Distribution and numbers of narwhals (*Monodon monoceros*) in Baffin Bay and Davis Strait

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Aerial surveys were conducted over Baffin Bay during May-October 1978–79 and off West Greenland and over southern Baffin Bay, Davis Strait and Hudson Strait during March 1981–82. Narwhals (*Monodon monoceros*) were dispersed throughout the pack ice in northern Davis Strait and Baffin Bay during late winter and spring and moved into nearshore areas in and adjacent to Lancaster Sound during late June and July. Important summering areas were identified in Buchan Gulf, Eclipse Sound, Admiralty Inlet, Prince Regent Inlet and Peel Sound, and possibly in Smith Sound and Home Bay, but there was considerable variation in the numbers of narwhals entering these areas each year. Narwhals remained in nearshore areas until late September or early October when they moved south in advance of and with the newly-forming pack ice. During autumn narwhals tended to migrate in large herds, moving both along the coast of Baffin Island and through offshore waters.

Our best estimates of the size of the narwhal population have come from surveys conducted in late spring when the whales are widely dispersed among the offshore pack ice. An estimated 34 363 (± SE 8282) narwhals were present in offshore areas of Baffin Bay that were surveyed four times in May-July 1979. This late spring estimate included narwhals that later summered on both the east and west sides of Baffin Bay and Davis Strait, but excluded animals that summered in northern Hudson Bay. It does not include animals outside the survey area nor is it corrected to account for animals below the surface.

Our aerial survey data indicate that 7.8–9.0% of narwhals in summering areas were calves. An estimate of calving rate is 0.29 calves/adult female/year based on sightings of 1-month-old calves without considering mortality between birth and the survey date. The mortality rate of calves from 1 month to 13 months of age is estimated as approximately 17%.

Key Words:
Narwhal, *Monodon monoceros*, distribution, movements, numbers, age, sex, reproduction, calf mortality.

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Introduction

The narwhal (*Monodon monoceros*) is an ice-associated cetacean that frequents dense offshore pack ice for 8–10 months of the year. Because the narwhal is essentially inaccessible to humans for much of the year, most information on the species has come from coastal observations during the summer open-water period. This has led to a fairly biased understanding of the distribution, movements and biology of the species. During the late 1970s and early 1980s, we conducted large-scale aerial survey programs in the Canadian High Arctic, Baffin Bay, and Davis Strait in conjunction with proposed offshore oil and gas exploration, production, and transportation proposals. These surveys provided coverage of the offshore pack ice frequented by narwhals during the winter and during spring migration. The surveys also included the open-water season and the onset of the fall migration of narwhals. The results of these surveys are presented here to provide an understanding of the distribution, annual movements, size, age and sex composition, and life history of the Baffin Bay narwhal population. This population includes all narwhals that summer in or adjacent to Baffin Bay and Lancaster Sound. It excludes whales that

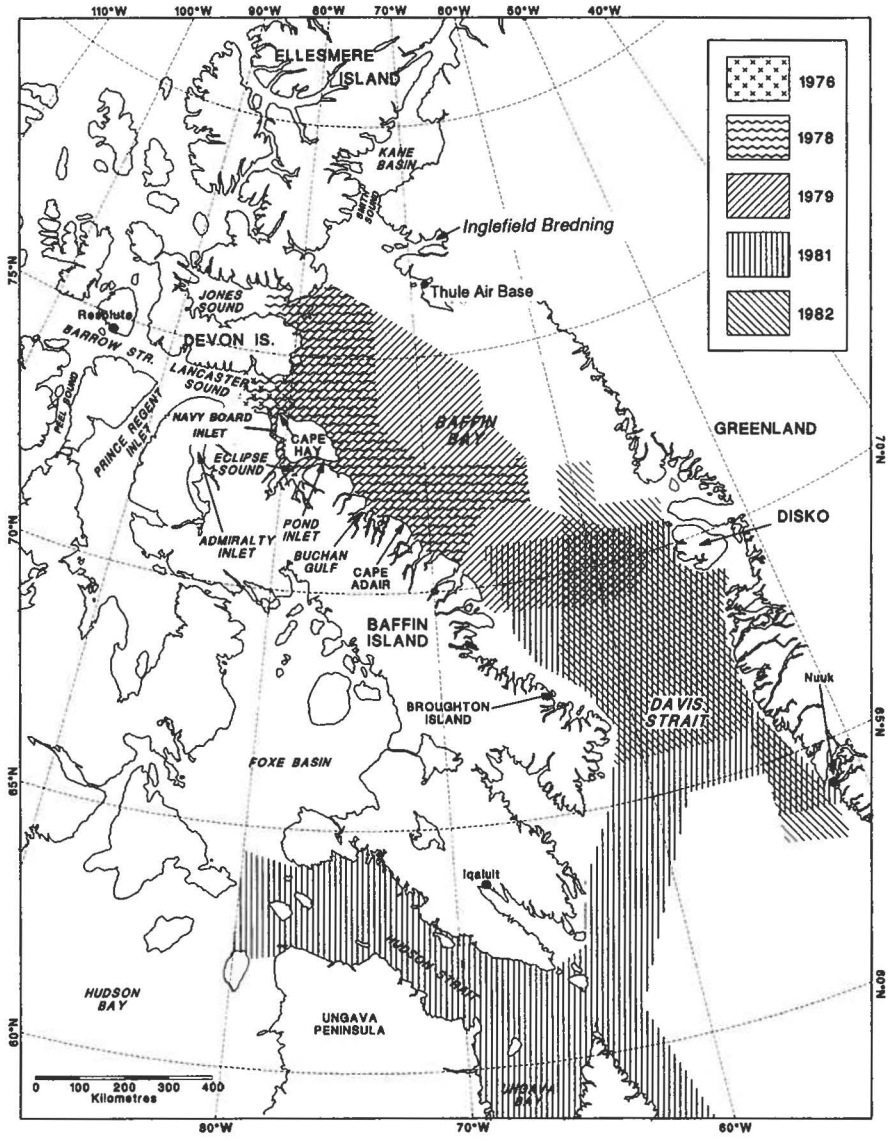


Fig. 1. Map of Baffin Bay, Davis Strait and surrounding areas showing the areas covered during systematic aerial surveys, 1976–1982. See text for other areas that were surveyed on one to a few occasions, 1975–1979.

summer in northern Hudson Bay and that probably winter in eastern Hudson Strait (Richard 1991).

The results from three major, and several smaller, aerial survey projects are reported in this paper. The first was a 5-month (May-September) study of the eastern half of Lancaster Sound conducted in 1976 for Norlands Petroleums Limited, Calgary, as part of an assessment of the potential effects of offshore hydrocarbon exploration in the area (Fig. 1). The second major project was the Eastern Arctic Marine Environmental Studies (EAMES) program conducted in Lancaster Sound and adjacent channels, Jones Sound and Baffin Bay in the May to early October periods of 1978 and 1979. EAMES was a multi- and inter-disciplinary study initiated by the Canada Department of Indian Affairs and Northern Development, Ottawa, and managed and funded by Petro-Canada Explorations, Inc., Calgary (see Sutterlin & Snow 1982 for a description). The third major survey project was conducted in March 1981 and 1982 to document the winter distribution of marine mammals in Davis Strait and southern Baffin Bay to facilitate selection of routes for year-round icebreaking liquid natural gas (LNG) carriers proposed by the Arctic Pilot Project, Calgary. Ancillary winter studies in March 1981 were conducted in southwestern Davis Strait and the northern Labrador Sea (funded by Petro-Canada Explorations, Inc.) and in Hudson Strait and northern Hudson Bay (funded by Canada Department of Fisheries and Oceans). Additional open-water surveys of channels in the central Canadian Arctic were conducted in 1976–77 for the Polar Gas Project.

Table 1. Survey effort and number of narwhals recorded on-transect[a] in Lancaster Sound, Baffin Bay and Davis Strait, 1978–1982.

Survey period	All coastal and ice-edge areas			All nearshore areas			Offshore Lancaster Sound			Offshore Baffin Bay and Davis Strait		
	Area surveyed (km^2)	On-transect[a] narwhals	Density (no./km^2)	Area surveyed (km^2)	On-transect narwhals	Density (no./km^2)	Area surveyed (km^2)	On-transect narwhals	Density (no./km^2)	Area surveyed (km^2)	On-transect narwhals	Density (no./km^2)
1978												
May and Jun	3638	2115	0.58	2050	312	0.15	3767	251	0.07	3903	231	0.06
Jul to mid-Aug	2169	4348	2.00	1047	353	0.34	1619	198	0.12	2120	116	0.05
mid-Aug to mid-Sep	2005	81	0.04	1054	3	0.00	808	0	0.00	1277	0	0.00
mid-Sep to Oct	1817	1159	0.64	1196	419	0.35	685	110	0.16	1187	105	0.09
1979												
May and Jun	2604	1279	0.49	54	6	0.11	2846	143	0.05	4900	561	0.11
end Jun to end Jul	1189	1355	1.14	208	146	0.70	1032	170	0.16	1377	104	0.08
Sep to Oct	9127	7969	0.87	1025	647	0.96	2231	257	0.12	1580	11	0.01
1981												
Mar – heavy pack ice										10416	246	0.024
Mar – open pack ice										3604	38	0.011
1982												
Mar – heavy pack ice										4858	144	0.030
Mar – open pack ice										11024	168	0.015

[a] Excludes narwhals seen outside the transect strip.

Materials and methods

The data presented here came primarily from the extensive aerial survey programs conducted in 1978–79 and 1981–82. These data were supplemented with observations from coastal vantage points in summer and autumn. We also conducted surveys of Lancaster Sound in 1976; results of these surveys are summarized in Davis *et al.* (1978) but some previously unpublished 1976 data are included here.

Survey coverage

Fig. 1 shows the area included in systematic surveys each year and Table 1 gives the survey coverage (km^2) in coastal/ice-edge, nearshore and offshore waters each year. Coastal/ice-edge transects were flown parallel to and centred 200 or 400–600 m seaward of the coast/ice edge when the survey altitude was 45 or 90 m above sea level (a.s.l), respectively. Nearshore transects were flown parallel to and centered 1400 or 1600 m seaward of the coast/ice edge. Offshore transects were flown along lines of latitude or longitude without regard for the presence or absence of open-water leads. The survey effort is summarized for periods when narwhals were present in the offshore pack ice (March to June), moving into summering areas (July to mid-August), present in summering areas (mid-August to mid-September), and moving out of summering areas (mid-September to October).

In 1978 and 1979 the transects were repeatedly surveyed at 7–10 day intervals from May to October; the systematic coverage of offshore areas was more extensive during May-June than during July-October. In addition to the systematic coverage of areas indicated in Fig. 1, we surveyed the coasts of Ellesmere Island and Greenland from 76°30' N latitude to southern Kane Basin on 31 May, 1 June and 5 July 1978 (see Figs 6 and 7, later); narwhal summering areas in Prince Regent Inlet, Admiralty Inlet, Eclipse Sound, Jones Sound and Lancaster Sound during July-September of 1978 and 1979; and the coast of eastern Baffin Island from Pond Inlet to Broughton Island on 13 and 18 September 1979. Most areas surveyed in 1981 and 1982 were surveyed once, but the open pack ice south of Disko was surveyed twice in 1982.

Aerial survey procedures

All surveys were conducted from a DeHavilland Twin Otter equipped with standard windows, a VLF navigation system, radar altimeter, and (during most surveys) a colour radar. The VLF navigation system determined aircraft position and was essential for surveys in offshore locations. The radar altimeter helped to maintain a constant altitude; this was important to estimate the distances of narwhal sightings from the aircraft. The radar helped to maintain the position of the aircraft relative to ice edges or coastlines.

Either two or three observers were present during each survey; one observer sat in the co-pilot's seat (right front) and the second observer sat in the second seat behind the pilot on the left. A third observer was occasionally present in the second seat behind the co-pilot's seat. Observ-

ers dictated information for each sighting into portable tape recorders. For each sighting, the species, total number of individuals, number of individuals in each group, behaviour, direction of movement, general and specific habitat, relative age, sex, distance from the centre of the transect, and any other relevant comments were recorded.

All transects were divided into two-minute intervals using a timing device that was audible to observers. Data were recorded, mapped and summarized by two-minute intervals (5.3–9.3 km segments, depending on the speed of the aircraft).

1978–79

The majority of surveys conducted during 1978–79 were designed to document distributions of both marine birds and marine mammals. Because many birds could not be seen or identified from altitudes >50 m a.s.l., most coastal and some offshore surveys were flown at 45 m a.s.l. and ground speeds of 160–185 km/h. However, surveys that were primarily for marine mammals were conducted at 90 m a.s.l. and 220–260 km/h (pack-ice surveys) or 150 m a.s.l. and 200–280 km/h. The primary search area (transect width) was 200, 400 or 800 m on either side of the aircraft during surveys conducted at 45, 90 or 150 m a.s.l., respectively. A line directly below the aircraft was the inner boundary of the transect. The front observer recorded animals that were directly below the aircraft and therefore in a blind spot for the rear observer. Sightings beyond the transect width were recorded when possible.

During low-level surveys conducted in the springs of 1978 and 1979, particularly along the Lancaster Sound ice edge during late June to mid-July, extremely large numbers of marine birds and mammals of many species were encountered. Counts of narwhals along coasts and ice edges during these periods may underestimate considerably the actual numbers present; counts in nearshore and offshore areas better reflect the actual numbers present because observers were not inundated by observations of other species.

1981–82

All 1981–82 surveys were conducted at 150 m a.s.l. and 200–240 km/h; the primary search area included strips 800 m wide on either side of the aircraft, for a transect width of 1.6 km.

In 1981, at the same time as the above surveys were being conducted, part of northern Hudson Bay, Hudson Strait and the northeast coast of Labrador were surveyed. The survey methods were identical to those described for Davis Strait and Baffin Bay and the coverage is shown in Fig. 1. The data on white whales (*Delphinapterus leucas*) in Hudson Strait were reported by Finley *et al.* (1982). Data for white whales in Davis Strait are reported in Heide-Jørgensen *et al.* (1993). Results for narwhals for the entire area are reported here.

Shore-based observations

Observations of migrating marine mammals were made from a 209 m a.s.l. observation post located at Cape Adair, NE Baffin Island (Fig. 1). Observations were made from 13 September to 7 October 1978 (260 h) and from 20 September to 16 October 1979 (277 h). Observations were continuous during daylight hours, except during periods of poor visibility. Binoculars, spotting telescopes and (1979 only) a surveyor's theodolite were used to facilitate spotting, identification and counting of marine mammals.

We conducted observations of spring-migrating narwhals from a cliff 9 km west of Cape Hay on northern Bylot Island (Fig. 1) from 28 July to 9 August 1978 and Greendale & Kerr (1979) attempted observations from the same location from 25 June to 2 August 1979. However, in 1979 persistent fog from 14 July to 2 August prevented observations during the main migration of narwhals.

Relative age and sex composition

Relative age and sex were recorded for some narwhals sighted during aerial surveys. Relative age was estimated based on size and colour of the animal: large light-coloured animals with mottling or spots were called adults and small dark-coloured animals with faint spots were called subadults (*cf.* Mansfield *et al.* 1975). Experienced observers can distinguish calves and yearlings from other subadult narwhals. Newly-born calves (neonates) appear white or light gray because of the presence of the neonatal skin; after it is sloughed, they appear to be slate gray (Reeves & Tracey 1980) and can be distinguished from other subadults by their small size (approx. 40% of mother's length). Yearlings are noticeably larger than calves (50–60% of mother's length), appear more rotund, and are much darker (neonatal skin present on calf) or lighter coloured (neonatal skin sloughed by calf). During our surveys of summering areas in August and early September the neonatal skin was present on calves and they were readily distinguishable from yearlings by experienced observers.

Our surveys were conducted by observers with varying experience and ability to estimate the relative age of narwhals. As a result, we have not used age-classification data from bird surveys (45 m a.s.l.) unless they were recorded by the senior author. We used all data from mammal surveys (>50 m a.s.l.) because most were obtained by experienced marine mammal observers.

Narwhals with tusks were assumed to be males and those without tusks were assumed to be females, although a small proportion of tusked animals are females (Mansfield *et al.* 1975) and an occasional adult male may not have a tusk (Reeves & Tracey 1980).

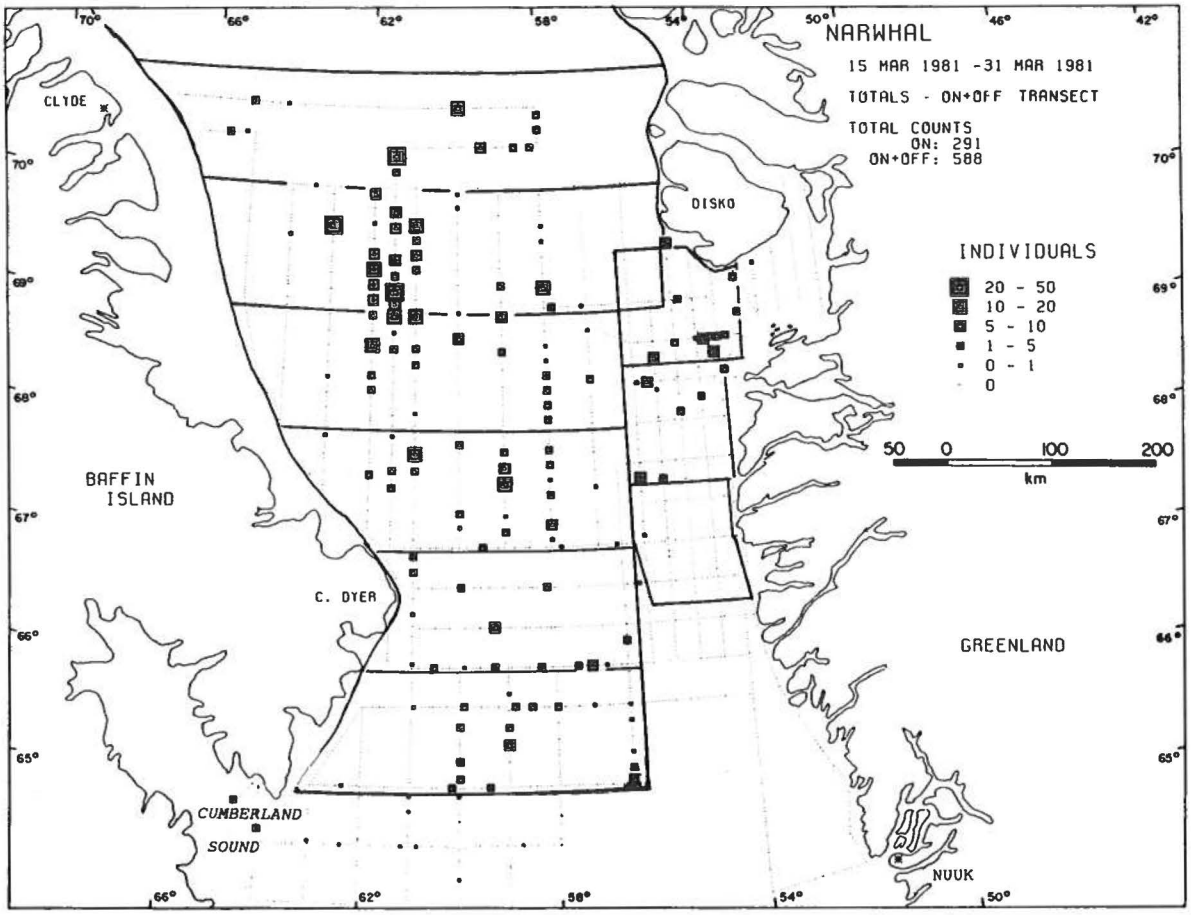


Fig. 2. Survey routes and narwhal sightings in southern Baffin Bay and northern Davis Strait, 15–31 March 1981. On this and subsequent figures individual symbols indicate the number or density of narwhals in a 2-minute transect segment. Each symbol may include sightings of several groups.

Group size

Narwhals that were within one body length of each other were defined as comprising a pod; activities (such as turns or dives) of animals in pods tended to be synchronous. Aggregations of pods were called herds; within herds, pods of narwhals were separated by 5–10, or more, whale lengths. Different pods within a herd frequently behaved differently.

Estimates of numbers in survey areas

Ideally, surveys to estimate numbers of animals should be conducted using randomly chosen transect lines (Cochran 1977, Caughley 1977, Eberhardt 1978). However, the major objective of our surveys was to determine the distributions of the different marine mammal species in the surveyed areas. In such situations, systematic survey patterns are desirable (Caughley 1977, Eberhardt 1978) provided that transects are designed to cross, rather than follow linear features of the habitat that affect animal abundance, *e.g.* coasts, ice edges, leads in sea ice or depth contours. We excluded surveys of coastal/ice-edge and nearshore transects from our estimates of numbers because these transects followed physical features that strongly influenced narwhal distribution. Because transect lengths varied, the ratio estimation procedure (Cochran 1977, Eberhardt *et al.* 1979) was used to estimate densities and numbers of narwhals present in offshore areas. Because densities varied among strata, we used the separate ratio method for sampling without replacement to estimate the total number of narwhals present during selected periods. Caughley & Grigg (1981) describe the method and calculations as applied to a sampling design similar to ours. Our estimates do not include coastal and ice-edge areas or offshore areas outside of our survey

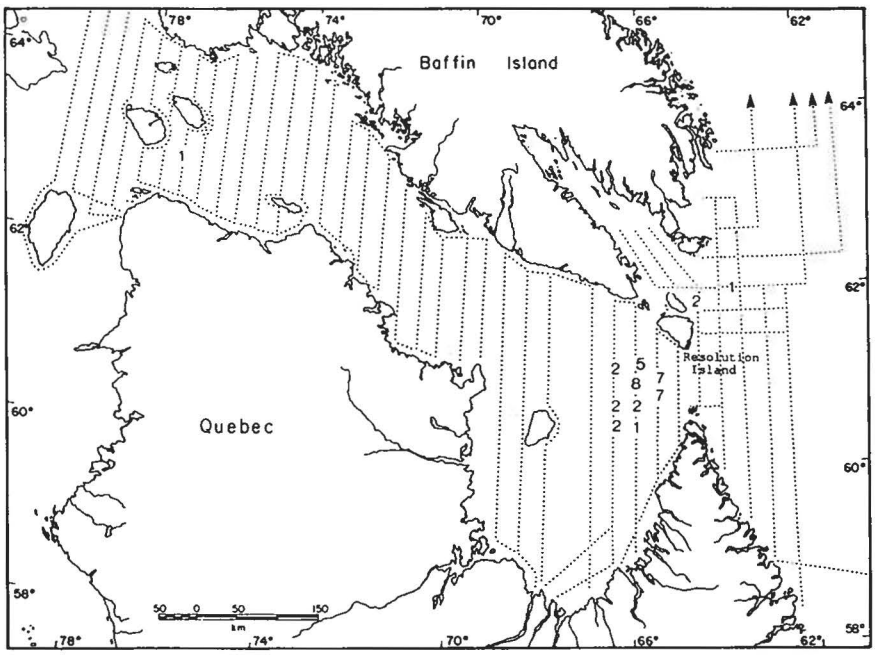


Fig. 3. Survey routes and narwhal sightings in southwestern Davis Strait and Hudson Strait, 14–30 March 1981. Numbers indicate individuals sighted in 2-minute intervals.

strata (see Fig. 11, later), nor do they account for animals that were below the surface at the time of the survey.

Results

Distribution and movements

Late winter 1981

Narwhals were widely dispersed in small groups throughout the pack-ice areas surveyed during the late winter of 1981 (Fig. 2). The average pod size was 2.08 (N=289), including a few groups recorded south of the areas that were included in extrapolations (Fig. 2). Narwhals were found in highest densities in areas where ice cover was 90–99% and only one narwhal was seen in an open-water area. Although narwhals were found among the loose pack ice south of Disko, they were found in highest densities among the heavy pack ice farther west in southern Baffin Bay.

Our surveys in 1981 also included the pack ice along SE Baffin Island, in Hudson Strait and along the NE Labrador coast. Small numbers of narwhals were recorded among the pack ice east of Cumberland Sound (Fig. 2) and in eastern Hudson Strait southwest of Resolution Island, but they were rare or absent in other areas south of 65°N (Fig. 3).

Late winter 1982

Although the overall study area was similar in March of 1981 and 1982, survey effort in 1982 was concentrated in the area along the coast of Greenland from Nuuk to Disko. Less coverage of the offshore pack ice in southern Baffin Bay was obtained. The distribution of narwhals appears to have been similar in 1981 and 1982 (Figs 2 and 4). Densities of narwhals were lower in the open pack ice along the coast of Greenland (0.015/km^2) than in the close pack ice farther north and west (0.030/km^2). The only area where significant numbers of narwhals were found in the open pack ice was south and southwest of Disko, where they occurred in both years. Within each of the two main categories of ice, the mean pod size was similar in 1981 and 1982: 2.42 and 2.44, respectively, in open pack ice and 2.04 and 2.08 in close pack ice. The difference in the distribution of pod sizes between open and close pack ice was not significant ($\chi^2 = 7.85$, df = 5, $P>0.05$).

Spring 1978

The surveys in 1978 were concentrated along the coasts and ice edges and in nearshore areas. Narwhals were not recorded during the first low-altitude aerial survey of coastal and ice-edge areas conducted 4–7 May 1978 and only 70, including sightings outside of the survey strip, were recorded during the second survey of the same route on 8–14 May. However, large numbers of narwhals were present among the offshore pack ice in Baffin Bay by mid-May; 0.12 narwhals/km^2 were recorded during sur-

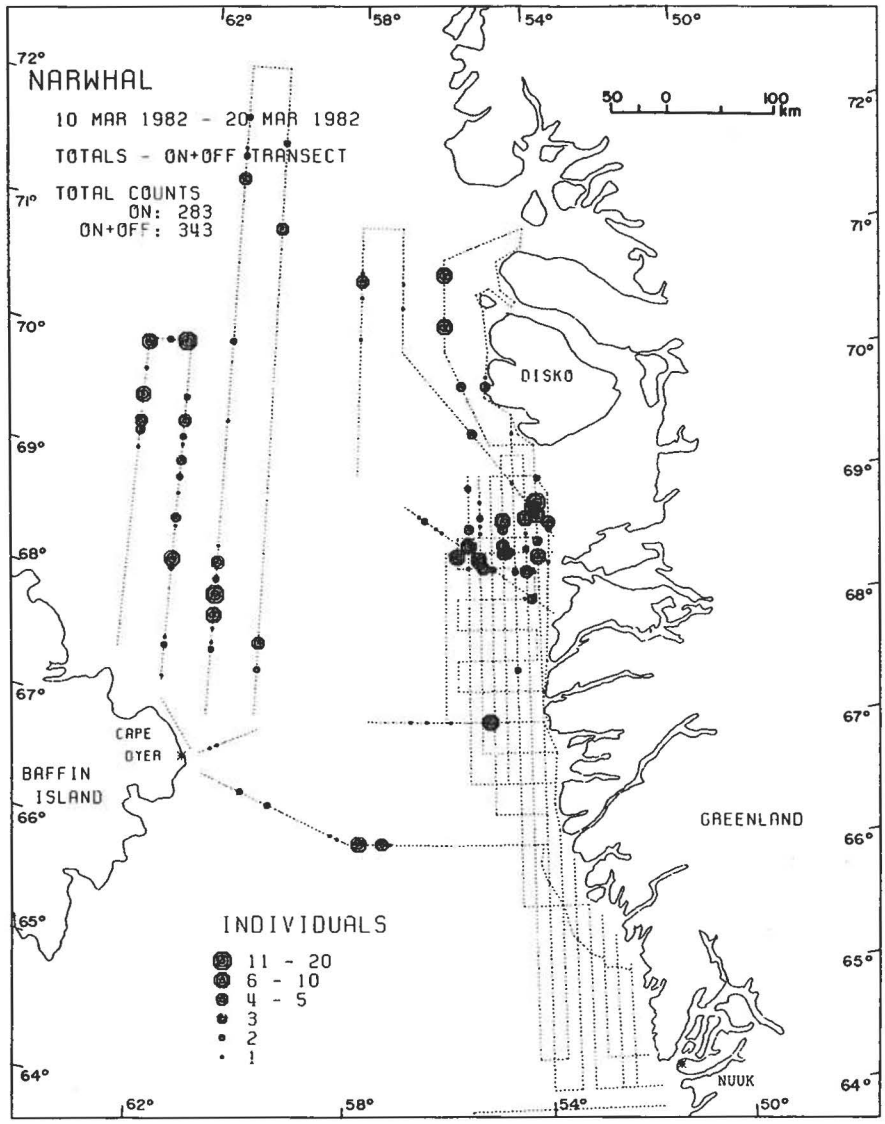


Fig. 4. Survey routes and narwhal sightings in southern Baffin Bay and northern Davis Strait, 10–20 March 1982. Legend: see Fig. 2.

veys of the offshore pack ice conducted at 90 m a.s.l. on 12–14 May. Our low-altitude surveys documented a gradual movement of narwhals into coastal and ice-edge areas in and adjacent to Lancaster Sound from early May until late July (Table 2). Distributional evidence and headings of animals sighted suggested that most of these narwhals came from the offshore pack ice at latitudes between 73°30'N and 74°30'N (Fig. 5, see also 1979 data in Figs 8–12). Few were seen in offshore waters north of 74°30'N.

Some of the narwhals that arrived in Lancaster Sound from the offshore pack ice appeared to move north along the east coast of Devon Island, the ice edge across Jones Sound and SE Ellesmere Island to Smith Sound. Surveys conducted in northern Baffin Bay on 31 May-1 June and 5 July 1978 detected 282 and 325 narwhals, respectively, along the east coast of Ellesmere Island but none along the coast of Greenland except at the Hvalsund ice edge (2 and 573, respectively, Figs 6 and 7). In addition, most narwhals sighted in offshore waters of Baffin Bay west of 75°W were swimming west; few were seen moving north. Along the Smith Sound ice edge, we saw 120 narwhals on 31 May-1 June and 1216 on 5 July 1978.

The weekly surveys in the spring of 1978 sampled only a small part of the total area of offshore pack ice; however, densities of narwhals recorded in the pack ice did not decrease as the numbers increased in coastal and fast-ice areas. Densities recorded in the pack ice were 0.03–0.05/km^2 during each of five surveys from 18 May to 21 June, and increased to 0.17/km^2 on 1 July. After 1 July few narwhals were seen in the pack ice in Baffin Bay. However, they must have been present in areas that

Table 2. Numbers and densities of narwhals on coastal and ice-edge transects, 4 May-2 August 1978.

Survey period	Coastal and ice-edge transects		
	Area surveyed (km^2)	On-transect narwhals	Density (no./km^2)
4– 7 May	372	0	0.00
8–14 May	431	42	0.10
15–18 May	372	35	0.09
22–26 May	384	106	0.28
29 May-2 Jun	356	90	0.25
8–11 Jun	409	49	0.12
12–16 Jun	440	268	0.61
19–23 Jun	438	936	2.14
26–30 Jun	436	589	1.35
3– 8 Jul	457	857	1.88
10–17 Jul	374[a]	1322[a]	3.53[a]
21–26 Jul	308[a]	696[a]	2.26[a]
28 Jul-2 Aug	537	1425	2.65

[a] These surveys were not completed because of low ceilings and fog.

were not surveyed because movements into Lancaster Sound from the offshore pack ice continued until late July or early August (see *Summer* sections, below).

A fast-ice edge remained intact across eastern Lancaster Sound until after 8 July in 1978. Until then, numbers of narwhals recorded along coastal and ice-edge transects tended to increase over time because narwhals arriving from the offshore pack ice could not move westward into Lancaster Sound (Table 2). The decline in numbers between the 19–23 and 26–30 June survey periods was probably due to the northward movements of narwhals from the Jones Sound ice edge to Smith Sound (*i.e.* north of our regular survey area). When cracks developed in the Lancaster Sound fast ice during the 9–18 July period, we saw narwhals moving west of the survey area through these cracks.

Spring 1979

By 9 May, when surveys were initiated, most of the narwhal population was probably present in the pack ice in Baffin Bay in or adjacent to our offshore survey area (Figs 8 and 9; see **Numbers of narwhals** – *Spring surveys*). The distribution of heavy pack ice (>75% ice cover) in June of 1979 as determined from satellite imagery is shown in Fig. 11; it was slightly more extensive in May when imagery was not available. Few narwhals were recorded on coastal and ice-edge transects on 12–15 and 17–22 May. Numbers of narwhals in coastal and ice-edge areas increased gradually during the spring period in 1979 (Table 3), similar to the pattern in 1978. However, extreme cold in combination with calm winds on 22 and 23 May froze most leads and cracks in the heavy pack ice and probably caused most narwhals to retreat into areas of lighter ice cover to the east and south (Fig. 10 vs Fig. 9). Many narwhals appear to have remained in the eastern part of our survey area, and possibly to the east of it, during the last two surveys of the Baffin Bay pack ice conducted on 19–23 June and 28 June-2 July (Figs 11 and 12). However, most narwhals had apparently moved into northern and central Baffin Bay because few narwhals were present along the most southerly offshore transect during either of these last two offshore surveys.

In 1979, the mean pod sizes of narwhals were significantly smaller in offshore Lancaster Sound (1.65, N =113) and Baffin Bay (2.02, N = 390) than in coastal and ice-edge areas both in (2.52, N = 522) and outside of Lancaster Sound (2.91, N = 538, $P<0.01$; Kruskal-Wallis ANOVA and Dunn's Multiple Comparison, Hollander & Wolfe 1973). Most of the large symbols on Figs 8–12 represent several sightings of small groups of narwhals

Table 3. Numbers and densities of narwhals along coastal/ice-edge and offshore transects in Baffin Bay and Lancaster Sound, 9 May-15 July 1979.

Survey period	Coastal and ice-edge transects			Offshore transects		
	Area surveyed (km^2)	Number of narwhals	Density (no./km^2)	Area surveyed (km^2)	Number of narwhals	Density (no./km^2)
9 May	136	3[a] (10)[b]	0.02	56	6 (6)	–
12–15 May	445	34 (64)	0.08	1133	154 (266)	0.14
17–22 May	562	72 (78)	0.13	1521	179 (273)	0.12
24–26 May	53	0 (0)	–	1321	68 (121)	0.05
1 Jun	261	143 (143)	0.55	101	0 (0)	0.00
10–14 Jun	573	431 (439)	0.75	2439	170 (219)	0.07
19–23 Jun	574	596 (646)	1.04	1173	116 (200)	0.10
28 Jun-2 Jul	589	722 (741)	1.23	1665	167 (305)	0.10
8–15 Jul	549	519 (578)	0.95	744	107 (138)	0.14

[a] Number on transect.
[b] Number on+off transect.

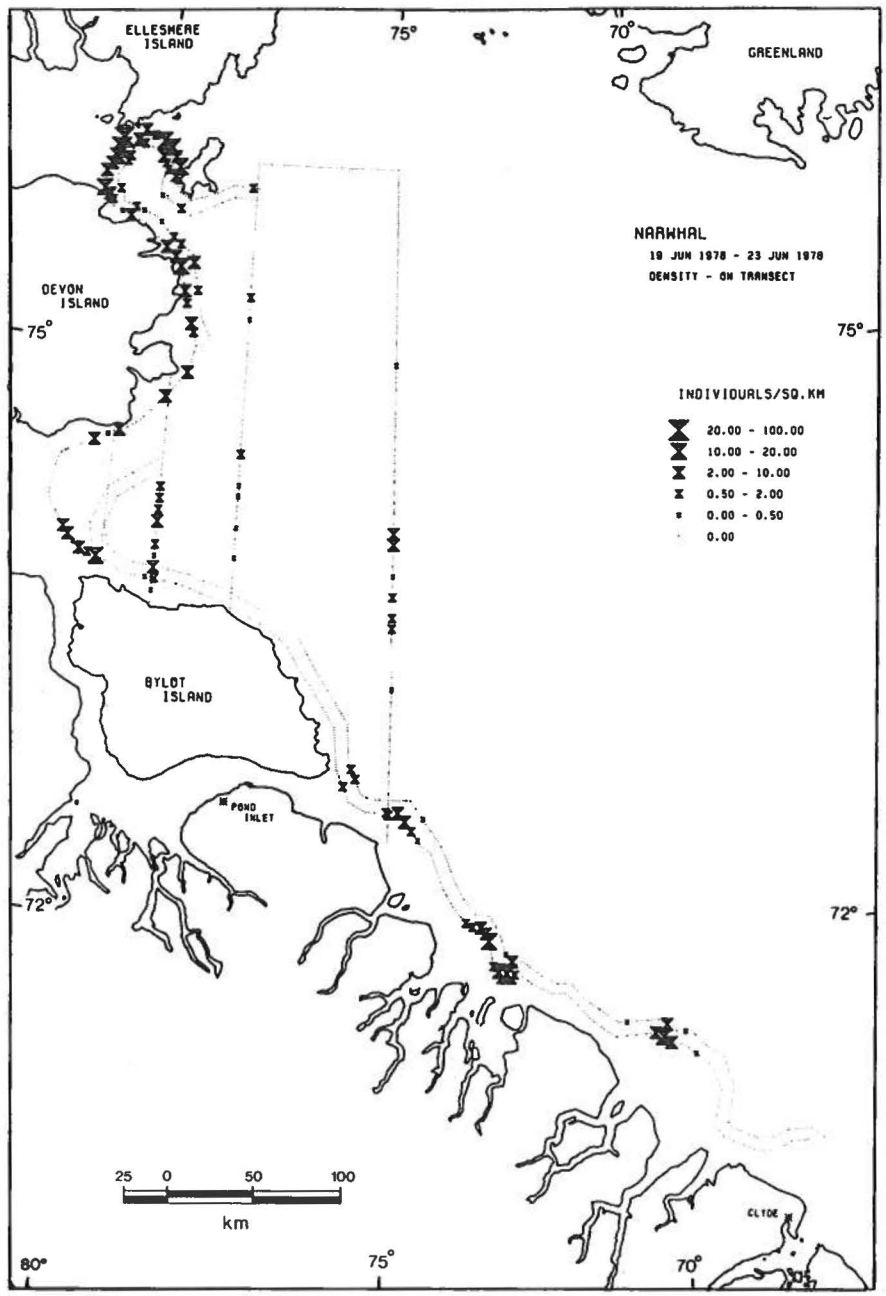


Fig. 5. Survey routes and narwhal densities in NW Baffin Bay, 19–23 June 1978. Nearshore transects, which were parallel to and 1.4 km from the landfast ice edge, are plotted seaward of their actual position to enhance legibility.

within a 5–9 km segment of transect rather than one or a few sightings of large groups.

Summers 1974–76

Our surveys in 1974–76 indicated that movements of narwhals into Lancaster Sound started in late May to mid-June. Surveys were not frequent enough to determine the periods of peak movements in 1974 and 1975; however, peak movements were in late June to mid-July in 1976 (Davis *et al.* 1978).

Summer 1978

In 1978, the major movements of narwhals into Lancaster Sound appear to have occurred from mid-July to early August, when poor weather prevented us from completing our surveys. Break-up of the fast ice in Lancaster

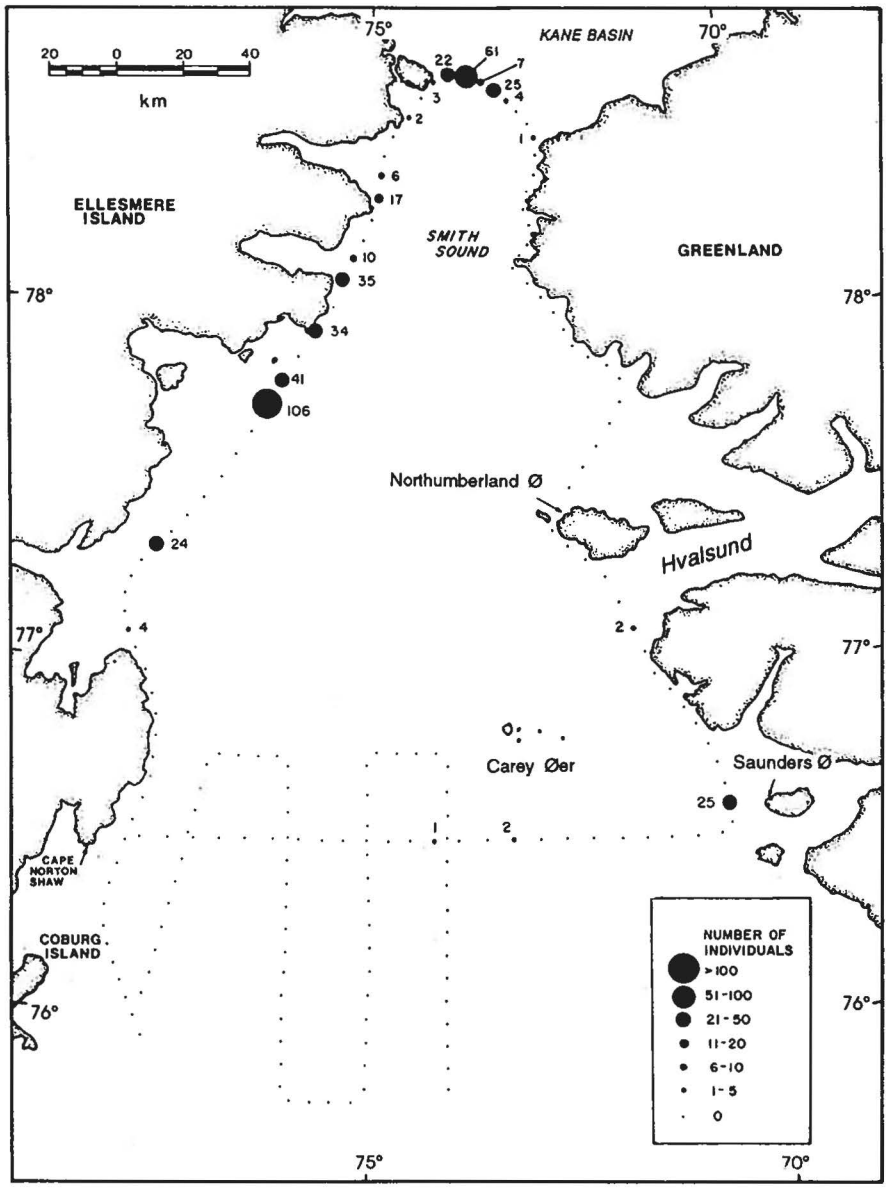


Fig. 6. Survey routes and narwhal sightings in northern Baffin Bay, 31 May-1 June 1978.

Sound occurred between 9 and 18 July. Small numbers of narwhals were recorded moving west through offshore Lancaster Sound during incomplete surveys on 21–26 July. Although none were recorded in offshore areas during surveys on 28 July-2 August, 651 narwhals were counted on coastal and nearshore transects along northern and northeastern Bylot Island. During periods of good visibility from 28 July to 9 August, 2709 narwhals were counted passing within view of our land-based observation site west of Cape Hay on northern Bylot Island. If similar rates of passage occurred during periods of observations and during periods when observations were not conducted due to poor visibility, 4844 narwhals passed the observation site from 28 July to 9 August.

Most of the narwhals that summer in Eclipse Sound enter that area through Pond Inlet rather than Navy Board Inlet. During a 30 July 1978 survey of the fast-ice edge across Pond Inlet and of cracks west of there, we counted 622 narwhals. Most of them were moving west through newly-formed cracks. During the same survey period no narwhals were seen in Navy Board Inlet or Eclipse Sound where ice cover was 80–90%.

Summer 1979

Fog and low cloud cover prevented aerial surveys or shore-based observations from mid-July to mid-August in 1979. The land-fast ice edge remained intact across Lan-

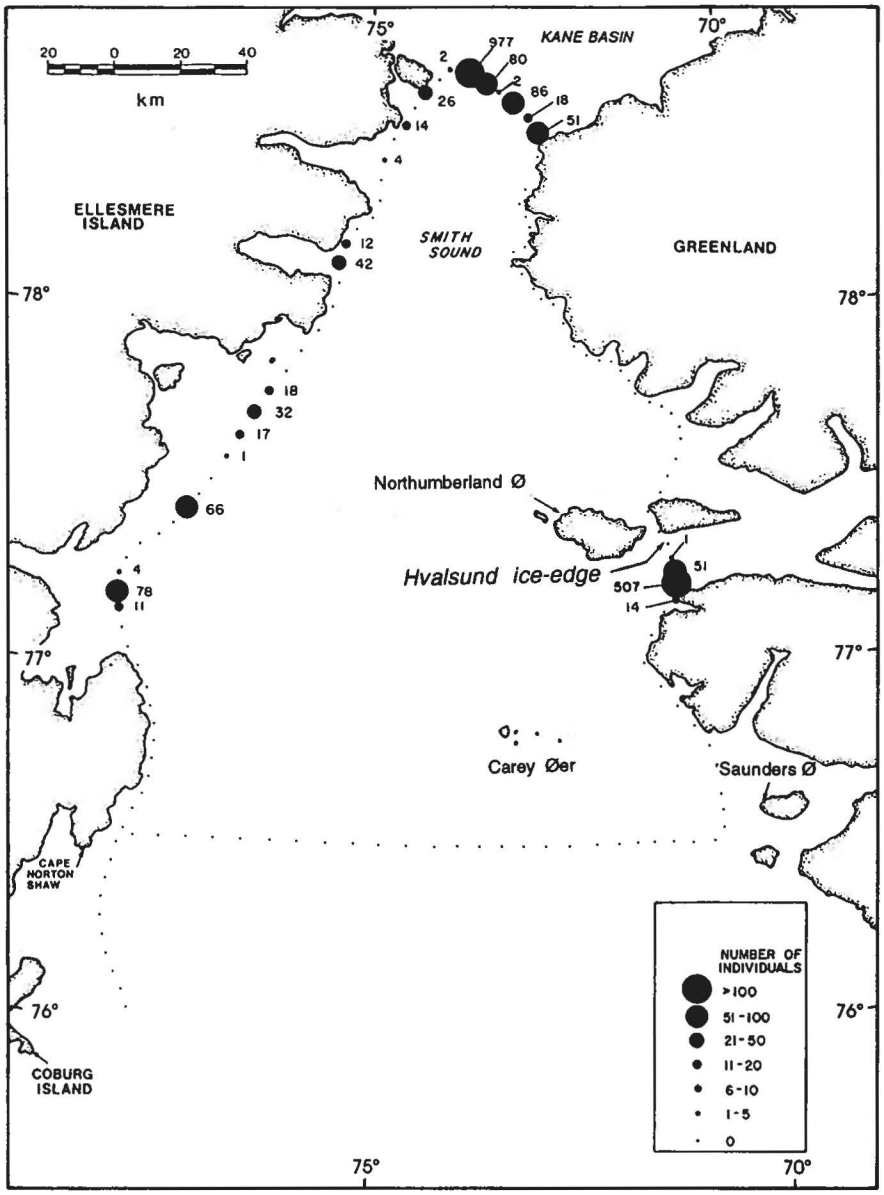


Fig. 7. Survey routes and narwhal sightings in northern Baffin Bay, 5 July 1978.

caster Sound until 2 August when cracks started to form. The majority of narwhals are suspected to have entered Lancaster Sound during early to mid-August in 1979.

Our systematic and opportunistic surveys identified several summering areas of narwhals, some of which had not been documented previously (Fig. 13). Unlike white whales, which frequently use shallow estuaries during summer, narwhals remain in deeper waters during summer (Mansfield *et al.*. 1975, Born 1986, Born *et al.* 1994). They sometimes enter deep fiords such as Tay Sound or Buchan Gulf but are most often found in larger water bodies such as Eclipse Sound, Milne Inlet, Admiralty Inlet and others listed in Table 4 (later). Our surveys were not designed to estimate the numbers of narwhals present in most of these areas. However, Table 4 gives maximum counts obtained during this study and estimates, where available, for numbers of narwhals summering in these areas.

Our data suggest that narwhals do not usually summer in Jones Sound. When fast ice blocked access to summering areas in 1978 and 1979, large numbers of narwhals were recorded along ice edges blocking access to Lancaster Sound, Pond Inlet, Buchan Gulf and Inglefield Bredning but numbers of narwhals along the Jones Sound ice edge were low: only 8 on 24 July 1978 and 36 on 9 July 1979. This occurred even though several hundred had been recorded there earlier in the year, and even though the ice edge was intact. In addition, opportunistic surveys

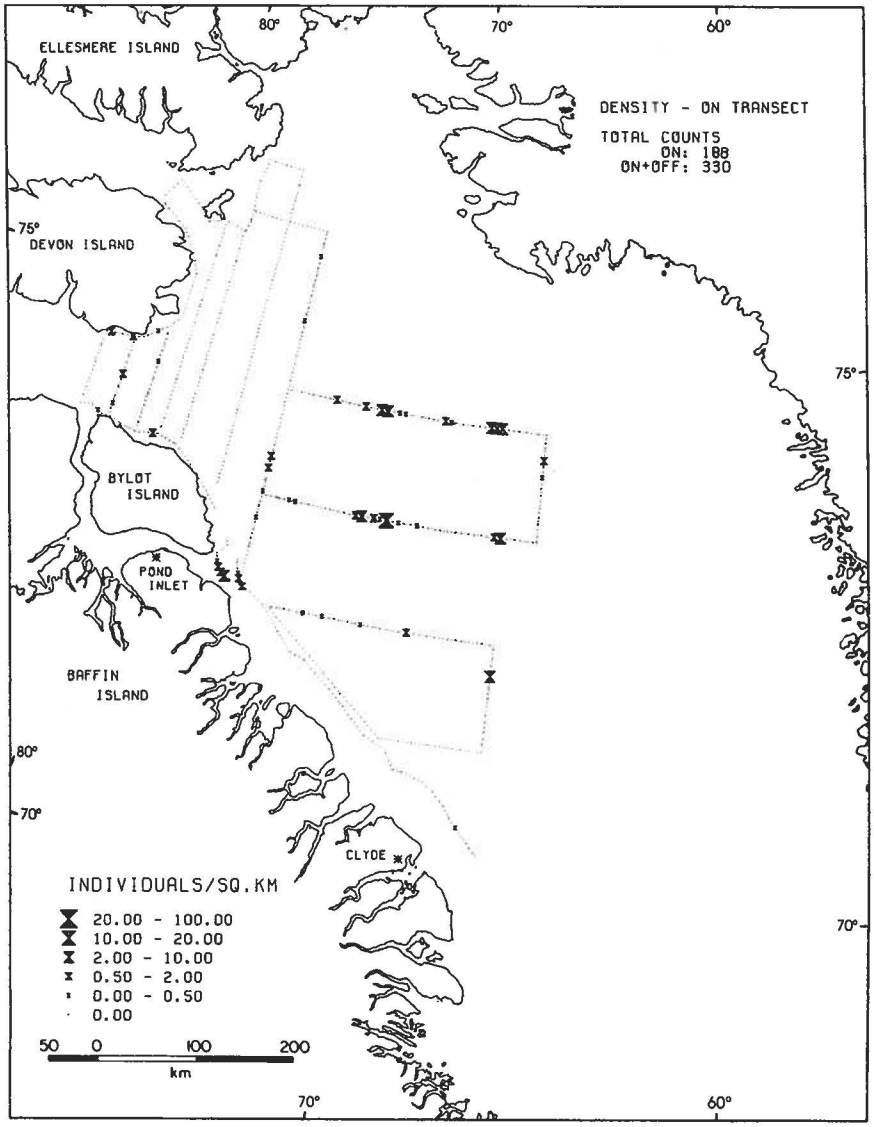


Fig. 8. Survey routes and narwhal densities in NW Baffin Bay, 12–15 May 1979.

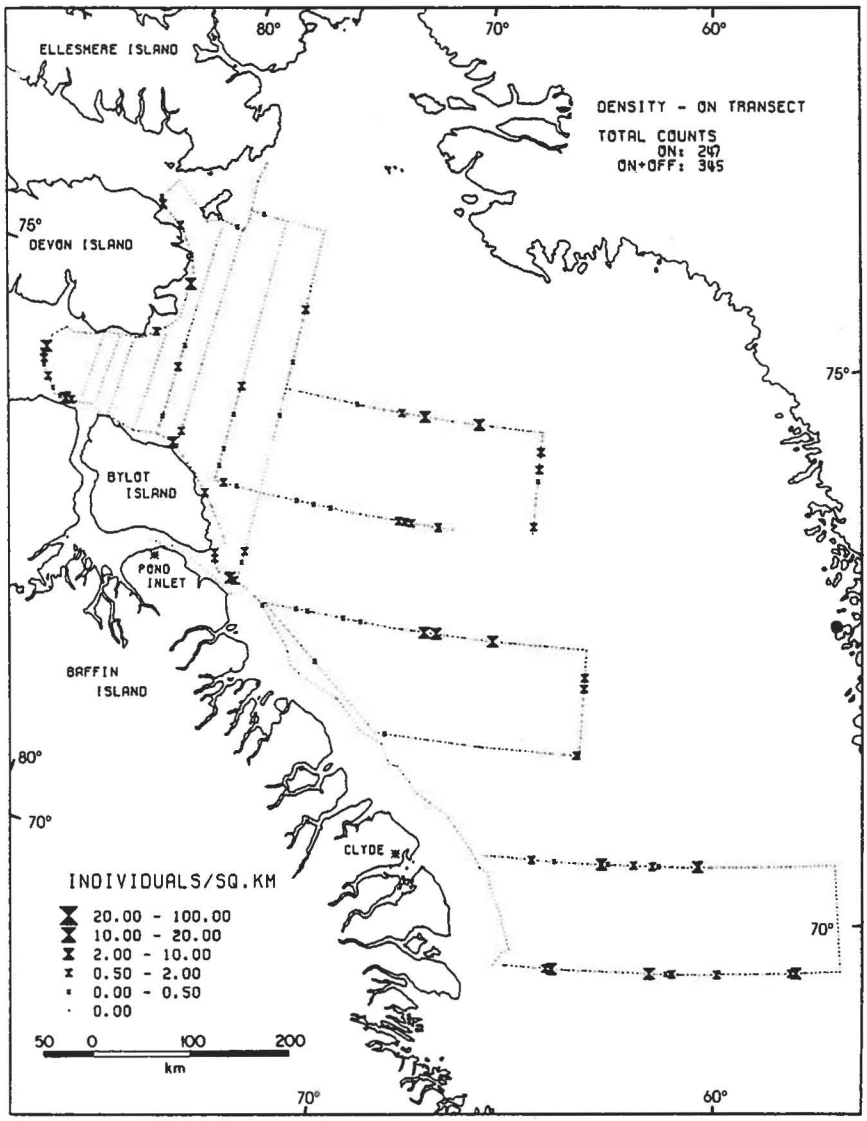
of Jones Sound during the summer and early autumn of 1977–79 detected no narwhals on 22 August 1977 and 21 August 1979 and only 11 and 22 on 15 September 1978 and 14 September 1979, respectively.

Autumn 1978

In 1978, narwhals started to move out of summering areas during the 23–27 September period. During late September and early October, before the offshore areas started to freeze, most narwhals followed either the north or south coast of Lancaster Sound eastward into Baffin Bay. Many then followed the coast of Baffin Island southeastward. Some continued east and offshore from SE Devon Island into Baffin Bay; for example, on 29 September 60–90 narwhals were seen moving east into Baffin Bay from the southeast corner of Devon Island even though no ice was present. Few narwhals were recorded swimming north along the east coast of Devon Island during autumn, even though narwhals were common along the south coast of Devon Island during late September and early October. This suggests that few if any narwhals migrated north along eastern Devon Island in autumn. During the 7–10 October survey, after new ice had started to form in offshore Lancaster Sound and along NE Baffin Island, narwhal movements were dispersed throughout the offshore pack ice and no longer followed the coast of Baffin Island.

Shore-based observers recorded narwhals moving south past Cape Adair on northeast Baffin Island during a four-day period from 29 September to 2 October in 1978. During this period, 4963 narwhals were recorded; all but

Fig. 9. Survey routes and narwhal densities in NW Baffin Bay, 17–22 May 1979.



21 were recorded as part of four major pulses. About 97% of the narwhals seen were within 700 m of shore, 3% were 700–1500 m from shore and only 18 (0.4%) were farther than 1500 m from shore. Some narwhals may have moved past Cape Adair at night and therefore would not have been counted. Also, aerial surveys indicated that many narwhals moved past Cape Adair after the shore-based observations were terminated on 7 October.

Autumn 1979

In 1979, narwhals were first observed leaving summering areas in Lancaster Sound during the 18–21 September survey when 572 narwhals were recorded along the south coast of Devon Island. On 24–26 September a major movement from Admiralty Inlet across Lancaster Sound to the south coast of Devon Island was documented (Fig. 14). A total of 672 narwhals was recorded along the south coast of Devon Island; 91% of these were moving strongly eastward. In addition, substantial numbers were recorded moving northeast through Lancaster Sound between Admiralty Inlet and the south coast of Devon Island. Extrapolation of numbers recorded on offshore transects to areas between those transects yields an estimate of approximately 1200 narwhals in offshore areas. This does not include numbers that were probably south and west of the survey area based on the observed distribution of sightings (Fig. 14, later). Some of the narwhals from Admiralty Inlet did not cross Lancaster Sound to the north side but appeared to follow the coasts of Baffin and Bylot islands to the east and south (Fig. 14).

By 28–29 September, pan ice had started to form

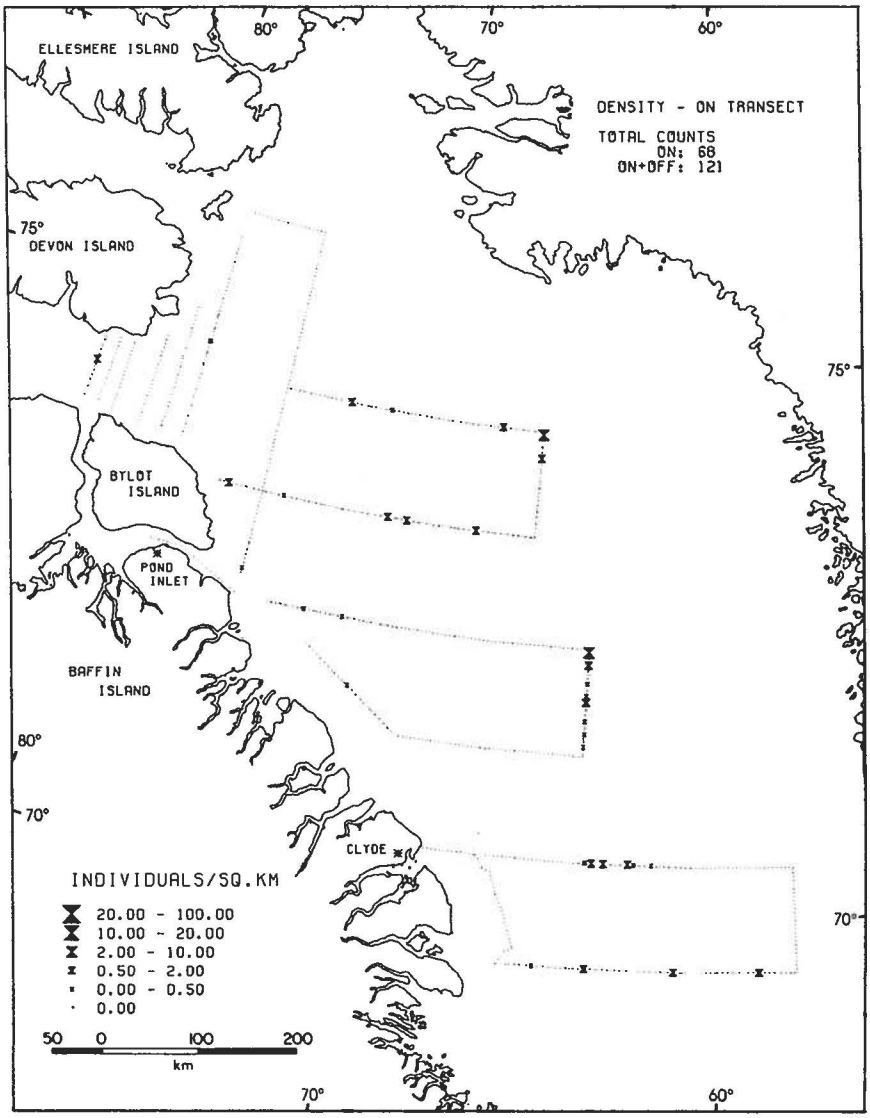


Fig. 10. Survey routes and narwhal densities in NW Baffin Bay, 24–26 May 1979.

offshore in Lancaster Sound. From this time on, few narwhals were sighted along either coast of Lancaster Sound. They were dispersed among the offshore ice. Narwhals that summered in Buchan Gulf apparently started to leave their summering area on these dates as 154 narwhals were seen just outside of Buchan Gulf.

A total of 4491 narwhals (including on- and off-transect sightings) was counted in Pond Inlet and an additional 900 were counted along NE Baffin Island between Navy Board Inlet and Cape Adair during an aerial survey on 1 October 1979. The number present in Pond Inlet was higher than the actual count. The survey covered all coastal areas but only 12% of the offshore waters where large numbers were present.

A large group of narwhals was observed moving north along the east coast of Bylot Island on 2 October; 2893 were counted during a single pass over the group but a complete count was not attempted. The 2 October group was probably the same, or part of the same, group seen in Pond Inlet the previous day.

Narwhals were recorded moving southeast along the Baffin Island coast from 27 September to 17 October 1979; most of the animals were in a few large groups. Observers at Cape Adair recorded 9 narwhals on 27 September, 1415 on 30 September, 185 on 2 October, groups of 283 and 117 on 10 October, and 800 on 13 October. All except the ones seen on 2 October were moving southeast along the coast. Poor weather prevented observations for most of 9 and 11–13 October, when many narwhals appear to have migrated southeast along the coast of Baffin Island. Aerial surveys detected groups of 350 and 550 narwhals that were 115 and 80 km

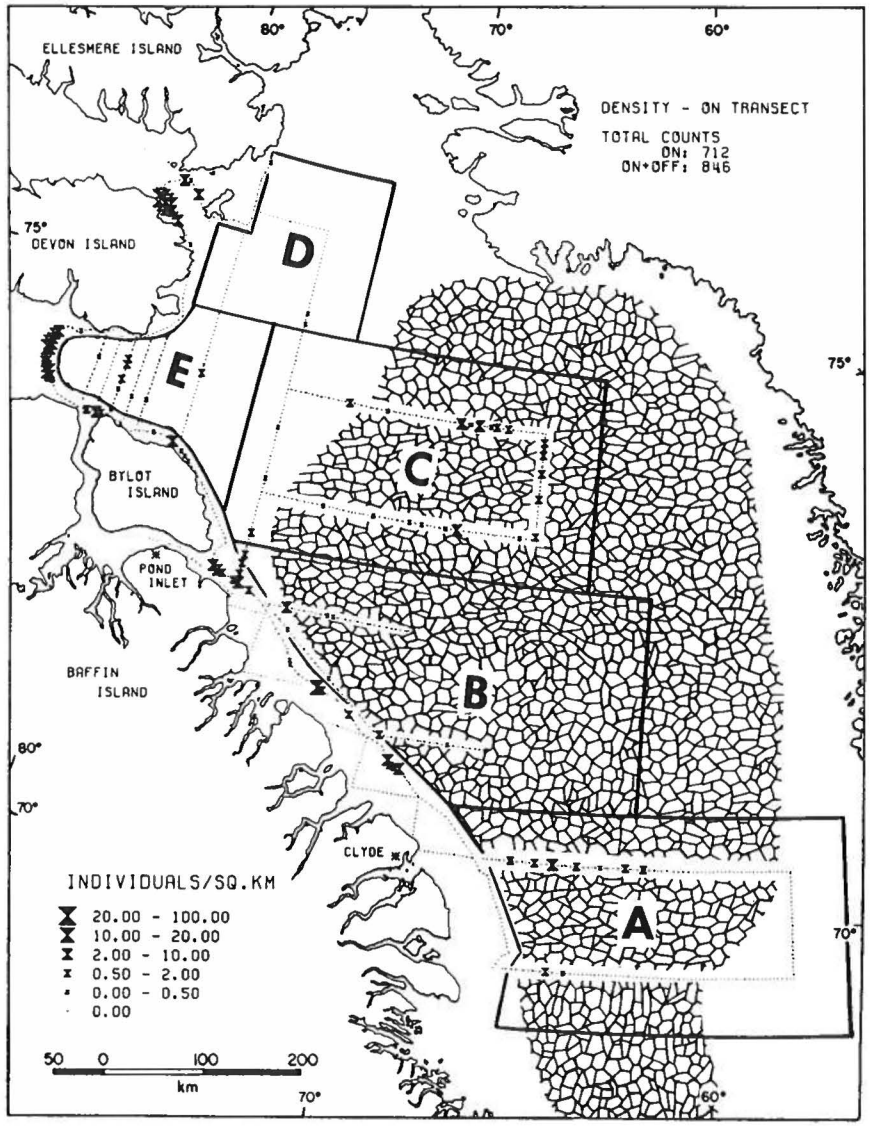


Fig. 11. Survey routes and narwhal densities in NW Baffin Bay, 19–23 June 1979. The outlined areas are the blocks to which extrapolations were made (see Table 8) and the shaded area indicates the extent of 75% pack ice in late June 1979 as determined from NOAA satellite imagery.

northwest of Cape Adair on 4 and 10 October, respectively; these groups were not detected by observers at Cape Adair. The 10 October survey also detected a group of 400 narwhals south of Cape Adair; only 117 of these were recorded from Cape Adair. Based on the combined aerial and shore-based observations narwhals appear to have continued to move at night and during periods of fog. Thus, the net southward movement of 2439 narwhals that was observed from Cape Adair in 1979 seriously underestimated the numbers of narwhals using this coastal route.

Narwhal movements during the autumn were more directed and appeared to be faster than those during other times of year. We do not have rates of movement for other times of year but we determined the minimum speeds of several large groups of narwhals that were resighted during the autumn migration. We have reliable estimates for two groups of narwhals that moved at ~12 km/h over a period of 3–4 h and for two groups that moved at 7 km/h over periods of 2–4 h (Table 5). In addition, the large group sighted in Pond Inlet on 1 October must have moved at a net speed of 7 km/h (based on the position of the centre of the group on each date) to reach the position where it was assumed to have been resighted on 2 October. However, the group had reversed course between sightings and its average speed was probably considerably greater.

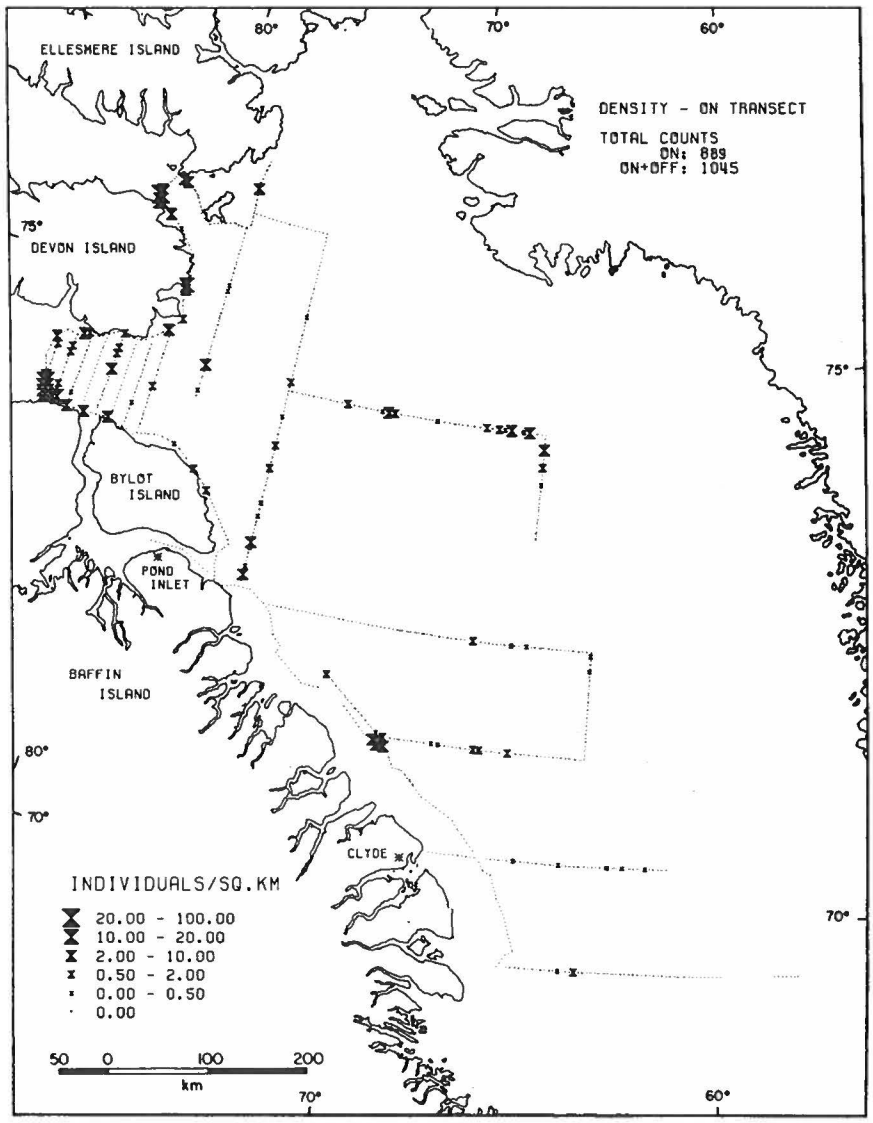


Fig. 12. Survey routes and narwhal densities in NW Baffin Bay, 28 June-2 July 1979.

Relative age and sex composition

The relative age and the sex of narwhals were recorded whenever possible. The data on sex ratios are biased toward males. If we were not certain of the sex we did not classify an animal to sex. When an animal was seen briefly, the presence of a large conspicuous tusk identified the animal as a mature adult male. Many animals without large tusks could not be sexed when seen briefly because they could have been either females or males with short tusks.

Offshore winter

In 1981 and 1982, 70 and 79%, respectively, of narwhals that were aged were adults and 68 and 61%, respectively, of the animals sexed were females (Table 6). These proportions were similar in the two types of habitat surveyed; 72 and 76% of narwhals were classified as adults and 68 and 60% as females in close and open pack ice, respectively. However, females with 7- to 8-month-old calves tended to avoid the open pack ice in favour of the close pack ice ($\chi^2 = 4.92$, $P<0.05$); calves formed 2.5 and 10.5% of all narwhals classified to an age category (N=80 and 209, respectively) in the open and close pack ice, respectively. The low number of males among the narwhals that were sexed in winter suggests that large num-

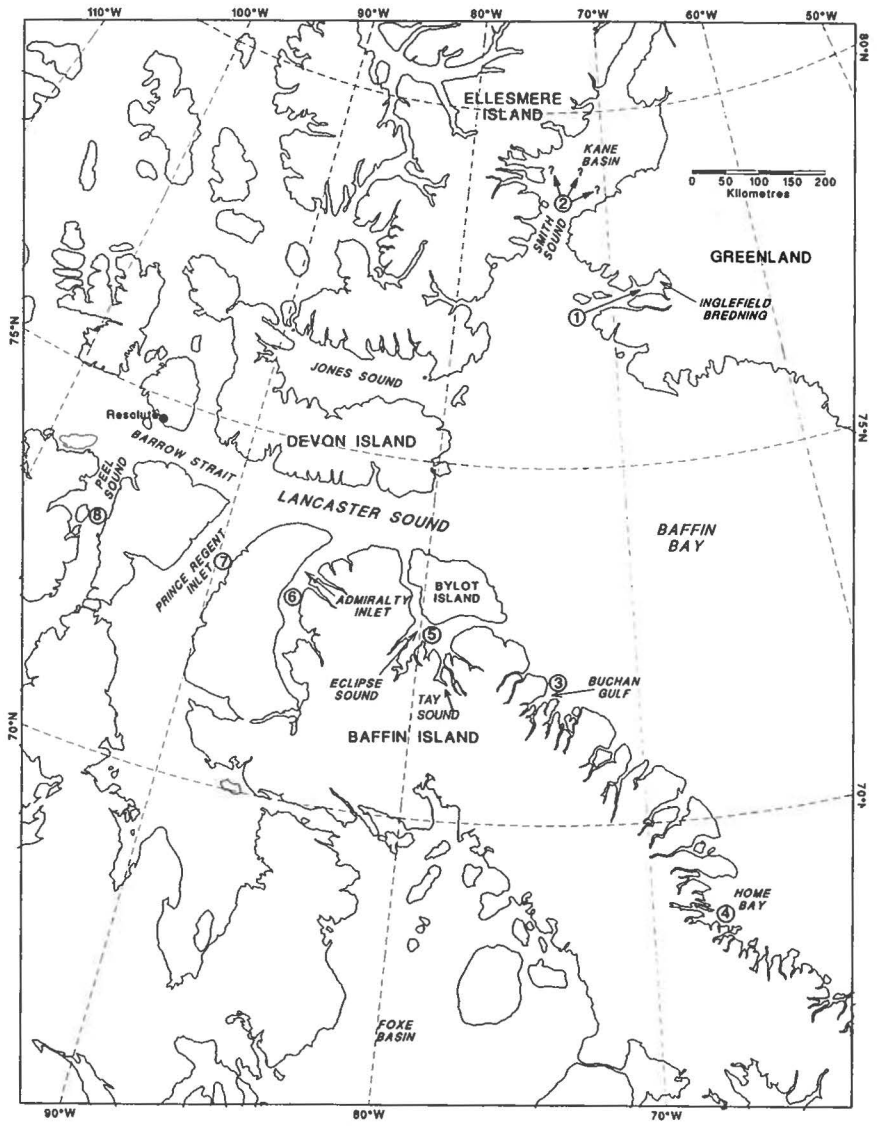


Fig. 13. Summering areas used by narwhals in 1976–1979. See Table 4 for information concerning surveys of each area.

bers of narwhals were present somewhere outside of the area surveyed.

Offshore spring

Adults comprised 74% of narwhals aged during offshore surveys of the pack ice in spring and the ratio of males: females was 48:52 (Table 6); the sex ratio was not significantly different from unity ($\chi^2 = 0.38$, $P>0.50$). The areas covered by these surveys appear to have included all age and sex categories, and therefore were not biased by the absence of a particular age or sex group. Data presented below indicate that adult males began moving into summering areas from the pack ice before females with young and subadults; therefore, fewer males may have been present in offshore areas during surveys conducted from 19 June to 2 July.

Migration to summering areas

Data from our surveys indicate that adult male narwhals entered Lancaster Sound before females with young and subadults. Furthermore, when entering Lancaster Sound adult males tended to move into coastal and ice-edge areas, whereas females with young and subadults tended to move through offshore waters (Table 6).

Few neonates were born before narwhals started to move into summering areas even though these movements were later in 1978 and 1979 than in most years. Only three neonates (<1% of all sightings) were recorded

Table 4. Estimates of numbers of narwhals present in summering areas surveyed during 1978 and 1979. Estimates and counts do not include correction factors to account for animals at the surface but not seen by observers or for animals below the surface at the time of the survey.

Location[a]	Date	No. Counted	Estimate of no. present	Comments	Other estimates (rounded to the nearest 100)
1. Inglefield Bredning (Greenland)	5 July 1979	573	>573[b]		4000 in 1984 (Born 1986) 800–1400 in 1985 (Born *et al.* 1994: aerial surveys) 1500 in 1985 (Born *et al.* 1994: ground counts) 2700–4400 in 1986 (Born *et al.* 1994) 500 in 1988 (Born *et al.* 1994: ground counts)
2. Smith Sound	5 July 1979	1216	>1500[b]	Includes 325 along Ellesmere Isl.	None
3. Buchan Gulf	11–15 Aug 1978	302	300		None
4. Home Bay	18 Sep 1979	95	>95	Widely dispersed; partial count	None
5. Eclipse Sound	24 Aug 1978	519	622	Good conditions	1200 in 1984 (Richard *et al.* 1994)
	8–9 Sep 1979	887	>3100	Poor conditions during part of survey, estimate low.	
6. Admiralty Inlet	24 Aug 1978	1362	7000		9700 in 1975 (Fallis *et al.* 1983)
	3 Sep 1979	231	>>1473	Partial survey and poor conditions	5600 in 1984 (Richard *et al.* 1994)
7. Prince Regent Inlet	17–18 Aug 1979	26	>569	Partial survey and poor conditions	9800 in 1984 (Richard *et al.* 1994)
	30 Aug-4 Sep 1979	85	>1614	Partial survey and poor conditions	10,800 in 1981 (Smith *et al.* 1985)[c]
8. Peel Sound	4 Sep 1976	378	900	Excellent conditions	1700 in 1984 (Richard *et al.* 1994)

[a] See Fig. 12 for locations.
[b] These counts were early in the season before major movements into summering areas had occurred (see Born 1986).
[c] This estimate is believed to be high (see text).

before mid-July in the two years. The earliest neonate and its presumed mother were recorded along the Pond Inlet ice edge on 19 June 1979. Other early records of presumed mothers with neonates were amidst the pack ice east of Pond Inlet on 28 June 1979 and amidst the pack ice along our most southerly offshore transect on 2 July 1979.

Summering areas

During surveys of summering areas of narwhals in 1978 and 1979, 67% (range = 63–74%, Table 6) of the 1230 animals aged were classified as adults, 19% (12–22%) as large subadults, 6.5% (3.7–7.7) as yearlings and 7.8% (5.9–10.2) as newborn calves. Females comprised 40% and males 60% of the animals that were sexed. This sex ratio is significantly different than unity ($\chi^2 = 34.1$, $P<0.001$). However, we believe that the observed ratio is biased by the ease of identifying adult males that was mentioned above. The surveys were conducted in late August and early September so that virtually all calves of the year should have been included. Based on the combined summer data from 1978 and 1979 (Table 6), the Gross Annual Recruitment Rate (GARR) was 0.085 calves/non calf/year. An estimate of the birth or calving rate, which considers only the ratio of calves to adult females for a species that calves seasonally, is 0.29 calves/adult female/year. However, this probably underestimates the true birth or calving rate because some calf mortality undoubtedly occurred after birth but before our surveys.

Autumn migration

Movements of narwhals during autumn migration were more rapid than at all other times of year. This made estimation of the relative age and sex of subadult animals difficult; as a result, we have not included age and sex data from autumn surveys in Table 6. The large herds of narwhals that were encountered seemed to consist of all age and sex categories, but the animals within pods seemed to be segregated by age and sex.

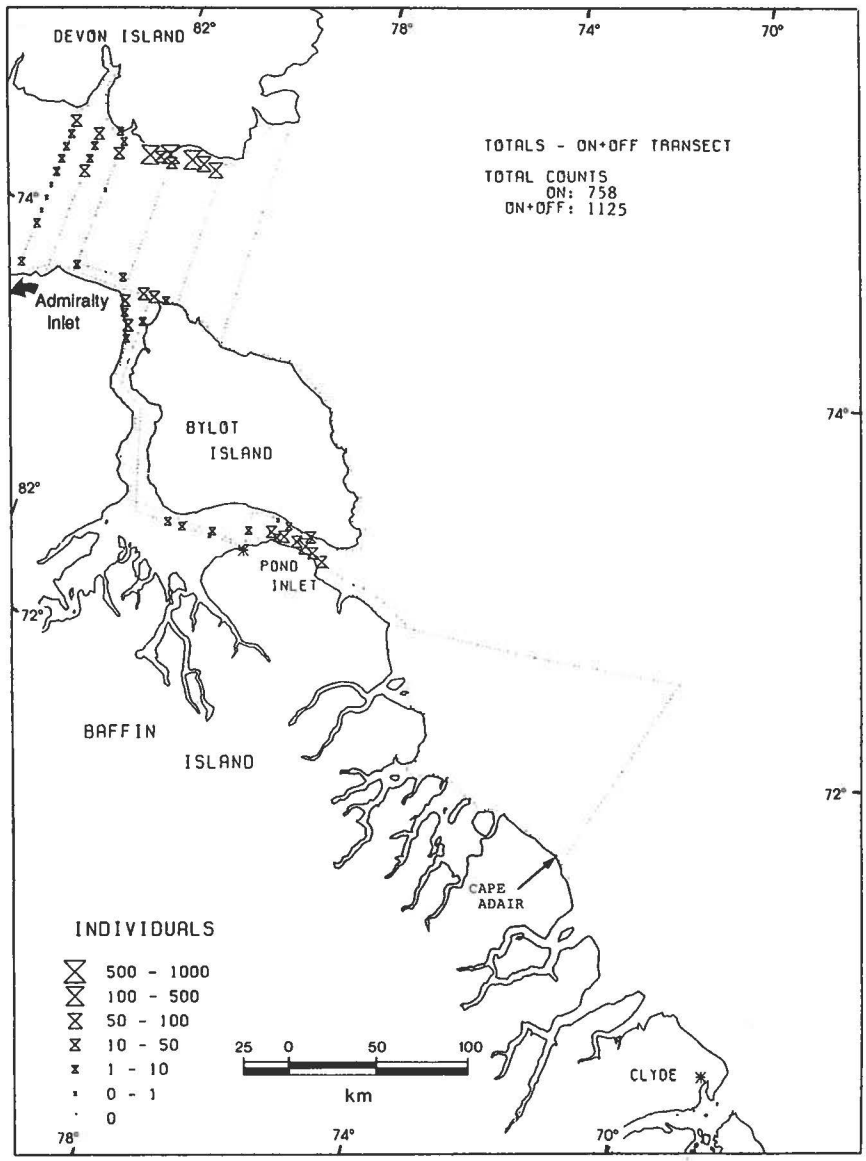


Fig. 14. Survey routes and narwhal sightings in NW Baffin Bay, 24–26 September 1979.

Table 5. Speeds of movement of narwhals sighted along NE Baffin Island, 30 September-10 October 1979.

Date of Sighting	Method of sighting initial/final	Elapsed time between sightings (h:min)	Distance travelled (km)	Speed (km/h)
30 Sep (group of 12)	G/A[a]	1:51	12.5	6.7
30 Sep (large group)	G/A	2:36–4:18	17.5–32.0	6.8–7.4
1–2 Oct	A/A	17:00	>>115[b]	>>6.8[b]
2 Oct	A/G	2:50	>32	>11.3
4 Oct	A/A	0:45	3.6	4.8
10 Oct	G/A	3:35–4:09	44–50	12.0–12.3

[a] A:sighted from the Twin Otter; G:sighted by observers at Cape Adair.
[b] This group had reversed course when it was resighted 2 October. The actual distance travelled and speed are probably much greater than those given (see text).

Table 6. Percent of narwhals in different age and sex categories recorded during surveys of Davis Strait, Baffin Bay and Lancaster Sound and vicinity, March-October 1978–1982.

	Age					Sex		
	Adults	Large subadults	Yearlings	Calves	Number aged	Males	Females	Number sexed
Winter								
Baffin Bay – Davis Strait (1981)	69.9	19.4	ND[a]	10.8[a]	186	32.5	67.5	117
Baffin Bay – Davis Strait (1982)	78.6	17.5	ND	3.9	103	38.6	61.4	57
Spring and early summer								
Baffin Bay (1979)	73.8	20.4	5.8[b]	NA[b]	80[c]	48.3	51.7	319
Lancaster Sound offshore (1979)	54.2	45.8	0.0	NA	36[c]	21.1	78.9	57
Lancaster Sound coastal (1979)	89.0	5.5	5.5	NA	82[c]	80.8	19.2	276
Summer								
Eclipse Sound (1978)	74.2	12.0	3.7	10.1	89	67.2	32.8	67
Admiralty Inlet (1978)	62.8	21.8	6.9	8.5	578	60.8	39.2	403
Central Arctic (1979)	73.1	11.8	6.7	8.3	108	51.9	48.1	79
Eclipse Sound (1979)	69.7	18.0	6.4	5.9	406	59.8	40.2	301
Admiralty Inlet (1979)	69.4	12.8	7.7	10.2	49	52.6	47.4	38
Total Summer Surveys	67.1	18.6	6.5	7.8	1230	59.8	40.2	888

[a] ND – in March, calves are approximately 7–8 months old, and yearlings (19–20 months old) are difficult to distinguish from other subadults.
[b] NA – calves are 10–12 months old and are called yearlings; most calves-of-the-year are born in late July-early August, although some are born as early as late June.
[c] Only age data collected by the senior author were used during these periods; see methods.

Numbers of narwhals

Winter surveys

The two major strata surveyed during the winters of 1981 and 1982 were open pack ice (<90%) and close pack ice (≥90%); these strata were further subdivided by latitude. The 1982 surveys extended farther north into central Baffin Bay than the 1981 surveys (Figs 2 and 4). Totals of 6027 and 8045 narwhals were estimated to have been present in the surveyed areas during 14–31 March 1981 and 10–20 March 1982, respectively. Large areas with suitable pack ice were present in Baffin Bay, north of our study area (see Fig. 1). The presence of this available habitat and the observed distribution of narwhals, suggests that substantial numbers wintered north of the survey areas in both years. In addition, some narwhals were probably present south of the survey area in 1982. A total of 450 (± SE 89) was estimated to have been present in the pack ice between 65 and 66°N during our 1981 surveys. An additional 650 were present south of 65°N based on extrapolations from scattered sightings, primarily in Hudson Strait and Davis Strait, south of Cumberland Sound (Fig. 3). These latter animals may be part of the Hudson Bay population (Richard 1991).

Spring surveys

Totals of 29 931 (± SE 7008) to 38 988 (± SE 6629) narwhals were estimated to have been present in surveyed areas of Baffin Bay during four surveys from 12 May to 2 July 1979 (Table 8). Estimates from surveys conducted 24–26 May and 10–14 June are not included because many narwhals apparently had moved east of the survey area when leads froze due to extremely cold weather. The combined estimate for the four surveys was 34 363 (± SE 8282).

Discussion

Distribution and movements

Late winter

Little was known about the distribution and movements of narwhals during the winter, spring and early summer previous to our surveys. Vibe (1967) and Kapel (1975, 1977) considered that narwhal wintering areas extended from Disko Bugt south to about 65°N. 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. Our surveys suggest that narwhals probably winter throughout the close pack ice in Davis

Table 7. Estimates of numbers of narwhals present in areas surveyed in northern Davis Strait and southern Baffin Bay, March 1981 and 1982.

Survey block[a]	Area in block (km^2)	Area surveyed (km^2)	No. transects	No. narwhals on-transect	Density[b] (no./km^2) ± SE	Estimated[b,c] number ± SE
Close pack ice, 15–31 March 1981						
70°N-71°N	49,354	1005.3	8	32	0.0318±0.0126	1571±623.7
69°N-70°N	47,464	2257.6	16	66	0.0292±0.0117	1388±553.3
68°N-69°N	40,641	2058.5	13	50	0.0243±0.0067	988±271.8
67°N-68°N	33,005	1661.4	10	53	0.0319±0.0104	1052±343.9
66°N-67°N	26,064	1492.2	12	18	0.0121±0.0043	314±112.7
65°N-66°N	32,392	1941.8	11	27	0.0139±0.0028	450± 88.9
Totals	228,920	10,416.8	70	246		5763±952.8
Open pack ice, 17–24 March 1981						
68°30'N-69°30'N	8044	1175.2	13	35	0.0298±0.0127	240±101.8
67°30'N-68°30'N	10,000	1212.9	13	1	0.0008±0.0008	8± 7.8
66°30'N-67°30'N	9605	1215.5	12	2	0.0016±0.0016	16± 15.0
Totals	27,649	3603.6	38	38		264±102.1
Close pack ice, 10–20 March 1982						
71°N-72°15'N	72,670	560.3	6	9	0.0161±0.0089	1167± 643.5
70°N-71°N	49,354	971.7	6	37	0.0381±0.0167	1879± 825.0
69°N-70°N	47,464	1144.8	7	20	0.1747±0.0062	829± 294.9
68°N-69°N	40,641	830.4	5	25	0.0301±0.0165	1224± 670.9
67°N-68°N	33,005	765.0	5	34	0.0444±0.0285	1467± 942.0
66°N-67°N	26,064	586.1	4	19	0.0324±0.0192	845± 500.1
Totals	269,198	4858.2	33	144		7411±1664.4
Open pack ice, 10–17 March 1982						
68°30'N-69°30'N	7211	1380.2	15	56	0.0406±0.0120	293± 86.7
67°30'N-68°30'N	10,000	2372.6	26	69	0.0291±0.0074	291± 74.7
66°30'N-67°30'N	9605	1916.2	22	10	0.0052±0.0036	50± 35.4
Totals	26,816	5669.0	63	135		634±119.8

[a] See Fig. 2 for location of survey blocks.
[b] Densities, estimated numbers and their standard errors are based on the ratio method.
[c] Estimates do not account for animals at the surface that were not seen or for submerged animals.

Strait and southern Baffin Bay, with relatively small numbers (<750) among the open pack ice south of Disko Bugt as far south as 68°N. The latter animals are predominantly females without young and subadults. We saw few narwhals south of 68°N along the Greenland coast even in 1982 when the pack ice extended farther south along the coast than normal. Heide-Jørgensen *et al.* (1993) found similar distributions and numbers of narwhals among the pack ice south of Disko during their surveys in 1990 and 1991. However they did not record narwhals south of 68°20'N where we had a few scattered sightings.

Finley & Renaud (1980) conducted three surveys of the North Water Polynia at the north end of Baffin Bay during March and April of 1978 and 1979 and found only one group of 12 narwhals. Their data are consistent with our results that indicate that narwhals avoid open water and ice-edge areas during the winter in preference to areas of 90–99% close pack ice. Hence, narwhals would not be expected in the polynia surveyed by Finley & Renaud (1980).

Spring

Narwhals were dispersed in small groups throughout the offshore pack ice in Baffin Bay and northern Davis Strait during spring. This distribution was unknown previous to our surveys.

Table 8. Estimated numbers of narwhals present in areas surveyed in offshore Baffin Bay and Lancaster Sound, 12 May-2 July 1979.

Survey block[a]	Area in block (km²)	Area surveyed (km²)	No. transects	No. narwhals on-transect	Density (no./km²) ± SE	Estimated number ± SE
12–15 May						
A	80,797	0	0	–	–	–
B	73,276	278	7	14	0.050±0.027	3692± 1944
C	80,119	355	11	135	0.380±0.148	30,451±11,873
D	24,699	223	12	2	0.009±0.006	221± 143
E	26,900	276	12	3	0.011±0.007	292± 194
Totals	285,791	1133	42	154		34,655±12,034
17–22 May						
A	80,797	338	9	65	0.192±0.056	15,543±4547
B	73,276	363	9	39	0.107±0.038	7876±2811
C	80,119	336	11	58	0.172±0.048	13,820±3856
D	24,699	182	10	5	0.027±0.022	679± 535
E	26,900	302	13	12	0.040±0.017	1,069± 452
Totals	285,791	1521	52	179		38,988±6629
19–23 June						
A	80,797	293	7	22	0.075±0.040	6057±3266
B	73,276	192	5	27	0.141±0.063	10,325±4633
C	80,119	355	11	50	0.141±0.049	11,278±3949
D	24,699	112	6	2	0.018±0.017	442± 426
E	26,900	221	8	15	0.068±0.041	1829±1099
Totals	285,791	1173	37	116		29,931±7008
28 June-2 July						
A	80,797	411	5	15	0.037±0.013	2951±1089
B	73,276	624	8	53	0.085±0.034	6224±2470
C	80,119	241	8	63	0.261±0.065	20,916±5236
D	24,699	117	6	3	0.026±0.017	635± 408
E	26,900	282	10	33	0.117±0.048	3152±1283
Totals	285,791	1674	37	167		33,879±6042

[a] See Fig. 11 for area included.

Movements into summering areas

Small numbers of narwhals (primarily males) move into coastal and ice-edge areas during May and early June. Larger numbers arrive in Lancaster Sound and adjacent coasts through offshore waters between 73°30' and 74°30'N from mid-June to early August. Some of those that arrive in June followed the east coast of Devon Island north to the Jones Sound ice edge, and from there, continue north to Smith Sound.

During 1978 and 1979 most narwhals moved west into Lancaster Sound during July to mid-August with peak numbers entering in late July and early August. The movements into Lancaster Sound appear to have been later than normal in 1978 and 1979. In 1976, Greendale & Brousseau-Greendale (1976) and Davis *et al.* (1978) documented peak movements of narwhals during early July with the main period of migration occurring from late June to mid-July. The delayed migration in 1978 and 1979 was probably due to the persistent fast-ice edge that remained across Lancaster Sound until 9–18 July in 1978 and 2 August in 1979.

Summer

Some of the summering areas of narwhals that were identified during our surveys have been surveyed comprehensively by others to estimate the numbers of narwhals present (Fallis *et al.* 1983, Smith *et al.* 1985, Born 1986, Born *et al.* 1994, Richard *et al.* 1994). Substantial year-to-year variation is evident both from our data alone and from comparisons among studies (Table 4). The largest summering populations are found in Admiralty Inlet, Prince Regent Inlet, Eclipse Sound, Inglefield Bredning and possibly Smith Sound-Kane Basin.

Three possible summering areas that we identified have not been systematically surveyed: Home Bay and Buchan Gulf along eastern Baffin Island and Smith Sound-Kane Basin. Of these areas, Kane Basin probably contains the largest number of narwhals; we counted

1226 narwhals along the Smith Sound ice edge and 325 along the east coast of Ellesmere Island south of there on 5 July 1979. In 1979, narwhals continued to move into Lancaster Sound until early August, so movements into Kane Basin may have continued after our last survey there, on 5 July. The presence and size of the group summering in Smith Sound-Kane Basin need to be confirmed by surveys conducted in mid-August to early September. It is possible that there is interchange between narwhals summering in Kane Basin and in Inglefield Bredning. Born (1986) estimated that at least 4000 narwhals summered in Inglefield Bredning in 1984, and Born *et al.* (1994) estimated that numbers in Inglefield Bredning were between 847 and 1366 in 1985 and between 2683 and 4369 in 1986. Although their surveys did not include Hvalsund, where some narwhals may summer, the large inter-year variation suggests that some whales that summered in Inglefield Bredning in 1984 and 1986 summered elsewhere in 1985.

Riewe (1977) suggested that Jones Sound is a summering area for narwhals in some but not all years. We saw few narwhals along the Jones Sound ice edge during the 3–4 weeks previous to break-up or during four surveys in late summer and early autumn. We suspect that narwhals may concentrate along the Jones Sound ice edge to feed during their spring migration north into Smith Sound and Kane Basin, but that only a few tens of narwhals normally summer in Jones Sound.

Autumn

Autumn migration from summering areas begins in late September just before summering areas begin to freeze. During autumn, narwhals tend to migrate in large herds ranging in size from a few hundred to several thousand animals. Narwhals that summer west of, or in the vicinity of, Lancaster Sound follow both coasts of Lancaster Sound eastward. A large proportion of the narwhals from Admiralty Inlet cross to the north side of Lancaster Sound and follow the south coast of Devon Island eastward into offshore Baffin Bay. Narwhals that follow the south coast of Lancaster Sound continue southeastward along the coast of Baffin Island. Observations from Cape Adair along NE Baffin Island suggest that a substantial proportion of the population follows the coast southward in some years; however, poor weather and darkness have prevented accurate estimation of the proportions of the population that use coastal and offshore routes. After freeze-up begins, narwhals disperse among the offshore pack ice where southward movements continue.

Swimming speed

We estimated the swimming speed of migrating narwhals as 5–12 km/h over periods varying from 0.8 to 17 h. We did not obtain estimates for other times of year but our impression was that movements during autumn were faster and more directed. Our estimated speeds are faster than those for narwhals in summering areas (Fallis *et al.* 1983) but are slower than those for rapidly-migrating (Koski & Davis 1979: 14 km/h) or fleeing white whales (Vladykov 1944: 14–18 km/h).

Relative age and sex composition

Our data indicate that narwhals are segregated by age and sex during some times of the year. During late winter, females are found farther south than males. In addition, females with 7- to 8-mo-old calves are found in areas of heavier ice conditions than are other females. During late spring, male narwhals precede females during movements toward summering areas; this temporal segregation was also recorded by Greendale & Brousseau-Greendale (1976). When moving into summering areas, adult males follow coasts and ice edges, whereas females and young move through offshore waters.

Silverman (1979) observed that although herds of narwhals in summering areas were not segregated by age or sex, pods or groups within the herds were segregated. We observed the same segregation within herds both during summer and during fall migration.

Based on our overall data from surveys of summering areas, which may be biased by overestimates of numbers of adult males, 67% of narwhals are estimated to be adults. Other surveys of summering areas have yielded similar proportions of adults and subadults (for a review see Born *et al.* 1994: Table 5).

Calf production

Data from summering areas suggest that the birth rate was 0.29 calves/adult female/year based on sightings of 1-mo-old calves. With an allowance for some early mortality and aborted fetuses, our data agree with those of Hay (1984) who found a range of pregnancy rates of 0.30–0.38/adult female. For the summering area of Scoresby Sund in eastern Greenland Larsen *et al.* (1994) reported a ratio of neonates to total number of females of 0.38. Kingsley *et al.* (1994) estimated 9.6% calves among 1395 narwhals that they classified and Born *et al.* (1994) estimated 14.9% among 228 animals. Silverman (1979) estimated that neonates made up 10.3% of the narwhals in Tremblay Sound during 1977 and 1978; males and females were 44% and 56% of her adult sample so that the sex bias in her sample was opposite to ours. Her data may slightly overestimate the proportion of calves in the total population. Our direct observations suggest that 1-mo-old calves form 7.8% of the sampled population but males may be over-sampled during our surveys. If the sex ratio of males:females is equal, and we equalize the sex ratio in our sample, calves make up 9.0% of all narwhals in late August to early September. With an allowance for

the potentially biased sampling in Silverman's (1979) study, her data are similar to ours but still have a higher proportion of calves. Based on a review of the narwhal literature, Strong (1988) suggested an annual population birth rate of 0.07 (*i.e.* calves would make up 6.5% (7/(100+7)) of all narwhals). Our data, which are from only two years, and the data of Silverman (1979), Born *et al.* (1994) and Kingsley *et al.* (1994) suggest that this estimate may be low. Collection of data on the age and sex ratios of narwhals from different summering areas should be a high priority of future surveys. Surveys should be either low-level photographic surveys (150 m a.s.l. with a 200–300 mm lens) or aerial count surveys by experienced observers; we have found that many observers can not reliably distinguish the various age classes that we used during this study.

Other life history data

Timing of calving

Our data suggest that most narwhals calve after mid-July when they normally would be in summering areas. Although the relative ages of few narwhals were estimated during our surveys in coastal/ice-edge areas, we would have recorded many neonates had they been common. Only three neonates (<1% of sightings) were recorded before mid-July during two years of intensive surveys yet 5.9 to 10.2% of animals in summering areas surveyed in late August to early September were neonatal calves. These data are consistent with those of Best & Fisher (1974). They listed dates and sizes of narwhal fetuses and neonates from the literature and found only one record of a neonate before July (28 June 1936, in Eales 1950). Best & Fisher (1974) found three records of near-term fetuses in early July but no other records of neonates until 12 July. Analyses conducted by Hay (1984) agree with our observations and those of Best & Fisher (1974). Using data on fetal sizes and growth rate, Hay (1984) estimated that narwhals calve from 30 June to 29 August. Data presented by Cosens & Dueck (1990) appear to suggest that neonatal calves are common in May and June at the mouth of Admiralty Inlet. They reported 22 narwhal neonates from 27 May to 25 June 1986; this was approximately 6% of the animals observed in groups that contained neonates (Cosens & Dueck 1990). However neonates were only 2% of all narwhals that they sighted during their surveys (Sue Cosens, Depart. of Fish. and Oceans, Winnipeg, pers. comm.). Their surveys were conducted over the same general area on most days, so that it is possible that some were sighted repeatedly. The sightings reported by Cosens & Dueck (1990) may represent a few mothers with neonates that moved toward summering areas in Admiralty Inlet earlier than other whales. It is also possible that a few of their sightings were narwhal yearlings that were mistaken for neonates (Sue Cosens, pers. comm.).

Calf mortality

Our data from the summering areas permit estimation of mortality during the first year of life. One-mo-old calves made up 7.8% of our 1978–79 sample and 13-mo-old yearlings made up 6.5%. Therefore, first year mortality is estimated at 17% ((7.8–6.5)/7.8). A second estimate of mortality can be made using the same data. Neonates were 8.7% of all narwhals recorded in summering areas in 1978 and yearlings were 6.6% of all narwhals recorded in summering areas in 1979. If neonates born in 1979 are excluded from the 1979 sample, yearlings were 7.2%. Again the mortality from age 1 mo to 13 mo is estimated to be 17% ((8.7–7.2)/8.7). These estimates of mortality are not independent since the second uses a subset of the data used for the first. They must be treated cautiously because mortality rates may vary among years and small changes in the proportion of calves or yearlings in either 1978 or 1979 would cause large changes in estimated mortality rates.

Numbers of narwhals

Narwhals were widely dispersed among the pack ice in Baffin Bay during May and June. Our best estimates of the size of the narwhal population come from surveys conducted at this time of year. These estimates include narwhals that later summer in both Canadian and Greenland waters. In 1979, we estimated that 29 931 (± SE 7008) to 38 988 (± SE 6629) narwhals were present in offshore waters of our study area during four different surveys (Table 8). The four individual estimates were remarkably similar given the low overall coverage. The mean number present was 34 363 (± SE 8282). In addition to the offshore animals, some narwhals were present along coasts and ice edges in and north of the study area and others may have been present in the offshore pack ice east of the surveyed area. Throughout the offshore surveys in all years and all seasons, narwhals strongly preferred ice cover of 90–99%, and less strongly, ice cover of 80–89%. The only suitable narwhal habitat that was not directly covered by our estimates during the late spring of 1979 was in eastern Baffin Bay, to the east of block B, and to the east and northeast of block C (Fig. 11). These areas are not large in comparison to the area included in the estimates. However, some additional narwhals were undoubtedly present in the unsurveyed areas, particularly during the 19–23 June survey when many were recorded in the eastern part of block C (Fig.11).

The estimates for offshore waters have not been corrected (1) for animals that were present near the water surface but were not seen by observers or (2) for animals that were below the surface and not recorded. They do include animals that were seen swimming below the surface, whether or not they surfaced in view of the observers. We believe that few animals near the surface

were missed during these surveys. Most of the survey area was covered with extensive ice pans, enabling observers to search the few cracks and leads, both ahead of and behind the aircraft. The prolonged search of these restricted open-water areas made it less likely that observers would miss an animal that was present on the surface; it also permitted detection of animals that were below the surface when the aircraft was perpendicular to them but that surfaced up to one minute before or after the normal viewing period.

Dueck (1989) studied the behaviour of narwhals during the open-water period in Admiralty Inlet and found that narwhals were visible at the surface only 38% (95% CI 29–52%) of the time. Born *et al.* (1994) found that narwhals were present at the surface for a similar (36%) proportion of the time while travelling. Thus, to correct instantaneous counts for the probability that a narwhal is below the surface, counts should be multiplied by 2.63–2.77 (1.00/0.38 or 0.36). Their data could be used to calculate a correction factor for submerged animals that allows for the extended search period during our surveys (see Eberhardt 1978). However, narwhal behaviour is likely different in offshore pack ice in spring than in open water in Admiralty Inlet and Inglefield Bredning in summer and any such calculation is of dubious validity.

Previous studies have not attempted to estimate the size of the entire narwhal population but several studies have estimated the numbers in various summering areas (Table 4; see also below) and the numbers of narwhals entering Lancaster Sound. Narwhals that enter Lancaster Sound summer primarily in Admiralty Inlet, Prince Regent Inlet and Peel Sound. Davis *et al.* (1978) used a combination of aerial surveys and ground-based observations to estimate the number of narwhals that entered Lancaster Sound in 1976. Their estimate of 20 000–30 000 animals was based on several conservative decisions and the actual number may have been higher.

Smith *et al.* (1985) attempted to estimate the number of narwhals in the Canadian High Arctic. They estimated that 11 142 (95% CL 9035–13 891) narwhals were present within their survey area in Lancaster Sound, Barrow Strait and Prince Regent Inlet and that an additional 2000 and 2117 were present in Peel Sound and Admiralty Inlet, respectively. Thus their total estimate was 13 200–18 000. Although Admiralty Inlet is a major summering area for narwhals entering Lancaster Sound (see below and Table 4), Smith *et al.* (1985) did not include Admiralty Inlet in their survey area and their allowance of 2117 for this area is likely low. In addition, for Prince Regent Inlet in early August, Smith *et al.* (1985) extrapolated densities recorded in northern Prince Regent Inlet to unsurveyed areas in central Prince Regent Inlet even though higher densities occurred on transects in the northern half of the area that was surveyed. Therefore, the Smith *et al.* (1985) estimate of 10 807 for Prince Regent Inlet may be an overestimate.

Richard *et al.* (1994) conducted photographic surveys of Peel Sound, Prince Regent Inlet, Admiralty Inlet and Eclipse Sound during 1984. Their combined estimate was 18 000 (90% CL 15 000–21 000) for the areas that they surveyed. The areas surveyed by Richard *et al.* likely contained most of the narwhals that entered Lancaster Sound in 1984. There was little ice in Barrow Strait and Lancaster Sound at the time of their survey, and their maps of narwhal distribution suggest that most narwhals had entered summering areas. They concluded that most of the biases in their estimates were negative and agreed with Davis *et al.* (1978) that the Canadian High Arctic narwhal population was probably 20 000–30 000 animals.

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