Abundance and stock composition of narwhals *(Monodon monoceros)* in Inglefield Bredning (NW Greenland)

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The abundance of narwhals *(Monodon monoceros)* was estimated in Inglefield Bredning (NW Greenland) during the open-water season. Land-based observations were made in August 1985 and 1988 and aerial surveys using line-transect methodology were flown during late August 1985 and early August 1986. Group sizes based on both land-based and aerial surveys are given in relation to behavior and the age and sex composition of groups. The aerial surveys in 1986 indicated that adults comprised about 68%, non-adults (including neonates) 32%, and neonates about 15% of the population present in Inglefield Bredning. On 20 August 1985 a direct land-based count of 1548 whales was obtained in the eastern part of Inglefield Bredning. The aerial surveys in August 1985 resulted in estimates of between 847 (95% CI 344–2085) and 1366 (95% CI 854–2276), uncorrected to account for those out of sight underwater. The aerial surveys in 1986 resulted in uncorrected estimates of between 2683 (95% CI 1029–6998) and 4369 (95% CI 2037–9341). Between late July and mid-August 1988, remarkably fewer narwhals were observed from land in the eastern parts of Inglefield Bredning. The maximum number of narwhals that could be accounted for during this period was 473 narwhals.

Key words:
Narwhal, *Monodon monoceros*, NW Greenland, line transect, aerial survey.

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Introduction

Narwhals (*Monodon monoceros*) occur in waters bordering northwestern Greenland during summer. Their presence in the Smith Sound area in July, prior to break-up of the fjord ice in Inglefield Bredning (Kangerlussuaq) in the Avanersuaq (Thule) area, was reported by Koski & Davis (1979, 1994) and Born & Knutsen (1990). Meldgaard & Kapel (1981) and Born (1987a) reported observations of narwhals in Melville Bugt during August. Although narwhals have been observed in large numbers along eastern Ellesmere Island (Canada) close to the Thule area, Inglefield Bredning is the major narwhal summering area in northwestern Greenland (Vibe 1950, Born 1986). Prior to ice break-up, which usually occurs about mid-July, the narwhals use lead systems in Hvalsund (Fig. 1) to penetrate the summering areas at the head of Inglefield Bredning. Although some narwhals migrate via Murchison Sund which is relatively shallow, the main migration usually occurs in the southern parts of the deeper Hvalsund. By the time of the formation of solid new ice, usually between late September and early October, the narwhals have left Inglefield Bredning (Born 1986). Observations of narwhals in Inglefield Bredning, with estimates of numbers, were reported by Vibe (1950), Bruemmer (1971), Durham (1979), Born (1986, 1987a), Heide-Jørgensen & Leatherwood (1987) and Born & Knutsen (1988). In Inglefield Bredning, hunting of narwhals is an important element of the maritime subsistence hunting by Inuit (Vibe 1950, Bruemmer 1971, Durham 1979, Born 1987b).

Information on group size and the sex and age composition of narwhal populations has implications for the evaluation of survey results and hence for the determination of population status. Such information has been

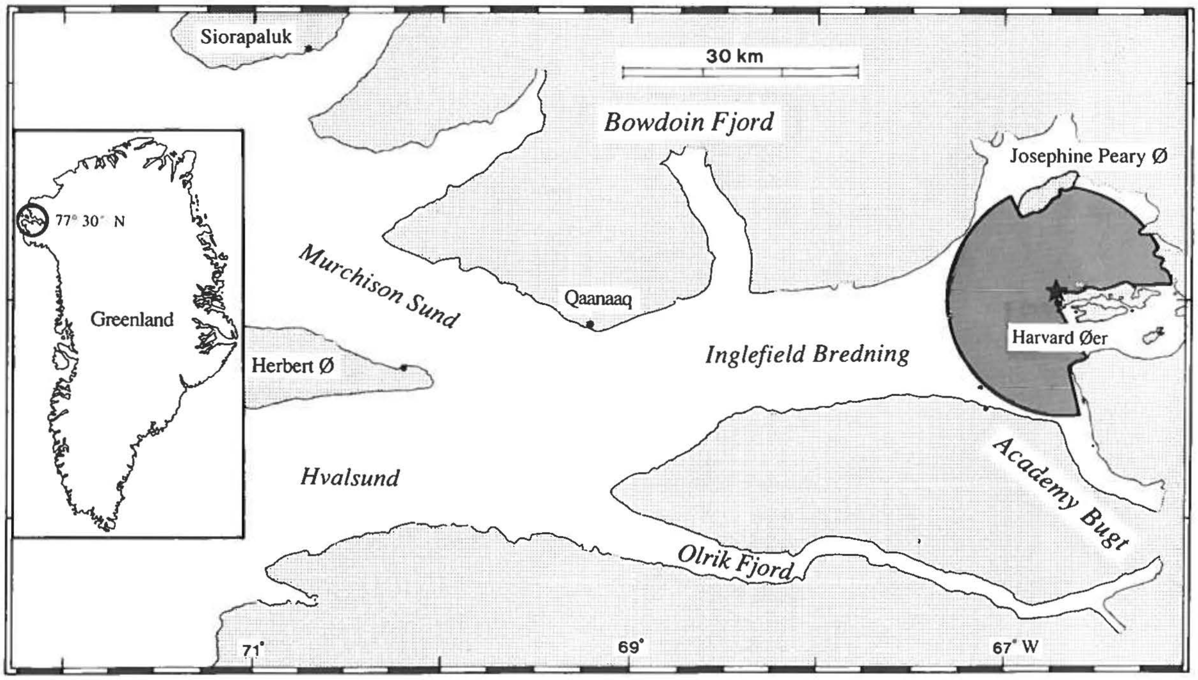

Fig 1. A: Inglefield Bredning study area with the observation site (⋆) on Harvard Øer (Qeqertat) used for land-based observations in 1984, 1985 and 1988. The perimeter of the observation area is shown.

presented from inshore narwhal summering areas in Canada (*e.g.* Silverman 1979, Fallis *et al.* 1983, Koski & Davis 1994, Kingsley *et al.* 1994) but not from Greenland. For comparative reasons such information collected in Inglefield Bredning in 1984, 1985 and 1988 is presented in this paper. We also present results of land-based surveys in August 1985 and 1988 and of aerial surveys in August 1985 and 1986, with the primary objective of estimating the number of narwhals in Inglefield Bredning.

Materials and methods

Land-based surveys

In 1985 and 1988 a continuous watch for narwhals was maintained from the 78-m high promontory of Nuussuaq, situated on the northwestern tip of Harvard Øer (Qeqertat) in Inglefield Bredning (Fig. 1; photo). This same site had been used for narwhal studies in August 1984 (Born 1986). Although much of the 1984 data was published by Born (1986), the estimates of group size were not; they are included here for comparative purposes. In 1985 observations were made for a total of 403 hours (59% of available time during the period) between 2 and 30 August. In 1988 a total of 105 hours (49% of available time) was used for observations between 30 July and 1 August, and from 6 to 11 August. In 1985, and during the first segment of the 1988 study, the team consisted of three observers. During the second segment in 1988 only two observers participated. In 1985 a Svarowski binocular telescope (30 × and 75 × magnification) and 7 × 50 Zeiss binoculars were used. In 1988 a Kowa SN-1 monocular zoom telescope (20 × - 60 ×) and Zeiss binoculars (7 × 42) were used.

A narwhal group (pod) was defined (after Silverman 1979) as one or more narwhals swimming in close proximity (no more than a few meters, and usually less than one meter, apart). An aggregation of two or more narwhal groups is called a herd.

We attempted to maintain watch round the clock in continuous light conditions. Observation was usually suspended when the sea state exceeded Beaufort 1, because it was no longer considered possible to detect and observe narwhals reliably at any distance. The entire observation area was searched carefully through the telescope at least once every hour. Depending on observation conditions (for example sea state or haze) and the number of observations, the scanning lasted between half an hour and one hour. Between the scannings the area was studied regularly by use of hand-held binoculars. For all observations of narwhals the following was recorded: time, position (compass direction to observation and estimated distance in km), direction of movement, behavior and herd and group size. Wind force (m/sec at observation level), sea state and cloud cover (in octas) were also noted. It was possible during good conditions (*i.e.* calm and clear with no haze or mirage) to detect and count narwhals out to a distance of 14–15 km from the observation site. Crude distances to observations were obtained by comparison with known distances to points on the surrounding coasts. However the relatively low angle and great distance involved in the majority of observations made it impossible to collect data on sex and age of the narwhals consistently.

During directed movement narwhals spend proportionally more time at the surface than they do when milling or remaining in the same area (Silverman 1979, Cosens & Dueck 1988). In 1985 we used methods described in Born (1986) to count narwhals in herds when the animals showed fast "directed movement". In 1988, when fewer narwhals were present within the study area, we also attempted to count narwhals in stationary herds. Whenever possible, numbers of animals in groups were counted. In cases where the behavior of a herd did not allow counting of individuals, we estimated the herd size by multiplying the total number of groups by the mean group size obtained for that particular behavior (see Results. Group size etc.).

Replicate counts of herds under similar observation conditions were made in 13 cases in 1985. These herds remained within the study area between the counting sessions, and no immigration to, or emigration from, the herds during the short period of time between the counts was observed.

Dive times for groups were recorded under circumstances where the group in question could not be mistaken with other groups. Time spent at the surface and submerged was noted with distance travelled at the surface and submerged, respectively. Crude estimates of distance were obtained by comparing the length of the group's track with lengths of individuals. Similar data on dive times obtained in 1984 and 1989 are included.

Aerial surveys

Survey coverage and procedures

Between 27 August and 3 September 1985 four systematic aerial surveys were flown in Inglefield Bredning and adjacent fjords (Figs 2 a & b; Table 1). On 25 August 1985 a reconnaissance survey was flown over Inglefield

A view to the west from the 78-m high observation site on Harvard Øer (Inglefield Bredning) used for observation of narwhals in 1984, 1985, 1987 and 1988. Photo: E. W. Born.

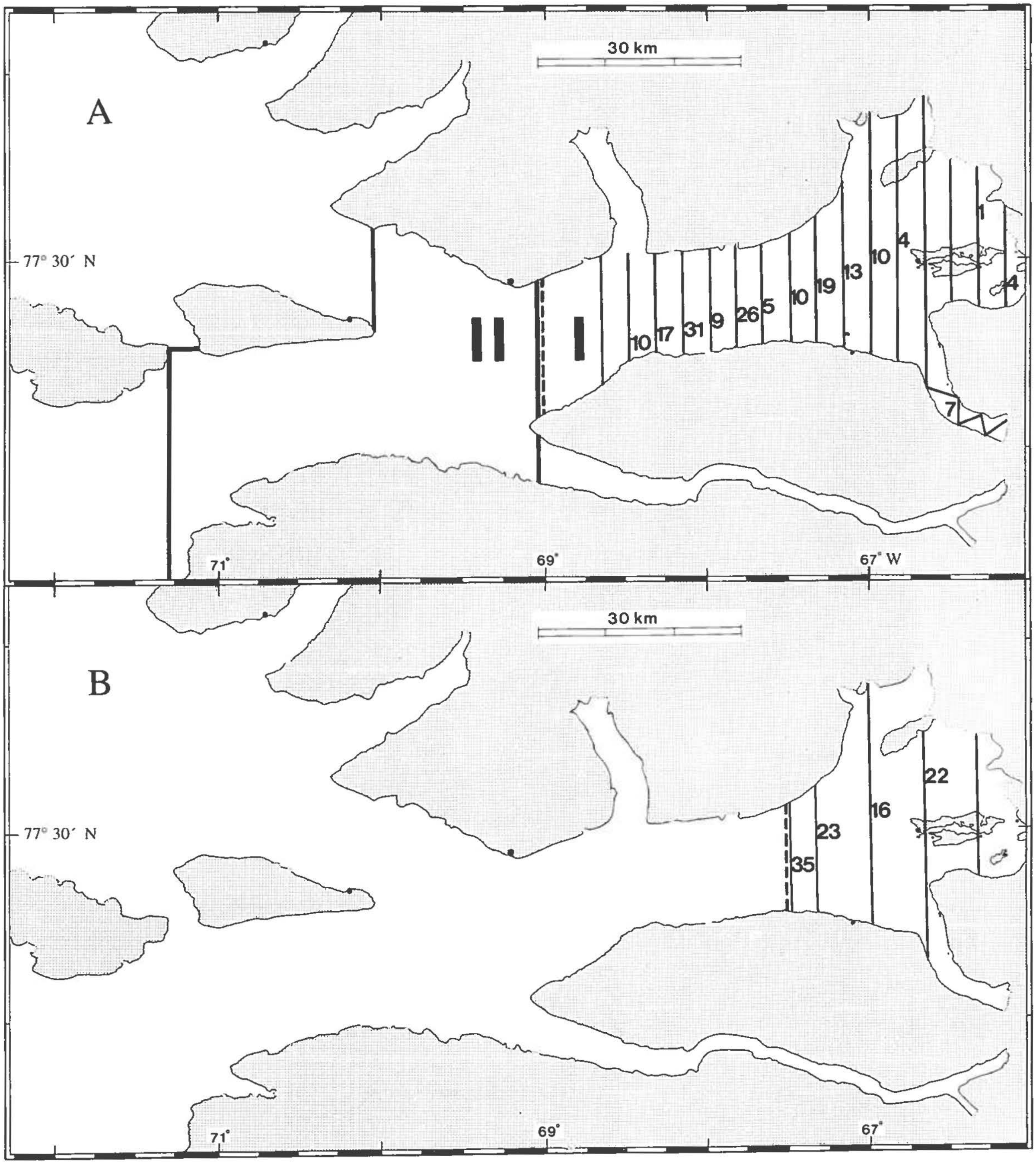

Fig. 2a. A: Inglefield Bredning with Strata I and II used for aerial surveys of narwhals in August 1985 and 1986. Figures at the transect lines refer to total number of narwhal groups observed on 27 August 1985. B: Survey lines flown on 28 August 1985. Legend: Solid lines = transects with sea state 0 and 1 (used for calculation of abundance of narwhals). Broken lines = borders of sample area (A) used for calculation of abundance of whales.

Bredning with the purpose of collecting data on narwhal group size. In 1986 five aerial surveys were conducted in the same areas between 6 and 10 August. Olrik Fjord and Murchison Fjord were not surveyed in either year because narwhals are known to be rare in these relatively shallow fjords.

In 1985 the fast fjord ice had disappeared from the study area before the surveys. Thus the ice coverage was

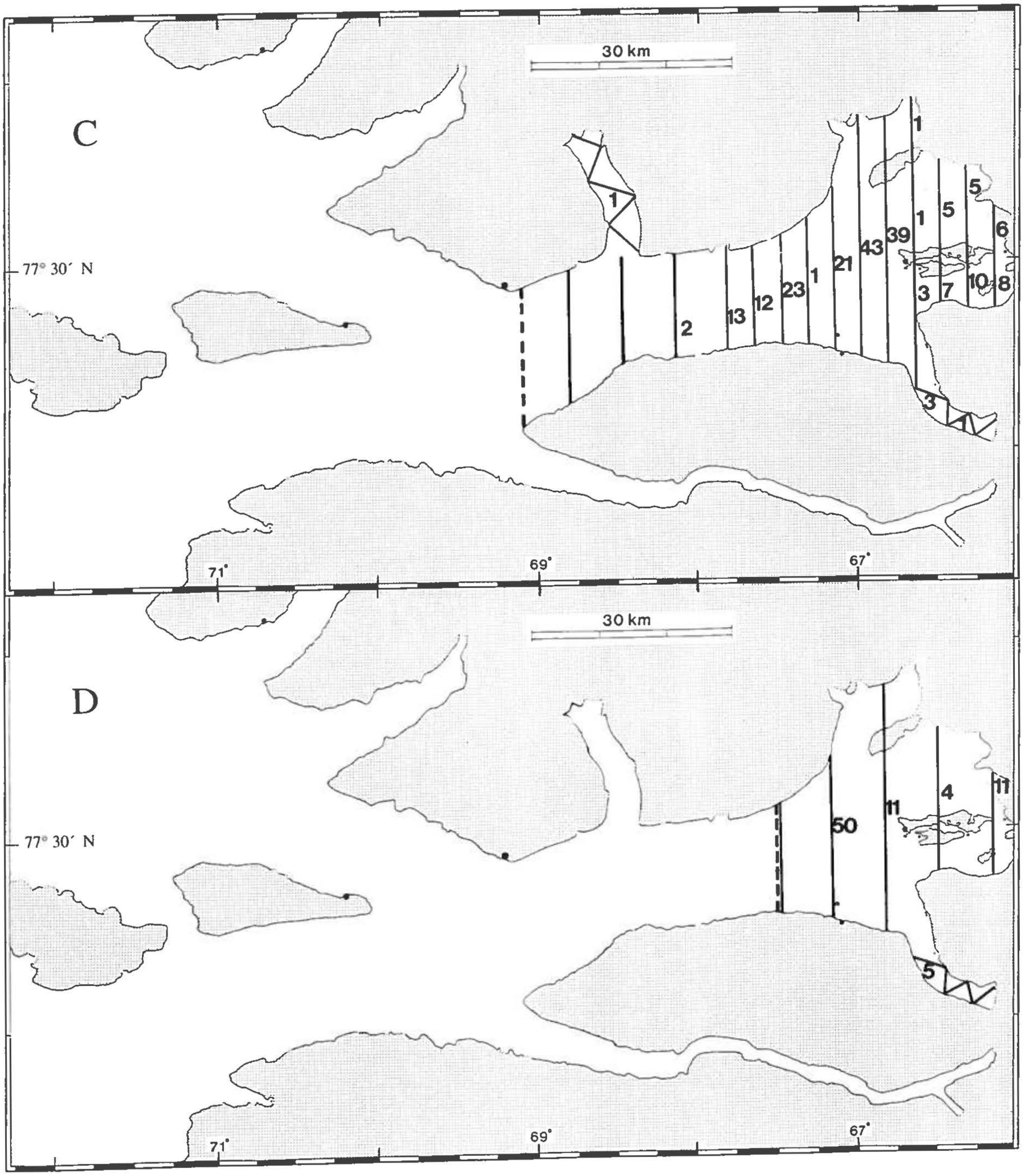

Fig. 2b. C: Inglefield Bredning with transect lines flown on 29 August 1985 with observations of groups of narwhals. D: Transect lines flown on 3 September 1985 and observations of groups of narwhals.
Legend: Solid lines = transects with sea state 0 and 1 (used for calculation of abundance of narwhals). Broken lines = borders of sample area (A) used for calculation of abundance of whales.

less than 10% and consisted entirely of ice bergs. Adverse weather prevented us from surveying the entire study area (which included Hvalsund) systematically, so we concentrated our effort on areas where high densities of narwhals were known to occur (Born 1986): Inglefield Bredning, Bowdoin Fjord and Academy Bugt (Figs 2 a & b). In August 1986 parts of Inglefield Bredning were still covered by fjord ice during the surveys (Figs 3 a & b).

Table 1. Aerial surveys flown over Inglefield Bredning (Thule area, NW Greenland) and adjacent fjords in 1985 and 1986 (see also Figs 2 a–b, and 3 a–b).

Year	Month	Day	Target altitude (m)	Area surveyed: Stratum (transect number) I	Stratum (transect number) II	Academy Bugt	Bowdoin Fjord
1985	Aug.	25	264	Survey to obtain group size data			
1985	Aug.	27	183	1–16	–	+	–
	Aug.	28	183	2–9	–	–	–
	Aug.	29	183	1–17	–	+	+
	Sep.	3	183	1–9	19–23, 25–29	+	–
1986	Aug.	6	305	1–18	–	+	+
	Aug.	6	305	–	19–32	–	–
	Aug.	8	305	7–14	–	–	+
	Aug.	9	305	1–18	–	+	+
	Aug.	9	305	1–18	–	+	+
	Aug.	10	915	6–18	–	+	+

In both years the survey lines were placed systematically with intervals of 10° longitude (distance between transects = 4.13 km) in Inglefield Bredning and Hvalsund. Inglefield Bredning was denoted stratum I and Hvalsund stratum II. When time allowed, Bowdoin Fjord and Academy Bugt were surveyed in a "zigzag" manner which was operationally convenient. However, due to time constraints the flight track followed the coast in these fjords in some cases in 1986.

In both years the surveys were carried out in a Partenavia P68 Observer, a high-wing, twin-engine aircraft with a plexiglass nose. In 1986 bubble windows were installed on each side at the rear observers' seats, thus allowing for the detection of narwhals on or close to the track line. Navigation was by a Litton 3000 Omega navigation system corrected by observations of recognizable land marks. All surveys were flown at an airspeed of 167 km/h (90 knots). In 1985 the systematic surveys were flown at a target altitude of 183 m (Table 1). The 1986 surveys were flown at a minimum of 305 m. A survey was also conducted at 915 m on 10 August 1986 when weather conditions were excellent (Table 1).

In 1985 there were two observers, both sitting in rear seats. In 1986 a different crew of three observers participated. The third observer sat in the co-pilot's seat and his effort was dedicated to recording ice cover, sea surface conditions and the size and composition of narwhal groups. The observers sitting in the rear seats recorded sightings of narwhal groups. By using inclinometers the rear observers measured the angle between the horizon and each narwhal group when the sighting was abeam the aircraft. If time allowed (depending on the concentration of groups) the observers also recorded direction of movement of the groups, reactions to the aircraft and other behavior, group size and group composition. When possible, narwhals were classified by their sex and relative age, based on size and coloration. Size categories used were: adults (3.5–5+ m; light mottled appearance); subadults (2–3.5 m; uniformly dark); neonates – young of the year (about 1.6 m, grayish brown). Animals with a tusk were regarded as males, all other adults as females. This information was collected in a consistent manner in 1986, but more sporadically in 1985. In 1985 all data collected by the two observers were recorded by one of the observers on a tape recorder. In 1986 data were recorded individually by the observers on cassette tape recorders.

Treatment of data from the aerial surveys

Line transect estimates of group density were made using the theory and techniques described in Burnham *et al.* (1980). For calculating probability density functions, f(x), sighting rates, N/L, and their associated empirical variances, we used the computer package "Distance" developed by Laake *et al.* (1991).

The distribution of perpendicular distances was fitted to the half-normal model, the negative exponential model, the hazard-rate model and a Fourier series. Adding of up to three adjustment terms was allowed. The model with the least adjustment terms, lowest coefficient of variation (CV) of f(0) and best goodness of fit determined by the chi-square distance between observed and expected distances was chosen. The chosen model was scaled to integrate to 1 to derive the f(x) which was evaluated at f(0) to obtain the Effective Search half-Width (ESW).

The stratum density of narwhals, D, was estimated as:

$$D = \frac{N \cdot f(0) \cdot C}{2 \cdot L} \quad (1)$$

where N is the number of sightings of groups, C is the mean group size and L is the linear distance (in km) that was searched.

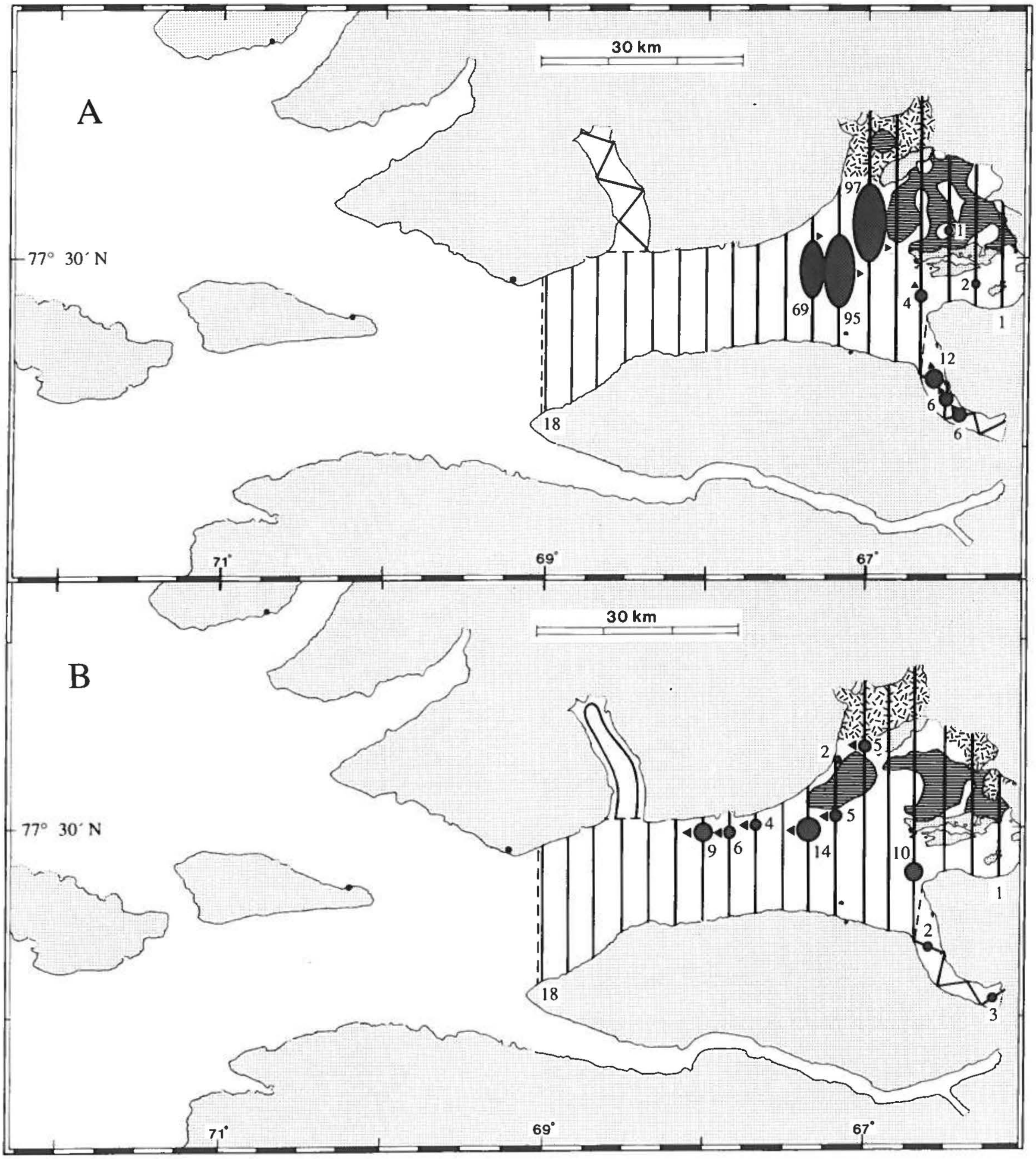

Fig. 3a. A: Transect lines flown during first aerial survey on 9 August 1986 with total number of groups of narwhals recorded by the rear observers. B: Transect lines flown during second aerial survey on 9 August 1986.
Legend: Arrows indicate main direction of movement of groups. Broken lines = borders of sample area (A) used for calculation of abundance of whales. ⛋ = 4–6/10 ice cover, ▤ = solid fjord ice ● = narwhal herd

Stratum variance of narwhal density and abundance was estimated according to Burnham *et al.* (1980):

$$var(D) = D^2(CV(f(0))^2 + CV(N/L)^2 + CV(C)^2) \quad (2)$$

where CV is the coefficient of variation calculated as the standard error in proportion to the mean.

We assumed that D has a log normal distribution, and we constructed the 95% confidence interval using the method developed by Burnham *et al.* (1987) where the

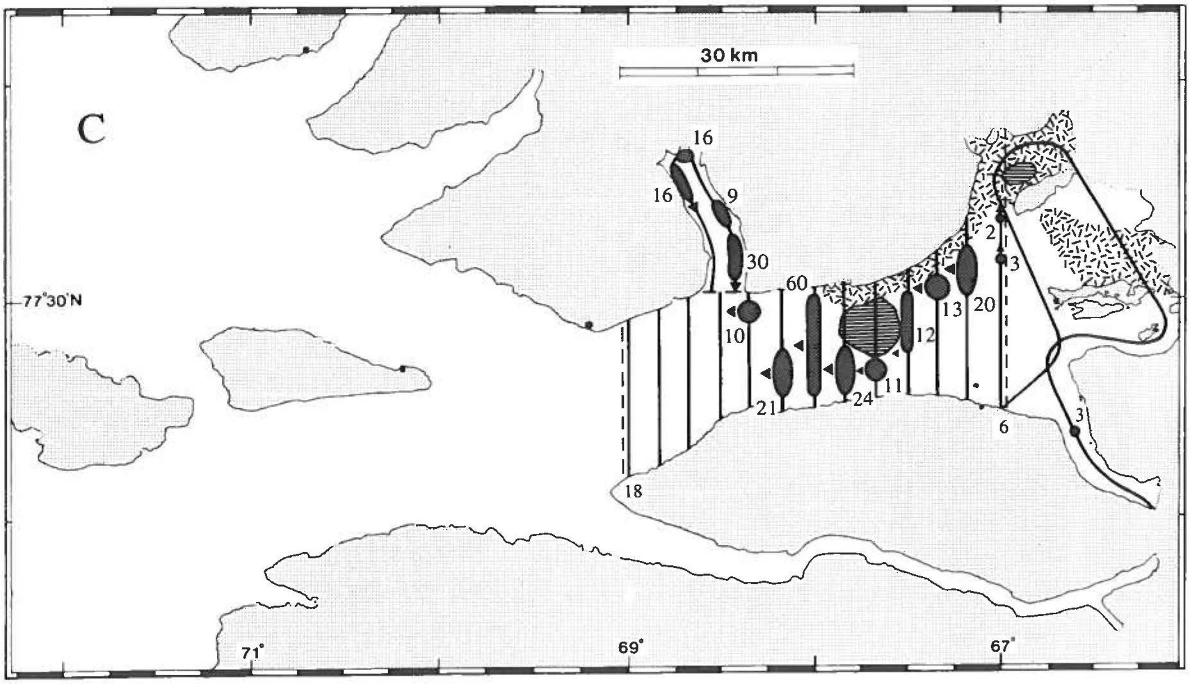

Fig. 3b. C: Transect lines flown during the aerial survey on 10 August 1986. Calculations of abundance of narwhals on this date (Table 9) refer to the area between transects 6 and 18. See also legend to Fig. 3 a.

lower and upper confidence limits are D/V and D · V, respectively, and:

$$V = \exp[1.96 \cdot \sqrt{\{ \mathrm{var}(\ln D)\}}] \quad (3)$$

where

$$\mathrm{var}(\ln D) = \ln[1+\mathrm{var}(D)/D^2] \quad (4)$$

For the data collected in 1985 we made an inside truncation at 150 m and an outside truncation at 1200 m from the track line. For the 1986 data an outside truncation was made at 2000 m from the track line.

Because the transects were short, a weighting factor was not applied to the counts for meridian convergence. For calculation of total number of narwhals, densities were extrapolated only to those parts of the fjord system (total sample area A) that were surveyed systematically during that particular survey (Figs 2a–b & 3a-b). Areas covered with solid fjord ice were subtracted from the total sample area (A) and the transect area (a).

A correction factor to compensate for submerged animals that were missed during the flights was *not* applied in any of the calculations, which thus apply only to the visible portion of the population.

Table 2. Narwhal group sizes from land-based counts in Inglefield Bredning, August 1984, 1985 and 1988. In 1988 group sizes were counted both during directed movement and when the groups were stationary (see text). * = counted when the group formed a feeding aggregation.

Year	Median	Mean	SD	Range	N	Remarks
1984	4.8	7.2	6.2	1–35	72	Directed movement
1985	6.8	8.9	8.2	1–63*	65	Directed movement
1988	4.8	5.7	2.8	1–15	122	Directed movement
1988	2.5	3.6	2.7	1–16	129	Stationary

Results

Group size, sex and age composition and dive times

Group sizes recorded during land-based surveys

Estimates of group size obtained during the land-based observations are presented in Table 2. In 1985 the frequency distribution of group size was significantly different from that in 1984, and also from the comparatively large male-female groups reported by Silverman (1979: fig. 8c) for the openwater season in Lancaster Sound (Kolmogorov-Smirnov (K-S) two-sample tests; $P < 0.05$). The frequency distribution of group sizes observed by us in 1984 did not differ significantly from that reported by Silverman (1979) for Lancaster Sound (K-S; $P > 0.05$).

Table 3. Narwhal group sizes from aerial surveys in Inglefield Bredning on 25 August 1985 and between 6 and 10 August 1986.

Year	Day (Aug.)	Median	Mean	SD	Range	N
1985	25	2.0	2.2	1.6	1–9	80
1986	6	2.7	4.1	3.4	1–12	15
	8	1.8	2.9	2.3	1–13	158
	9 (1st)	1.7	2.9	2.4	1–23	267
	9 (2nd)	5.1	6.5	4.4	1–32	85
	10	2.2	4.0	3.3	1–18	325

In 1988 group sizes were also recorded when groups within a herd were scattered widely over a large area. This behavior, where the herd is "stationary" and many of the groups are "circling" ("milling"), is thought to be associated with feeding and social activity (Silverman 1979). The narwhals often remained almost stationary, infrequently exposing a small portion of their back; such behavior was described as "hanging" and "back exposed" by Silverman (1979) and Cosens & Dueck (1991). In 1988 the frequency distribution of group sizes obtained during fast directed movement differed significantly from that when the herd was stationary (K-S, $P < 0.01$). Furthermore, noticeably more narwhals occurred singly during the stationary situation than during directed travel in all years. The frequency distribution of travelling group size in 1988 did not differ significantly from that in 1984 (K-S; $P > 0.05$) but did differ significantly from that in 1985 (K-S; $P < 0.05$).

Group sizes recorded during aerial surveys

Group sizes observed during the aerial surveys are given in Table 3. The mean group sizes in 1986 were somewhat larger than those in 1985, but the difference was not significant (Mann-Whitney U-tests, $P > 0.05$). The frequency distributions of group sizes obtained by the front observer and by the rear observers in 1986 did not differ significantly (K-S, $P > 0.05$). In none of the surveys were there statistically significant differences between group sizes observed in different sea states (K-S; sea states 0,1,2, 3 and 5; $P > 0.05$). Group sizes observed during the second survey on 9 August 1986 differed significantly from those observed during the other surveys (Mann-Whitney U-test, $P<0.05$). The somewhat smaller group sizes from the surveys in 1985 and on 6, 8, 9 (1st) and 10 August 1986 did not differ significantly from group sizes observed during the land-based surveys in 1988, when narwhals were counted in essentially stationary herds. Neither was there a significant difference between the relatively large group sizes observed during the second survey on 9 August and the group sizes obtained in 1988 when groups were counted during fast directed movement (Mann-Whitney U-tests, $P > 0.05$).

Table 4. Percentages of narwhals classified as adult, subadult and neonate by the front and the rear observers (only for classified animals) during aerial surveys in Inglefield Bredning in August 1986.

	Adults %	Subadults %	Neonates %	N=identified
Front observer	68.0	17.1	14.9	228
Rear right observer	74.0	2.9	23.1	238
Rear left observer	64.2	9.4	26.4	261

Sex and age composition of narwhals in 1986

Of all groups observed by the front observer 39% (31% of the narwhals) were classified by sex and relative age. The rear observers classified 24% of all groups and 21% of all narwhals. Neonates comprised 14.9% and 23–26 % of all narwhals that were categorized by sex and age class by the front observer and the rear observers, respectively (Table 4). Due to a difference in proportions of neonates and subadults, the age composition of the narwhals identified by the front and the rear observers differed significantly ($\chi^2 = 19.025$; $P < 0.01$; Table 4). As the collection of data on sex and age was a primary task of the front observer but was only a secondary task of the rear observers, the front observer's data are probably more reliable. During different surveys the percentage of neonates classified by the front observer varied between 1.9 ($N_{total\ narwhals} = 58$) and 36.7 ($N = 30$). Sixty-eight per cent of the narwhals categorized by the front observer were classified as adults, 32% as subadults. The proportions of adult males and adult females were comparable with those obtained during aerial surveys in the Canadian High Arctic during the inshore summering period (Table 5).

As also reported by Silverman (1979) for narwhals summering inshore in Tremblay Sound (Canada), all-male groups (mean = 5.6 narwhals/group) and mixed groups consisting of males and females (mean = 4.4) were the largest types of group in Inglefield Bredning.

Dive times

During directed movement narwhals in a group surfaced and dived synchronously, or at least within a few seconds of one another. On a few occasions it was possible to record dive times of groups under conditions where there was no risk of mistaking one group in the area from another. During directed movement groups were at the surface for an average of 151 seconds (SD = 148.9; range: 46–481; N = 8) and submerged for an average of 264 seconds (SD = 170.1; range: 40–540 sec.; N = 16). Thus the average surface time:subsurface time ratio for travelling groups was 1:1.7 (about 64% of the time was spent submerged).

Table 5. Percentages of narwhals classified as adult, subadult and neonate during aerial and land- based surveys in various areas and seasons. * = land-based surveys; others are aerial surveys.

Area	Month	Adult (%)	Subadults (%)	Neonates (%)	Adult males (%)	Adult females (%)	Source
Off Central West Greenland	March	67	33	–	22	68	McLaren & Davis 1981
Off Central West Grenland	March	79	21	–	39	61	McLaren & Davis 1983
Offshore Baffin Bay	May-July	74–88	26–12	–	48–51	49–52	Koski 1980
Offshore Lancaster Sound	May-July	59	31	–	–	–	Koski 1980
S. coast Lancaster Sound*	June-July	82	18	3.8	68	32	Greendale & Brousseau-Greendale 1976
Inglefield Bredning, NW Greenland	August	68	32	14.9	57	43	This study
Tremblay Sound, NE Canada*	August	54.5	45.5	10.3	57	43	Silverman 1979
Lancaster Sound, NE Canada*	August	–	–	2.7	63	37	Silverman 1979
Milne Inlet, NE Canada	August	74	26	10.0	67	33	Koski & Davis 1979
Admiralty Inlet, NE Canada	August	67.5	32.5	9.1	61	39	Koski & Davis 1979
Eclipse S., Admiralty Inlet, Central Canadian Arctic	Mid.Aug. Mid.-Sep.	67.1	32.9	7.8	59.8	40.2	Koski & Davis 1994
Scoresby Sund	September	–	–	23.5	–	–	Larsen *et al.* 1994
Scoresby Sund	September	–	–	10.9	–	–	Larsen *et al.* 1994

Estimates of numbers of narwhals

Land-based surveys in 1985 and 1988

Sea and weather conditions are important factors affecting the sightability of narwhals. In 1985 weather conditions generally were more moist and windy than experienced in 1984 and during the relatively short observation period in 1988. In 1985 the sea state was 0 and 1 for 47% and 40% of the observation time, respectively. In 1988 the sea state was 0 and 1 for 73% and 27% of the time, respectively. The difference between years was significant ($\chi^2 = 21.16$; DF = 2; P < 0.01).

Narwhals rarely occurred close to the observation site on the Harvard Øer. In 74% of the 65 cases when herds could be counted in 1985 they were between 5 and 11 km from the observation site. In 1988, 83% of the 41 herds were between 4 and 8 km away when they were counted.

As also experienced in 1984 (Born 1986), the number of narwhals occurring within the observation area varied from day to day. However on many days during August 1985 more than 1000 narwhals were counted, and on 20 August 1985 a single herd with 1548 whales was observed (Fig. 4). On several occasions replicate counts of the same herd were achieved. In such cases the minimal counts averaged 85% of maximal counts (SD = 15.6, range: 54–98%, N = 13). In cases when the same herd was counted twice during fast directed movement, the minimal count was on average 92% of the maximal count (SD = 8.6, range: 75–98 %, N = 8). On six occasions when a herd was counted during both fast directed movement and other behavior (stationary or slow directed movement), the count during fast directed movement was higher. The difference between minimal and maximal counts of a herd in 1985 was not significantly different (P > 0.05; t = 1.924; DF: 11) from the difference between replicate counts reported in Born (1986).

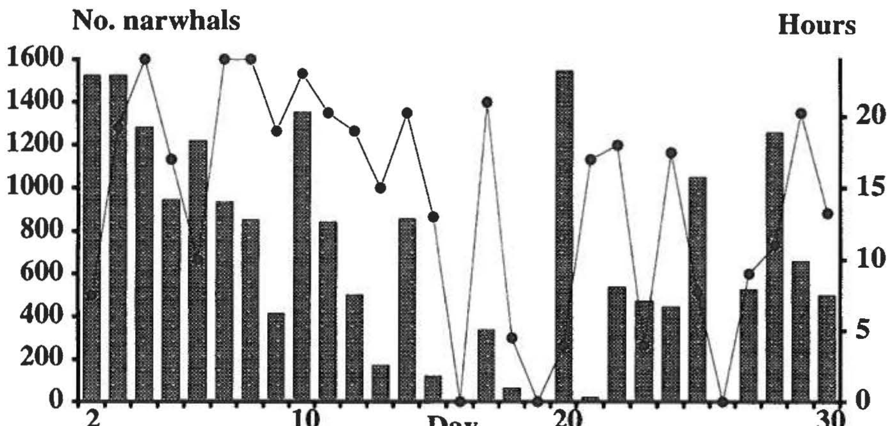

Fig. 4. Number of narwhals counted (bars) in the head of Inglefield Bredning in the period 2 to 30 August 1985, with cumulative observation time per 24 hours (dots).

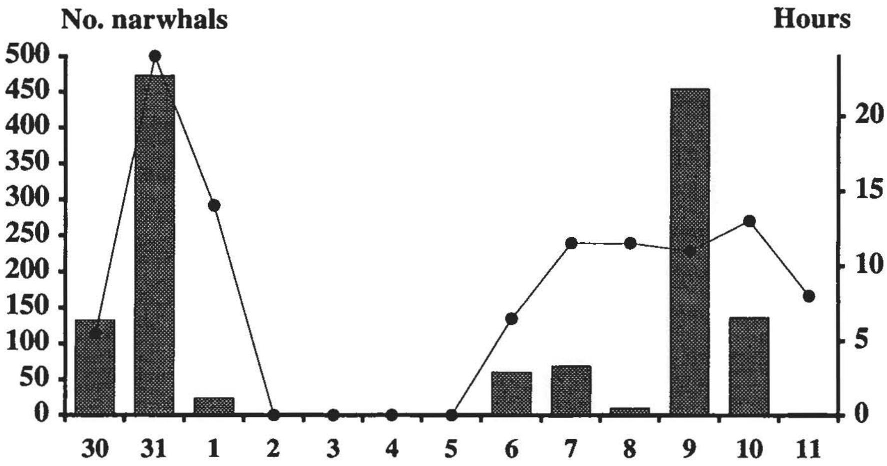

Fig. 5. Number of narwhals counted (bars) in the head of Inglefield Bredning in the period 31 July to 11 August 1988, with cumulative observation time per 24 hours (dots).

In 1988 the daily counts of narwhals within the study area fluctuated widely (Fig. 5). However the daily total number of narwhals was lower compared with the same period in 1984 (Born 1986) and in 1985 (Fig. 4). On 31 July 1988 a total of 353 narwhals in three herds consisting of a total of 55 groups were counted. At the same time another stationary herd consisting of 33 groups was observed. Multiplying by an average group size of 3.6 animals (Table 2), an estimated 120 whales were in this herd. Hence the highest number that could be accounted for at any time between 30 July and 11 August 1988 was about 473 narwhals on 31 July (Fig. 5).

Estimates of abundance based on aerial surveys in 1985 and 1986

The half-normal model was found to adequately estimate ESW for most of the stratifications of the sighting distances and hence it is used in the following. In both years detectability of narwhals decreased with increasing sea states. Both the medians of the frequencies of distance to observations of narwhals and the ESWs decreased from sea state 0 to 5 (Table 6).

In 1985 the data were not recorded in a manner that allowed tests of possible inter-observer differences. Hence the observers are assumed to have been equally efficient. However during the surveys in 1986 for which estimates of abundance of narwhals were achieved, the rear left observer detected about twice as many narwhal groups per linear km flown as the rear right observer (Table 7). Estimates of group size did not differ significantly among the three observers (K-S; $P > 0.05$).

For all three survey altitudes the sighting-distance data showed a deficiency of sightings close to the track line (Fig. 6). In calm seas narwhals were observed up to 3500 m and in some cases even up to about 10 km away. However as transects were placed 4.1 km apart, no observation beyond 2000 m from the flight track is included in the analyses. For the surveys at 183 m a bimodal distribution of sighting distances with peaks at 200–300 m and

Table 6. Sea-state specific Effective Search half-Widths (ESW) and medians of frequencies of distance to sightings of narwhals during aerial surveys in Inglefield Bredning and adjacent fjords in 1985 and 1986, respectively.

Sea state	1985					1986				
	ESW Altitude: 183 m*	CV	N	Median	N	ESW Alt.=305 m	CV	N	Median	N
0	375	0.30	98	476	119	1298	0.21	20	838	20
1	443	0.22	226	411	267	542	0.12	45	281	46
2	146	0.35	16	324	24	529	0.08	199	348	204
3	324	0.48	13	293	15	423	0.15	101	327	102
4	247	0.66	9	248	12	–	–	–	–	–
5	–	–	–	–	–	392	0.12	44	275	37
						Alt.=915 m				
1						1194	0.13	141	641	141
2						1039	0.14	31	884	31

Legend: *= ESWs were fitted to the half-normal model.
1985: Observation distances were truncated at 1200 m.
1986: Observation disatances were truncated at 2000 m.

Table 7: Observer-specific sighting rate, Effective Search half-Widths (ESW) and medians of frequencies of distance to observation of narwhals during aerial surveys in Inglefield Bredning and adjacent fjords in 1986.

Day (August)	Altitude (m)	Sighting rate (SD) (Groups/lin. km)*		ESW (CV) and Median (N)**			
				Right observer		Left observer	
		Right observer	Left observer				
9 (1st)	305	0.196 (0.350)	0.392 (0.257)	420 (0.07)	270 (90)	508 (0.11)	405 (192)
9 (2nd)	305			617 (0.53)	230 (13)	505 (0.15)	351 (45)
10	915	0.509 (0.607)	0.839 (0.625)	1244 (0.05)	839 (68)	935 (0.12)	518 (104)

Legend: *= Groups observed per linear km flown; transects without narwhals are excluded.
**= Groups observed. Observation distances truncated at 2000 m.

1200 m is indicated. Therefore, to obtain a probability density function that decreased monotonically, it was decided to truncate the 183 m survey at 1200 m.

During the aerial surveys conducted at 183 m in 1985 good sea-state conditions (0 and 1) generally prevailed. Because ESWs obtained for sea states 0 and 1 did not differ (Table 6) a common ESW for sea states 0 and 1 was derived and used to calculate abundance of narwhals on the respective dates (Table 8; Fig. 6).

The uncorrected point estimates in Inglefield Bredning and tributary fjords (Figs 2 a–b) between 27 August and 3 September 1985 range between 847 and 1366 narwhals (Table 8).

Although the 1985 estimates did not differ significantly (Table 8), the two surveys that covered only the eastern part of stratum I (Fig. 2a:B & 2b:D) revealed higher densities of narwhals than those covering the entire stratum I. This reflects the fact that narwhals occasionally concentrated in the eastern parts of Inglefield Bredning, as also was found to be true during the land-based observations.

Sea states were generally worse during surveys in 1986 than in 1985, and only about 4.7% and 29.9% of the effort was flown at sea states 0 and 1, respectively. Only a few narwhals were observed in areas with sea state 0. Calculations of ESWs include observations of narwhals in sea states 0 to 3.

During the surveys in 1986 the ESWs of the right observer varied inconsistently between surveys, whereas those of the left observer did not (Table 7). Because of this variability and because the right observer also missed a considerable proportion of the narwhals (Table 7), abundance calculations were made for these three surveys using only data recorded by the rear left observer.

The two surveys conducted at 305 m and the one at 915 m in 1986 gave almost identical estimates of narwhal density (Table 9). However due to differences in the areas surveyed, the 915 m survey provided a slightly lower estimate of abundance. Despite the inclusion in 1986 of data obtained in less favourable weather conditions, all the estimates of abundance from 1986 are larger, and some significantly so, compared with the 1985 survey results. Both at 183 m and 305 m altitudes a similar sampling effort at all distances from the track line was found, and therefore the increase in mean sighting rate (N/L) from 0.44 groups/km (95% CI 0.32–0.63) in 1985 to 0.63 (95% CI 0.40–1.01) in 1986 is a reliable estimator of an increased number of narwhals present in Inglefield Bredning in 1986 compared with 1985.

The two uncorrected point estimates of narwhals in Stratum I and tributary fjords on 9 August 1986 were 4369 and 2683 whales. These do not differ significantly and the combined estimate for the two surveys was 3539 narwhals (95% CI 1869–6722). The estimates of the visible population in the western part of Stratum I on 10 August was 1894 narwhals (95% CI 929–3752; Table 9).

On a single occasion it was possible to compare estimates of herd size obtained from the aerial surveys and the land-based surveys. On 28 August 1985, 1262 narwhals were counted in one herd at 7.5 hours from the observation site on land. This herd was observed continuously until it was covered by the aerial survey on the same day, at 13.2–13.9 hours (Fig. 2 a:B). The aerial survey resulted in an uncorrected estimate of 932 narwhals (95% CI 382–2012) in this herd (Table 8).

After the 1985 surveys some hunters in the area indicated that the engine noise of the survey aircraft had scared narwhals, causing them to dive and thereby interfering with the hunting of narwhals from kayaks. Hence, to reduce the risk of scaring the narwhals the surveys in 1986 were conducted at higher altitudes. However, even during the surveys at 305 m altitude in 1986, the narwhals often dived at distances of 500 to 1000 m in front of the aircraft, and we suspected that this was a reaction to the aircraft. When the aircraft passed over the narwhals, groups were observed approximately two to five meters under the sea surface, frequently descending. On some occasions newborn narwhals were observed alone at the surface while the mother had apparently dived, and this was interpreted by us as indicating an escape response. Of 161 groups observed by the front observer, about 18% were noted as diving in front of the

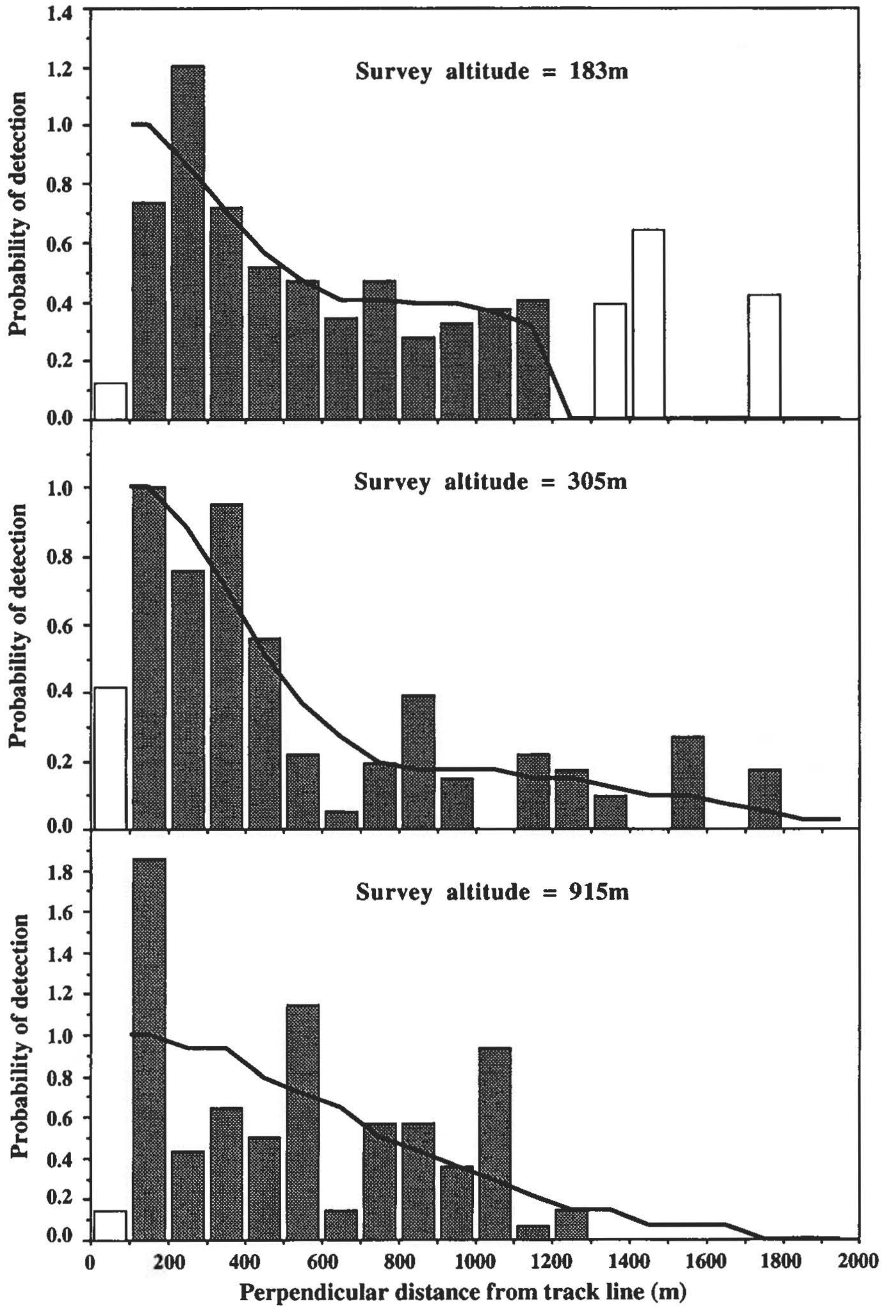

Fig. 6. Frequency distribution of narwhal sightings with distance from track line. At 183 m (1985) and 305 m (1986) altitude, sightings beyond 1200 m from the track line were excluded from the estimation of abundance. At 915 m (1986) sightings beyond 2000 m from the track line were excluded. At all altitudes sightings at the first 150 m from the track line were eliminated for calculations of abundance. Data have been fitted to the half-normal model: $g(x) = \exp[-y^2 / (2 \cdot A_1^2)]$. The fitted curves show the expected number of sightings and the histograms the actual observations. Also see Tables 8 and 9.

aircraft during the surveys at 305 m. Of a total of 518 groups observed by the rear observers, about 18% were submerged when the aircraft passed over them. During the survey at 915 m, 18% of 80 groups dived in front of the aircraft, whereas about 39% of 252 groups observed by the rear observers were diving, or underwater.

Discussion

Group size

Land- and ship-based observations indicate that narwhals usually occur in groups of 3 to 10 (*e.g.* Vibe 1950, Bruemmer 1971, Tomilin 1967, Meldgaard & Kapel 1981). Narwhals in Admiralty Inlet (Canada) moved in

Table 8. Estimates of abundance of narwhals based on aerial surveys over Inglefield Bredning and tributary fjords in late August and early September 1985. Sighting-distance data truncated at 150 and 1200 m from the track line were pooled for all four days and used to derive a common Effective Search half-Width (ESW) by fitting the half-normal model. Only effort and sightings from sea states 0 and 1 were included. The estimate of mean group size was obtained on 25 August during a survey mounted specifically for information on group size.

Month Day	August 27	August 28	August 29	September 3
Survey altitude (m)	183	183	183	183
A: Total sample area (km²)[1]	1435	825	1435	825
Effort (L,km)	233	104	306	94
No. of sightings (N)	66	57	141	54
Sighting rate (N/L)	0.28	0.55	0.46	0.57
Coefficient of variation	0.47	0.39	0.21	0.61
Mean group size (C,N = 80)	2.21	2.21	2.21	2.21
Coefficient of variation	0.08	0.08	0.08	0.08
ESW-pooled (1/f(0),m,N = 374)	535	535	535	535
Coefficient of variation	0.09	0.09	0.09	0.09
Density (groups/km²)	0.26	0.51	0.43	0.54
Density (narwhals/km²)	0.59	1.13	0.95	1.19
Coefficient of variation	0.49	0.41	0.24	0.62
Abundance estimate	847	932	1366	979
Confidence interval	344–2085	382–2012	854–2276	320–3011

[1] For areas surveyed, see Figs 2 a–b.

tight groups of 5 to 8 animals with distinct spaces between groups (Fallis *et al.* 1983). According to Greendale & Brousseau-Greendale (1976) group size varied from single animals to 21, but was usually 3 to 8, as narwhals migrated past Cape Hay (Bylot Island, Canada). The estimates of group size in our study are consistent with those obtained during land-based observations in Canada during the break-up and open-water periods. However we cannot explain why average group size was larger in 1985 than in any of the other years.

Table 9. Estimates of abundance of narwhals based on aerial surveys over Inglefield Bredning and tributary fjords in early August 1986. Sighting distance data were truncated at 150 and 2000 m from the track line. A common Effective Search half-Width (ESW; N= 227) was derived by fitting the half-normal model to the data from the two surveys on 9 August. ESW for the survey on 10 August was obtained by fitting the half-normal model to the data (N=77). Effort and sightings from sea states 0 to 3 were included.

Day	9(I)[1]	9(II)	*(I+II)	10
Survey altitude (m)	305	305	305	915
A: Total sample area (km²)[2]	1435	1435	1435	902
Effort (L,km)	179	167	346	114
No. of sightings (N)	178	47	225	103
Sighting rate (N/L)	0.99	0.28	0.65	0.91
Coefficient of variation	0.38	0.34	0.31	0.35
Mean group size (C) (N)[3]	2.89 (63)	6.28 (18)	3.58 (81)	3.23 (77)
Coefficient of variation	0.11	0.15	0.10	0.08
ESW-pooled (1/f(0),m)	472	472	472	713
Coefficient of variation	0.08	0.08	0.08	0.08
Density (groups/km²)	1.05	0.30	0.69	0.64
Density (narwhals/km²)	3.04	1.87	2.47	2.07
Coefficient of variation	0.40	0.38	0.34	0.37
Abundance estimate	4369	2683	3539	1894
Confidence interval	2037–9341	1029–6998	1869–6722	929–3752

[1] I = 1st survey on 9 August 1986; II = 2nd survey; *I+II = 1st and 2nd survey on 9 August combined.
[2] For areas surveyed, see Figs 3 a–b.
[3] Independent estimates of group size obtained by the front observer.

Estimates of group size obtained in Inglefield Bredning in 1988 are similar to those reported by Silverman (1979) for Tremblay Sound (NE Baffin Island) where average group size was 5.1 narwhals/group during "directed movement" and 3.5 narwhals/group during "localized movements". An average group size for all observations in 1988 in Inglefield Bredning of 4.6 narwhals/group (SD = 2.9; range: 1–16; N = 251) is similar to that given by Silverman (1979) of 4.1 narwhals/group (N = 635) for groups with both sexes and all ages.

During aerial surveys of narwhals in inshore summering areas, average group sizes varying between 2 and 3 animals/group, but often around 2, have been reported (*e.g.* Koski & Davis 1979, 1994, Cosens & Dueck 1991, Kingsley *et al.* 1994, Larsen *et al.* 1994). However under certain conditions narwhal group size estimated from aerial surveys is larger. In Lancaster Sound between 13 June and 10 August 1976, Johnson *et al.* (1976) observed that narwhal groups that occurred along coasts without fast ice tended to be larger (average group size 7.1- 9.0) than groups occurring in nearby areas with more ice. During a mass movement of narwhals on 29 August in Maud Bight average group size was 4.05 (Koski & Davis 1979). Group size also varies according to sex and age composition. As also seen in our study, Koski (1980) observed that groups containing only males tended to be larger (average 3.4) than male-female groups (2.8) or groups of females (2.4). Cosens & Dueck (1988) found that group size was larger (mean = 3.3) during disturbance by an ice-breaking vessel at the Lancaster Sound ice edge than during the non-disturbance situation (mean = 2.2). Average group size observed during our second survey over Inglefield Bredning on 9 August 1986 was significantly larger than that obtained during the other surveys (Table 3). The comparatively large group sizes are believed to reflect that during this particular survey a herd of narwhals was observed during a fast "mass movement", whereas during the other surveys the whales were either stationary or moving slowly.

The discrepancy between narwhal group sizes obtained from land-based surveys and those from aerial surveys might be explained by 1) the difference in angle of view and 2) the difference in time allowed for observations. During our land-based observations the low angle of view, in combination with the foreshortening from using powerful telescopes, presumably sometimes caused us to judge that whales which were more than "one whale length" apart belonged to the same group. Nevertheless we found no correlation between group size and distance to observation. During land-based observations in Canada (*e.g.* Silverman 1979) where observations were made from a higher platform and the narwhals occurred closer to the observation site, estimated group sizes also were larger than those reported for aerial surveys. Almost certainly, the difference between estimates of group size relates to the fact that from a fast-moving aircraft a momentary "static" view of the groups is obtained, whereas from land the maximum number of whales which surface together during the observation period is recorded.

Sex and age composition

The estimated sex and age composition of the narwhal population found during the aerial surveys in Inglefield Bredning in 1986 was similar to that reported for inshore summering areas in Canada (*cf.* Table 5). During our study 15% of the narwhals observed were classified as neonates by the front observer. Aerial surveys conducted in August and September in inshore areas resulted in estimates of percentage of neonates of total narwhals observed between 9.6 (Kingsley *et al.* 1994) and 23.5 (Larsen *et al.* 1984). In our study significantly more neonates were recorded by the rear observers. These observers concentrated on recording numbers of groups and narwhals and measuring angles to observations; they only recorded information on sex and age if time allowed. Most of the narwhals occurred in dense herds and generally little time was left for recording sex and age. It is therefore very likely that the rear observers unintentionally paid special attention to conspicuous animals such as adult males and neonates, so that these categories are over-represented in our data and the resulting estimates of sex and age composition are biased accordingly. Silverman (1979) found that segregation by sex does not usually occur between entire narwhal herds but rather occurs within a given herd. However, cow-calf groups comprised 27% of narwhals in Koluktoo Bay and 24% in Milne Inlet whereas this proportion was only 4% in Eclipse Sound. These observations indicate that females and young are a smaller proportion of narwhals in exposed waters than in more sheltered waters (Kingsley *et al.* 1994). Similarly, Vibe (1950) found indications that females with young showed special preference for the head of Inglefield Bredning while males tended to occur further west in less sheltered waters. Our aerial surveys covered primarily the more sheltered parts of the Inglefield Bredning and Hvalsund fjord complex. It cannot be excluded that during the 1986 aerial surveys, which were conducted during a very brief period, females with young predominated in Inglefield Bredning, resulting in an overestimate of the fraction of neonates in this summering stock.

Dive times

Our land-based observations indicate that travelling narwhals are at the surface for about 36% of the time. Depth profiles obtained from an adult female narwhal equipped with a satellite transmitter revealed that, during a 10-day period in August 1991, about 45% of its time was spent between 0 and 1 m from the surface (Martin *et al.* 1994).

Effects of aircraft engine noise

Narwhals react to underwater and airborne ship engine noise by "freezing" (*i.e.* they sink quietly beneath the surface with little audible respiratory sound; Finley *et al.* 1990). In Inglefield Bredning narwhals are hunted only from kayaks. There is, however, considerable boating activity during the hunting season because the hunting teams travel to and from the hunting grounds in motorized vessels, and hunters report that motor noise scares the narwhals. The lower estimate of mean group size obtained during the 1985 aerial surveys compared with 1986 can partially be explained by a greater number of animals diving as a reaction to the noise of the aircraft which flew at a lower altitude in 1985. Kingsley *et al.* (1994) noted that their survey aircraft (Bell 206 helicopter), even at 305 m altitude, disturbed narwhal groups and caused some whales to dive before the helicopter passed over them. Narwhals that are far below the water surface cannot be detected (see Richard *et al.* 1994) and consequently aerial surveys tend to underestimate the number of whales and their group size. If the narwhals really dived in response to our survey aircraft it would imply that the estimates of abundance of narwhals in Inglefield Bredning are negatively biased.

Other factors affecting the aerial-survey results

The lack of observations close to the track line during the surveys at 183 m in 1985 is easily explained by the flat windows used in the aircraft; these windows prevented observations within the first 100–150 m from the track line. However surveys in 1986 showed that narwhals were still missed in the areas close to the track line even though bubble windows had been installed. This could have been caused by inattention to the area near or under the aircraft, by avoidance reaction of narwhals close to the track line or by a combination of both.

Aerial surveys in Inglefield Bredning showed that under good sighting conditions narwhals could be seen at long distances. In other aerial surveys of narwhals using strip-census methods, half-strip widths of 400 m (Smith *et al.* 1985) and 800 m (Richard 1991) have been used. However our study indicates that the assumption in strip censusing that the probability of detection is constant across the half strip width is violated. Theoretically some of the potential bias caused by the narwhals' avoidance of the aircraft can be reduced in line-transect surveys where sightings close to the track line are omitted and distant sightings are included.

Because narwhals often occurred in one or a few large herds, the sightings were sometimes concentrated on relatively few transects (Fig 3 a:A). The major source of variation in the abundance estimates was the sighting rate, which usually contributed more than 50% of the variation. Furthermore it was suspected that some groups were missed as we flew over high-concentration areas because observers could not simultaneously measure angles to sightings and continue searching. Under such circumstances high-altitude photographic surveys (Richard 1991, Richard *et al.* 1994) may seem to have advantages in terms of counting the number of groups and in estimating group sizes. However this method also has limitations and tends to underestimate true numbers because when the photos are read the readers miss some narwhals on the film (for discussion see Richard *et al.* 1994).

Although our surveys were relatively imprecise, they still indicate an increase from 1985 to 1986 in the density of groups and the sighting rate, which are unaffected by the various group-size estimates.

Our surveys showed that surveys of narwhals at high altitudes (> 300 m) are preferable to surveys at lower altitudes. Narwhals apparently showed avoidance response to the low-flying survey aircraft, presumably causing underestimates of group size and narwhal densities. Furthermore, from a low-flying aircraft the field of view is relatively narrow; this reduces sighting time and increases the likelihood that narwhals will be missed.

Fluctuations in numbers of narwhals in Inglefield Bredning

The results of the surveys in Inglefield Bredning in the various years (Born 1986, this study) are influenced to an unknown degree by differences in survey methods and effort, but also by annual and seasonal fluctuations in the number of narwhals present in the fjord system. The land-based surveys covered only a limited part of the narwhal's range in Inglefield Bredning and tributary fjords, and narwhals were present outside the observation area during the observation sessions. During August narwhals are also observed in Hvalsund, and during this same month some animals apparently move from Inglefield Bredning into Smith Sund. An influx to Inglefield Bredning may also occur during August (Born 1986), so the geographical distribution of the stock during the short summer is fluid and variable both within and between years, as has also been observed in Canada (*e.g.* Fallis *et al.* 1983).

When narwhals were present in the observation area in 1985 the groups were more widely distributed and scattered in comparison with the situation in 1984. In 1984 the large herds showed a greater tendency to travel rapidly from one section of the observation area to another (Born 1986). Furthermore in 1985 they spent comparatively less time in the northern parts of the observation area between the Harvard Øer and Josephine Peary Ø. The reason for this apparent change in distribution and behavior is not clear. In contrast to the situation in August 1984, when the whales spent comparatively more time within the observation area at the head of Inglefield Bredning, frequently in large herds (Born 1986), they were more widely scattered and therefore less easy to count in 1985 and 1988.

It is likely that natural fluctuations in narwhal prey in Inglefield Bredning affect the number of whales summering in the area and also influence the whales' behavior and distribution. In Inglefield Bredning narwhals feed on polar cod (*Boreogadus saida*; Vibe 1950, Born 1986, Heide Jørgensen *et al.* 1994), arctic cod (*Arctogadus glacialis*; Heide-Jørgensen *et al.* 1994), Greenland halibut (*Reinhardtius hippoglossoides*; Vibe 1950), other fish, cephalopods and crustaceans (Heide-Jørgensen *et al.* 1994). During August they are often observed feeding on schools of polar cod or arctic cod (Born 1986, Born & Knutsen 1988). They often form "feeding frenzies" together with harp seals (*Phoca groenlandica*) and sea birds. There is, however, no quantifiable evidence that would allow us to determine the relationship and annual variation in number of narwhals and prey biomass in the Inglefield Bredning area.

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