Distribution and numbers of Canadian High Arctic narwhals *(Monodon monoceros)* in August 1984

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Aerial photographic surveys of the numbers and distribution of narwhals (*Monodon monoceros*) in fjords and inlets south of Parry Channel, N.W.T., Canada, were conducted between 17 and 29 August 1984. Narwhals were concentrated in waters 350 m or more in depth and were most abundant in Prince Regent Inlet and Admiralty Inlet. An estimate of 18 000 narwhals (90% CI 15 000–21 000) was obtained by combining estimates for the Eclipse Sound area, Admiralty Inlet, Prince Regent Inlet and Peel Sound. We evaluated the visibility of narwhal and white whale *(Delphinapterus leucas)* models submerged to different depths. Models of adult narwhals could be seen when submerged to 10 m but could only be clearly distinguished from white whales at depths of 2 m. Such results indicate a limit to counting submerged narwhals. This problem, along with other factors, constrains the estimation of population size.

Key words:
Narwhal, *Monodon monoceros*, distribution, photographic survey, Canadian High Arctic.

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Introduction

In the Canadian High Arctic, narwhals *(Monodon monoceros)* summer in deep fjords and channels south of Parry Channel (Lancaster Sound and Barrow Strait) from mid-July to September or October (Mansfield *et al.* 1975, Finley & Johnston 1977, Davis *et al.* 1980, Finley *et al.* 1980, Finley & Miller, 1982). A first approximation of the size of this population was obtained by extrapolation from counts of narwhals migrating through Lancaster Sound in 1976 (Davis *et al.* 1978) but more precise estimates are needed for management of the subsistence hunt practiced by local Inuit. Smith *et al.* (1985) flew surveys in Lancaster Sound and Prince Regent Inlet in August 1981 but did not cover the Eclipse Sound area, Admiralty Inlet and Peel Sound (Figs 1–2) which also have large summer narwhal concentrations (Davis *et al.* 1980, Fallis *et al.* 1983, Finley & Johnston 1977, Mansfield *et al.* 1975).

Between 17 and 29 August 1984 we flew a series of surveys in all four areas (Fig. 2). Counts of narwhals were also made at Inglefield Bredning, NW Greenland, during that period (Born 1986). The combination of these efforts provided the first extensive coverage of the Baffin Bay narwhal stock. Preliminary estimates for the Canadian part of these surveys were given by Strong (1988) and Barber (1989) analyzed the observed distribution of narwhals in relation to sea-surface temperature features occurring during these surveys.

In this paper we present details of the distribution of narwhals and estimates of numbers for the August 1984 Canadian surveys. The distribution is discussed and compared to other studies. Methods used to estimate numbers are discussed in the light of the bias demonstrated by a model experiment and of other known or potential counting and sampling biases.

White whales *(Delphinapterus leucas)* and narwhals are sympatric in Peel Sound and Prince Regent Inlet. Narwhals may be confused with white whales or missed entirely when they are submerged. A model experiment was conducted in July 1984 to study the visibility and ease of recognition on aerial photographs of narwhals submerged to varying depths. We present the results of this experiment here because they are important to the understanding of counting error in aerial surveys.

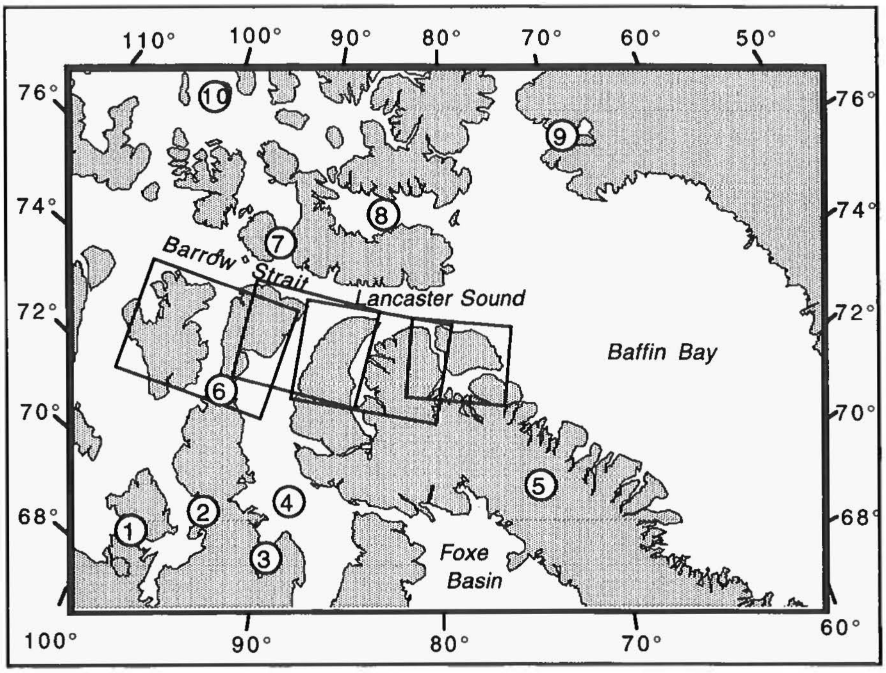

Fig. 1: Canadian High Arctic. Numbered locations are: 1- Gjoa Haven, 2- Spence Bay, 3- Pelly Bay, 4- Gulf of Boothia, 5- Baffin Island, 6- Bellot Strait, 7- Wellington Channel, 8- Jones Sound, 9- Inglefield Bredning (Greenland), 10- Maclean Strait. Insets delimit the survey areas shown in Fig. 2.

Materials and methods

Study area

Surveys were flown between 17 and 29 August 1984 in the Eclipse Sound area, Admiralty Inlet, Prince Regent Inlet and Peel Sound (Fig. 2). These four areas are bays or channels with zones of deep water that exceed 350 m in depth. At the end of August the Eclipse Sound area and Admiralty Inlet are normally ice-free, and Prince Regent Inlet and Peel Sound have ice in low concentrations (Markham 1981).

Aerial surveys

Surveys were flown in a DeHavilland Twin Otter (DHC6) equipped with a gyrostabilized 230.8 mm by 230.8 mm format camera (Wild-Leitz RC8) with a 153.8 mm lens mounted vertically at the rear camera port of the aircraft. The navigator used an Omega navigation system to locate transects and maintain headings; landmarks were used to confirm positions and update the navigation system. The pilot maintained a constant ground speed of 187 km/h and an altitude of 923 m throughout the transects. The camera was triggered by an intervalometer at 29 sec intervals to obtain a stream of photographs separated by a slight gap, each covering an area of 1385 m by 1385 m. Kodak Aerocolor 2445 colour negative film was used for all the

Table 1. Details of survey strata and narwhal population estimates, 17–29 August 1984.

Date (Aug.)	Stratum (see Fig. 2)	Transects	Census area (km²)	Coverage	Transects	Count	Density	Estimate	CV	Confidence limits lower 90%	upper 90%
17	Eclipse I	1W-13W	1502	19.34%	13	0	0	0	–	–	–
17	Eclipse II	14E-18E	2048	20.43%	5	111	0.26522	543	59%	166	1784
18	Eclipse III	19W	493	15.10%	1	102	1.37087	675	–	–	–
23	Admiralty	all	6319	8.44%	13	469	0.87925	5556	22%	3759	8213
25	Peel Sound I	1E-9E	7998	7.67%	11	65	0.10591	847	26%	531	1352
26	Peel Sound II	10W-15E	2252	7.96%	4	68	0.37922	854	23%	498	1464
27	Prince Regent I	1E-7E	8623	8.19%	7	447	0.65617	5461	29%	3139	9500
29	Prince Regent II	8E-11W	5742	9.18%	4	394	0.7476	4293	17%	2918	6316
	All blocks combined							17991	10%	14724	21258

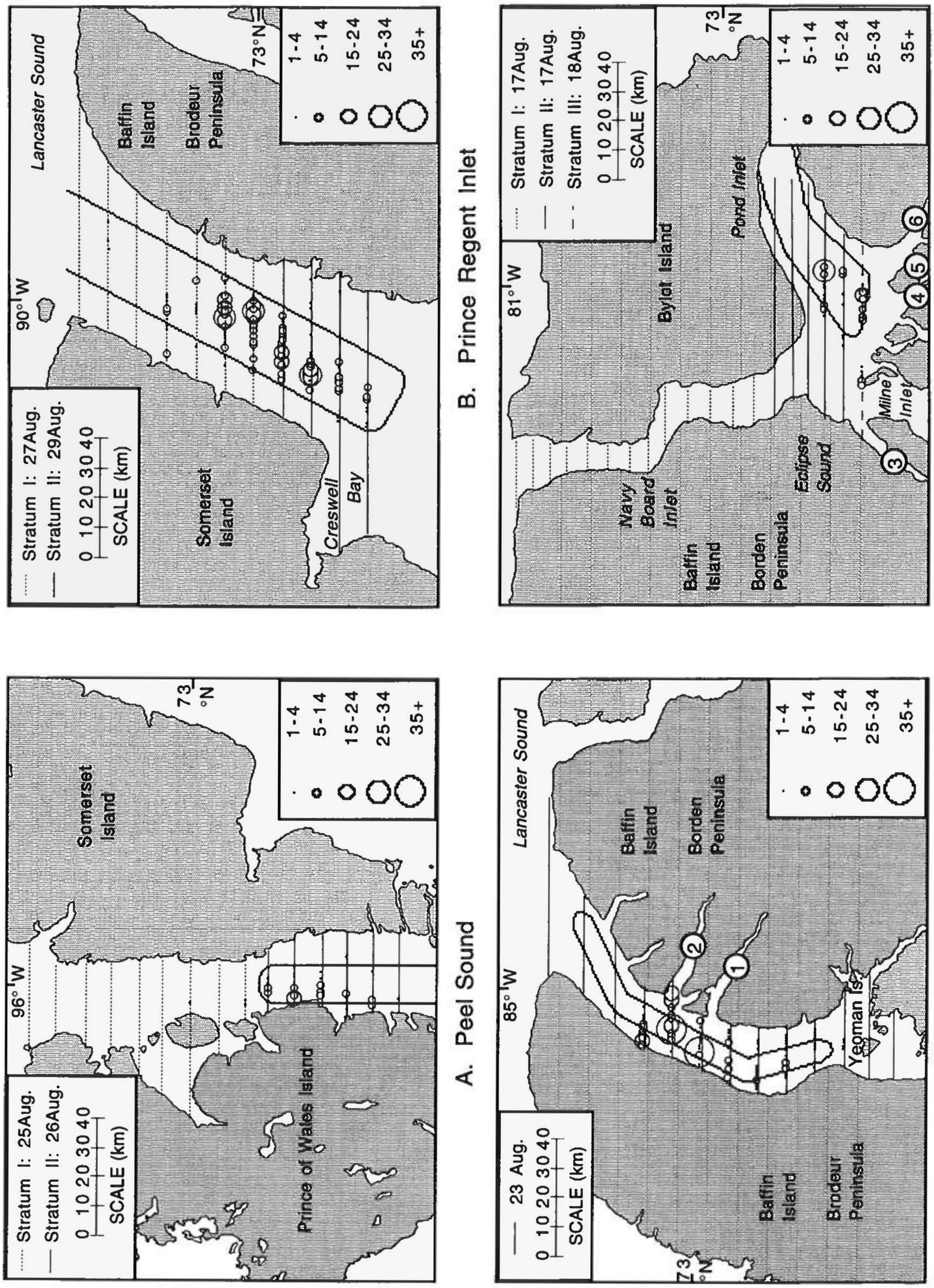

Fig. 2: Distribution of narwhal counts in survey areas. Note: circles represent categories of narwhals counted per photograph. Count categories are given in the legends. Numbered locations are: 1- Adams Sound, 2- Strathcona Sound, 3- Tremblay Sound, 4- Tay Sound, 5- Paquet Sound, 6- Oliver Sound. The line contours delimit the approximate locations of waters with depths greater than 350 m.

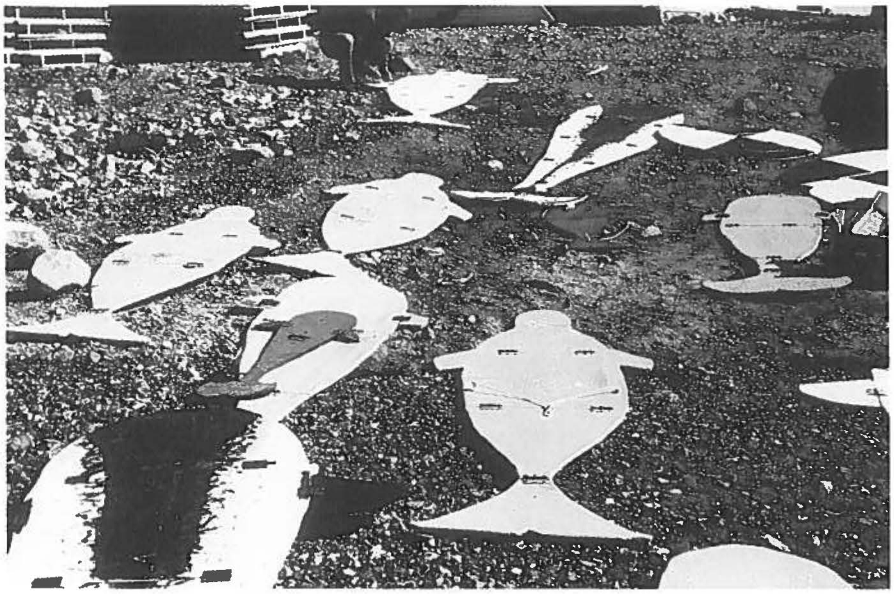

Fig. 3: Narwhal and white whale models used in the model experiment.

surveys. Surveys were flown during periods surrounding solar noon to maximize available light and minimize surface glare.

Systematic east-west transects were flown in daily strata, as described in Fig. 2a-d and Table 1. The first two strata in the Eclipse Sound area were flown on the same date (17 August 1984) but were kept separate to group transects of similar lengths and to minimize the effect of uneven transect areas on the variance of the estimate. Surveys were flown only when sea state for the stratum averaged 2 or less and did not exceed 3 on the Beaufort scale (wavelets, little or no whitecaps).

Photographic coverage consisted of transects spaced every 8' of latitude except in the Eclipse Sound area, where transects were spaced every 4' of latitude, yielding coverage of about 8% and 20% respectively (Table 1). The Eclipse Sound area was flown at a higher coverage to study the distribution of narwhals in more detail. In all areas but Admiralty Inlet, it took two or three days to complete the surveys.

Photographs were scanned for narwhals at a magnification of 10x using a Nikon SMZ-1 stereoscopic microscope mounted on a Richards GFL-940MC light table, and following a grid that divided the frame into nine equal-sized blocks. In addition to narwhal counts, the readers noted environmental conditions such as sea state (Beaufort index), ice concentration or the presence of fog. The heading of each whale relative to true north was also noted. For areas requiring two or more days to complete, we calculated the frequency of narwhal headings by survey stratum to determine if there was any directional trend in the orientation of narwhals when an area was covered in two or more days.

Methods described by Kingsley *et al.* (1985) and Smith *et al.* (1985) were used to obtain estimates of variance and confidence limits. We used methods suggested by Gasaway *et al.* (1986) to calculate an estimate of population size and one of population variance for all areas combined. These methods are described in detail in Appendix I.

Ninety-percent confidence limits are reported. Ninety-five percent confidence limits are traditionally given for population estimates but setting $\alpha = 0.10$ gives added power to test for population change (Peterman 1990). This is an important tool since in resource management the consequences of a Type II error (*i.e.*: accepting the null hypothesis of no decline in population size when it is wrong) are more serious than those of a Type I error (*i.e.*: rejecting the null hypothesis of no decline when it is true). The former may lead to over-exploitation and long-term harm to the resource.

Model experiment

Experiments were conducted at Repulse Bay (66°50'N, 86°30'W) on 30 July 1984 with life-sized models of narwhal and white whale adults, juveniles and calves to evaluate the visibility and ease of identification of the models of age classes of each species submerged to different depths.

The models were made by stretching white canvas on plywood forms cut in the shape and size of adult, juvenile and neonatal animals. Gray and black colour was added to imitate the natural colour of narwhals and white whales. The shape and colour of each model were made to approximate the dorsal aspect of each age class (Fig.3) and were based on aerial photographs of narwhals and white whales and on photographs of animals landed by

Table 2. Frequency of narwhals with North (330°–30°) and South (150°–210°) headings in each stratum.

Date (August)	Stratum	North Frequency	North Proportion	South Frequency	South Proportion	Total Frequency	Chi-Square Goodn.-of-Fit
17	Eclipse Sound II	7	7%	48	46%	105	$p < 0.005$
18	Eclipse Sound III	5	5%	37	39%	96	$p < 0.005$
25	Peel Sound I	2	33%	0	0%	6	$p > 0.100$
26	Peel Sound II	15	12%	38	31%	122	$p < 0.005$
27	Prince Regent Inlet I	81	20%	48	12%	413	$p < 0.005$
29	Prince Regent Inlet II	67	18%	66	18%	365	$p < 0.005$

local hunters in various localities in the N.W.T. Model lengths (Table 3) were based on data from Hay (1984) for narwhals and from Sergeant & Brodie (1969) for white whales.

Models were submerged and stabilized on a horizontal plane at predetermined depths using floats and anchors. A set of randomly assorted white whale and narwhal models of various age classes (2 adults, 2 juveniles and 2 neonates of each species) were anchored along a cable and submerged to 2 m, 5 m and 10 m. Vertical aerial photographs were taken from four altitudes (Table 3). The photographs were read by an experienced reader who did not know the depths or age classes of the models. The reader noted all visible whale models and determined their species and age class where possible.

Results

Aerial surveys

All surveys were flown on days with low surface winds (Beaufort index <4) and good visibility conditions. Ice cover was lower than expected for that time of year (Markham 1981). In all but one survey area, the water surface was free of ice except for a few occasional patches of loose pack (<10%). Peel Sound had ice scattered along its entire length in low concentration (<10%). On 18 August in the Eclipse Sound area only one transect was partially surveyed owing to dense fog which covered the middle section of that transect and all transects to the south. High winds (Beaufort index ≥4) over the stratum in the following days caused the cancellation of the survey.

In Peel Sound (Fig. 2a) narwhals were found to be concentrated in the south part of the channel, from the center to the coast of Prince of Wales Island. Of the four areas, Prince Regent Inlet (Fig. 2b) had the largest number of narwhals. Their distribution followed the longitudinal axis of the inlet and the largest numbers were found in the center. Few narwhals were counted near the coasts of Baffin Island and Somerset Island

In Admiralty Inlet visual reconnaissance flights were conducted in Adams and Strathcona sounds on 22 August, but no narwhals were seen. During systematic photographic surveys on 23 August narwhals were distributed throughout Admiralty Inlet, north of the mouth of Strathcona Sound to Yeoman Island (Fig. 2c). The largest numbers were counted near Strathcona and Adams sounds.

Table 3. Narwhal and beluga models visible and identifiable on aerial photographs taken at four different altitudes.

Altitude of camera	360 m			370 m			680 m			990 m		
Depth of models	2 m	5 m	10 m	2 m	5 m	10 m	2 m	5 m	10 m	2 m	5 m	10 m
Model type												
420 cm adult beluga	*	*		*	*		*	*		*	*	
460 cm adult narwhal	*			*			*			*		
Adult unknown species			*			*			*			*
250 cm juvenile beluga	*			*			*			*		
250 cm juvenile narwhal	*			*			*			*		
Juvenile unknown species					*			*			*	
160 cm neonate beluga												
160 cm neonate narwhal												
Neonate unknown species				*	*							
Unknown species/class	*	*										

Note: an asterisk indicates that the model type was visible on film.

In the Eclipse Sound area visual reconnaissance flights were flown in Tay Sound, Paquet Bay and Oliver Sound on 15 August but no narwhals were seen. In systematic surveys flown on 17 August narwhals were not found in stratum I or in the northern three transects of stratum II (Fig. 2d). Narwhals were in relatively large groups in the southern two transects of stratum II on 17 August and in the single transect flown in stratum III on 18 August (Fig.2d).

The 90% confidence limits for all strata combined suggest a total visible (*i.e.* not corrected for whales that were submerged out of sight) population of between 15 000 and 21 000 narwhals (Table 1), of which about half were in Prince Regent and a third in Admiralty Inlet.

The frequency of south orientation (12%) of narwhals in Prince Regent Inlet's survey stratum I is less than expected from random orientation (Table 2). This is opposite to what one would expect if large numbers of narwhals were moving toward stratum II during the survey. Stratum II of the Eclipse Sound area (Table 2) had a higher than expected proportion of narwhals pointing south (46%). This indicates that movement to stratum III, which was flown the next day, could have taken place.

Model experiment

Irrespective of photograph altitude, adult models of both species were visible at a depth of 10 m (Table 3) but adult models of narwhals and white whales could only be distinguished to species at depths of 2 m and 5 m, respectively. Juvenile models of both species were only seen and recognized at 2 m from all altitudes. Neonate models submerged at 2 m and 5 m were seen only on low-altitude photographs (370 m) and could not be identified to species.

Discussion

Distribution

In all four survey areas (Fig. 2) narwhals were aggregated in a portion of the area and these aggregations appear related to bathymetry. In southern Peel Sound narwhals were concentrated along the western edge of a zone of water about 380 m deep (Fig. 2a). Narwhals were also concentrated over the deep central waters of Prince Regent Inlet, where depths average 400 m (Fig. 2b). In Admiralty Inlet most narwhals were also near the deepest waters of the inlet, zones where depth averages about 500 m (Fig. 2c). The largest numbers were counted near the mouths of Adams Sound and Strathcona Sound where depth increases to 600 m. In the Eclipse Sound area narwhals were most concentrated over the deep waters of Pond Inlet which average about 400 m (Fig. 2d).

Other authors have reported a similar distribution of narwhals in late summer. During surveys of southern Peel Sound on 28 August and 4 September 1976 Finley & Johnson (1977) observed narwhals in the same zone of deep water. From 172 narwhals observed on six transects on 4 September 1976 they estimated the density of narwhals to be about 0.54 narwhal/km^2, a density greater than that estimated for our 26 August 1984 survey (0.38 narwhal/km^2; Table 1: Peel Sound II). Most of the narwhals observed during Smith *et al.*'s (1985) August 1981 systematic surveys were also in the deep waters of Prince Regent Inlet. Dueck (1989) reported densities of between 0.4 and 1.29 narwhals/km^2 from systematic surveys of Admiralty Inlet on 17 August 1983, 21 August 1984 and 14 August 1985. In all three surveys most narwhals were in or near the deep waters, but in 1984 and 1985, they were most concentrated south of the mouths of Adams Sound and Strathcona Sound. Dueck's (1989) counts indicate some variation in the distribution of narwhals in Admiralty Inlet. There are no other systematic surveys with which to compare our results but Kingsley *et al.* (1994) observed relatively fewer narwhals in Eclipse Sound than in fjords and bays to the south of it.

Our results combined with the above-mentioned studies indicate a preference for deep water. The choice of deep water by narwhals may be related to bottom-feeding activity. Vibe (1950) reported that the summer diet of narwhals in northwestern Greenland consists partly of Greenland halibut *(Reinhardtius hippoglossoides)*, a deepwater fish. Finley & Gibb (1982) sampled narwhals in Eclipse Sound during the open-water period and reported that four of 11 narwhal stomachs had remains of polar cod *(Arctogadus glacialis)*, another deep-water fish (*A. glacialis* is usually called arctic cod in Europe). They concluded that narwhals did not feed very much during the open-water period. However the narwhals that they sampled were taken on the west side of Eclipse Sound, at least 30 km from Pond Inlet. If narwhals had been feeding in Pond Inlet, they could have fully digested their prey by the time they reached the west side of Eclipse Sound. Finley & Gibb (1982) did find remains of Greenland halibut and redfish *(Sebastes marinus)* in stomachs of narwhals captured in the deep waters of Pond Inlet earlier in the season. Heide-Jørgensen *et al.* (1994) found *Arctogadus glacialis* to be the dominant food item of the narwhals in Inglefield Bredning (NW Greenland) during summer.

Population size

Our estimates provide an index of the population size of Canadian High Arctic narwhals. An estimate of true population size is constrained by several factors.

First and foremost is the fact that narwhals spend considerable time at depths where they cannot be detected or identified on vertical photographs. The model experiment shows that at standard photographic survey altitudes (>680 m), models of narwhal and white whale adults and juveniles can be detected at depths of 10 m and 5 m, respectively, but species identification of both adults and juveniles is only possible at depths within 2 m of the surface. Neonate models of both species can not even be detected at 2 m depths. There is a clear bias due to under-counting of juveniles and neonates that are not near the surface. In areas where narwhals and white whales are sympatric, such as Prince Regent Inlet and Peel Sound, species identification of submerged animals can be a problem.

The dive durations of adult narwhals likely also contribute to the underestimation of their numbers, even though they comprise the largest portion of the population. Depth profiles obtained from an adult female narwhal equipped with a satellite transmitter revealed that, during a 10-day period in August 1991, 44% of its time was spent at depths greater than 6 m (Martin *et al.* 1994). From cliff and helicopter observations Dueck (1989) estimated the probability of narwhals being visible to an observer during a visual survey. His sighting probability (0.38, 95% CI 0.29–0.52) was derived from observations made at oblique angles, and as such is probably lower than if it had been derived from vertical observations, owing to poorer water penetration at oblique angles.

Second, bias occurs when photographs are read because readers miss some narwhals that are visible on the film. Double-count experiments using white whale photographic survey data showed that, on photographs taken in clear offshore waters of the Beaufort Sea, the probability of a reader's counting a white whale when it is visible on the film was 0.84 (Richard, unpubl. data). For visual surveys conducted in the same area Norton & Harwood (1985) reported a probability of 0.4 that a white whale would be counted when it was visible in a strip-census survey. A similar bias may exist in our narwhal photographic counts but we have not made double-counts of these survey photographs.

Third, counting biases may be caused by narwhals' movement out of a survey stratum during the survey or from one stratum to the next between flights. Such biases could cause either under- or over-estimates. Our analysis of narwhal orientation shows no indication of mass movement between strata in Prince Regent Inlet, but it is possible that some movement took place. There is indication of movement from stratum II to stratum III of the Eclipse Sound area. Although a high frequency of common headings does not necessarily mean that narwhals did move to the next survey stratum, it is cause for caution in the interpretation of our estimates. If such a movement did occur, it could have caused double-counting and biased the total estimate for the Eclipse Sound area. In this case the number of narwhals involved is relatively small and therefore the potential bias on the overall population estimate is relatively small.

Movement out of survey strata is also possible during surveys. Narwhals have been observed to make mass movements in response to weather, ice distribution or the presence of killer whales (*Orcinus orca*) but, in contrast, narwhals fitted with telemetry instruments have also been observed to spend several weeks in the same area during summer (Kingsley *et al.* 1994). The extent to which movement has affected our surveys is unknown. However it may be balanced by a simultaneous immigration to the surveyed areas.

Fourth, the southern part of Eclipse Sound, Milne Inlet and adjacent bays and fjords were not surveyed. Some of these areas are known to be preferred by narwhals in summer but the total numbers occurring in these areas are not large (Kingsley *et al.* 1994).

Finally, we only covered areas known to have relatively high densities of narwhals in August. Narwhals have a wide distribution in the Canadian Arctic archipelago in late summer (Fig.1). They have been observed in low numbers north of our study area, in Barrow Strait, Maclean Strait, Wellington Strait and Jones Sound (Mansfield *et al.* 1975, Roe & Stephen 1977, Davis *et al.* 1978, Koski 1980, Sergeant & Williams 1983) and south of it, in Bellot Strait, the Gulf of Boothia and northern Foxe Basin (Anders 1965, Finley & Johnston 1977, Sergeant & Williams 1983). Narwhals are also hunted in some years in Gjoa Haven, Spence Bay and Pelly Bay (Mansfield *et al.* 1975, Smith & Taylor 1977, Strong 1989). The unpredictable occurrence and low numbers of narwhals in a given year do not justify the allocation of survey effort to these areas. For example, Koski (1980) reported narwhal observations in Barrow Strait between 17 and 20 August 1979 but Smith *et al.* (1985) did not observe any narwhals on their 6 and 14 August 1981 transects through Barrow Strait.

Most of the above sources of error will cause an underestimation of true population size. Consequently our overall estimate of 18 000 narwhals is only an index of the population size. If biases are relatively constant from year to year, indices derived from annual surveys could be used to track narwhal population changes. Studies of narwhal movement and diving behaviour are badly needed to understand the extent to which some of these biases vary and affect the index.

The ability to detect changes also hinges on the precision of the estimates and our survey estimates have low precision (high variance) owing to the low density and clumped distribution of narwhals (Fig. 2) and the low sampling fraction. It is not clear whether we could reduce the sampling variance in future surveys by stratifying the survey areas into sub-areas of high and low density. Even though narwhals often concentrate near the deepest parts of their summering areas, their distribution is dynamic and unpredictable (Finley & Johnston 1977, Dueck 1989, Kingsley *et al.* 1994). Reconnaissance surveys to find high-density sub-areas just prior to the census flights might enhance the chance of effective stratification.

An alternative to stratification is to repeat surveys several times to reduce the sampling variance (Gerrodette 1987). However if movements occur into or out of survey areas between successive flights, then the numbers estimated are not the same and combined estimates are not valid. A second and preferred alternative suggested by Kingsley *et al.* (1994) is to use several planes simultaneously to survey each area at high coverage. Neither of these alternatives comes without a substantial increase in cost, but unless population estimates can be made more reliable, they will only detect large changes in population size.

Our results lead us to conclude that the size of the Canadian High Arctic narwhal population is most likely greater than or equal to 20 000 animals since the 90% lower confidence limit is 15 000 and most sources of error probably result in an under-estimate. Born (1986) counted a maximum of about 4 000 narwhals on 18 August 1984 in Inglefield Bredning, which is only a part of the summer range of narwhals in northwestern Greenland (Vibe 1950, Meldgaard & Kapel 1981). This suggests that the total Baffin Bay narwhal population is at least 19 000 narwhals and may well exceed 22 000 narwhals.

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Appendix I : Formulas used to calculate estimates of population size.

Except where indicated, the following formulas and notation were taken from Kingsley *et al.* (1985). Average density within strata was calculated as:

$$\hat{R} = \frac{\sum_{1}^{I} \sum_{1}^{J} t_{ij}}{\sum_{1}^{I} \sum_{1}^{J} a_{ij}} \tag{1}$$

where $\hat{R}$ = average density of the survey area,
t_{ij} = whale count in photograph j on transect i,
a_{ij} = area of photograph j on transect i.

Transect counts were not weighted for meridian convergence since our transects were oriented east-west.

The variance of $\hat{R}$ is calculated by:

$$V_S = \left(1 - \frac{n}{N}\right)\left(\frac{I \sum_{1}^{I-1} (d_i - d_{i-1})^2}{2(I-1)\left(\sum_{1}^{I} \sum_{1}^{J} a_{ij}\right)^2}\right) \tag{2}$$

where $d_i = Y_j - \hat{R} X_i$,
n = number of transects flown (I),
N = total number of transects possible across the survey area.

The term (1 – n/N) is the finite population correction and is effectively equal to (1 – survey fraction).

V_s is an estimate of variance based on serial differences between neighbouring transects (S_2^2 in Kingsley *et al.* 1985). V_s is less biased than Cochran's (1977) variance estimator when neighbouring transects are positively correlated, a situation likely to occur when animal distribution is clumped (Kingsley & Smith 1981), as was the case in our study (Fig. 2).

Error coefficients of variation (CV; E in Kingsley *et al.* 1985) were calculated as follows:

$$CV = \frac{\sqrt{V}}{R} \tag{3}$$

To obtain confidence limits of mean density, we assumed that true mean density and sampling variance were proportional, and that this proportion (P) could be estimated from the ratio of sampling variance to sampling estimate of density (Cochran 1977, Smith *et al.* 1985):

If $$P = \frac{V}{\hat{R}} \tag{4}$$

then $$\hat{R} = R_L - t\sqrt{PR_L} \tag{5}$$

and $$R_L - t\sqrt{\frac{V}{\hat{R}}}\sqrt{R_L} - \hat{R} = 0 \tag{6}$$

where R_L = confidence limit of the density estimate,
t = critical point of Student's t distribution.

Equation 6 is a quadratic with two solutions, the upper and lower confidence limits:

$$R_L = \left(\frac{\frac{-t\sqrt{V}}{\sqrt{\hat{R}}} \pm \sqrt{\frac{t^2 V}{\hat{R}} + 4\hat{R}}}{2}\right)^2 \tag{7}$$

For each survey stratum the population estimate T and confidence limits were calculated as follows:

$$\hat{T} = \hat{R}\,A \tag{8}$$

and

$$T_L = R_L\,A \tag{9}$$

where A = survey stratum area.

Population estimates $\hat{T}_n$ and variance estimates $V(\hat{T}_n)$ for each stratum were summed to obtain estimates of the total population $\hat{T}_t$ and its variance $V(\hat{T}_t)$ (Gasaway *et al.* 1986):

$$\hat{T}_t = \hat{T}_1 + \hat{T}_2 + \ldots + \hat{T}_n \tag{10}$$

and

$$V(\hat{T}_t) = V(\hat{T}_1) + V(\hat{T}_2) + \ldots + V(\hat{T}_n) \tag{11}$$

The degrees of freedom associated with the summed estimate (Satterthwaite 1946) were calculated as follows:

$$\upsilon_t = \frac{[V(\hat{T}_1) + V(\hat{T}_2) + \ldots + V(\hat{T}_n)]^2}{\dfrac{V(\hat{T}_1)^2}{\upsilon_1} + \dfrac{V(\hat{T}_2)^2}{\upsilon_2} + \ldots + \dfrac{V(\hat{T}_n)^2}{\upsilon_n}} \tag{12}$$

Confidence limits were calculated by:

$$CL = \hat{T}_t \pm t\sqrt{V(\hat{T}_t)} \tag{13}$$