Summer distribution and movements of narwhals (*Monodon monoceros*) in Eclipse Sound and adjacent waters, North Baffin Island, N.W.T.

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Each year from 1987 to 1991 and in 1993, 3–6 helicopter surveys were flown in August to study the distribution and movements of narwhals (*Monodon monoceros*) in their summering grounds in western Eclipse Sound, Milne Inlet, Koluktoo Bay and Tremblay Sound. Their summer distribution is influenced by ice cover. They prefer waters that while giving them shelter from the wind, are over deep bottoms. Narwhals associate with ice in Eclipse Sound, a large expanse of water, while it persists, but do not frequent Tremblay Sound, a narrow fjord, when it has ice cover. When Eclipse Sound is ice-free, narwhals frequent smaller water bodies. Favoured areas in the ice-free season have in common the characteristics of being steep-sided and deep. Narwhals associate in small groups, but these groups aggregate to form larger herds that generally move together. In the short term, movements and distribution are greatly affected by the near presence of killer whales (*Orcinus orca*), which narwhals seek to avoid.

Key words:

Narwhal, Monodon monoceros, distribution, behaviour, Baffin Island, killer whale, Orcinus orca.

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Introduction

Narwhals (*Monodon monoceros*) occupy fjord complexes during the open-water season (Mansfield *et al.* 1975, Silverman 1979, Born 1986, Koski & Davis 1994). Females with young show special preference for the heads of fjords (Vibe 1950). It is not known for certain what factors influence the distribution and movements of narwhals at that time of year, although tidal cycles, feeding, calving, ice conditions and hunting have all been suggested (Vibe 1950, Finley 1976, Silverman 1979).

Knowledge of the distribution and movements of narwhals in their summering grounds is of practical interest for several reasons. 1) It potentially provides insight about why whales occupy their summer habitat. 2) It may aid in identifying types of habitat that should be given special protection. 3) Distributions that are difficult to explain can cause researchers to investigate seemingly unlikely, or less directly related, factors for an explanation. 4) It can lead to more effective design of aerial surveys for population estimation. Mass movements may also affect the precision of aerial census surveys which may take several days to complete.

We flew aerial surveys in western Eclipse Sound and two adjoining fjord systems (Fig.1) in August 1987–1993 to study narwhal distribution and movements. We were particularly interested in the influence of ice cover and wind. Observations of killer whales (*Orcinus orca*) were also noted. Survey observations were complemented by incidental observations made in the course of vocalisation, behaviour and radio-tagging studies in Tremblay Sound in 1984–1987 and 1989–1991 and in southern Milne Inlet in 1988 and 1993.

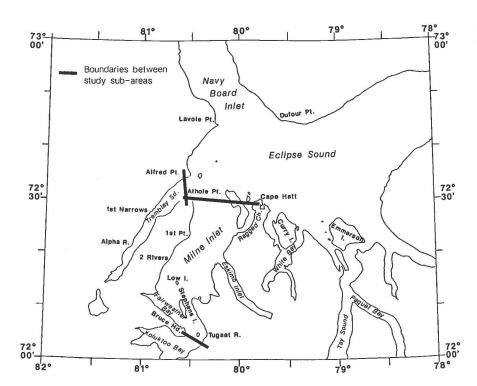


Fig. 1. Study area in northern Baffin Island.

Materials and methods

Study area

The full survey route sampled the western end of Eclipse Sound, Tremblay Sound, Koluktoo Bay and Milne Inlet (Fig. 2). Some surveys flown in early August, before fuel had been cached within the survey area, could not cover the full route. Three surveys in 1988 were prevented by bad weather from flying the full route in Eclipse Sound. In two surveys each in 1989, 1990 and 1991 the route in Milne Inlet was varied to cover the western near-shore waters more thoroughly, fewer transects being flown from side to side. The southern end of Navy Board Inlet was crossed by a single transect.

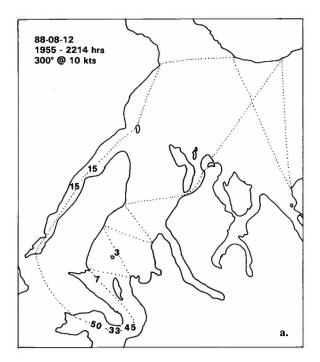
Weather and ice conditions

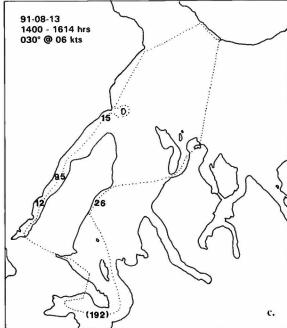
In most years Tremblay Sound, Koluktoo Bay and Milne Inlet are cleared of ice by river inflows while the ice in Eclipse Sound remains fast. When the ice in Eclipse Sound breaks up, north or northeast winds can sometimes drive ice into Milne Inlet and Tremblay Sound, where it may stay until south winds cause clearing. The surveys described here took place after the ice in Eclipse Sound had broken up. In 1987 this break-up occurred 2–3 weeks

later than usual. Mean ice cover was 25% (SD 33%, N = 220) for the four surveys in 1987; 8% of the ice was multi-year. In the first survey that year Tremblay Sound had 15% ice cover and Koluktoo Bay had no ice, while Eclipse Sound had 57% ice cover and Milne Inlet averaged 41%. During the following three surveys in 1987, Eclipse Sound had less ice cover, while in the other three bodies of water the ice cover increased in the second survey and then decreased in the third and fourth.

Break-up of the sea ice occurred early in 1988 and 1989, and no ice was recorded on any survey. In 1990 there was ice in southwestern Eclipse Sound, northern Tremblay Sound and northern Milne Inlet during the first survey on 2 August, but southern Tremblay Sound and southern Milne Inlet were ice-free. This ice cover had cleared by the time of the next survey on 12 August. In 1991 the last ice disappeared during the first week of August. In 1993 Koluktoo Bay and Tremblay Sound were clear of ice, and Eclipse Sound had only light ice cover on 16 August. Continuous north winds moved the ice out of Navy Board Inlet, increased the ice cover in Eclipse Sound and brought heavy multi-year pack ice to Tremblay Sound from 17 August and to southern Milne Inlet from 19 August.

Strong winds affect all aspects of aerial survey for marine mammals, so light winds were preferred. However as one objective of the surveys was to determine if narwhals select summering areas that will give them shelter during windy periods, we flew several surveys when wind speeds exceeded 8 m/s. One of four surveys in





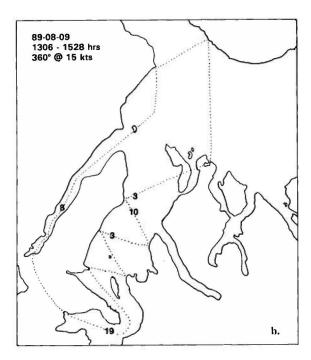


Fig. 2. Example survey routes in western Eclipse Sound, Milne Inlet and adjacent waters: a) 1987–1988, b) 1989 and 1993, c) 1990–1991. Box legend: date (yr-mo-day), start and end times of survey, wind direction (° true) and speed (knots) at time and place of survey start. Narwhal counts in two-minute intervals are marked on flight line.

1987 and three of six surveys in 1988 deviated from the planned pattern because of high winds or fog. Of the four water bodies surveyed Eclipse Sound was the largest and the most prone to bad weather.

Survey methods

Surveys were flown in a Bell 206 "Jet Ranger" helicopter at an indicated airspeed of 166–176 km/h and at altitudes of 244 or (usually) 305 m above sea level (a.s.l.). We found that if we flew below 244 m narwhals reacted so

Table 1. Mean sizes for cow-calf groups and for other narwhal groups by water body, western Eclipse Sound and adjacent waters, 1987–88 and 1993.

	No. of Individuals	No. of	Group Size	
	individuais	Groups -	Mean	SD
Cow-calf group	os			
Eclipse Sound	6	3	2.0	0
Koluktoo Bay	128	58	2.2	0.7
Milne Inlet	146	70	2.1	1.0
Tremblay Sd	83	25	3.3	2.7
Total	363	156	2.3	1.4
All other group	os			
Eclipse Sound	133	64	2.1	1.6
Koluktoo Bay	339	163	2.1	1.7
Milne Inlet	452	203	2.2	2.0
Tremblay Sd	471	193	2.4	2.0
Total	1395	623	2.2	1.9

quickly to the helicopter that we could not get accurate counts; even at 305 m a.s.l. narwhals on the flight track reacted to the helicopter by starting to dive even before the helicopter passed over them. However flying higher would have decreased our ability to identify and count animals.

In 1987 and 1988 observers sat in the back seat of the helicopter and scanned a 690 m strip on each side of the aircraft for narwhals. The surveyed strip was defined by window marks that had been established by triangulation while the aircraft was on the ground. The number and age class (calf, i.e. young of the year, older juvenile or adult) were recorded; when time permitted, sex (tusked or nontusked), activity (localized or directed) and direction of movement (if any) were also recorded. We identified calves as very small animals (about, or less than, half of adult length) swimming very close to another whale. Whales within one body length of each other were considered to comprise a group. Four types of group were distinguished: adult all male; adult all female; mixed male and female; and "cow-calf" groups, consisting of females with calves and other accompanying animals, including older juveniles, females without young and occasional adult males. Data were tabulated for periods of two minutes (transect intervals) during a survey; at the cruising speed of the helicopter each interval would have covered approximately 7.8 km². In 1987 a third observer sat in the front seat and recorded weather, ice conditions and waypoint times. In 1988 one of the observers in the back seat recorded that information. Wind speed and direction, cloud cover (in tenths) and type, and temperature were recorded at the start of each survey and updated as required. Ice cover (in tenths) and ice types (first-year and multi-year) were recorded for each two-minute interval.

From 1989 through 1993 most surveys were carried

out by a single observer in the left front seat of the helicopter who recorded ice cover, sea state and counts of narwhals on a 500 m strip below and to the left of the aircraft for an estimated interval area of 3 km². Narwhal observations were recorded, with their times, as they occurred; so were changes in ice cover or sea state. The time was also recorded when each navigational waypoint was passed. Two-minute interval data were constructed after the flight from the timed records. For some surveys supplementary observations were made by another observer in the right rear seat. They were not included in the quantitative analyses but were included in the presenceabsence contingency table analyses. Four primary observers carried out the surveys reported here: Verbeek and Ramsay in 1987; Cleator, Ramsay and Kingsley in 1988; Kingsley in 1989, 1990 and 1993; and Ramsay or Kingsley in 1991.

Data analysis

Dummy-variable stepwise linear regression (Draper & Smith 1981) was used to examine the data set for consistent patterns of narwhal density or distribution due to year, date, water body, ice cover or sea state, including the effects of the presence of ice in Eclipse Sound on narwhal numbers in other water bodies. In order to at least partly stabilise the variance of the data, which was highly skewed, the fourth root of the two-minute-interval counts was used as the dependent variable. Strict critical levels were used, usually 0.01%, to identify effects, because of the large size of the data set and the problem of non-independence (serial correlation) of two-minute intervals. These results were interpreted to give information on the directions (increase or decrease) of density variations due to the factors listed above.

The association between ice cover and narwhal distribution was also examined using contingency tables of the presence or absence of narwhals in one water body and of ice in the same or a different one, treating each survey as an observational unit. Contingency coefficients and chisquared statistics were calculated.

Results

Group size and composition

As calves are much smaller than adults, the observers had no difficulty distinguishing them from adults but they were harder to see. The presence or absence of a tusk was not always easy to determine, so all groups other than cow-calf groups were pooled for analysis of group size. Mean group sizes were small — mostly 2.0–2.4; the largest group sizes were in Tremblay Sound where cowcalf groups averaged 3.3 (Table 1). Variation in group

Table 2. Mean narwhal density per two-minute survey interval and mean ice cover on survey lines for Eclipse Sound, Tremblay Sound, Milne Inlet and Koluktoo Bay, 1987–1993.

Date (Aug.)	Eclipse Sound			Tremblay Sound		
	No. of intervals	Mean (SD) narwhals/ interval	Mean ice cover (%)	No. of intervals	Mean (SD) narwhals/ interval	Mean ice cover (%)
87–06	30	0.43 (1.15)	57.6	6	0.17 (0.37)	15.0
87-15	30	1.23 (3.40)	17.0	7	0.0	55.7
87–20	30	0.0	0	7	1.86 (4.55)	38.6
87–24	18	0.22 (0.71)	0.5	6	14.00 (18.62)	0
88-02	6	0.50 (1.12)	0	8	14.13 (27.37)	0
88-08	3	0.33 (0.47)	0	5	0.80 (1.17)	0
88-12	26 29	0.0	0	6	5.00 (7.07)	0
88–16 88–19	29	1.31 (5.52) 0.0	0	8	2.63 (5.07) 29.63 (40.25)	0
88–23	27	0.04 (0.19)	0	8	6.88 (9.80)	0
89-04	23	0.09 (0.41)	5.7	7	21.00 (51.44)	0
89-09	17	0.0	0	12	0.67 (2.24)	ő
89–18	35	0.0	ŏ	13	5.77 (19.41)	ő
90-02	20	5.20 (10.92)	16.5	5	0.0	16.0
90-12	15	0.0	0	9	1.33 (2.87)	0
90–16	15	0.0	0	7	2.29 (5.60)	0
91–07	10	0.0	0	12	30.75 (27.77)	0
91–11	9	0.0	0	11	5.91 (11.62)	0
91–13	15	0.0	0	9	13.89 (29.19)	0
91–15	22	0.0	0	7	9.43 (21.89)	0
91-17	16	0.0 0.0	0	6 9	5.83 (12.60)	0
93–17 93–19	16 16	0.31 (1.21)	9.4 10.0	9	0.0 0.0	28.9 20.0
93-19	14	1.36 (4.89)	17.9	10	0.0	44.0
93–23	14	1.29 (3.88)	12.1	7	0.0	17.1
Date (Aug.)	Milne Inlet			Koluktoo Bay		
Date (Aug.)		Milne Inlet			Koluktoo Bay	
Date (Aug.)	No. of intervals	Milne Inlet Mean (SD) narwhals/ interval	Mean ice cover (%)	No. of intervals	Koluktoo Bay Mean (SD) narwhals/ interval	Mean ice cover (%)
	3300	Mean (SD) narwhals/ interval	cover (%)	intervals	Mean (SD) narwhals/ interval	cover (%)
37–06	No. of intervals	Mean (SD) narwhals/			Mean (SD) narwhals/ interval	cover (%)
37–06 37–15 37–20	17	Mean (SD) narwhals/ interval 0.47 (1.24) 0.24 (0.94) 5.88 (8.77)	41.2	intervals 4	Mean (SD) narwhals/ interval	cover (%)
37-06 37-15 37-20 37-24	17 17 16 17	Mean (SD) narwhals/ interval 0.47 (1.24) 0.24 (0.94) 5.88 (8.77) 7.63 (14.76)	41.2 49.4 10.6 3.5	4 4 4 4 4	Mean (SD) narwhals/ interval 9.75 (15.17) 6.75 (7.79) 3.25 (1.92) 0.0	0 22.5 17.5 0
37-06 37-15 37-20 37-24 38-02	17 17 16 17	Mean (SD) narwhals/ interval 0.47 (1.24) 0.24 (0.94) 5.88 (8.77) 7.63 (14.76) 6.24 (24.94)	41.2 49.4 10.6 3.5 0	4 4 4 4 4 4	Mean (SD) narwhals/ interval 9.75 (15.17) 6.75 (7.79) 3.25 (1.92) 0.0 15.25 (25.84)	0 22.5 17.5 0
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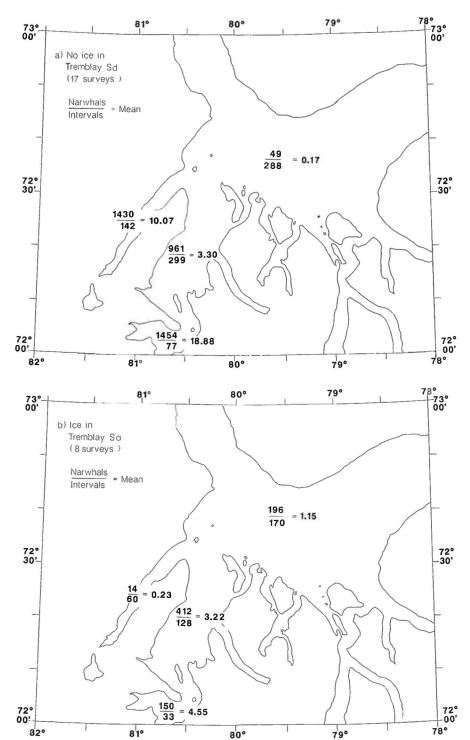


Fig. 3. Summary distribution of narwhals in the survey area: a) after ice had cleared from study area and b) when pack ice was present in Tremblay Sound or Eclipse Sound.

size was so large that differences were not statistically significant.

Cow-calf pairs or groups averaged overall 20.0% of the total groups classified, and accounted on average for 20.6% of individual whales. Calves were 9.6% of classified individuals, and accompanying whales were 11.0%. In Koluktoo Bay and Milne Inlet females with young formed the same proportion of groups (26.2% and 25.6%; $\text{Chi}_{1}^{2} = 0.02$) and of individuals (27.4% and 24.4%; $\text{Chi}_{1}^{2} = 1.23$) classified (Table 1). In Eclipse Sound,

where few narwhals were counted or classified, females and young formed a smaller proportion of groups (4.5%) and of individuals (4.3%). In Tremblay Sound females and young formed 11.5% of groups and 15.0% of individuals classified, between the Milne Inlet-Koluktoo Bay values and those for Eclipse Sound.

Distribution and movements of narwhals

Survey totals of narwhals seen ranged from 5 to more than 600. The survey mean number of narwhals per 2-min. survey interval ranged from 0.1 to 13.4. The numbers of narwhals recorded varied between surveys both within and between years; however the dummy-variable regression selected only the survey of 2 August 1990, when many narwhals were seen in the ice in Eclipse Sound, as being different from the others.

The mean number of narwhals/interval also varied significantly between water bodies (Table 2, Fig. 3). Eclipse Sound had the lowest overall mean, 0.54/interval, Milne Inlet 3.30, Tremblay Sound 7.15 and Koluktoo Bay the highest, 14.58. In 1988 Eclipse Sound had the lowest mean number of narwhals/interval in five of six surveys, and in 1989-1991, other years in which the ice cleared early, few narwhals were counted in Eclipse Sound. An exception was the first survey in 1990, on 2 August, when Eclipse Sound still had 16% average ice cover and a mean of 5.2 narwhals/interval was recorded. The ice did not clear until very late in 1987 and Eclipse Sound had the lowest mean narwhals/interval in only one survey out of four; 1993 was also a late ice year, and narwhals were observed in Eclipse Sound, in the pack ice, in three surveys out of four. In the late ice years of 1987 and 1993 no narwhals were sighted in Tremblay Sound in 5 surveys out of 8, and fewer than usual (1.5% and 16.7% of the weighted mean narwhals/interval for 19 surveys on which narwhals were sighted in Tremblay Sound) in two others. Only in the last survey in 1987, when the ice had left, did we record normal numbers (125.7% of the mean). In 1988 narwhals were relatively abundant in Tremblay Sound: it ranked second to Koluktoo Bay. In 1991 Tremblay Sound, south of the First Narrows, was continuously, and densely, frequented (Table 2). In most surveys Koluktoo Bay had large numbers of whales, usually densely distributed in the same small area. The fitted dummy-variable regression model confirmed these results, with positive coefficients for the dummy variables "water body is Koluktoo Bay" and "water body is Tremblay Sound", and a negative coefficient for the variable "water body is Eclipse Sound".

The aggregated results of the 6 years of surveys showed a consistent pattern of distribution in the openwater season. There were three preferred centres of aggregation. One was the northern part of eastern Koluktoo Bay, under the southern face of Bruce Head. Distribution

in this area sometimes extended eastward around the point of Bruce Head and into southern Milne Inlet (which had on average 5.76 narwhals/interval) or toward western Koluktoo Bay. A second preferred area was Tremblay Sound, south of the First Narrows. On most surveys narwhals were observed there, and they were present in this area throughout August in 1991. A less favoured extension of this area was in the mouth of Tremblay Sound north of the First Narrows as far as Alfred Point. We seldom saw narwhals south of the Alpha River. The third area was in west central Milne Inlet. Narwhals were usually recorded within the area defined by Low Island, Two Rivers and First Point (mean 4.01 narwhals/interval in western Milne Inlet).

Areas where we rarely saw narwhals during the openwater season included eastern and northern Milne Inlet (mean 0.93 narwhals/interval). They were often absent from eastern and northern Milne Inlet when they were concentrated on the western side. We also counted few narwhals (mean 0.56 /interval) in Eclipse Sound in the open-water season. The most likely part of Eclipse Sound to be frequented by narwhals was north of Cape Hatt and Ragged Island. Northwestern Eclipse Sound and southern Navy Board Inlet were less frequented: we only twice, out of 19 flights that went into this area, saw narwhals to the northwest of a line from Alfred Point to the southernmost point of Bylot Island.

The areas frequented by narwhals in Milne Inlet and Koluktoo Bay, within which narwhals were observed on surveys, form a continuum stretching from northeastern Koluktoo Bay round Bruce Head, northwestward toward Two Rivers and First Point, and further north up the west side of Milne Inlet. Narwhal movements were observed from camps and capture sites, and from survey aircraft, between different parts of this range. Live-capture teams stationed on Bruce Head in 1988 and 1993 recorded movements round the point, which is used as a netting and hunting site by Inuit. North-south directional movements of narwhals in western Milne Inlet were seen from the survey helicopter. Many narwhals were observed in northeastern Koluktoo Bay, sheltered by Bruce Head from the light north wind that was blowing, at 2100 h on 14 August 1988 during a flight to track a VHF radio. Another flight at 1100 h on the next day found no narwhals in that area, exposed to the south wind that had arisen; narwhals were found in central Milne Inlet in calm water. First Point in western Milne Inlet is a site used by Inuit for narwhal hunting camps, because narwhals pass close along shore in this area.

Ice cover

After ice cover disappeared, narwhals were distributed differently from how they were when ice was still present (Fig. 3). Contingency table analysis of the relation between the presence of ice and the presence of whales in Eclipse Sound, treating each survey as an observational unit, showed a positive association (coefficient of con-

tingency (CC) 51%; Chi²₁ = 6.5*). The same analysis for Tremblay Sound showed a strong negative association (CC -82%; Chi²₁ = 16.8***). Ice cover in Eclipse Sound was associated with ice cover in Tremblay Sound (c.c. 78%). Contingency table analysis for narwhals and ice in Milne Inlet (CC 11%) and Koluktoo Bay (7%) did not give significant results because Koluktoo Bay very seldom had ice cover, whether narwhals were seen there or not, and Milne Inlet almost always had narwhals, regardless of ice cover. However the presence of whales in Koluktoo Bay was negatively associated with the presence of ice in Eclipse Sound (CC -50%; Chi²₁ = 6.0*). The results of dummy-variable regression identified two ice cover factors that affected distribution: ice-cover in Tremblay Sound appeared to be associated with lower narwhal density in Tremblay Sound, and ice cover in Eclipse Sound appeared to be associated with lower narwhal density in Koluktoo Bay. The positive association of ice and narwhals in Eclipse Sound was not evident in the results of dummy-variable regression because densities in Eclipse Sound were never high, even when ice was present. There was no association of narwhals with high ice cover within Eclipse Sound.

Wind speed

The Beaufort sea state was entered into the regression analyses. Increasing sea state reduced narwhal sightings (dummy variable "Beaufort > 1" had coefficient -0.14, P = 0.38%).

Killer whales

Killer whales influence the behaviour and distribution of narwhals (Reeves & Mitchell 1988). They occur in the study area when the waters are ice-free; according to Reeves & Mitchell (1988) they do so "on a regular basis". In Eclipse Sound on 30 August 1980, 30-40 killer whales cooperatively attacked a herd of "over 300" narwhals, killing at least one (Steltner et al. 1984.) Reports and records available to us for 1984-1991 and 1993 indicate the presence of killer whales in the Eclipse Sound area as follows: 1985 - Campbell et al. (1988), J. Ford (Vancouver Public Aquarium, pers. comm.); 1988 - reports from hunters on 16 August, while we were on Bruce Head, of killer whales in southern Milne Inlet; 1990 – 5 killer whales were reported in the straits of Pond Inlet in the evening of 7 August; and 1991 - 15 killer whales were sighted in the strait east of Stephens Island on a survey on 17 August.

Unusual behaviour and distribution that we observed to be associated with the presence of killer whales included (1) unusually rapid directed movement round Bruce Head into Koluktoo Bay, seen from shore on the evening of 16 August 1988 and (2) crowding of narwhals in to Fairweather Bay, where they were not seen at any other time, on 17 August 1991.

Discussion

Group size and composition

Compared with our overall mean group size of 2.3 (N = 597), Koski & Davis (1979) calculated a larger mean group size (2.9, N=165) from aerial-survey data collected in Milne Inlet on 24 August 1978. They also reported larger group sizes in coastal and ice-edge areas both within (2.5) and outside (2.9) Lancaster Sound (Koski & Davis 1994). Silverman (1979) calculated a much larger average group size of 4.1 (N=635) from cliff-top observations in Tremblay Sound in August 1977 and 1978. The sampling system used in these observations was to record "total numbers of narwhals passing by, group size, group composition. . ." (Silverman 1979, p. 11). However observations from the land are comparable with observations from the air only if all groups in a study area are regularly recorded by scan sampling. If each group that passes, or comes within sight, is recorded once, then observations from slow-moving or stationary platforms will record a larger proportion of travelling groups. If narwhals in directed travel tended to aggregate into larger groups (cf. Silverman 1979, p. 102), this would raise the estimate of mean group size for landbased data and make caution necessary in comparing them with aerial-survey data. Our subjective impression from shore-based observations in Tremblay Sound and at Bruce Head was that travelling groups, especially of males, were larger and disproportionately evident. In contrast, cow-calf pairs were so cryptic that they were caught several times in live-capture nets before those watching the nets were aware that any narwhals were close by. Other aspects of behaviour and factors such as ice conditions, prey distribution and density of narwhals may also influence group size (Silverman 1979) and account for differences in mean group size between studies. We noted that mean group size sometimes varied between surveys in the same area in the same year.

Silverman (1979) reported that sex and age segregation does not usually take place between herds, but that narwhals seem rather to form segregated groups within herds. However our results from 1987-88 and 1993 indicate that while cow-calf groups comprised 27% of narwhals seen in Koluktoo Bay and 24% in Milne Inlet (Table 1), in Eclipse Sound this proportion was about 4%. In Tremblay Sound, overall, an intermediate proportion was observed. These observations support the hypothesis that females and young are a smaller proportion of narwhals seen in the exposed waters of Eclipse Sound than in more sheltered waters. The population of white whales (Delphinapterus leucas) in the St Lawrence estuary, where group composition has been intensively studied in the entire summering area, tends to segregate into a component of adult males inhabiting the deeper, colder northeastern part of the range, and cow-calf and mixed groups in warmer, shallower water (Michaud 1993).

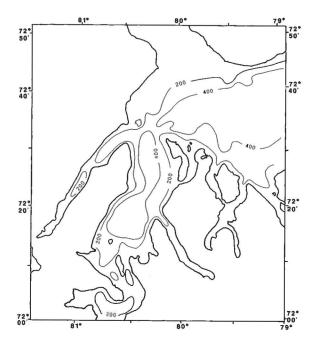


Fig. 4. Bathymetry of Eclipse Sound, Milne Inlet and adjacent waters.

Koski & Davis (1994) estimated 7.8% to 9% young of the year in selected observations made by expert observers in summer aerial surveys flown at 45, 90 or 150 m a.s.l. There were 10.3% "neonates" (young of the year) and 6.3% "calves" (defined by Silverman (1979, p. 25) as one- or two-year-olds) among 1469 narwhals classified in cliff-top observations in Tremblay Sound in 1977–78 (Silverman 1979, Table 10). We estimated 9.6% calves but, flying as high as we did, may have missed some calves; we also may have misidentified some small yearlings as calves. These estimates are consistent with models of monodontid population dynamics which indicate gross annual birth rates of 7% to 14% (Hay 1984, Burns & Seaman 1985, Kingsley 1989).

Finley & Gibb (1982) suggested that the preference of narwhals for particular areas in and around Eclipse Sound in summer may be related to calving. July and August constitute the calving period for narwhals (Hay 1984), and it has been suggested that protected fjords and inlets may be important for rearing young (Silverman 1979). Our survey data showed that cow-calf groups were more common in Koluktoo Bay, Milne Inlet and Tremblay Sound than in Eclipse Sound, supporting this suggestion.

Numbers, distribution and movements

These surveys were not designed to estimate absolute abundance. The survey route was not an unbiased sample

of the study area. In Tremblay Sound and Koluktoo Bay we were surveying areas where high densities were expected. Only in Milne Inlet and Eclipse Sound did we fly a survey pattern that was independent of the expected distribution of whales. The survey pattern in Milne Inlet used promontories of land as survey waypoints and therefore may have under-sampled nearshore waters.

Numbers of narwhals in any summering area vary from year to year (Koski & Davis 1994, Born et al. 1994). In this series of surveys the number counted varied also from survey to survey within years, partly because of variation in viewing conditions. For example during the 19 August 1988 survey the lack of wind and relatively low and diffuse light made narwhals appear light-coloured against a background of dark water. The calm, high-contrast conditions facilitated detection and probably contributed to the high numbers recorded in that survey. However variations were also caused by the movement of herds of narwhals into and out of the survey area, or onto and off the survey transect pattern, between surveys.

Fallis *et al.* (1983) flew aerial surveys for narwhals in Koluktoo Bay, Milne Inlet and Tremblay Sound on 12 August 1975 and 11 August 1976. Their counts were comparable to ours except for a cow-calf group, or herd, of nearly 200 that they saw in the mouth of Tremblay Sound in 1975. This is larger than any group recorded during our surveys. Koski & Davis (1979) counted 507 narwhals while surveying all of Milne Inlet on 24 August 1978. We counted up to 143 narwhals in the Inlet in 1987–88, and 340 on 18 August 1989.

We expected that strong winds would reduce the counts of narwhals. We also hypothesised that narwhals, accustomed for much of the year to the calmer water found in pack ice, would seek sheltered waters in windy weather. Beaufort sea state entered into the dummyvariable stepwise regression with a significant negative coefficient. However several possible factors are confounded in this result: 1) rough water makes marine mammals, even at the surface, hard to see; 2) in rough water, narwhals may spend more time at depth below the zone of wave turbulence and be less visible for this reason; 3) the distribution of narwhals may change in windy weather if narwhals actively seek sheltered calm water. We have difficulty separating these factors using our data set. Fluctuations in the number of narwhals that could be counted in Inglefield Bredning, Greenland, were associated with variations in sea state (Born 1986).

Narwhals preferred some bodies of water in the study area over others. Koluktoo Bay had the highest mean number of narwhals/interval, and Tremblay Sound, when ice-free, was also much frequented. Eclipse Sound, the largest water body, had the lowest density. Deep water is found in almost all parts of our study area. Both Tremblay Sound and Koluktoo Bay are more than 200 m deep and are bounded by steep underwater slopes (Fig. 4). Deep water in Tremblay Sound, and the steep western shore, extend north to Alfred Point. Milne Inlet is also steep

underwater on its west side. However there are some parts of the study area that are not as deep. Southern Navy Board Inlet, where we never observed narwhals, and northwestern Eclipse Sound and eastern Milne Inlet, where we rarely saw them, are shallower, with shelving shores. Narwhals apparently do not occur in Eskimo Inlet, which is shallow, but they have been reported in Tay Sound (Miller 1954). Born (1986) cited local knowledge that narwhals do not frequent the shallow Olrik, McCormick and Robertson fjords in the municipality of Avanersuaq (Thule area), where white whales occur instead. The distribution of narwhals in other summering areas of the Canadian high Arctic in 1984 appeared to be related to water depth: narwhals were more concentrated near the deepest areas of water bodies (Richard et al. 1994). "Narwhals characteristically have a deep-water distribution in the Arctic" (Sergeant 1979). The narwhal is physiologically adapted to deep diving, with oxygenstorage capabilities that have been evaluated, from physiological parameters such as the myoglobin content of muscle, as permitting aerobic dives lasting about 20 min (Williams et al. 1987). Dive data obtained from satellitelinked time-depth recorders in 1991 and 1993 indicate that narwhals make repeated dives to the bottom of deep fjords in summer (Martin et al. in press, Kingsley unpubl. data). It is possible that these areas provide a feeding niche where deep-diving narwhals experience less competition from other arctic marine mammals, Sergeant (1979), comparing narwhals with white whales, found that narwhals feed in deeper water, perhaps because they have a competitive advantage there. The distribution of food stocks has been suggested as influencing the summer distribution of white whales in Alaskan waters (Seaman & Burns 1981). We have no data on the distribution of food stocks in our study area at this time of year, and analyses of stomach contents of animals taken by hunters have suggested that narwhals feed little in the Eclipse Sound area during the open-water season (Mansfield et al. 1975, Finley & Gibb 1982, Weaver & Walker 1988). If these data are unbiased, preference shown by narwhals for this area may not be related to feeding (Finley & Gibb 1982). However regurgitation might account for the absence of food in the stomachs of some narwhals killed by hunters (Vibe 1950). In summer narwhals in Inglefield Bredning are reported to feed on polar cod (Boreogadus saida), arctic cod (Arctogadus glacialis), Greenland halibut (Reinhardtius hippoglossoides) and shrimp (Vibe 1950, Heide-Jørgensen et al. 1994). Satellite-radiotagged narwhals in Tremblay Sound in 1991 spent 70% of their time diving deep, possibly related to feeding (Martin et al. in press).

Narwhals have been reported to move into and out of fjords throughout the summer (Silverman 1979); this tendency was also apparent from our shore-based observations in Tremblay Sound during 1984–1987 (Kingsley unpubl. data). Livecapture teams working or camped on the extremity of Bruce Head also noted movements, sometimes apparently of significant numbers of nar-

whals, round the point into or out of Koluktoo Bay. Reports of narwhals in Inglefield Bredning (Born 1986, Born et al. 1994) also emphasized movement from one sector of the observation area to another or into and out of tributary fjords. Vibe (1950) and Silverman (1979) suggested that these movements into and out of fjords may be related to foraging activities or to the tidal cycle. Our ground-based observations agreed with those of others, but our aerial-survey results did not entirely agree. On 16 out of 16 surveys made when Tremblay Sound was icefree, narwhals were found there, and in Koluktoo Bay on 14 of 15 surveys flown when Eclipse Sound was ice-free. Other information was obtained from satellite-radio-tag data: in 1991 two of two radio-tagged female narwhals stayed continuously for three weeks between Alpha River and Athole Point in Tremblay Sound; they did not leave Tremblay Sound (Kingsley unpubl. data). Conversely a sub-adult male narwhal radio-tagged at Bruce Head on 24 August 1993 stayed within radio-shot of the tagging site for two days. He then moved to western Milne Inlet, and five days later into central Eclipse Sound (Kingsley un-

We have some evidence that narwhals do move into and out of Koluktoo Bay, backed up by indications of where they go - into southern and western Milne Inlet. But if narwhals move out of Tremblay Sound, we have little indication of their destination, whether north to Navy Board Inlet, round Athole Point into Milne Inlet, or northeast into central Milne Inlet. We frequently surveyed the western coast of Eclipse Sound, and crossed the southern end of Navy Board Inlet, without seeing narwhals, but we did not survey the inshore waters around Athole Point. We once saw narwhals close inshore in western Milne Inlet north of First Point. Information from local hunters is conflicting. Some say that narwhals from Tremblay Sound move north along the western shore of Eclipse Sound into central Navy Board Inlet, and there are traditional summer-season narwhal hunting camps - Kaunak and Komukouri - on the western shore of Eclipse Sound (Finley et al. 1980, Finley & Miller 1982). However other hunters say that the narwhals hunted at Low Point (Nadluat) in central Navy Board Inlet are part of a separate group that moves within a region extending further north towards Lancaster Sound.

Distribution relative to ice

Finley (1976) reported that in the late summer narwhals strongly prefer water containing pan ice, and Silverman (1979) suggested that they may do so because the ice offers protection from wind and predators. As long as ice remained in Eclipse Sound, narwhals were found there, usually associated with the ice. However the association of narwhals with ice cover, in this study, only applied to Eclipse Sound. Ice cover in Tremblay Sound, which usually coincided with ice cover in Eclipse Sound, had a clear negative effect on narwhals, and they stayed out of

Tremblay Sound when it was ice-covered. Narwhals may prefer wide, deep waters like Eclipse Sound, but, finding themselves exposed to predators or rough weather when such areas are ice-free, move then into more enclosed areas. Alternatively narwhals may have a preference for steep shorelines of deep narrow inlets, but avoid such areas when they are infested with ice because they perceive a danger of ice entrapment. The observation of a negative association between narwhal presence in Koluktoo Bay and ice cover in Eclipse Sound is an indication, but not proof, that the former hypothesis is more likely. Additional support for it is given by the winter distribution of narwhals, which tends to favour offshore ice-covered waters (Koski & Davis 1994).

Narwhals may move into areas recently cleared of ice to take advantage of newly-available food sources. This may be especially important for nursing females. Although adult males lead major northward and westward spring migrations into the Canadian Arctic archipelago (Greendale & Brousseau-Greendale 1976), our observations from shore in Tremblay Sound in 1984–86 (Kingsley unpubl. data) indicated that females with young were usually the first animals to arrive there once the ice disappeared.

Distribution and movements relative to wind

Once the ice in the study area disappeared, the narwhals seemed to seek out smaller bodies of water (e.g. Koluktoo Bay) or areas containing islands or other topographical irregularities (e.g. southern end of Milne Inlet) that offered shelter from the wind, from a variety of directions, without the whales having to travel very far. The results of dummy-variable regression indicated that fewer narwhals were seen when the Beaufort sea state was higher. However, known visibility biases are confounded with possible behavioural biases, making interpretation of this result difficult. Two observations support the hypothesis that the distribution of narwhals may be affected by wind. First, while narwhals were usually found in Koluktoo Bay, they consistently favoured the calmer water under the south face of Bruce Head and avoided the rougher water where north winds blew down through the pass further to the west. Second, narwhals moved from Koluktoo Bay into Milne Inlet between 2100 h on 14 August 1988 and 1100 h on 15 August apparently in response to a change in wind direction. On the evening of 14 August we saw narwhals in calm water in northern Koluktoo Bay; the wind then was from the north and the high ridge sheltered the bay. On the next day the wind was from the south. Koluktoo Bay was exposed to it, and the water was rough. During a helicopter flight to locate a VHF radio transmitter that we had attached to a narwhal the day before, we saw no narwhals in Koluktoo Bay, but many in central and western Milne Inlet, where the water was quite calm. On 16 August narwhals were still in southern Milne Inlet, and the wind was still blowing from the south.

Movements in response to killer whales

The proximity of killer whales affects the behaviour of other marine mammals. Ringed seals are said to haul out on land only when killer whales are near, and narwhals are said by the Inuit to have a suite of characteristic behaviour patterns when avoiding killer whales. This includes moving into heavy ice or close to ice edges or shorelines, and slow, quiet movement (Reeves & Mitchell 1988, Finley et al. 1990). Long-finned pilot whales (Globicephala melas) have been reported to "hide" from killer whales by swimming very close to a shoreline (Bloch & Lockyer 1988), and what succeeds for one prey species may serve another. Our observations indicate that narwhals may also crowd into small bays, that they do not usually frequent, when killer whales are nearby. We observed more than 200 narwhals crowded into Fairweather Bay, southwestern Milne Inlet, when killer whales were east of Stephens Island in 1991. Narwhals were also reported by local hunters to use Z Lagoon at Cape Hatt when killer whales were in the vicinity. On 24 August 1987 200-300 narwhals were reported to be in Z Lagoon, but we had no confirmed sighting of killer whales in the area at the time. All our surveys passed over Cape Hatt, but we did not see narwhals in Z Lagoon in any other survey.

Although killer whales, as a species, are adept at hunting in ice-infested waters, it has been suggested that in eastern Canadian and Greenlandic waters they are less apt to enter ice fields than in Antarctic or Alaskan waters (Heide-Jørgensen 1988). Whether or not this is so, narwhals could be harder for killer whales to detect in ice-covered waters than in open waters. And if swimming close to shore helps narwhals to avoid detection by killer whales, then areas with complex shorelines should be favoured.

Conclusions

Narwhals favour larger, deeper water bodies as long as ice cover persists, probably because the ice cover helps them to avoid predators, perhaps also because it shelters them from wind, although this is still unproven. When ice cover disappears, they seek smaller water bodies but prefer those that are deep and bounded by steep shores. They tend not to use the smaller water bodies as long as ice cover persists in the larger ones. Although the distribution of narwhals is usually predictable, it is highly clumped, and may change over short periods of time. Reaction to the presence of killer whales causes the distribution to become more clumped and less predictable. The indications for aerial survey are two-fold: 1) careful stratification and 2) multi-aircraft surveys to complete surveys in a short time.

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References

- Bloch, D. & Lockyer, C. 1988. Killer whales (*Orcinus orca*) in Faroese waters. Rit Fiskideildar 11: 55–64.
- Born, E. W. 1986. Observations of narwhals (Monodon monoceros) in the Thule area (NW Greenland), August 1984. Rep. int. Whal. Commn 36: 387–392.
- Born, E. W., Heide-Jørgensen, M. P., Larsen, F. & Martin, A. R. 1994. Abundance and stock composition of narwhals (*Monodon monoceros*) in Inglefield Bredning (NW Greenland). – Meddr Grønland, Biosci. 39: 51–68.
- Burns, J. J. & Seaman, G. A. 1985. Biology and ecology. Pt II of Investigations of belukha whales in coastal waters of western and northern Alaska. – Final report prepared for NOAA, Outer Continental Shelf Environmental Assessment Program, contract NA-81-RAC-00049 by Alaska Dept Fish and Game, Fairbanks, Alaska. 129 pp.
- Campbell, R. R., Yurick, D. B. & Snow, N. B. 1988. Predation on narwhals, *Monodon monoceros*, by killer whales, *Orcinus orca*, in the eastern Canadian Arctic – Can. Field-Nat. 102: 689–696.
- Draper, N. L. & Smith, H. 1981. Applied regression analysis. 2nd ed. – Wiley, New York, NY: 709 pp.
- Fallis, B. W., Klenner, W. E. & Kemper, J. B. 1983. Narwhal surveys and associated marine mammal observations in Admiralty Inlet, Navy Board Inlet, and Eclipse Sound, Baffin Island, N.W.T. during 1974 and 1976. Can. Tech. Rep. Fish. Aquat. Sci. 1211: 20 pp.
- Finley, K. J. 1976. Studies of the status of marine mammals in the central district of Franklin, N.W.T. June-August 1975. – Rep. prep. by LGL Ltd. – Polar Gas, Toronto, Ontario, unpubl.: 189 pp.
- Finley, K. J., Davis, R. A. & Silverman, H. B. 1980. Aspects of the narwhal hunt in the eastern Canadian Arctic. – Rep. int. Whal. Commn 30: 459–464.
- Finley, K. J. & Gibb, E. J. 1982. Summer diet of the narwhal (*Monodon monoceros*) in Pond Inlet, northern Baffin Island. Can. J. Zool. 60: 3353–3363.
- Finley, K. J. & Miller, G. W. 1982. The 1979 hunt for narwhals (*Monodon monoceros*) and an examination of harpoon gun technology near Pond Inlet, northern Baffin Island. Rep. int. Whal. Commn 32: 449–460.
- Finley, K. J., Miller, G. W., Davis, R. A. & Greene, C. R. 1990. Reactions of belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, to ice-breaking ships in the Canadian high Arctic. In: Smith, T. G., St Aubin, D. J. & Geraci, J. R. (eds.). Advances in Research on the Beluga Whale, *Del-*

- phinapterus leucas. Can. Bull. Fish. Aquat. Sci. 224: 97-117
- Greendale, R. G. & Brousseau-Greendale, C. 1976. Observations of marine mammals at Cape Hay, Bylot Island during the summer of 1976. Environment Canada, Fish. Mar. Serv. Tech. Rep. 680. 25 pp.
- Hay, K. A. 1984. The life history of the narwhal (Monodon monoceros L.) in the eastern Canadian Arctic. Unpublished PhD thesis. McGill University, Montreal, Québec: 255 pp.
- Heide-Jørgensen, M.-P. 1988. Occurrence and hunting of killer whales in Greenland Rit Fiskideildar 11: 115–135.
- Heide-Jørgensen, M. P., Dietz, R. and Leatherwood, S. 1994. A note on the diet of narwhals (*Monodon monoceros*) in Inglefield Bredning (NW Greenland) – Meddr Grønland, Biosci. 39: 213–216.
- Kingsley, M. C. S. 1989. Population dynamics of the narwhal Monodon monoceros: an initial assessment (Odontoceti: Monodontidae.). – J. Zool. 219: 201–208.
- Koski, W. R. & Davis, R. A. 1979. Distribution of marine mammals in northwest Baffin Bay and adjacent waters, May-October 1978. Rep. prep. by LGL Ltd for PetroCanada, Calgary, Alberta. Unpublished: 243 pp.
 Koski, W. R. & Davis, R. A. 1994. Distribution and numbers of
- Koski, W. R. & Davis, R. A. 1994. Distribution and numbers of narwhals (*Monodon monoceros*) in Baffin Bay and Davis Strait. – Meddr Grønland, Biosci. 39: 15–40.
- Mansfield, A. W., Smith, T. G. & Beck, B. 1975. The narwhal (*Monodon monoceros*) in eastern Canadian waters. J. Fish. Res. Board Can. 32: 1041–1046.
- Martin, A. R., Kingsley, M. C. S. & Ramsay, M. A. In press. Diving behaviour of narwhals on their summer grounds. Can. J. Zool. (In press).
- Michaud, R. 1993. Distribution estivale du béluga du Saint-Laurent; synthèse 1986–1992. – Rapp. tech. can. sci. hali. aquat. 1906: 22 pp. + Annexe.
- aquat. 1906: 22 pp. + Annexe.

 Miller, R. S. 1955. A survey of the mammals of Bylot Island,
 Northwest Territories Arctic 8: 166-176.
- Reeves, R. R. & Mitchell, E. 1988. Distribution and seasonality of killer whales in the eastern Canadian Arctic. – Rit Fiskideildar 11: 136–160.
- Richard, P. R., Weaver, P. A., Dueck, L. & Barber, D. A. 1994. Distribution and numbers of Canadian High Arctic narwhals (Monodon monoceros) in August 1984. – Meddr Grønland, Biosci. 39: 41–50.
- Seaman, G. A. & Burns, J. J. 1981. Preliminary results of recent studies of belukhas in Alaskan waters. – Rep. int. Whal. Commn 31: 567–574.
- Sergeant, D. E. 1979. Seasonal movements and numbers of cetaceans summering in Lancaster Sound, Arctic Canada. – Paper SC/31/SM/19 presented to the Scientific Committee of the International Whaling Commission. Available from IWC, The Red House, Cambridge, UK, CB4 4NP: 20 pp. + tables + figs.
- Silverman, H. B. 1979. Social organization and behaviour of the narwhal, *Monodon monoceros* L. in Lancaster Sound, Pond Inlet, and Tremblay Sound, Northwest Territories. – Unpublished M.Sc. thesis. McGill University, Montreal, Québec: 144 pp.
- Steltner, H., Steltner, S. & Sergeant, D. E. 1984. Killer whales. Orcinus orca, prey on narwhals, Monodon monoceros: an eyewitness account. – Can. Field-Nat. 98: 458–462.
- Weaver, P. A. & Walker, R. S. 1988. The narwhal (Monodon monoceros L.) harvest in Pond Inlet, Northwest Territories: hunt documentation and biological sampling, 1982–83.
 Can. Manus. Rep. Fish. Aquat. Sci. 1975: 26 pp.
- Williams, T. M., Cornell, L. H., Hall, J. D. & Antrim, J. 1987.
 Summary of research conducted in the Pond Inlet area during August 1987. – Tech. Rep. 87–204, Sea World Research Institute, San Diego, Calif.: 16 pp.
- Vibe, C. 1950. The marine mammals and the marine fauna in the Thule district (northwest Greenland) with observations on ice conditions 1939–41. Meddr Grønland 150(6): 115 pp.