5 and 6). Narwhal #20162 remained in this area for two days, whereas narwhal #3961 continued south along Baffin Island: following a route similar to that of narwhal #6335 in 1997, it visited Scott Inlet (250–700 m), Sam Ford Fiord (400–600 m), and the continental slope (500–1000 m) east of Home Bay and Kangeeak Point. As in 1997, the whales showed no interest in the shallow areas (less than 200 m) of the continental shelf along Baffin Island and the shallow Hecla and Griper Bank (only 14 m deep). Narwhal #3961 started to move east off Broughton Island but then decided to head farther south to Cape Dyer, where contact was lost on 4 November.

After the two days' stay in Royal Society Fiord, #20162 returned north on 22 September towards an area east of Pond Inlet, where it stayed from 26 September to 4 October (Figs. 4d, 6, 8). It then moved north to an area east of Bylot Island, at the north end of the deep, narrow basin. On 8 October, it returned to the mouth of Pond Inlet, then moved north again, this time to the deepwater areas farther east of Bylot Island, where it stayed until 21 October. Narwhal #20162 then moved southward towards Royal Society Fiord, taking essentially the same route that it had taken a month earlier in company with #3961. Thereafter, it moved farther east towards the 1500 m contour, which it followed, without visiting any of the Baffin Island fiords, until it reached the latitude of Broughton Island. It moved 6 latitudinal degrees south (more than 650 km) in 16 days (Fig. 8).

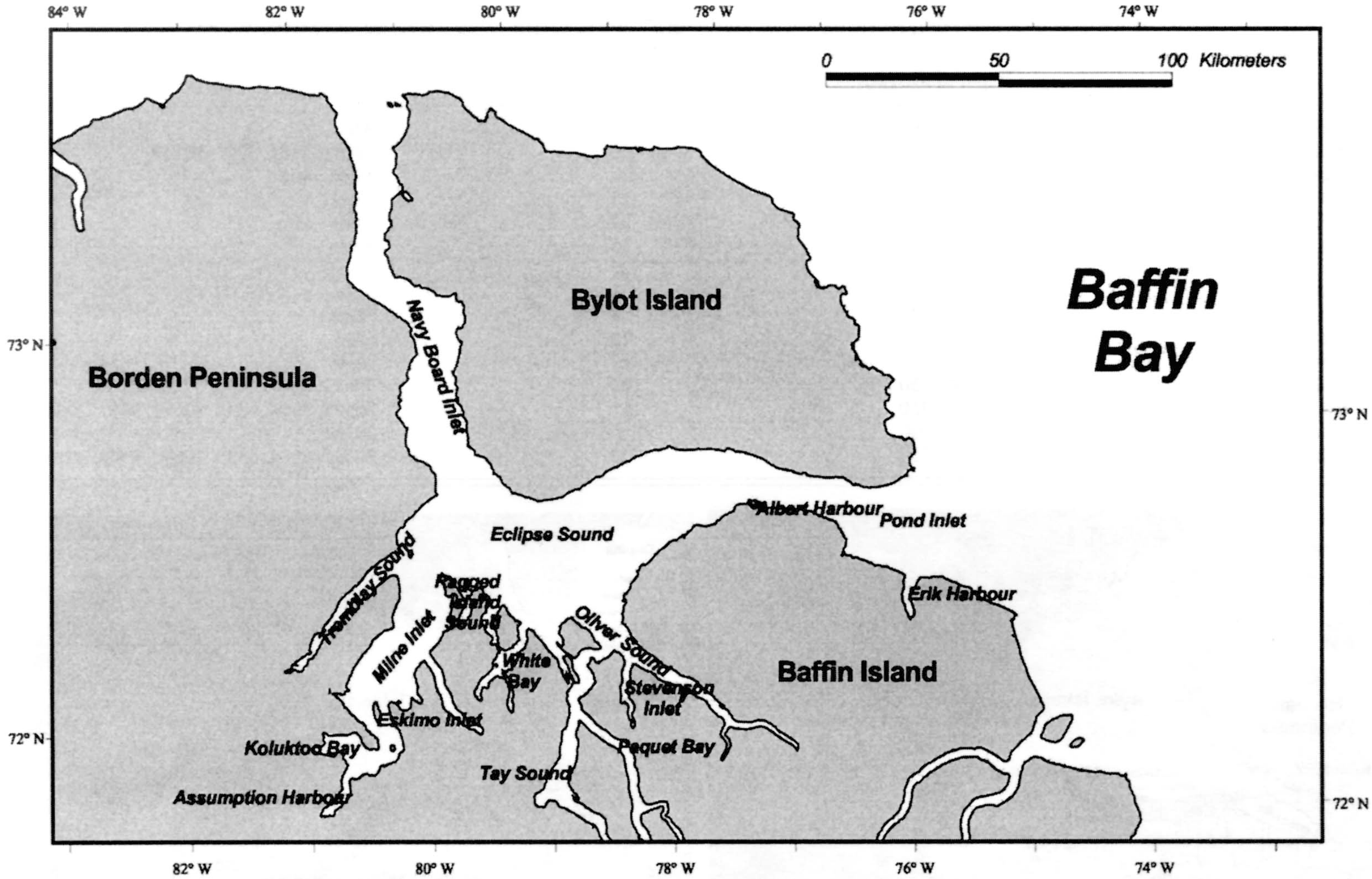

FIG. 2. Map showing place names in the Bylot Island area.

The whales that had time to visit the fjords of Baffin Island on their way south clearly preferred the deep fjords that extend close to the continental slope. Their rapid southward migration may have precluded visiting deep fjords situated or extending farther west (see Table 4).

Offshore Wintering Areas

After narwhal #6335 had reached its southern limit, it continued moving east until it reached the area used by the narwhals from Melville Bay. It arrived there, however, on 7 November, two weeks earlier than the Melville Bay narwhals. As the last contact with #6335 was on that date, it is impossible to conclude, from the 1997 data, whether it (and other narwhals) remained in the area for the winter.

Narwhal #20162 started moving east towards the 1000 m contour off Greenland on 5 November 1998, arriving there on 10 November (Figs. 6 and 7). This was the same area (69˚ N, 59˚ W) frequented by the "Canadian" narwhal (#6335) tagged in 1997 and by the two male narwhals from Melville Bay, and the arrival dates of all four whales were within a two-week period of November (Figs. 6 and 7). Narwhal #20162 stayed between 59˚ and 60˚ W and travelled south and north along the 1000 m contour between 67˚ and 70˚ N. It reached 68˚18′ N, 60˚ W on 10 November. From there it went south and arrived at its most southern latitude, 67˚48′ N, on 15 November. Over the next two weeks, it went north to its most northern wintering latitude, 69˚36′ N. Between 29 November and 7 January, narwhal #20162 went south and north twice between 68˚30′ N and 69˚30′ N. It then moved south to 68˚ N, perhaps because of severe ice conditions (NOAA satellite ice map from January 1999). It stayed at that latitude from 18 to 30 January, after which the transmitter stopped operating (Figs. 6 and 7).

Timing and Rate of the Southward Movement

The rate of southward movement by "Canadian" narwhals was similar to that of the narwhals from Greenland (Dietz and Heide-Jørgensen, 1995). However, the narwhals from the Bylot Island area started their southward movement approximately one month earlier (22–29 September) than the Melville Bay whales (ca. 22 October). One exception was male narwhal #20162, which went back north and stayed another month east of Bylot Island. As most narwhals from the Bylot Island area moved only 4.5˚ (500 km) south, compared with 7.5˚ (833 km) for the Melville Bay narwhals, the Bylot Island area animals took less time than the narwhals from Melville Bay (3 weeks vs. 4–5 weeks) to reach their southernmost positions (Fig. 8).

TABLE 2. The fjords of the Bylot Island area, showing depth and length characteristics and visits by narwhals in 1997 and 1998.

Fjord	Depth Range (m)	Length (km)	Visited by Narwhal No:
Tremblay Sound	90–260	41	All
Milne Inlet	150–850	52	3960, 20696, 3961, 20162
Koluktoo Bay	150–320	20	3960, 3961
Assumption Harbour	150–170	15	None
Eskimo Inlet	30–285	24	None
Ragged Island Sound	40–110	15	None
White Bay	40–410	26	None
Tay Sound	100–640	61	None
Paquet Bay	300–430	54	None
Oliver Sound	?	72	6335
Stevenson Inlet	?	19	None
Navy Board Inlet	100–550	120	3963
Eclipse Sound	100–750	111	20691, 3964, 6335, 20696, 3961, 20162
Albert Harbour	10–090	4	20162
Pond Inlet	100–750	52	20691, 3964, 6335, 20696, 3961, 20162

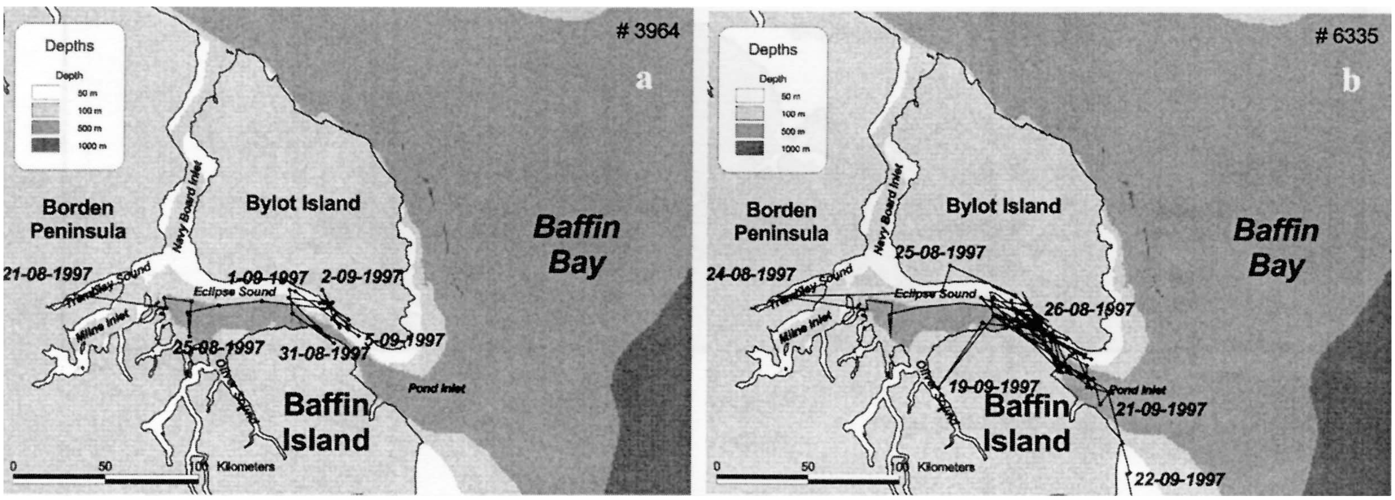

FIG. 3. a: Movements of adult male narwhal #3964 (length: 370 cm, tusk: 63 cm), tracked for 430 km from 21 August through 5 September 1997. b: Close-up of the Bylot Island area movement of adult male narwhal #6335 (length: 440 cm, tusk: 137 cm) from 24 August to 23 September 1997. See Figure 6 for the complete track of this whale. Only good-quality positions (Class 1–3) are shown.

Performance of the Backpack Transmitters

Three backpack transmitters of the second generation were deployed (on #20682 and #20691 in 1997 and on #20692 in 1998), and their average transmitter longevity was 41 days. Although 11 923 transmissions (on average) were sent from each of the three platform transmitter terminals (PTTs), only two Class 1–3 positions and 67 Class 0 positions were obtained in total from these three whales (Table 4).

However, the fourth-generation transmitter (#20696) deployed in 1998 provided three times as many uplinks (33261) on average, resulting in as many as 470 "good" positions (Class 1–3) and 473 positions with unknown accuracy (Class 0). This large difference must be ascribed to the design of the fourth-generation transmitters, which placed the PTT centrally on the saddle (see Fig. 1c). This placement elevated the antennae 3–4 cm higher than on the second-generation transmitters, which had the PTT unit and the battery package on opposite sides of the saddle. We therefore stopped using the second-generation design in subsequent studies on narwhals, as their lack of a protruding dorsal ridge leaves the antennae and saltwater switch too low in the water.

Performance of the Tusk-Mounted Transmitters

As the second- and third-generation transmitters had the same shape and PTT, differing only in the range of the pressure transducer and in colour, we did not compare their longevity. One tusk-mounted transmitter in 1997 (#6335) and two in 1998 (#3961 and #20162) showed fairly good longevity, ranging from 78 to 165 days. But three other tusk transmitters (#3963, #3960, and #3964) transmitted for only 6, 7, and 31 days, respectively: less time than the shortest lasting backpack transmitters. On the basis of the 1997 results, we believed that the small size of the tusks (63–83 cm external lengths) contributed to the premature failure of the tusk-mounted transmitters. However, the failure of #3960 in 1998, after only 7 days, showed that transmitters mounted on a large tusk (148 cm) could fail prematurely as well.

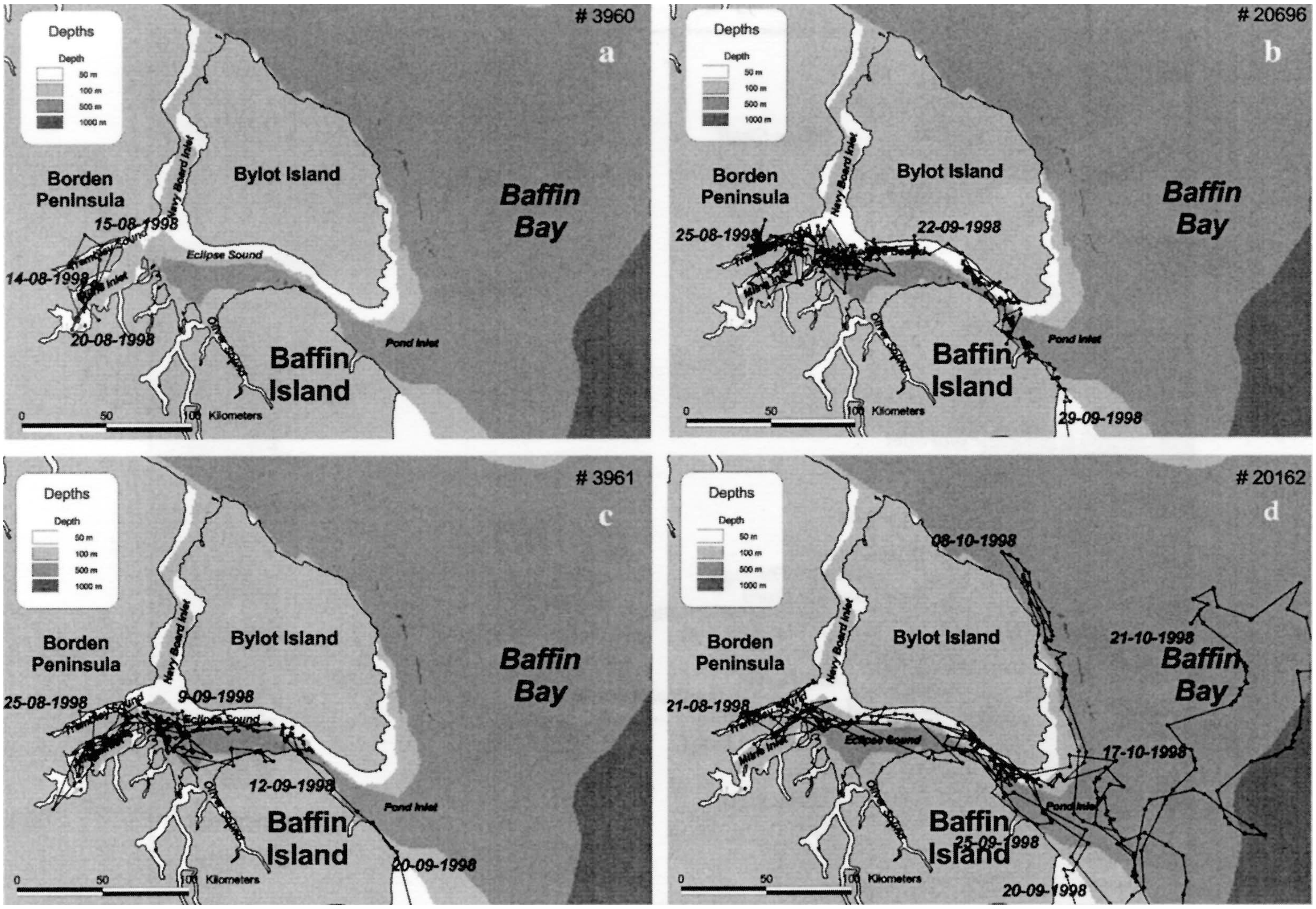

FIG. 4. a: Movements of adult male #3960 (length: 400+ cm, tusk: 148 cm), tracked for 228 km from 14 to 20 August 1998. b: Close-up of the Bylot Island area movement of adult female #20696 (length: 440 cm) from 25 August through 29 September 1998. c: Close-up of the Bylot Island area movement of adult male #3961 (length: 500 cm, tusk: 210 cm) from 25 August through 20 September 1998. d: Close-up of the Bylot Island area movement of adult male #20162 (length: 475 cm, tusk: 190 cm) from 21 August through 22 October 1998. See Figure 6 for complete tracks of whales #20696, #3961, and #20162 (b-d). Only good-quality positions (Class 1–3) are shown.

The fact that a transmitter operated for more than 18 months on a narwhal with a tusk 84 cm long (tagged in 1994) indicates considerable variability in the longevity of the tusk-mounted tags. This information also indicates that the mounting of a PTT on the tusk of a narwhal is not likely to affect the behaviour or survival of the animal. The cause of the transmission failure of the long-lasting transmitters #6335 (76 days), #3961 (78 days), and #20162 (162 days) is also unknown. The climatic conditions at the time of failure (November–February), with low temperatures and up to 10/10 of ice coverage, could have damaged the electronics, the antennae, or the attachment. As no reduction in the monitored voltage was observed, battery failure was not believed to be the cause of the transmission failure.

Backpack Transmitters vs. Tusk-Mounted Transmitters

The tusk-mounted transmitter had greater longevity than the backpack transmitters (61 vs. 43 days) and a larger number of days with good locations (57 vs. 25 days), but the differences were not significant ($p = 0.5869$ and $p = 0.3629$ respectively; unpaired T-test). However, the longevity of the six tusk-mounted transmitters showed greater variability (6–165 days) than that of the four backpack transmitters (32–49 days).

The number of good positions per day (Class 1–3 positions/Good position days) was very poor for the second generation of backpack transmitters (0–0.2 positions/day), intermediate for the tusk-mounted transmitters (0.2–5.4 positions/day) and best for the fourth generation of backpack transmitters (9.6 positions/day). However, data in these three groups were insufficient for a meaningful statistical test.

None of the transmitters showed battery drainage within the period monitored. All ten transmitters showed a higher battery voltage at the end of their operating period compared with the first measurements of voltage. We therefore concluded that none of the units stopped transmitting because of battery failure. It is likely that the backpack transmitters terminated because they fell off as the pins migrated out through the dorsal ridge.

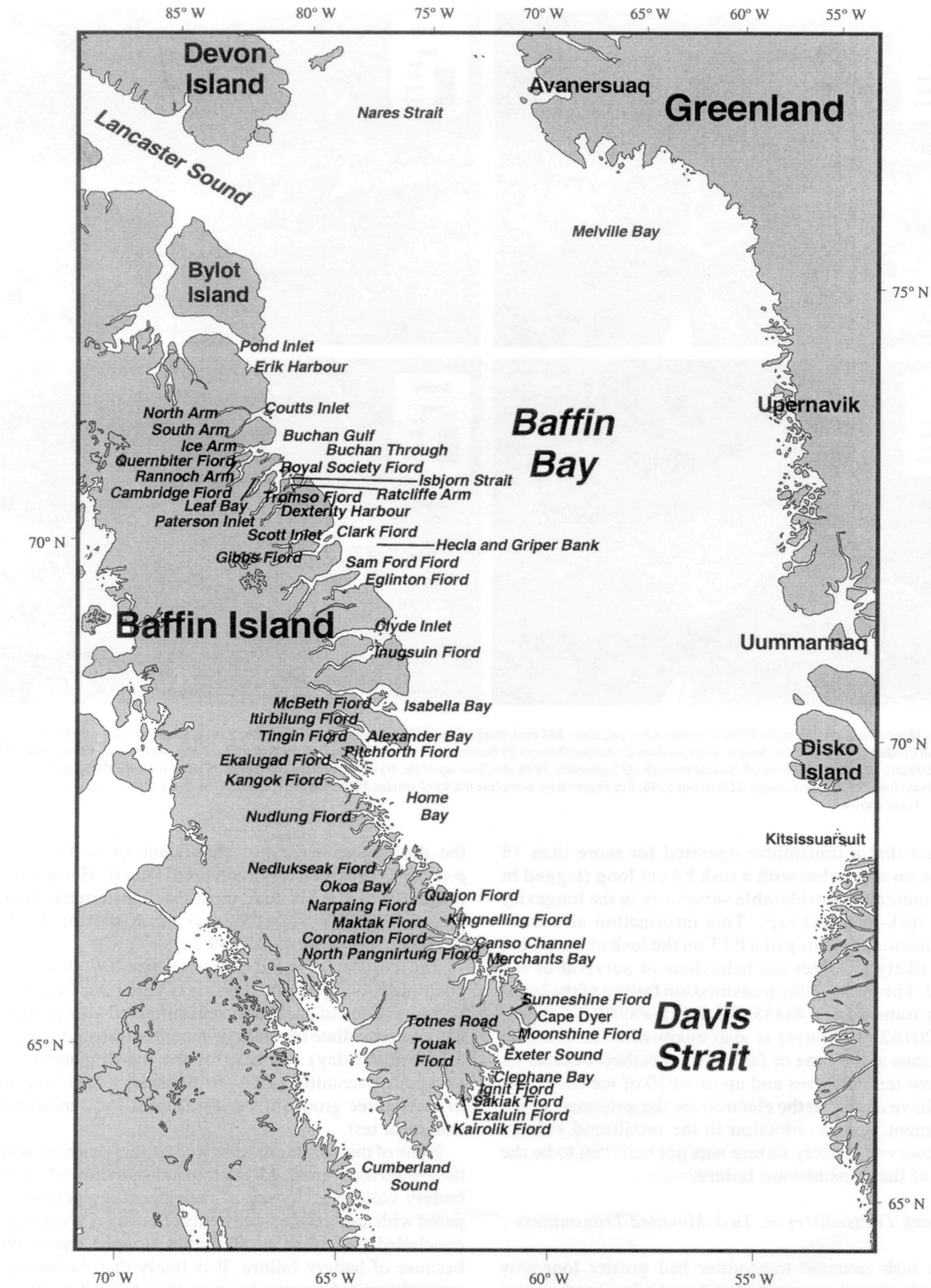

FIG. 5. Map showing place names along Baffin Island.

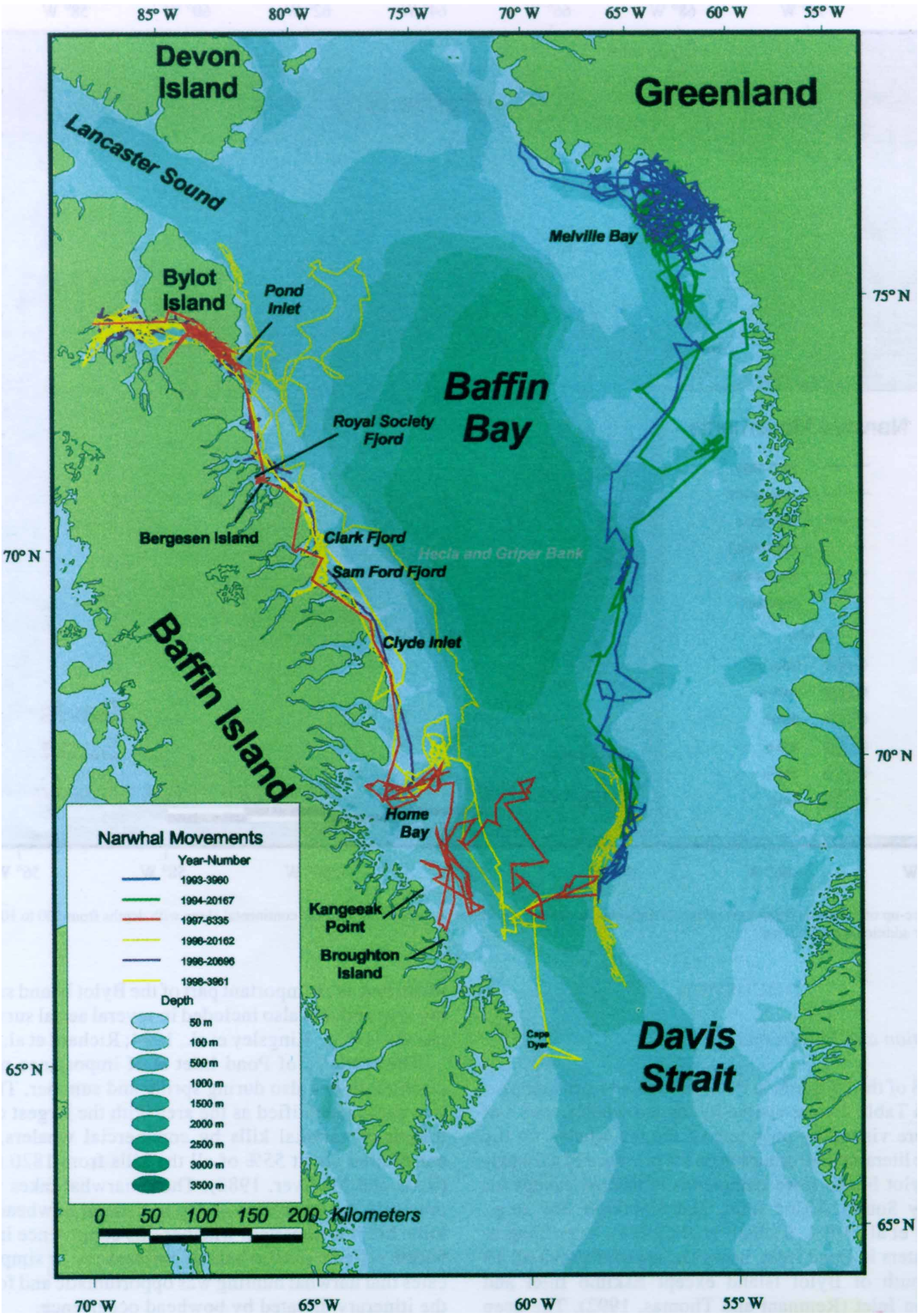

FIG. 6. Autumn movements of three adult narwhal males (#6335; #3961; #20162) and an adult female (#20696) tracked for 4062 km, 4516 km, 7017 km, and 2742 km, respectively, during 1997 and 1998. Also shown are the tracklines of two other male narwhals tracked from Melville Bay in West Greenland in 1993 (#3960) and 1994 (#20167); (see Dietz and Heide-Jørgensen, 1995). Only good-quality positions (Class 1–3) are shown.

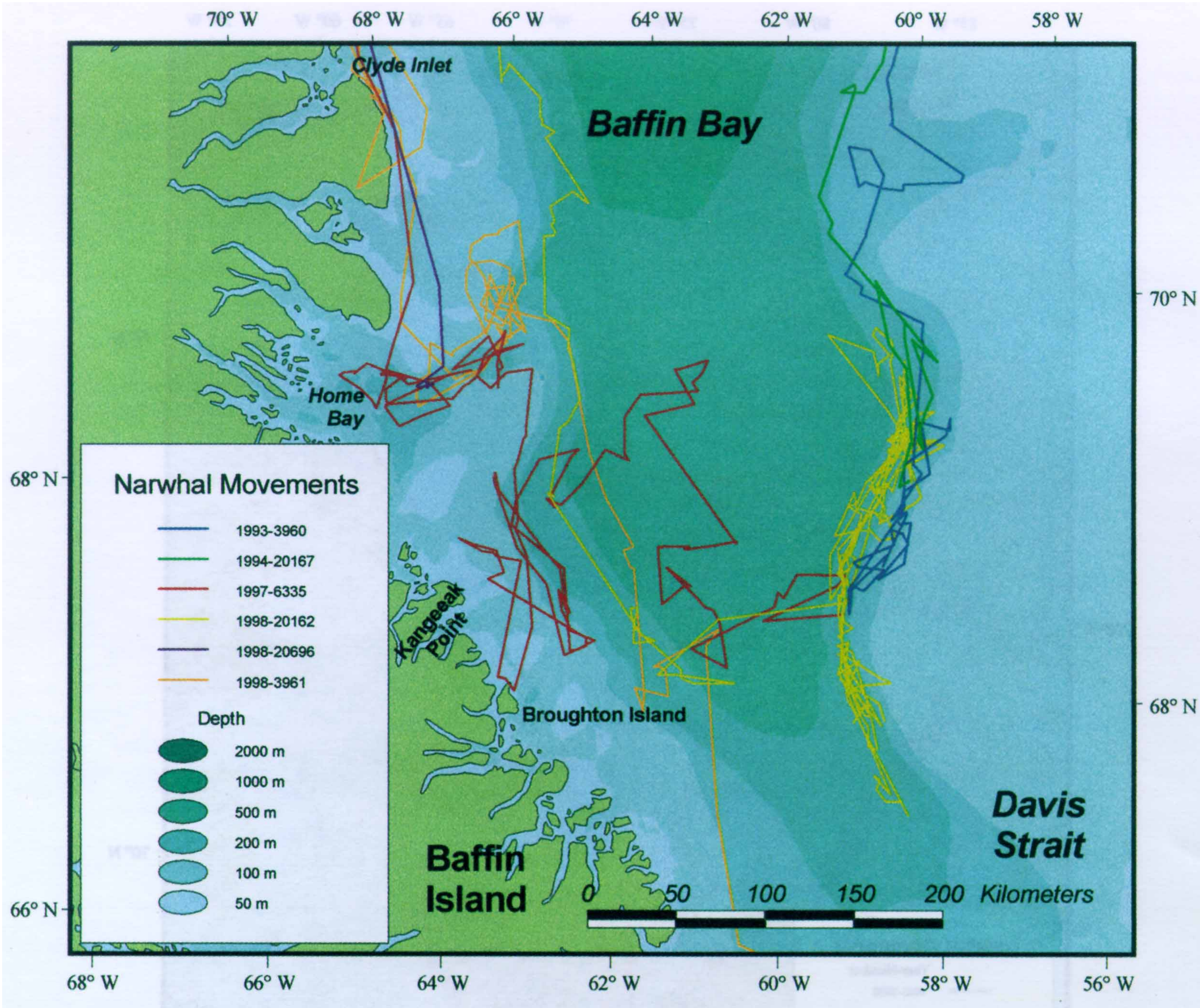

FIG. 7. Close-up of the Davis Strait movements of narwhals from Figure 6, showing their affinity for the continental slope with depths from 500 to 1000 m. See Figure 8 for additional information.

DISCUSSION

Distribution and Movements

Only 8 of the 15 fjords in the Bylot Island fjord complex shown in Table 2 were visited by tagged whales, and 3 of those were visited by only one of the ten whales. In the scientific literature, information on the presence of narwhals in the Bylot Island fjord complexes is limited except for Tremblay Sound, Milne Inlet, and Koluktoo Bay (e.g., Kingsley et al., 1994; Richard et al., 1994). According to Inuit hunters in Pond Inlet, however, narwhals visit all 15 fjords south of Bylot Island except Eskimo Inlet and Stevenson Inlet (Remnant and Thomas, 1992). The deep fjord Tay Sound (to 640 m) has been described as an important summering ground for narwhals (Miller, 1955; J. Mucktar, pers. comm. 1998). Eclipse Sound has also been identified as an important part of the Bylot Island summering area and was also included in several aerial surveys for narwhals (e.g., Kingsley et al., 1994; Richard et al., 1994).

The entrance of Pond Inlet is of importance not only during fall, but also during spring and summer. This area was earlier identified as the area with the largest concentration of narwhal kills by commercial whalers, which constituted about 55% of all the kills from 1820 to 1910 (Ross and MacIver, 1982). These narwhal takes were in precisely the same area as the registered bowhead whale kills, but it is uncertain whether this congruence in distribution reflects similar habitat preferences, or simply indicates that narwhal hunting was opportunistic and followed the itinerary dictated by bowhead occurrence.

In both 1997 and 1998, the tagged whales stayed within the Bylot Island area during the summer, without frequenting Lancaster Sound or the more western summering areas

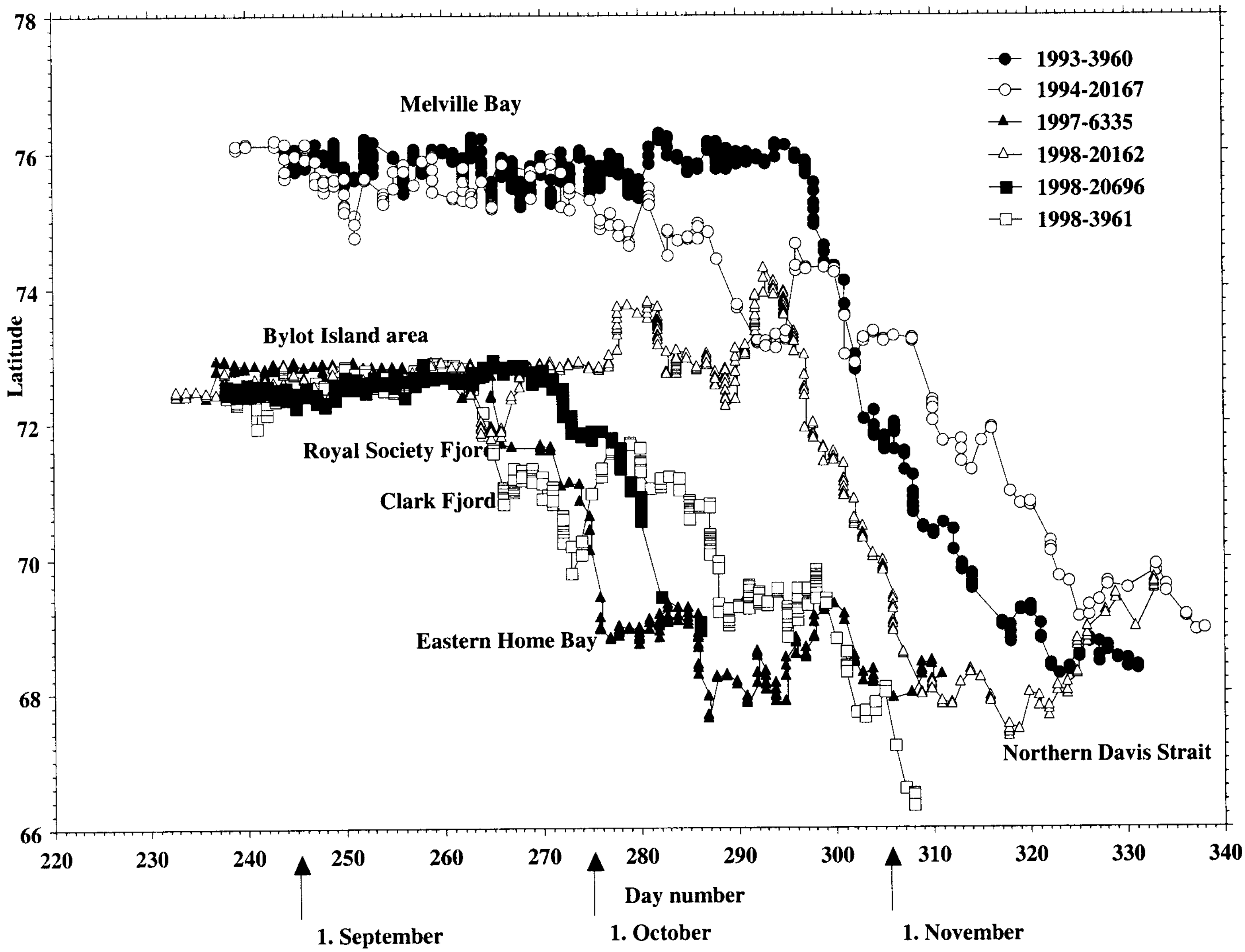

Fig. 8. Comparison of the change in latitudes over time for the narwhals from the Bylot Island area (#6335, #3961, #20162, and #20696) and for two whales from Melville Bay (#20167 and #3960) reported by Dietz and Heide-Jørgensen (1995).

in and around Admiralty Inlet, Prince Regent Inlet, Peel Sound, and the fjords south of Pond Inlet. Five narwhals previously tagged in Tremblay Sound and Milne Inlet also remained within the Bylot Island area without frequenting other summering areas during the monitored period (up to 26 days) in August and early September (Kingsley, 1993; Martin et al., 1994). Inuit hunters indicate that narwhals have a distribution within the Bylot Island area extending from the mouth of Navy Board Inlet to the mouth of Pond Inlet (Remnant and Thomas, 1992). Remnant and Thomas (1992) and Stewart et al. (1995) interviewed hunters from the other Canadian summering areas, but received no reports of summer observations in Lancaster Sound. In those studies, however, the hunters were not specifically asked about the connection between the summering populations. It is therefore not possible to conclude anything from the interview information about the connection between narwhals from the Bylot Island area and those from the other known summering areas around Admiralty Inlet, Resolute, Prince Regent Inlet, or Peel Sound (Remnant and Thomas, 1992; Stewart et al., 1995). Systematic aerial surveys carried out in Lancaster Sound in 1975, 1976, and 1981 likewise resulted in no observations of narwhals there during August and the first part of September (Johnson et al., 1976; Renewable Resources Consulting Services Ltd, 1976; Davis et al., 1978; Smith et al., 1985; Strong, 1988). However, some animals may move between the summering areas.

Even if there is some degree of separation among the summering stocks in and around Admiralty Inlet, Resolute, Prince Regent Inlet, and Peel Sound, most of the whales have to move through Lancaster Sound during their spring and autumn migrations. The exceptions are those narwhals that enter the Bylot Island area through Pond Inlet during the breakup of fast ice. It is possible that narwhals mingle at the entrance to Lancaster Sound in spring, but to what extent this mingling affects their choice of summering habitat and results in genetic exchange is uncertain.

TABLE 3. Eastern Baffin Island fjords, showing depth and length characteristics and visits by narwhals in 1997 and 1998. ? indicates that depth information is not available.

Fjord	Depth Range (m)	Length (km)	Visited by Narwhal No:
Erik Harbour	300	13	None
Coutts Inlet, Nonerth Arm	200–400	50	None
Coutts Inlet, South Arm	150–350	52	None
Buchan Through	500–700	0	6335, 3961, 20696, 20162
Buchan Gulf	200–800	41	6335, 3961, 20696, 20162
Buchan Gulf, Ice Arm	200–300	17	3961
Quernbiter Fiord	150–300	26	None
Cambridge Fiord, RanNonech Arm	100–450	15	None
Cambridge Fiord	200–700	56	None
Royal Society Fiord	150–500	48	6335
Royal Society Fiord, Leaf Bay	100–250	13	None
Paterson Inlet	100–500	52	6335
Tromso Fiord	200–300	39	None
Isbjorn Strait	200–400	20	None
Dexterity Harbour	020–100	19	None
Ratcliffe Arm	200–350	13	None
Dexterity Fiord	100–280	63	None
Scott Inlet	250–700	26	6335, 3961, 20696
Clark Fiord	100–700	54	6335
Gibbs Fiord	200–700	46+	None
Sam Ford Fiord	400–600	28+	6335, 3961, 20696
Eglinton Fiord	100–250	48	None
Clyde Inlet	200–500	83	None
Inugsuin Fiord	100–600	93	None
Isabella Bay	050–500	46	None
McBeth Fiord	150–500	67	None
Home Bay	200–800	52	6335, 3961, 20696
Alexander Bay	100–500	24	None
Itirbilung Fiord	?	43	None
Tingin Fiord	?	43	None
Pitchforth Fiord	?	4	None
Ekalugad Fiord	010–450	56	None
Kangok Fiord	?	28	None
Nudlung Fiord	?	37	None
Nedlukseak Fiord	100–200	37	None
Okoa Bay	200–300	44	None
Narpaing Fiord	?	44	None
Quajon Fiord	?	20	None
Kingnelling Fiord	?	19	None
Maktak Fiord	050–300	31	None
Coronation Fiord	050–300	28	None
Nonerth Pangnirtung Fiord	?	48	None
Canso Channel	100–200	19	None
Kangert Nonerth	?	33	None
Merchants Bay	?	20	None
Durban Harbour	050–100	9	None
Sunneshine Fiord	050–150	33	None
Moonshine Fiord	?	20	None
Totnes Road	?	31	None
Exeter Sound	?	19	None
Clephane Bay	?	35	None
Ignit Fiord	?	22	None
Sakiak Fiord	?	13	None
Exaluin Fiord	?	13	None
Touak Fiord	?	33	None
Kairolik Fiord	?	17	None
Cumberland Sound	?	315	None

Southeast of Pond Inlet, the hunters of Clyde River indicate the summer presence of narwhals in most of the fjords frequented during the autumn migration, including Scott Inlet, Clark Fiord, Gibbs Fiord, Sam Ford Fiord, Eglinton Fiord, Clyde Inlet, Inugsuin Fiord, McBeth Fiord, the Alexander Bay area, and Ekalugad Fiord (Fig. 5). Coutts Inlet and Buchan Bay were not listed by the 34 Pond Inlet residents interviewed as areas traditionally used by narwhals in summer and autumn (Remnant and Thomas, 1992). However, the Coutts Inlet area and farther south towards Clyde River were designated as "new" sighting areas, where narwhals had increased since the mid-1980s. According to J. Mucktar (pers. comm. 1998), both Buchan Gulf and Coutts Inlet are visited by a considerable number of narwhals in the summer. Buchan Gulf was surveyed between 11 and 15 August 1978, and 300 narwhals were

TABLE 4. Performance of satellite transmitters attached to narwhals in Tremblay Sound, NE Canada, in August 1997 and 1998.

Transmitter No./Type	Sex	Date of Instrumentation	Date of Last Good Position (Class 1–3)	Date of Last Uplink	Good Position Obtained (Days)	Transmitter Longevity (Days)	Class 1 Positions < 450 m	Class 2 Positions < 300 m	Class 3 Positions < 150 m	Class 1–3 Positions < 450 m	Class 0 Positions > 1000 m	Number of Uplinks
Backpack transmitters												
1997:												
20682/2. Gen.	Female	August 8	August 10	September 11	0	32	0	0	0	0	46	16165
20691/2. Gen.	Male	August 21	August 26	October 3	5	43	1	0	0	1	6	2875
1998:												
20692/2. Gen.	Female	August 19	October 3	October 5	46	48	1	0	0	1	15	16730
20696/4. Gen.	Female	August 25	October 10	October 13	49	49	276	149	45	470	473	33261
All backpack transmitters					100	172	278	149	45	472	540	69031
Average for backpack transmitters					25	43	70	37	11	118	135	17258
Tusk-mounted transmitters												
1997:												
3963/2. Gen.	Male	August 19	August 24	August 25	5	6	1	0	0	1	3	1078
3964/2. Gen.	Male	August 21	September 5	September 21	15	31	22	6	1	29	49	6995
6335/2. Gen.	Male	August 24	November 7	November 8	75	76	208	20	8	236	391	37029
1998:												
3960/3. Gen.	Male	August 14	August 20	August 21	6	7	15	5	4	24	82	4299
20162/2. Gen.	Male	August 21	January 30 '99	February 2 '99	162	165	362	129	45	536	541	62145
3961/3. Gen.	Male	August 25	November 4	November 4	78	78	291	103	30	424	320	32763
All tusk-mounted transmitters					341	363	899	263	88	1250	1386	144309
Average for tusk-mounted transmitters					57	61	150	44	15	208	231	24052
All transmitters in 1997–98					441	604	1177	412	133	1722	1926	213340
Average for all transmitters in 1997–98					44	60	118	41	13	172	193	21334

estimated to have been present there (Koski and Davis, 1994). A large group of narwhals was seen going up Coutts Inlet and moving along the glacier fronts in late August 1984 (R.R. Reeves, pers. comm. 2000). Haller (1967) stated that narwhals were common from Home Bay north to the Clyde River area, where they appeared from summer to early fall. Farther south, the Broughton Island hunters provided information on the summer presence of narwhals in Nudlung Fiord, the mouth of Nedlukseak Fiord, and Merchants Bay, all areas that were not visited by our tagged whales during autumn (Remnant and Thomas, 1992). On present evidence, we can not dismiss the possibility that the narwhals distributed during summer all the way from Peel Sound eastward and southward to Merchants Bay represent one large and widely distributed population. However, it is likely that there are several or many smaller population units, which, even if they mingle during other times of the year, return to specific inlets, embayments, or fjord complexes during the summer.

Exchange is less likely with other summering populations, such as those in Foxe Basin, because of the significant physical land barriers (Mansfield et al., 1975). In early papers, Sergeant (1979a, b) talks of a large northern narwhal component in the Lancaster Sound area and small southern component inhabiting northern Hudson Bay, but it is uncertain whether exchange may occur through Fury and Hecla Strait during summer and whether the segregation persists throughout winter. Small numbers of narwhals may, however, winter in Hudson Strait (McLaren and Davis, 1981; Strong, 1988).

Contact with the Greenland summer populations in Melville Bay and Inglefield Bredning, or with possible populations in the Nares Strait and its associated fjord complexes, is also uncertain. But since not one of the 24 narwhals tagged so far in Canada and Greenland has shown summer movements across country borders, such summer exchange seems unlikely (Kingsley, 1993; Martin et al., 1994; Dietz and Heide-Jørgensen, 1995). Additional tagging and increased tag longevity will certainly shed additional light on these questions.

All evidence points to a southward migration along the east coast of Baffin Island in late September (e.g., Strong, 1988; Remnant and Thomas, 1992). Whales in our study began moving south from the mouth of Pond Inlet around 22–29 September, which is consistent with the observations by Johnson et al. (1976) of eastward movements through Lancaster Sound around 26–28 September. Davis (1980, cited in Strong, 1988) claimed that the autumn migration starts in September or October. The timing of the southward migration at Pond Inlet is also in good accordance with the Inuit information from this area (Remnant and Thomas, 1992). Koski and Davis (1994) reported departure periods from Admiralty Inlet to be 23–27 September in 1978 and 18–21 September in 1979. Many of the narwhals were reported to follow the coast of Baffin Island southeastward, but some continued moving offshore from SE Devon Island towards Baffin Bay (Koski and Davis, 1994).

Most of the areas visited by the tracked narwhals during their southward migration have also been described as summering areas. For example, Clyde River and Broughton Island residents reported the summer presence of narwhals in all fjords between Scott Island and Home Bay, as well as in the three fjord complexes west of Home Bay and in Merchants Bay south of Broughton Island (Remnant and Thomas, 1992). Wenzel (1991) states that narwhals may appear at any time from mid-August through September around Clyde River. As borders between spring, summer, and autumn are not well defined, at least some of the summer observations may represent late spring or early autumn observations. For example, Home Bay was described as a summering area by Koski and Davis (1994), who surveyed it on 18 September 1979, but this observation could represent an early portion of the southward migration. This "population" was estimated to be more than 95 animals (Koski and Davis, 1994).

According to Koski and Davis (1994), almost 5000 narwhals passed Cape Adair between 29 September and 2 October 1978. This timing agrees well with that of our four tagged narwhals as they moved southward along Baffin Island in 1997–98.

The few autumn kills of narwhal by commercial whalers along the eastern Baffin Island coast might reflect the fact that narwhals migrate southward somewhat later than bowheads (and thus, after the whalers have passed). According to Ross and MacIver (1982), the narwhals appeared after the whalers had cleared Cape Dyer.

The most southern position of our tagged narwhals was just south of Cape Dyer at about 66˚ N on 6 November 1998. This is consistent with the claim of Strong (1988) that narwhals are seldom seen south of 65˚ N in the Davis Strait.

The narwhals from Canada showed a preference for deep fjords and for the continental slope (1000–1500 m) along eastern Baffin Island. This same preference was shown by the narwhals from Melville Bay that moved south along the continental slope west of Disko Island (Dietz and Heide-Jørgensen, 1995). We find it remarkable that narwhals are so strongly linked to the narrow bathymetry corridors in Baffin Bay and Davis Strait, which constitute only a small proportion of the total water volume available between Canada and Greenland. A similar preference for a well-defined section (350–975 m isobath) of the continental slope was documented for Risso's dolphin (*Grampus griseus*), another cephalopod predator inhabiting the northern Gulf of Mexico (Baumgartner, 1997). This area constituted only 2% of the surface area of the entire gulf. It was argued that such shelf edges and upper continental slopes are frequently sites for increased biological activity. The upwelling in such areas introduces nutrients from deeper shelf or slope waters into the euphotic zone, stimulating increased primary production and thus supporting secondary production as well. Species with such a specialized distribution, including the narwhal, are particularly susceptible. Disturbance or intense fishing within these areas may force the whales to deeper and less favourable areas, which may negatively affect their foraging. Information on such critical areas can be used in their management and protection to avoid negative impacts from human activities.

The preferred wintering ground observed in this study, with its distinct pattern relative to the bathymetry, has been shown previously only for a few animals tracked from Melville Bay (Dietz and Heide-Jørgensen, 1995). Ours was the first study to document that populations summering in Canada and Greenland share a common wintering area. Our winter observations did not extend beyond 30 January and were restricted to the continental slope between 67˚48′ N and 69˚36′ N.

Few reliable winter observations of narwhals in Baffin Bay and Davis Strait have been published, but they suggest that wintering occurs in the offshore pack ice with a southern limit from 65˚ to 70˚ N. One published winter record is from the account of the North Polar Expedition during the southward drift of the U.S. *Polaris* from northern Baffin Bay to the Labrador Sea between October 1872 and April 1873 (Davis, 1876). Narwhals were seen on 7 February as the ship drifted south of 68˚50′ N and then again on March 14 and 15 in latitudes from 64˚32′ to 64˚19′N, opposite the mouth of Cumberland Sound. No longitudes were given, as chronometers were not available at that time. However, the east coast of Baffin Island, probably Cape Dyer, was visible from the ship on 19 February, as it passed the Arctic Circle on approximately 66˚30′N (Davis, 1876). Turl (1987) found large numbers of narwhals in the close pack ice in west and central Davis Strait (between 66˚30′ and 68˚15′N) in February–March 1976.

Information from aerial surveys in the late winter and early spring (mid-March to late May) suggests that narwhals winter throughout the close pack ice in Davis Strait and southern Baffin Bay down to 68˚ N, without any clear concentration areas (Heide-Jørgensen et al., 1993; Koski and Davis, 1994).

It is unclear whether this more scattered distribution of narwhals in late winter and early spring represents a reinvasion into the dense pack ice from the more southern winter quarter, or whether other narwhal stocks so far not tracked are using these areas outside the continental slopes as their wintering quarters. Tagging of other summering stocks with transmitters of increased longevity should help to answer these questions.

Stock Identity

The narwhals tracked in this study were almost stationary in the deepwater area of Eclipse Sound and adjacent fjords for most of August. They moved east to the deep areas in Pond Inlet in early September and stayed there until their southward migration began in late September. From late September, they moved south along Baffin Island and visited a few fjords, possibly selected for their depth, productivity, or glacial activity. They made short stays in these fjords but continued their southward heading towards Davis Strait. The only exception was the individual that, after leaving Pond Inlet, first moved north to an abyss east of Bylot Island then headed south in early October along the continental slope. All of the whales moved east when they reached the southern end of the deep trough in Baffin Bay. They wintered on the eastern slope of the deep trough, together with narwhals that summered on the Greenland side of Baffin Bay.

With the ten animals tracked, we could not document an exchange with narwhals on other summering grounds (e.g., Admiralty Inlet or the eastern coast of Baffin Island) during August. Such an exchange may take place for some animals, in some years, earlier in the season, or between years (i.e., whales could visit different summering grounds in different years). Within the Bylot Island area, our whales seemed to be moving freely among the fjords known to be inhabited by narwhals in summer, so they apparently belong to a common stock. This may also be true of the narwhals in Pond Inlet in September.

During the summering period and the autumn southbound migration, the narwhals visited only 16% of the available fjords. The southbound migrating narwhals used a rather narrow corridor and a specific timing, either traveling along the coast between the few selected fjords or taking an offshore route along the slope of the Baffin Island continental shelf in water 1000–1500 m deep. The tagged animals did not visit the deepest part of Baffin Bay (> 2000 m deep) within the monitored period.

When on the wintering grounds, the narwhals made shorter trips within a restricted area along the north-south oriented slope of the Greenland continental shelf, the same area used by narwhals from Greenland.

These data suggest that some population structure may persist among Baffin Bay narwhals, with specific habitats for summering and wintering grounds and migrations that are well defined both spatially and temporally. In view of these restricted movements and the limited home range during stationary periods, the impact of harvest practices, competing fisheries, and habitat changes should be reviewed.

The mating season of narwhals is uncertain, but likely falls between May and July (Dietz et al., 1994). We have so far no tracking data from that period, but catch and survey data suggest that the narwhals are either still on their wintering grounds or moving towards their summering areas in those months. Large concentrations of narwhals are known to occur at fast-ice edges in both Greenland and Canada, just before the whales move into the summering areas, and this may allow opportunities for mating by animals from different areas. No thorough attempt has been made to investigate genetic differences between whales that use different summering habitats in Canada. Palsbøll et al. (1997) examined 427 narwhals, sampled in five regions, for mtDNA, but only 29 of these were from Canadian waters. The low nucleotide diversity and low number of Canadian samples did not permit internal Canadian comparisons, and no differences were found between the pooled Canadian sample and samples from the Avanersuaq district. However, the homogeneity tests identified five "entities": northern Baffin Bay, Melville Bay and Upernavik, Uummannaq, the 1994 "Sassat" at Kitsissuarsuit, and eastern Greenland (Palsbøll et al., 1997).

Independent of the question of genetic exchange, it is also important to know whether the whales return to the same summering grounds year after year, whether the site fidelity is equally strong for both sexes, and whether narwhals have the ability to re-inhabit localities that are locally depleted.

Performance of the Transmitters

For backpack transmitters, the average attachment period of 43 days for the two years was slightly longer than that obtained from five backpacks deployed on narwhals in Greenland waters in 1993–94, for which the average longevity was 38 days (range: 25–44 days; Dietz and Heide-Jørgensen, 1995). Two first-generation transmitters and three second-generation transmitters were used in the Greenland study. No statistical difference (unpaired t-test) on longevity, location classes, or number of uplinks could be found between first- and second-generation transmitters during the four years of investigation. The fourth-generation transmitter used in the present study certainly showed a considerable improvement on all measured categories; however, with a single unit, sample size was inadequate for a meaningful statistical comparison to previous transmitter generations.

The backpack transmitter longevity of the present study was longer than that for similar mountings on narwhals in Tremblay Sound in 1991 and at Svalbard in 1998 (Martin et al., 1994; Lydersen et al., 1999), but shorter than that for transmitters mounted on belugas (Richard et al., 1998, 2001; Lydersen et al., 1999). The larger dorsal ridge of the belugas—and possibly a stronger epidermis—can explain this difference.

For tusk-mounted transmitters, the average number of days providing good positions (57) in the Canadian study was similar to the average from the Greenland study (64 days; Dietz and Heide-Jørgensen, 1995). Only the transmitter on #20162 in the Canadian study lasted longer (162 days) than the longest-lasting tusk transmitters in the Greenland study, which provided good-quality positions for 87 days in 1993 and 100 days in 1994 (Dietz and Heide-Jørgensen, 1995). No significant differences (unpaired T-test) were found in the longevity, location classes, or number of uplinks between the first tusk-mounted generation used in Melville Bay in 1993 and generations 2 and 3, used in Melville Bay in 1994 and in Tremblay Sound in 1997 and 1998. This result was due to the small total number (N = 10) in the comparison and to three short-performing transmitters in Tremblay Sound in 1997 and 1998.

Three tusk-mounted units in the Canadian study transmitted for 6, 7, and 31 days: less time than the shortest-performing tusk-mounted transmitter (32 days) in the Greenland study. It remains uncertain why these three Canadian transmitters stopped prematurely. Three of the four transmitters mounted in Greenland terminated because of battery drainage, which was monitored from status messages monitored every 15th uplink (Dietz and Heide-Jørgensen, 1995). None of the transmitters mounted on narwhals in Canada terminated because of battery failure.

In general, the narwhal tusk must be regarded as an ideal substratum for attachment compared to skin penetration. Brear et al. (1993) and Currey et al. (1994), who analyzed the mechanical properties of the narwhal tusk in detail, concluded that the tusk tissues are of low stiffness but very tough, suiting the tusk for loading on impact. The longest-lasting transmitter was on a male narwhal tagged during the Dietz and Heide-Jorgensen study. This transmitter provided scattered uplinks for more than 18 months, indicating that tusks have the potential for long-term attachment. However, the short performances of tusk-mounted transmitters indicate that tusk surface structure and variability of the stainless steel band tension may also produce short-term data series with even shorter longevity than the backpack transmitters.

The termination during winter of the longest-lasting tusk transmitters is likely to be caused by the severe ice conditions that narwhals inhabit at this time of the year. One possibility could be breakage of the antennae, as found on a retrieved walrus transmitter in 2000 in East Greenland (E. Born, pers. comm. 2000). To what extent the ice may cause loosening of the attachment or malfunction of the electronics still remains unknown.

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REFERENCES

BAUMGARTNER, M.F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. Marine Mammal Science 13(4): 614–638.

BORN, E.W., HEIDE-JØRGENSEN, M.P., LARSEN, F., and MARTIN, A.R. 1994. Abundance and stock composition of narwhals (*Monodon monoceros*) in Inglefield Bredning (NW Greenland). Meddelelser om Grønland, Bioscience 39:51–68.

BREAR, K., CURREY, J.D., KINGSLEY, M.C.S., and RAMSAY, M. 1993. The mechanical design of the tusk of the narwhal (*Monodon monoceros*: Cetacea). Journal of Zoology, London 230:411–423.

CURREY, J.D., BREAR, K., and ZIOUPOS, P. 1994. Dependence of mechanical properties on fibre angle in narwhal tusk, a highly oriented biological composite. Journal of Biomechanics 27(7):885–897.

DAVIS, C.H. 1876. Narrative of the North Polar Expedition (U.S. Ship *Polaris*). Edited by G.M. Robeson. Washington, D.C.: U.S. Government Printing Office. 696 p.

DAVIS, R.A., RICHARDSON, W.J., JOHNSON, S.R., and RENAUD, W.E. 1978. Status of the Lancaster Sound narwhal population in 1976. Report to the International Whaling Commission 28. SC/29/Doc 22:209–215.

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. Canadian Journal of Zoology 73:2106–2119.

DIETZ, R., HEIDE-JØRGENSEN, M.P., BORN, E.W., and GLAHDER, C. 1994. Occurrence of narwhals (*Monodon monceros*) and white whales (*Delphinapterus leucas*) in West Greenland. Meddelelser om Grønland, Bioscience 39:69–86.

GOULET, A.-M., HAMMILL, M.O., and BARRETTE, C. 1999. Quality of satellite telemetry locations of gray seals (*Halichoerus grypus*). Marine Mammal Science 15(2):589–594.

HALLER. A.A.1967. Baffin Island – East Coast: An area economic survey. Ottawa: Industrial Division, Department of Indian Affairs and Northern Development.

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. United States Department of the Interior, Fish and Wildlife Service, Fish and Wildlife Technical Report 30. 52 p.

HEIDE-JØRGENSEN, M.P., and DIETZ, R. 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behaviour in Baffin Bay. Canadian Journal of Zoology 73(11):2120–2132.

HEIDE-JØRGENSEN, M.P., LASSEN, H., TEILMANN, J., and DAVIS, R.A. 1993. An index of the relative abundance of wintering belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, of West Greenland. Canadian Journal of Fisheries and Aquatic Sciences 50(11):2323–2335.

JOHNSON, S.R., RENAUD, W.E., DAVIS, R.A., and RICHARDSON, W.J. 1976. Marine mammals recorded during aerial surveys of birds in eastern Lancaster Sound, 1976. Toronto, Ontario: LGL Limited. 180 p.

KINGSLEY, M.C.S. 1993. Satellite radio tagging of narwhal in Koluktoo Bay, August 1993. Technical Report from Department of Fisheries and Oceans, Mont-Joli, Quebec, Canada. 6 p.

KINGSLEY, M.C.S., and RAMSAY, M.A. 1988. The spiral in the tusk of the narwhal. Arctic 41(3):236–238.

KINGSLEY, M.C.S., CLEATOR, H.J., and RAMSAY, M.A. 1994. Summer distribution and movements of narwhals (*Monodon monoceros*) in Eclipse Sound and adjacent waters, North Baffin Island, N.W.T. Meddelelser om Grønland, Bioscience 39: 163–174.

KOSKI, W.R., and DAVIS, R.A. 1994. Distribution and numbers of narwhals (*Monodon monoceros*) in Baffin Bay and Davis Strait. Meddelelser om Grønland, Bioscience 39:15–40.

LYDERSEN, C., KOVACS, K., and GJERTZ, I. 1999. Studies of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in Svalbard. NAMMCO SC/7/BN/24. 27 p.

MANSFIELD, A.W., SMITH, T.G., and BECK, B. 1975. The narwhal, *Monodon monoceros*, in the eastern Canadian Waters. Journal of Fisheries Research Board Canada 32:1041–1046.

MARTIN, A.R., KINGSLEY, M.C.S., and RAMSAY, M.A. 1994. Diving behaviour of narwhals on their summer grounds. Canadian Journal of Zoology 72:118–125.

McCONNELL, B.J., CHAMBERS, C., NICHOLAS, K.S., and FEDAK, M.A. 1992. Satellite tracking of gray seals (*Halichoerus grypus*). Journal of Zoology 226:271–282.

McLAREN, P.L., and DAVIS, R.A. 1981. Distribution of wintering marine mammals in southern Baffin Bay and northern Davis Strait, March 1981. Unpubl. report by LGL Limited for the Arctic Pilot Project, Calgary, Alberta. 85 p.

MILLER, R.S. 1955. A survey of the mammals of Bylot Island, Northwest Territories. Arctic 8(3):167–176.

PALSBØLL, P., HEIDE-JØRGENSEN, M.P., and DIETZ, R. 1997. Genetic studies of narwhals, *Monodon monoceros*, from West and East Greenland. Heredity 78:284–292.

REMNANT, R.A., and THOMAS, M.L. 1992. Inuit traditional knowledge of the distribution and biology of High Arctic narwhal and beluga. North/South Consultants Inc., 202-1475 Chevrier Blvd, Winnipeg, Manitoba R3T 1Y7, Canada. 96 p.

RENEWABLE RESOURCES CONSULTING SERVICES LTD. 1976. Aerial surveys of marine mammals of Lancaster Sound, 1975–1976. Unpubl. report for Norland Petroleum Ltd., Calgary. 100 p.

RICHARD P., WEAVER, P., DUECK, L., and BARBER, D. 1994. Distribution and numbers of Canadian High Arctic narwhals (*Monodon monoceros*) in August 1984. Meddelelser om Grønland, Bioscience 39:41–50.

RICHARD, P.R., HEIDE-JØRGENSEN, M.P., and ST. AUBIN, D. 1998. Fall movements of belugas (*Delphinapterus leucas*) with satellite-linked transmitters in Lancaster Sound, Jones Sound, and Northern Baffin Bay. Arctic 51(1):5–16.

RICHARD P.R., HEIDE-JØRGENSEN, M.P., ORR, J.R., DIETZ, R., and SMITH, T.G. 2001. Summer and autumn movements and habitat use by belugas in the Canadian High Arctic and adjacent areas. Arctic 54(3):207–222.

ROSS, W.G., and MacIVER, A. 1982. Distribution of the kills of bowhead whales and other mammals by Davis Strait whalers, 1829 to 1910. Technical Report for Arctic Pilot Project. Unpubl. report available from the Dept. of Geography, Bishop's University, Lennoxville, Quebec J1M 1Z7. 75 p.

SEMPELS, J.-M. 1982. Coastlines of the eastern Arctic. Arctic 35(1):170–179.

SERGEANT, D.E. 1979a. Seasonal movements and numbers of cetaceans summering in Lancaster Sound, Arctic Canada. International Whaling Commission, Committee on Small Cetaceans Working Paper No. 11. 20 p.

———. 1979b. Summary of knowledge on populations of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros* L.) in Canadian waters. International Whaling Commission, Committee on Small Cetaceans Working Paper No. 8. 6 p.

SERVICE ARGOS INC. 1989. Guide to ARGOS system, September 1989. Toulouse, France: CLS ARGOS.

SMITH, T.G., HAMMILL, M.O., BURRAGE, D.J., and SLENO, G.A. 1985. Distribution and abundance of belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, in the Canadian High Arctic. Canadian Journal of Fisheries and Aquatic Sciences 42:676–684.

STEWART, B.S., LEATHERWOOD, S., YOCHEM, P.K., and HEIDE-JØRGENSEN, M.P. 1989. Harbour seal tracking and telemetry by satellite. Marine Mammal Science 5:361–375.

STEWART, D.B, AKEEAGOK, A., AMARUALIK, R., PANIPAKUTSUK, S., and TAQTU, A. 1995. Local knowledge of beluga and narwhal from four communities in the Arctic. Canadian Technical Report of Fisheries and Aquatic Sciences 2065. 48 p.

STRONG, J.T. 1988. Status of the narwhal, *Monodon monoceros*, in Canada. Canadian Field-Naturalist 102(2):391–398.

THOMPSON, D.W. 1963. On growth and form. 2nd ed. Cambridge: Cambridge University Press. 1097 p.

TURL, C.W. 1987. Winter sightings of marine mammals in Arctic pack ice. Arctic 40(3):219–220.

WENZEL, G. 1991. Animal rights, human rights: Ecology, economy and ideology in the Canadian Arctic. Toronto: University of Toronto Press. 206 p.