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Abundance of narwhals (*Monodon monoceros*) on the hunting grounds in Greenland

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Narwhals (*Monodon monoceros* L.) occur in the Atlantic sector of the Arctic where for centuries they have been subject to subsistence hunting by Inuit in Greenland and Canada. Scientific advice on the sustainable levels of removals from narwhal populations provides the basis for quotas implemented in both Greenland and Canada. The scientific advice relies heavily on extensive aerial surveys that are the only feasible way to acquire data on narwhal densities and abundance throughout their range. In some areas lack of information on abundance, in combination with high exploitation levels, has caused conservation concerns leading to restrictions on the international trade in narwhal tusks. Narwhals also are regarded as highly sensitive to habitat disturbance caused by global warming. This study analyzed data from aerial sighting surveys covering four major narwhal hunting grounds in Greenland. The surveys were conducted as double observer experiments with 2 independent observation platforms, 1 at the front and 1 at the rear of the survey plane. The sighting data were analyzed using mark–recapture distance sampling techniques that allow for correction for whales that were missed by the observers. The surveys also were corrected for animals that were submerged during the passage of the survey plane, using diving and submergence data from satellite-linked time–depth recorders deployed on 2 free-ranging narwhals. The abundance of narwhals on the wintering ground in West Greenland in 2006 was 7,819 (95% confidence interval [*CI*]: 4,358–14,029). The abundances of narwhals in Inglefield Bredning and Melville Bay, northwest Greenland in 2007 were 8,368 (95% *CI*: 5,209–13,442) and 6,024 (95% *CI*: 1,403–25,860), respectively. The abundance of narwhals in East Greenland in 2008 was 6,444 (95% *CI*: 2,505–16,575). These surveys provide the first estimates of narwhal abundance from important hunting areas in East and West Greenland and provide larger and more complete estimates from previously surveyed hunting grounds in Inglefield Bredning. The estimates can be used for setting catch limits for the narwhal harvest in West and East Greenland and as a baseline for examining the effects of climate change on narwhal abundance. DOI: 10.1644/09-MAMM-A-198.1.

Key words: abundance estimation, aerial survey, Arctic, climate change, Greenland, mark–recapture distance sampling, narwhal, satellite tracking

The narwhal (*Monodon monoceros* L.) is a medium-sized odontocete whale that occurs year-round mainly in high Arctic or sub-Arctic areas of the North Atlantic and adjacent waters. It is distributed widely from around Franz Josef Land in the east, around Svalbard, along East Greenland, in central and northern parts of West Greenland, along the east coast of Baffin Island, in the Canadian high Arctic archipelago, and in northern Hudson Bay and Hudson Strait (Heide-Jørgensen 2001). During the summer narwhals generally move north into areas that are inaccessible during winter because of formation of dense pack ice or fast ice. In winter narwhals are found in the moveable pack ice in the Greenland Sea, Hudson Strait, and Baffin Bay–Davis Strait. Often in winter they are located in deep water where they dive to 2,000 m in search of prey

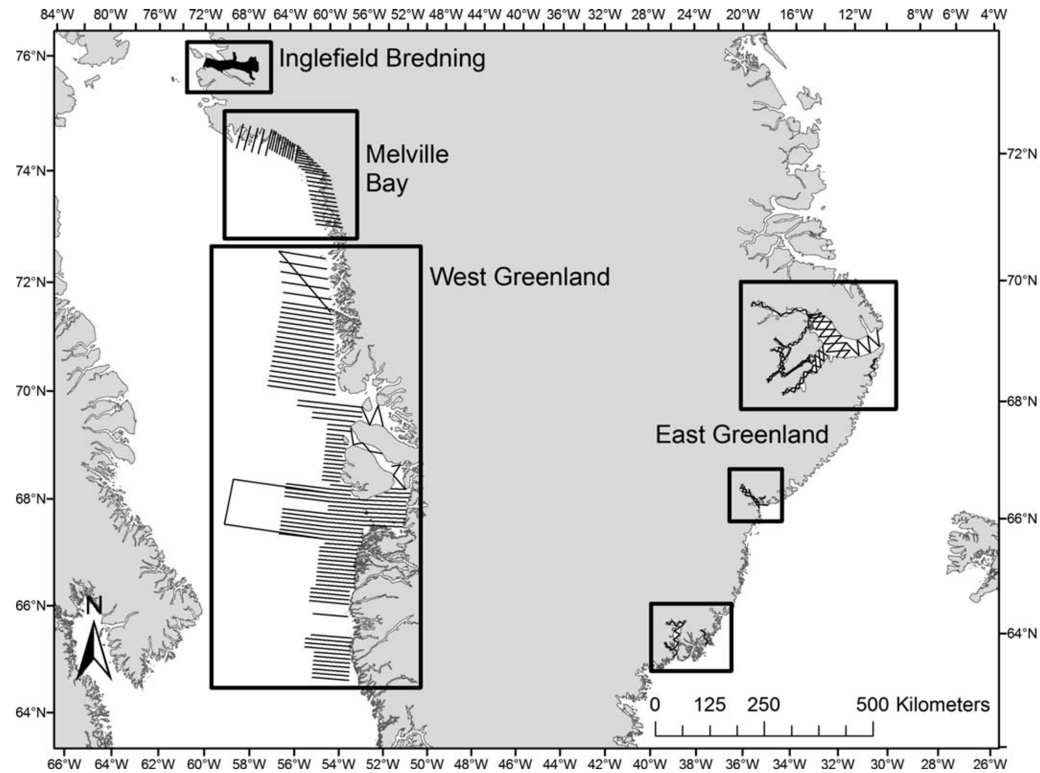

FIG. 1.—Overview of narwhal aggregations surveyed in this study with major locality names indicated.

species like Greenland halibut (*Reinhardtius hippoglossoides*) and squid (*Gonatus* sp.—Laidre and Heide-Jørgensen 2005). Their high affinity for ice-covered areas and their ability to conduct deep dives make them unique among cetaceans (Laidre et al. 2003). These specializations, together with small population size and restricted core areas of distribution, were identified recently as features that make narwhals particularly sensitive to climate changes (Laidre et al. 2008).

Narwhals inhabiting the Arctic areas of the North Atlantic constitute a metapopulation of several smaller subpopulations showing high site fidelity to certain summering grounds (Heide-Jørgensen et al. 2003). Some mixing or exchange between subpopulations can occur on the wintering grounds. Narwhals return to the same summering grounds year after year which makes it possible to assess the status of the narwhal subpopulations in each of these summering grounds.

Narwhals are subject to harvest by Inuit hunters in Greenland and Canada, and both the hunt itself and the export of narwhal tusks lead to concerns about the sustainability of the exploitation (Reeves and Heide-Jørgensen 1994). The current (2003–2007) reported harvest of narwhals amounts to approximately 420 annually in Canada, 400 in West Greenland, and 110 in East Greenland. These catches are taken from specific summering aggregations, from migrating whales comprised of several different summer aggregations, or from wintering grounds where, presumably, some mixing of whales from different summer aggregations occurs (Heide-Jørgensen et al. 2002). Scientific advice on the sustainable levels of removals from narwhal populations is provided by the North Atlantic Marine Mammal Commission and the Canada–Greenland Joint Commission for the Conservation and Management of Narwhal and Beluga, and partly on the basis of that advice, quotas are implemented in both Greenland and Canada. Because of the absence of unbiased abundance estimates the long-term sustainability of these catches has been difficult to assess. Narwhals are listed in Appendix II of the Convention on International Trade in Endangered Species (CITES), which ''lists species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled.'' However, the European Union has banned all import of narwhal products since 2004 because of concern about the sustainability of the harvest. In 2004 the first quotas were implemented in West Greenland, and they have been revised annually since. In 2009 quotas were installed for East Greenland.

In 2005 new regulations from CITES required the scientific authority of the state of export to issue a ''nondetrimental finding'' if it can be documented that export will not be detrimental to the survival of species being traded. The lack of abundance estimates and scientific assessment of all narwhal stocks in Greenland forced the Greenland Home Rule government to issue a negative nondetrimental finding in 2006, which prohibits export of narwhal products from Greenland.

In Greenland, narwhals are hunted by two communities in East Greenland (Ittoqqortormiut, 70°30′N, 22°00′W, and Tasiilaq, 66°N, 38°W) and by several communities in West Greenland from Disko Bay to Qaanaaq (77°30′N, 69°W; Fig. 1). The hunt in West Greenland targets aggregations of narwhals that move south in the fall (Uummannaq), winter in the pack ice off Disko Bay and Uummannaq, or are heading toward summering grounds in Melville Bay (Upernavik) and Inglefield Bredning. In East Greenland it is unknown if the narwhals hunted in the communities Tasiilaq and Ittoqqortormiut constitute a single stock with seasonal migrations or if they are separate aggregations of whales (Dietz et al. 1994).

Davis Strait and Baffin Bay have a large number of overwintering narwhals. They arrive in the area in late fall and remain at certain localities along the coast until spring. The winter occurrence of narwhals in West Greenland has been used to index the population trends in the stock that is hunted at several sites along the coast based on 8 surveys between 1981 and 1999 (Heide-Jørgensen and Acquarone 2002; Heide-Jørgensen and Reeves 1996; Heide-Jørgensen et al. 1993). The time series has shown a declining trend in abundance since 1981, and thus continued surveys are necessary to update the index and trend.

In summer, narwhals in West Greenland are found at two major coastal regions: Inglefield Bredning and Melville Bay. Previous abundance estimates exist from Inglefield Bredning (Heide-Jørgensen 2004), but previous surveys of Melville Bay failed to detect whales, making it impossible to derive abundance estimates despite a harvest in the bay. Narwhals visit Uummannaq in November, but attempts to survey narwhals in Uummannaq in November have failed because of the darkness at that time of the year.

Less is known about narwhals in East Greenland, and most information comes from harvest statistics that indicate several coastal summering areas: the fjord system of Scoresby Sound and the Kangerlussuaq, Sermilik, Sermiligaaq, and Kulusuk fjords. Scattered observations indicate that narwhals might occur as far south as Umivik (64°30′N, 41°W) in summer and that they also occur at several fjords along the Blosseville Coast between 70°N and 67°30′N; however, the density in these areas is considered to be low (Dietz et al. 1994). It is not known if several separate narwhal aggregations persist in these areas or if the same whales use several of the fjords and coastal regions of East Greenland. North of Scoresby Sound narwhals are frequently found in Young Sound (74°N) and along the coast as far north as Nordost Rundingen (82°N—Dietz et al. 1994; http://www2.dmu.dk/Pub/FR721.pdf). Narwhals north of Scoresby Sound are protected by the Northeast Greenland National Park, no hunting takes place and no attempts have been made to assess the abundance of narwhals in the national park.

To obtain estimates of the total abundance of narwhals at all major summer hunting grounds and on the wintering ground in West Greenland, visual aerial surveys were conducted between 2006 and 2008 using similar analytical and data collection methods. These surveys provide estimates of the major aggregations of narwhals in Greenland but do not include all areas; some areas in northeast Greenland were not included as they are believed not to be subject to hunting. Also, parts of the wintering grounds in West Greenland could not be covered for logistical reasons.

Low-flying, fixed-winged aircraft have proven to be the best platforms for surveying the abundance of narwhals in remote and ice-covered areas. The advantages are that large areas can be covered in relatively short windows of favorable weather conditions and that the otherwise noise-sensitive narwhals do not avoid the aircraft before the passage of the plane. Both visual and photographic aerial surveys of narwhals have been conducted in Canada (Richard 1991; Richard et al. 1994) and Greenland (Heide-Jørgensen 2004; Heide-Jørgensen et al. 1993), and each has its advantages. In the surveys reported here visual aerial line-transect methods were used. Narwhals spend time underwater and are not always available for detection (availability bias), and in addition, observers do not detect all animals (perception bias). Total abundance estimates of narwhals were developed taking into account both perception bias and availability bias.

Materials and Methods

Survey platform.—All visual aerial line-transect surveys were conducted as a double-platform, or double-observer, experiment with independent observation platforms at the front and rear of the survey plane. The survey plane was a DeHavilland Twin Otter, and target altitude and speed were 213 m and 168 km h^{-1}. Two observers sat in the front seats just behind the cockpit, and 2 observers sat in the rear seats at the back of the plane. The distance between front and rear observers was approximately 4 m, and a long-range fuel tank and recording equipment installed between the front and rear seats prevented visual or acoustic cueing of sightings between the two platforms. All 4 observers had bubble windows that allowed them to view the track line directly below the aircraft.

The observers collected data on sightings (species, group sizes, and characteristics), recorded declination angles to sightings when abeam using inclinometers, and kept a record of sighting condition (sea state and visibility). In 2006 information from observers was recorded on 4 different tape recorders, together with time stamp signals of position from a Garmin 100 global positioning system (GPS; Garmin Inc., Olathe, Kansas). In subsequent surveys data from the 4 observers were recorded on a specially designed, 4-channel video- and audio-recording computer (sDVRms) developed by Redhen (www.redhen.com). The Redhen system was connected to a GPS, and all sightings were logged in a GPS logfile. Although all observations were spoken into a common recording system, the observers could not hear each other.

Survey of the West Greenland wintering ground in 2006.—The first survey was conducted in West Greenland between 21 March and 19 April 2006. The survey design consisted of transects aligned east–west, systematically placed from the coast of West Greenland and across the banks (Fig. 2). The survey covered an area from Maniitsoq to northern Upernavik in West Greenland, including Disko Bay, Vaigat, and Uummannaq. A total of 14 strata was constructed in this area following stratification in previous surveys (Heide-Jørgensen and Reeves 1996). The realized effort was slightly less than

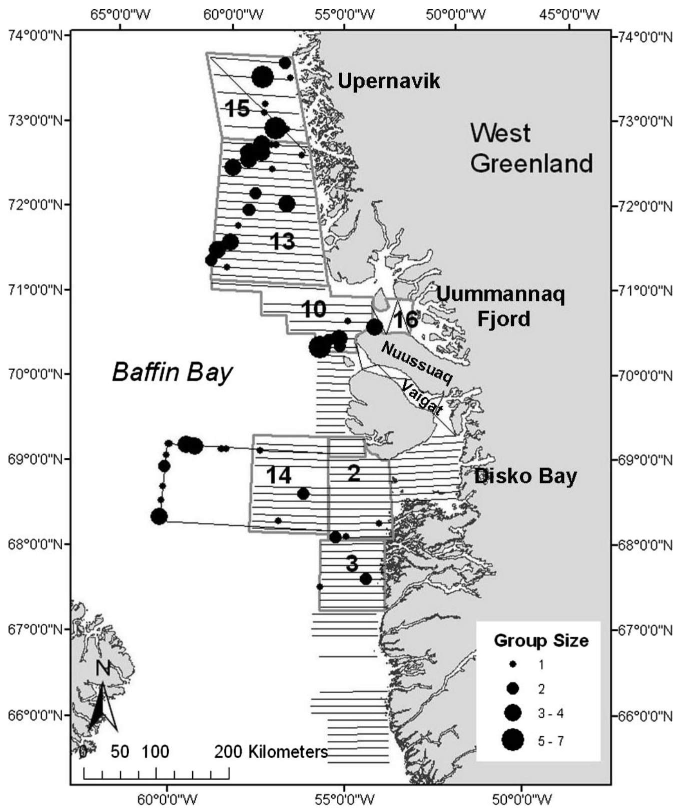

FIG. 2.—Transect lines, strata numbers in bold, and distribution of sightings in the survey of narwhals in West Greenland, March–April 2006.

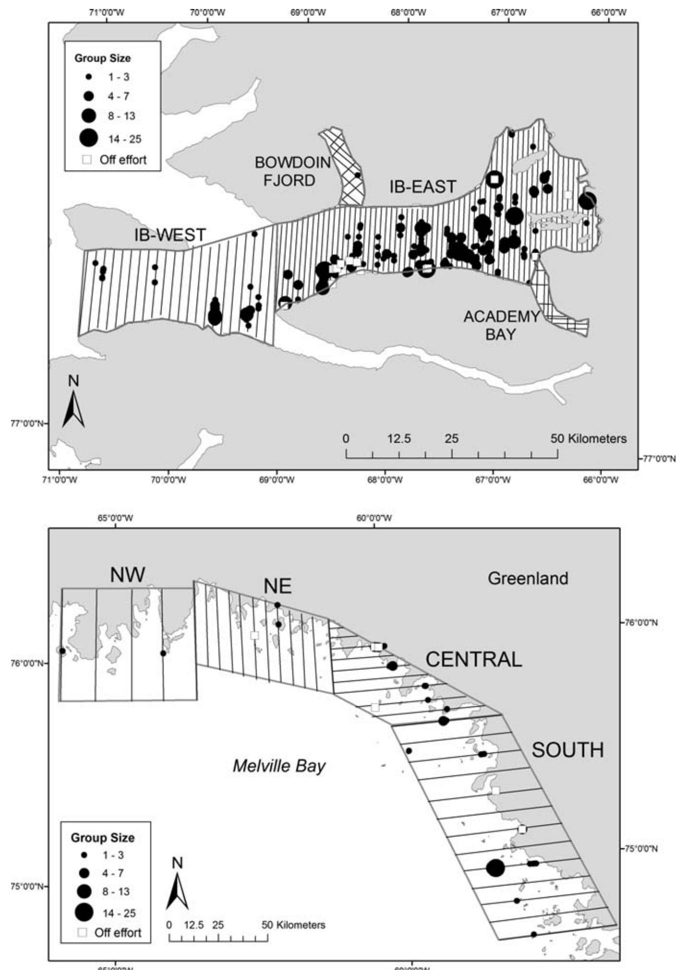

FIG. 3.—Strata, transect lines, and sightings of narwhals (including off-effort sightings between transects) in Inglefield Bredning (upper panel) and Melville Bay (lower panel) during the aerial survey in August 2007.

originally planned because of unfavorable weather conditions (sea states >3 and horizontal visibility <1 km), and only 8 strata produced narwhal sightings. Three long transects were extended west to 61°W to obtain distributional data on narwhals but were not used for estimation of abundance.

Surveys of Melville Bay and Inglefield Bredning in 2007.—The second survey was conducted in northwest Greenland between 13 and 24 August 2007. The survey design was planned to cover Melville Bay and Inglefield Bredning (Fig. 3) systematically, with Melville Bay surveyed twice (11–14, 20, 23 August) and Inglefield Bredning surveyed five times (15–16, 21 August). Melville Bay is essentially one long glacial front with few bedrock promontories intersecting the glacial fronts. No precise maps of the borders of the glaciers exist, and the positions of the glaciers are also subject to considerable changes. The transects were planned to intersect the glacial fronts at approximate perpendicular angles. The largest survey effort was allocated to the central and northeastern strata (~5.5 km between transects) because of their expected higher abundance of narwhals compared with the south and northwestern strata (~9 and 15 km between transects).

Inglefield Bredning was surveyed with transects aligned north–south going from coast to coast. Two side fjords, Bowdoin and Academy Bay, were surveyed in a zig-zag manner. The western stratum in Inglefield Bredning was covered with a survey intensity of 2 km between transects, with every fifth transect covered in each survey. Transects in the eastern part of Inglefield Bredning were spaced 1.2 km apart with each survey covering 20% of the transects. The survey was completed in optimal conditions (sea states <3 and visibility >10 km). The time between the first detection of a group of whales and when it passed abeam was estimated by the survey leader for a subset of sightings. The purpose was to estimate the average time a group of whales was visible to the observers.

Survey of East Greenland in 2008.—The third survey was conducted in East Greenland between 8 August and 19 August 2008 and used similar techniques and equipment to those in the 2007 survey. Only the fjord system of Scoresby Sound, the fjords along the Blosseville Coast, the Kangerlussuaq fjord, and the fjords south of 65°N were covered (Figs. 4–6). In all areas a systematic coverage was attempted, but along the coast of Blosseville a reconnaissance flight about 1 km offshore was conducted in addition to the fjords. Available maps from East Greenland did not match the GPS positions from the aircraft, and instead dead reckoning was used in small areas like the fjords along the Blosseville Coast. Transect lines in these

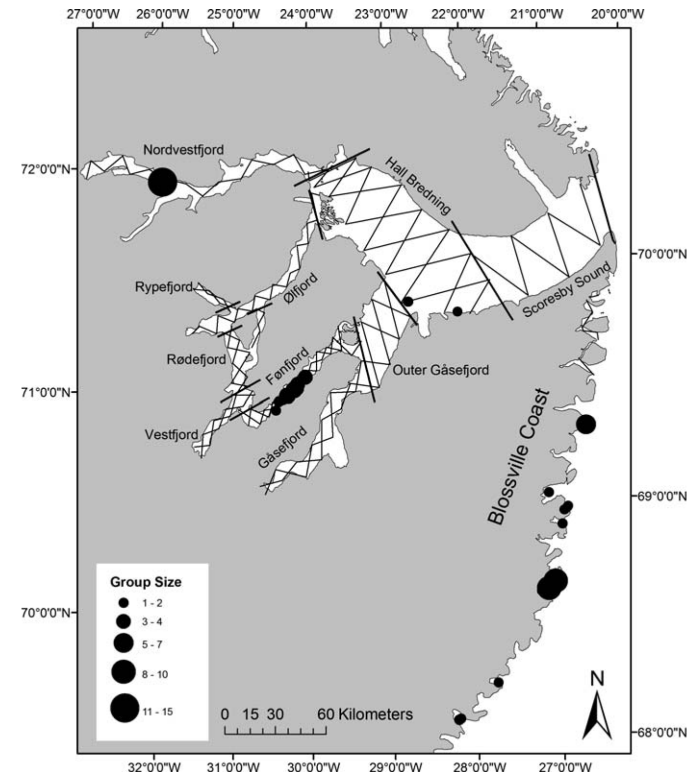

FIG. 4.—Strata with areas, transect lines, and sightings of narwhals in Scoresby Sound and along the northern part of Blosseville Coast during the aerial survey in August 2008.

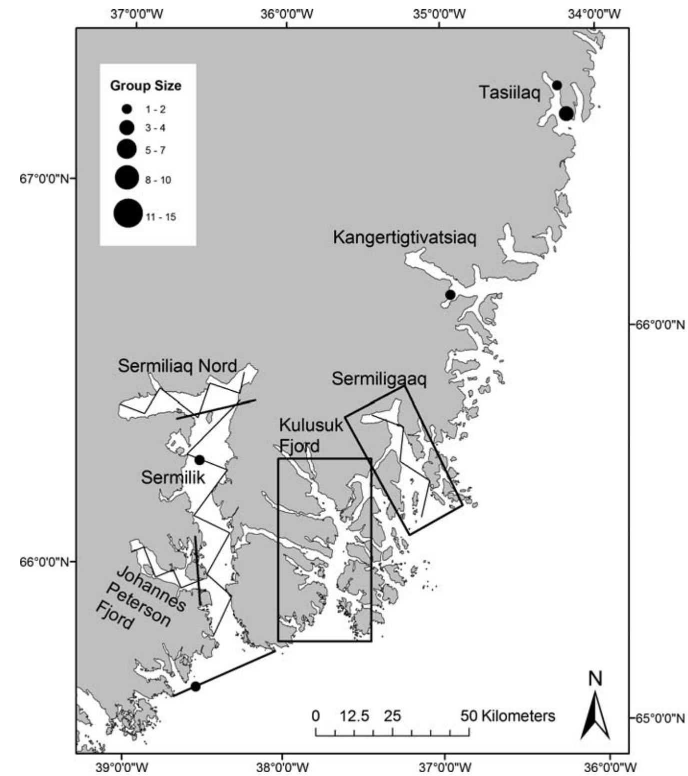

FIG. 6.—Strata with areas, transect lines, and sightings of narwhals in Sermilik, Sermiligaaq, Kangertigtivatsiaq, and Tasiilaq during the aerial survey in August 2008. Notice that Tasiilaq also is a community located in the Sermiliaq Fjord.

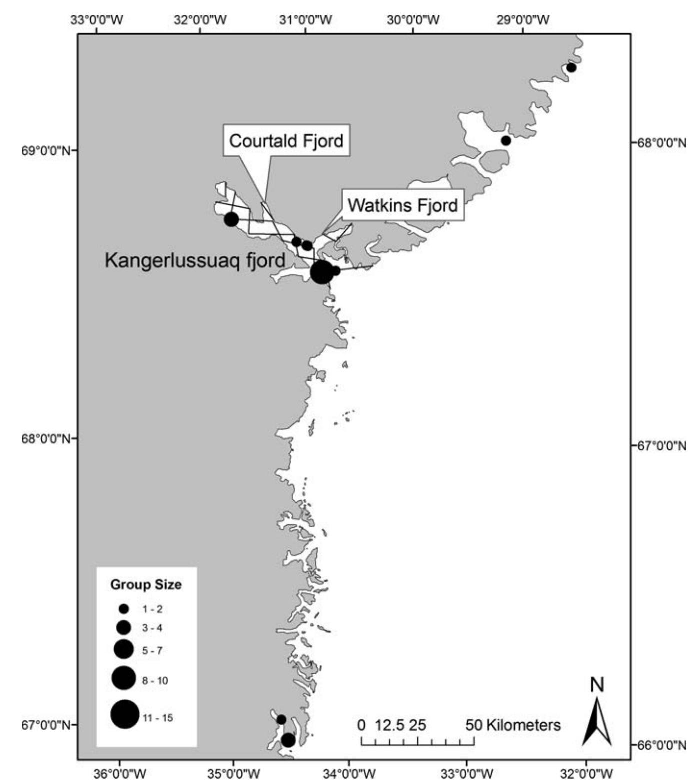

FIG. 5.—Delineation of the strata in Kangerlussuaq and the southern part of the Blosseville Coast, with sightings of narwhals during the survey in August 2008.

fjords were constructed in a zig-zag manner beginning at the outer coast and ending at the glacial front. Only effort recorded during sea states <3 and visibility >10 km was included.

Collection of data on the availability correction.—Two female narwhals were captured in nets (Dietz and Heide-Jørgensen 1995) in Melville Bay in August–September 2007. The whales were tagged with satellite-linked time–depth recorders (SLTDR, SPLASH-tag from Wildlife Computers, Redmond, Washington) that were bolted through the dorsal ridge of the whales with nylon pins. As well as providing satellite positions of the 2 whales, the tags also collected data on the time spent at or above 2-m depth, the depth to which narwhals can be detected reliably on the track line (Heide-Jørgensen 2004; Richard et al. 1994). Data were collected in 1-h increments over a 24-h period rounded to the nearest 5% of total time by hour and with a maximum of 95% of total time that the whales were above the threshold depth. Data were relayed through the Argos data collection and location system and decoded using Argos message decoder (Wildlife Computers). Daily averages were calculated and used for deriving monthly averages that matched the survey dates.

Perpendicular distance measurements.—The declination angles (ψ) recorded by the observers were converted to the perpendicular distance of the animal to the track line (x) using the following equation taken from Lerczak and Hobbs (1998a, 1998b):

$$x = \cos(\psi)\left\{(R+v)\sin(\psi) - \sqrt{R^2\sin^2(\psi) - 2(2R+v)\cos^2(\psi)}\right\},$$

where R is the radius of Earth (6,370 km) and v is the altitude of the airplane (213 m). Sightings where angles of declinations had not been recorded were deleted before analysis. Sightings where group size had not been recorded were given the average group size. Sightings without a Beaufort value recorded were assigned a sea-state value on the basis of the sea state on neighboring parts of the same transect.

Detection function estimation.—Double-platform surveys can be used to estimate detection probability on the track line using mark–recapture (MR) methodology. Distance sampling (DS) methods (Buckland et al. 2001) can be used to estimate detection probability away from the track line while assuming that detection on the track line is certain (denoted by $g(0) = 1$). Thus, the combination of MR and DS (MRDS) methods can be used to estimate abundance without assuming that $g(0) = 1$ (Laake and Borchers 2004). Here, the 2 observers in the front of the plane were considered to be 1 platform and are referred to as observer 1, and the 2 observers in the rear were considered to be the other platform, or observer 2. With the independent observer configuration used in these surveys, detections by observer 1 serve as a set of trials in which a success corresponds to detection by observer 2 and vice versa. Decisions about sightings detected by both observers (duplicates) were based on coincidence in timing (within 3 s), distance from track line (±200 m) and group size (±3 whales). Analysis of these trials and duplicates allow the probability of detection on the track line to be estimated and the shape of the detection function away from the track line to be estimated from the distribution of perpendicular distance.

Although observers 1 and 2 were acting independently, detection probabilities of observers can be correlated because of factors such as group size (for example, both observers are more likely to see only large groups at long distances). If detections were dependent on such factors and this was not modeled, the resulting detection probability and abundance estimate will be biased. Because it may not be possible to record all variables affecting detection probability, dependencies can persist even when the effects of all recorded variables are modeled. Laake and Borchers (2004) and Borchers et al. (2006) developed an estimator on the basis of the assumption that detections were independent only on the track line (i.e., at the point $x = 0$), which they called a point independence model. This estimator was more robust than the alternative, which assumed that detections were independent at all perpendicular distances. Therefore, detection probability was estimated using this point independence assumption with an independent observer configuration implemented in Distance 6.0 (Thomas et al. 2009).

A point independence model involves estimating two functions, a multiple covariate DS detection function for detections pooled across platforms, assuming certain detection on the track line, and a MR detection function to estimate the probability of detection on the track line for each of the independent observers. The probability that a group, at given distance x and covariates z, was detected by an observer given that it was seen by the other observer, was modeled using a logistic form:

$$p_{l|3-l}(x,z) = \frac{\exp\left(\beta_0 + \beta_1 x + \sum_{k=1}^{K} \beta_{k+1} z_k\right)}{1 + \exp\left(\beta_0 + \beta_1 x + \sum \beta_{k+1} z_k\right)},$$

where l can take the values 1 or 2 to represent the observers, $\beta_0, \beta_1, \ldots, \beta_K$ represent the parameters to be estimated, and K is the number of covariates. If observer is included as a covariate, the probability of detection for each observer can be estimated separately, otherwise, the probability of detection is assumed to be the same for both observers. When perpendicular distances and group sizes differed between duplicates, the average distance and group size of the duplicate pair was used.

Covariates also can be included in the DS model (Marques and Buckland 2004), and both the half-normal and hazard-rate functional forms can be used for the DS model with Akaike's information criterion (AIC) used for selecting the model with the lowest AIC.

Estimating density and abundance.—In the case of duplicates the mean group size of the duplicate pair was used (rounded down to the nearest integer) and group density (D_{Gi}) and abundance (N_{Gi}) for stratum i were estimated as follows:

$$\hat{D}_{Gi} = \frac{1}{2wL_i}\sum_{j=1}^{n_i}\frac{1}{\hat{p}_{ij}} \text{ and } \hat{N}_{Gi} = \hat{D}_{Gi}A_i,$$

where w is the truncation distance, L_i is the total effort in stratum i, n_i is the total number of detections in the stratum i, $\hat{p}_{ij}$ is the estimated probability of detecting group j in stratum i, and A_i is the size of stratum i. The variance of $\hat{N}_{Gi}$ was based on the method developed by Innes et al. (2002) using the estimator R2 in Fewster et al. (2009).

To account for availability bias, abundance was corrected (denoted by the subscript ''c'') using

$$\hat{N}_{cGi} = \frac{\hat{N}_{Gi}}{\hat{a}(0)},$$

where the parameter $\hat{a}(0)$ is the estimated proportion of time animals are available for detection, i.e., within the upper 2 m of the water column. The coefficient of variation (CV; standard error in proportion to the mean) of N_{cGi} is given by

$$CV\left(\hat{N}_{cGi}\right) = \sqrt{CV^2\left(\hat{N}_{Gi}\right) + CV^2(\hat{a}(0))}.$$

Similarly, the density (D_i) and abundance (N_i) of individual animals in stratum i were obtained using

$$\hat{D}_i = \frac{1}{2wL_i}\sum_{j=1}^{n_i}\frac{s_{ij}}{\hat{p}_{ij}} \text{ and } \hat{N}_i = \hat{D}_iA_i,$$

where s_{ij} is the size of group j in stratum i. These estimates were corrected for availability bias in the same way as group abundance, and it was assumed that narwhals were diving synchronously within a group. The expected group size in stratum i is given by

Table 1.—Time at surface collected from 2 female narwhals instrumented in Melville Bay in August or September 2007. Monthly averages are calculated from daily averages on the basis of 24-hour recordings of the fraction of time spent at >2-m depth. Body length of #20162 was 420 cm and that of #10946 was 390 cm.

Individual	August[a]	September	October	November	December	January	February	March	April	May	June	July
20162												
n (days)	31	24	26	29	27	30	16	24	26	31	28	31
$\bar{X}$ (all day)	0.16	0.22	0.23	0.18	0.19	0.16	0.16	0.17	0.19	0.20	0.16	0.13
SD	1.04	1.51	1.17	0.86	0.85	0.87	1.3	1.18	1	1.42	1.1	1.1
$\bar{X}$ (daytime)	0.15	0.23	0.24	0.18	0.19	0.17	0.16	0.18	0.20	0.20	0.16	0.13
SD	0.88	1.37	0.90	0.75	0.85	0.89	1.53	1.21	0.78	1.27	1.07	1.12
10946												
n (days)	2	30	30	29	29	na[b]	na	na	na	na	na	na
$\bar{X}$ (all day)	0.25	0.20	0.21	0.20	0.17							
SD	4.87	1.40	1.20	1.08	0.8							
$\bar{X}$ (daytime)	0.25	0.20	0.21	0.20	0.17							
SD	3.87	1.40	0.97	1.24	0.76							

[a] For 20162 the August data are from 2008 and for 10946 the August data are from 2007.
[b] na, not applicable.

$$\hat{E}[s_i] = \frac{\sum_{j=1}^{n_i} \frac{s_{ij}}{\hat{p}_{ij}}}{\sum_{j=1}^{n_i} \frac{1}{\hat{p}_{ij}}}. \quad (1)$$

In 2006 the group size for three sightings was unknown, and the abundance and density of individual animals in each stratum was obtained using the mean group size in stratum *i*, $\bar{s}_i$, as follows:

$$\hat{N}_i = N_{Gi} i \bar{s}_i \text{ and } \hat{D}_{Gi} i s_i.$$

These estimates were corrected for availability bias as before. The 95% *CI*s for estimates of density and abundance were calculated following the derivation of Burnham et al. (1987).

Results

Availability factors for narwhals in West and East Greenland.—One transmitter (#10946) lasted from August through December 2007 and provided data on the time at surface for 120 days or 2,880 hourly recordings (Table 1). The other transmitter (#20162) lasted for a full year and gave data for 323 days or 7,752 hourly recordings. We observed no difference between the monthly mean time at surface for the full 24-h period or for a period truncated to match the hours when the survey was flown (i.e., 1000–2000 h). The surfacing time during winter months was lower than during the summer period.

Survey of the West Greenland wintering ground in 2006.—The survey began on 21 March 2006 in the southern strata (Fig. 2); however, only limited effort was conducted in this region because of inclement weather conditions. Most of the survey covering the northern areas was conducted between 7 April and 24 April.

Narwhals were seen only sporadically south of Disko Bay, none were seen in Vaigat, and 1 (no position) was seen in Disko Bay (Fig. 2). A concentration of narwhals was found off Nuussuaq and in the outer part of Uummannaq Fjord. Large densities were observed in Upernavik and in the dense pack ice in northern Upernavik. Narwhals also were abundant on 3 reconnaissance transects flown over offshore areas west of Disko Bay. In total, observer 1 made 57 sightings, observer 2 34 sightings, and both observers 25 sightings (Table 2). Except for one group of 7 whales, all narwhal groups ranged between 1 and 4 in size (Table 3). The overall estimate of mean group size was 1.7 ($CV = 0.08$), and mean group size in each stratum varied between 1 and 3 whales (Table 4). Data on time between first detection of a group of whales and when it passed abeam are missing, but considering the low time seen in later surveys it would have little effect on the correction of the availability bias.

Table 2.—Summary of survey effort and number of sightings of narwhals made by each platform in each region. Note that the number of unique sightings is the number of sightings seen by observer 1 plus the number seen by observer 2, minus duplicates.

Region	Survey	Effort (km)	Number seen by observer 1	2	Duplicates	Number of unique sightings
West Greenland wintering ground		10,293	57	34	25	66
Melville Bay	1	1,787	9	5	4	10
	2	1,787	13	16	7	22
	All	3,574	22	21	11	32
Inglefield Bredning	1	420	13	17	6	24
	2	422	49	56	35	70
	3	368	75	58	41	92
	4	325	32	40	26	46
	5	306	34	57	27	64
	All	1,841	203	228	135	296
East Greenland		2,376	50	50	29	71

TABLE 3.—Distribution of group sizes of narwhals for unique sightings in each region. The maximum recorded group size was 19 animals.

Group size	West Greenland wintering ground	Melville Bay	Inglefield Bredning	East Greenland
1	37	21	73	52
2	15	4	96	6
3	7	3	40	4
4	4	1	32	5
5		1	16	
6–9	1	1	29	2
10–19		1	10	2
Total	64[a]	32	296	71

[a] Group size for 2 sightings was unknown.

Detection function for the survey of the West Greenland wintering ground.—Although MRDS models do not require $g(0)$ to be 1, they do rely on the probability of detection on the track line being at a maximum (or minimum). Ensuring that this requirement is fulfilled can be problematic in an aerial survey where it can be difficult to see directly below the plane. However, the distributions of perpendicular distances for each observer (Fig. 7) did not indicate problems with detection close to the track line.

The hazard-rate key function had a lower AIC than the half-normal key function; therefore this was selected for subsequent models (Table 4). Model 3 was selected, as it had the lowest AIC. This model used all the data, including the 2 sightings with unknown group size. Fitting models with group size as a covariate in the DS model led to little improvement in AIC (a reduction of about 1), and so, in view of this and sample size being relatively small, a model that did not include group size was chosen (Fig. 8). The perception bias for each observer was estimated to be 0.55 ($CV = 0.13$) and for both observers combined was 0.80 ($CV = 0.08$).

Abundance on the West Greenland wintering ground.—The largest abundance of narwhals was found in stratum 13 in Upernavik. The second largest abundance was found in stratum 15 off Uummannaq. The total abundance corrected for perception bias but uncorrected for availability bias was 1,407 narwhals (95% *CI*: 788–2,513). On the basis of the surface time for the whale with the tag still operating in March and April (Table 1), a mean availability of narwhals down to 2-m depth was estimated to be 0.18 ($CV = 0.04$). The total abundance corrected for both perception and availability bias summed across all strata was 7,819 narwhals (95% *CI*: 4,358–14,029; Table 5).

Surveys of Melville Bay and Inglefield Bredning in 2007.—Both Melville Bay and Inglefield Bredning were divided into 4 strata, and each region was surveyed more than once (Fig. 3; Table 2). Melville Bay was surveyed twice, and the same track lines were used each time. Each survey was treated as an independent sample. Surveys occurred 6 days apart, and satellite tracking has shown that animals can move a considerable distance in this time. Inglefield Bredning was surveyed on 5 occasions using different track lines in the east and west strata and 3 sets of track lines in Academy Bay and Bowdoin Fjord. Again, these were considered independent samples.

TABLE 4.—Akaike information criterion (AIC) values after fitting explanatory variables to the distance sampling (DS) and mark–recapture (MR) models. The final models chosen are given in bold, and ΔAIC indicates the difference between the chosen model and the specified model. HN indicates a half-normal form for the DS model, and HZ indicates a hazard-rate form. The explanatory variables are perpendicular distance (D), group size (S), region (R), Beaufort sea state (BF), side of plane (SD), and observer (O). A subscript indicates that the variable is fitted as a factor variable with the number of factor levels denoted in the subscript.

Model	DS model	MR model	AIC	ΔAIC
West Greenland winter survey 2006				
1	HN: D	D	1,051.68	6.02
2	HZ: D	D	1,049.44	3.78
3	**HZ: D + BF**	**D**	**1,045.66**	**0.00**
4	HZ: D	D + BF	1,050.31	4.65
5	HZ: D + BF	D + BF	1,046.53	0.87
Melville Bay and Inglefield Bredning 2007				
1	HN: D	D	2,886.52	20.11
2	HZ: D	D	2,888.10	21.69
3	HN: D + S	D	2,888.51	22.10
4	HN: D + R_2	D	2,871.16	4.75
5	HN: D + BF	D	2,887.51	21.10
6	HN: D + SD_2	D	2,883.04	16.63
7	HN: D + R_2 + SD_2	D	2,870.35	3.94
13	HN: D	D + S	2,883.46	17.05
14	HN: D	D + R_2	2,887.08	20.67
15	HN: D	D + BF	2,887.69	21.28
16	HN: D	D + SD_2	2,887.40	20.99
17	HN: D	D + O_2	2,885.65	19.24
18	HN: D	D + O_2 + S	2,882.58	16.17
19	**HN: D + R_2 + SD_2**	**D + O_2 + S**	**2,866.41**	**0.00**
East Greenland 2008				
1	HN: D	D	1,006.39	25.83
2	HZ: D	D	1,009.14	28.58
3	HN: D + S	D	1,007.06	26.50
4	HN: D + S_2	D	1,007.78	27.22
5	HN: D + SD_2	D	1,003.04	22.48
6	HN: D + R_2	D	991.62	11.06
7	HN: D + R_2 + SD_2	D	985.42	4.86
8	HN: D	D + S	1,006.54	25.98
9	HN: D	D + S_2	1,004.41	23.85
10	HN: D	D + R_2	1,006.01	25.45
11	HN: D	D + SD_2	1,003.24	22.68
12	HN: D	D + O_2	1,008.29	27.73
13	HN: D	D + SD_2 + S_2	1,001.54	20.98
14	HN: D + R_2	D + SD_2 + S_2	986.76	6.2
15	**HN: D + R_2 + SD_2**	**D + SD_2 + S_2**	**980.56**	**0.00**

The differences between perpendicular distances and group sizes for duplicates were examined (Fig. 9). We did not observe any systematic pattern between the platforms (which could occur, for example, if the measurements from observer 1 were always greater than observer 2). As mentioned previously, the average for each duplicate pair was used where differences occurred. The distribution of group sizes indicates that more than half of all sightings were of groups of either 1 or 2 animals (Table 3).

Detection functions for Melville Bay and Inglefield Bredning surveys.—Because of the small number of sightings in Melville Bay, sightings from both regions were combined

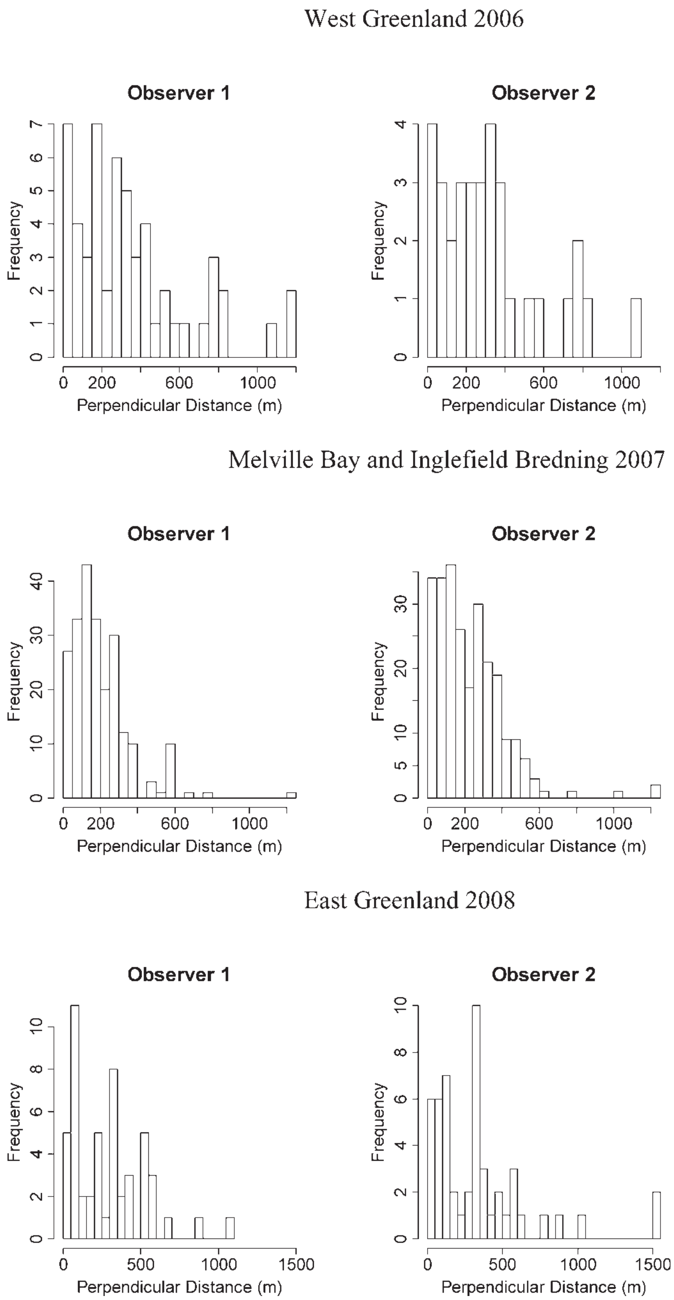

FIG. 7.—Perpendicular distance distributions calculated from the abeam angles recorded by each observer for West Greenland wintering ground (top plots), Melville Bay and Inglefield Bredning (middle), and East Greenland (bottom).

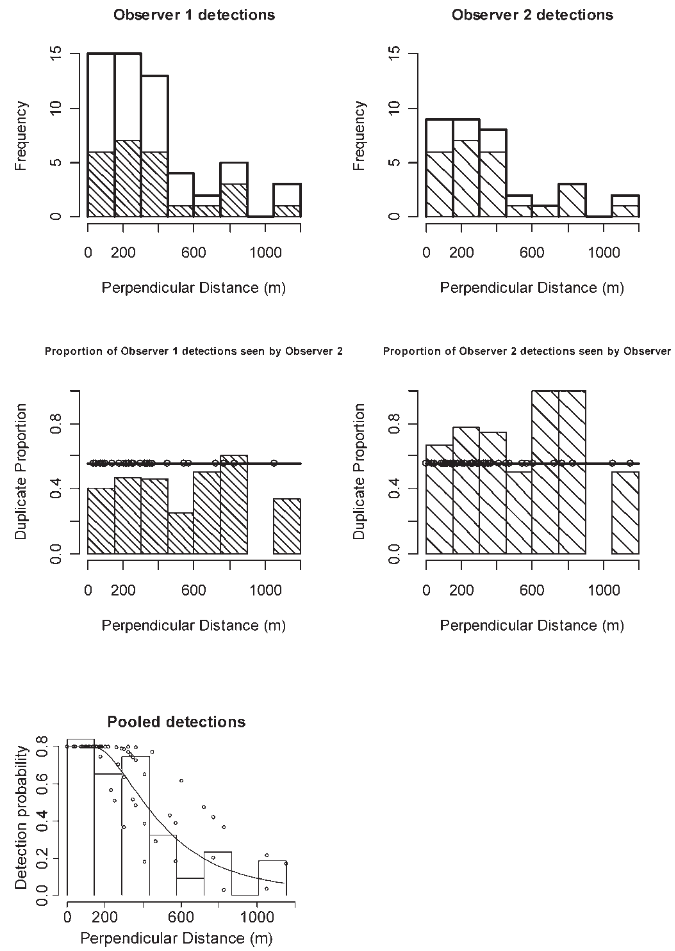

FIG. 8.—Detection function plots for the survey in West Greenland wintering ground 2006. Duplicate detections are indicated in the shaded areas—as a number in the top plots and as a proportion in the middle plots. Points (circles) are the probability of detection for each sighting given its perpendicular distance and other covariate values. Lines are the fitted models. In the pooled detection plot (bottom) the line is a smooth function fitted to the points.

and a single detection function was estimated. Slightly fewer detections were made ≤100 m from the track line than >100 m, particularly for observer 1, suggesting a reduced detectability straight below the plane (Fig. 7). To ensure that the probability of detection was at a maximum on the track line, the perpendicular distances were left-truncated at 100 m (i.e., all detections within 100 m were excluded and then 100 m was subtracted from all remaining perpendicular distances). The data also were right-truncated at a perpendicular distance of 400 m to avoid small estimated detection probabilities. The number of sightings after truncation is shown in Table 5.

For the DS model both half-normal and hazard-rate functions were fitted. Explanatory variables were included to model any dependency between detections. The available explanatory variables were group size, Beaufort sea state (as a factor with levels 0 to 4), side of plane (left and right), and region (Melville Bay or Inglefield Bredning). The same explanatory variables were included in the MR model in addition to a variable indicating observer (2 levels). Too few sightings in some strata precluded the use of stratum as an explanatory variable.

For the DS model, region and side of plane were the most important explanatory variables. For the MR model, group size and observer were the most important explanatory variables (Table 4). The estimated detection function plots can be seen in Fig. 10. The average probability of detection on the track line was estimated for each observer, and this indicated that observer 2 had a slightly higher probability of detection on the track line than observer 1; 0.83 ($CV = 0.04$) for observer 2 compared with 0.77 ($CV = 0.05$) for observer 1.

TABLE 5.—Summary statistics of survey results and narwhal abundance estimates from Greenland. Abundance estimates from West Greenland March–April 2006 are corrected for availability with $\hat{a}(0) = 0.18$ ($CV = 0.04$), and sightings from stratum 11 were included in the calculation of the detection function and mean group size only. Abundance estimates for Melville Bay and Inglefield Bredning in August 2007 are corrected for availability bias with $\hat{a}(0) = 0.21$ ($CV = 0.09$). Abundance estimates for East Greenland in August 2008 are corrected for availability bias with $\hat{a}(0) = 0.21$ ($CV = 0.09$). Sightings were truncated at 800 m. The encounter rate and density estimates for ''All'' strata include strata where no whales were detected (see text). Number of sightings is after truncation, and *CV*s are given in parentheses.

Region	Stratum	Area (km^2)	Tran-sects	Effort (km)	Number unique of sightings	Encounter rate (groups/km)	Mean or expected group size	Abundance of groups	Density of groups (groups/km^2)	Abundance of whales	Density of whales (whales/km^2)	Abundance of whales corrected for availability bias
West Greenland	1	1,496	2	91	0							
	2	9,669	12	1,329	3	0.0023 (0.25)	1.33 (0.26)	17 (0.57)	0.0017 (0.57)	22 (0.62)	0.0023 (0.62)	123 (0.62)
	3	8,613	10	837	1	0.0012 (0.99)	2.00 (0.00)	14 (1.01)	0.0016 (1.01)	27 (1.01)	0.0032 (1.01)	152 (1.01)
	4	6,376	5	419	0							
	5	8,041	1	84	0							
	6	5,935	10	857	0							
	7	8,205	10	1,076	1	0.0009 (0.74)	1.00 (0.00)	6 (0.76)	0.0007 (0.76)	6 (0.76)	0.0007 (0.76)	32 (0.76)
	9	5,792	12	491	0							
	10	10,779	6	523	6	0.0115 (0.76)	2.17 (0.18)	94 (0.77)	0.0087 (0.77)	204 (0.80)	0.0189 (0.80)	1,134 (0.80)
	11				19		1.42 (0.11)					
	12	3,612	6	234	0							
	13	27,544	18	2,384	26	0.0109 (0.32)	1.92 (0.12)	445 (0.40)	0.0161 (0.40)	854 (0.42)	0.0310 (0.42)	4,745 (0.42)
	14	14,168	12	1,296	5	0.0039 (0.38)	1.2 (0.17)	47 (0.42)	0.0033 (0.42)	56 (0.45)	0.0039 (0.45)	311 (0.45)
	15	13,256	5	536	4	0.0075 (0.47)	3.00 (0.67)	75 (0.49)	0.0057 (0.49)	226 (0.83)	0.0171 (0.83)	1,256 (0.83)
	16	2,148	3	138	1	0.0073 (0.99)	1.00 (0.00)	12 (1.00)	0.0055 (1.00)	12 (1.00)	0.0055 (1.00)	66 (1.01)
	Total	125,634	112	10,293	66	0.0046 (0.20)	1.72 (0.08)	709 (0.29)	0.0056 (0.29)	1 407 (0.30)	0.0112 (0.30)	7,819 (0.31)
Melville Bay	Central	2,133	10	764	3	0.0039 (0.70)	1.71 (0.40)	61 (0.72)	0.0288 (0.72)	105 (0.75)	0.0493 (0.75)	501 (0.76)
	Northeast	2,755	11	863	1	0.0012 (1.00)	1 (0.00)	26 (1.02)	0.0092 (1.02)	26 (1.02)	0.0092 (1.02)	121 (1.02)
	Northwest	4,860	5	563	1	0.0018 (1.00)	1 (0.00)	53 (1.04)	0.0109 (1.04)	53 (1.04)	0.0109 (1.04)	253 (1.04)
	South	6,614	12	1,384	6	0.0043 (0.83)	5.20 (0.22)	208 (0.85)	0.0314 (0.85)	1,081 (0.98)	0.1635 (0.98)	5,149 (0.99)
	All	16,362	38	3,574	11	0.0031 (0.51)	3.64 (0.38)	348 (0.58)	0.0213 (0.58)	1,265 (0.85)	0.0773 (0.85)	6,024 (0.86)
Inglefield Bredning	Academy Bay	65	13	74	0	0		0 (0.00)		0 (0.00)		0 (0.00)
	Bowdoin Fjord	85	13	78	1	0.0129 (0.97)	1 (0.00)	2 (1.00)	0.0260 (1.00)	2 (1.00)	0.0260 (1.00)	11 (1.01)
	East	1,478	62	1,278	178	0.1393 (0.21)	3.29 (0.09)	449 (0.22)	0.3039 (0.22)	1,477 (0.25)	0.9992 (0.25)	7,033 (0.27)
	West	918	21	410	20	0.0488 (0.49)	2.91 (0.18)	96 (0.49)	0.1044 (0.49)	278 (0.50)	0.3032 (0.50)	1,325 (0.51)
	All	2,546	109	1,840	199	0.1082 (0.20)	3.21 (0.08)	547 (0.21)	0.2149 (0.21)	1,757 (0.23)	0.6902 (0.23)	8,368 (0.25)
All		18,908	147	5,414	210	0.0388 (0.23)	3.38 (0.18)	895 (0.26)	0.0473 (0.26)	3,022 (0.38)	0.1598 (0.38)	14,392 (0.39)

Table 5.—Continued.

Region	Stratum	Area (km^2)	Transects	Effort (km)	Number unique of sightings	Encounter rate (groups/km)	Mean or expected group size	Abundance of groups	Density of groups (groups/km^2)	Abundance of whales	Density of whales (whales/km^2)	Abundance of whales corrected for availability bias
East Greenland	Sermilik North	311	10	43								
	Sermilik Fjord	1,259	30	212	2	0.0094 (0.69)	1.00 (0.00)	30 (0.77)	0.0237 (0.77)	30 (0.77)	0.0237 (0.77)	142 (0.78)
	Johan Petersen Fjord	122	5	17								
	Sermiligaq	307	16	90								
	Kulusuk Fjord	320	4	27								
	Kangertigtivatsiaq	303	5	33	1	0.0301 (1.13)	1.00 (0.00)	32 (1.15)	0.1060 (1.15)	32 (1.15)	0.1060 (1.15)	153 (1.15)
	Tasiilaq Fjord	175	7	26	2	0.0756 (0.73)	1.64 (0.42)	34 (0.80)	0.1963 (0.80)	57 (0.78)	0.3227 (0.78)	269 (0.79)
	Nigertuluk	65	6	18								
	Kangerlussuaq	672	26	168	8	0.0475 (0.69)	2.91 (0.37)	90 (0.72)	0.1334 (0.72)	261 (0.88)	0.3885 (0.88)	1,243 (0.87)
	Courtauld Fjord	28	2	9								
	Watkins Fjord	76	4	16								
	Blosseville Coast	1,511	75	305	11	0.0360 (0.34)	1.31 (0.00)	170 (0.38)	0.1125 (0.38)	223 (0.44)	0.1479 (0.44)	1,064 (0.45)
	Hall Bredning	4,849	41	787	1	0.0013 (0.99)	1.00 (0.82)	22 (1.01)	0.0045 (1.01)	22 (1.01)	0.0045 (1.01)	103 (1.01)
	Fønfjord	586	50	223	38	0.1703 (0.36)	1.62 (0.11)	100 (0.39)	0.1705 (0.39)	162 (0.40)	0.2765 (0.40)	772 (0.41)
	Gåsefjord	1,047	10	98								
	Øfjord	793	18	84								
	Rødefjord	512	15	77								
	Rypefjord	130	6	27								
	Vestfjord	320	6	26								
	Nordvestfjord	1,330	15	90	3	0.0335 (1.01)	3.64 (0.08)	156 (1.03)	0.1172 (1.03)	567 (1.04)	0.4261 (1.04)	2,699 (1.04)
All		14,716	351	2,376	66	0.0278 (0.25)	2.14 (0.21)	624 (0.34)	0.0430 (0.34))	1,353 (0.50)	0.0920 (0.50)	6,444 (0.51)

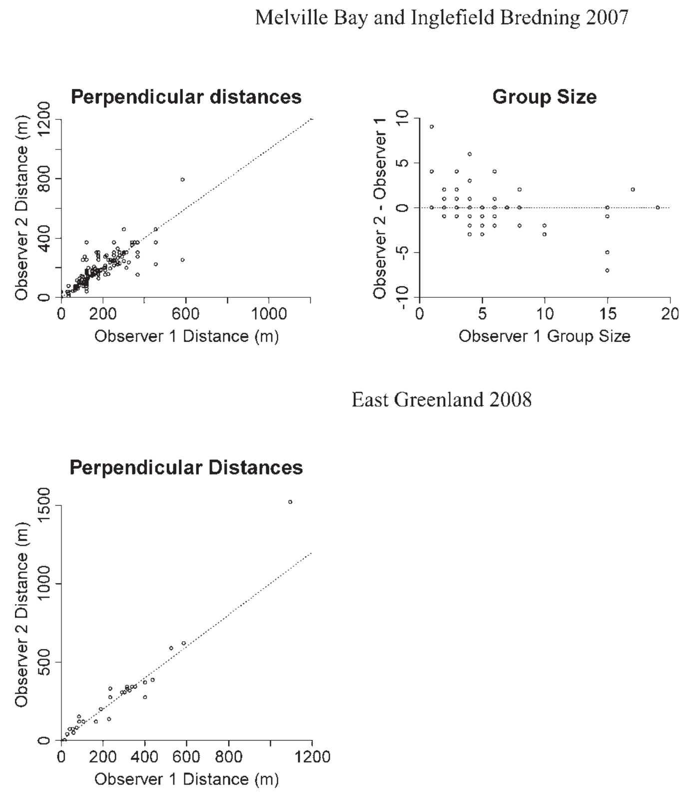

Fig. 9.—Differences in the perpendicular distances and group sizes (differences) recorded by observers 1 and 2 for duplicate sightings. The dotted line indicates no difference.

The probability of detection on the track line for both observers combined was estimated to be 0.96 ($CV = 0.02$).

Abundance estimates from Melville Bay and Inglefield Bredning.—On the basis of the surface time for the 2 whales in August and September (Table 1), a mean availability of narwhals down to 2-m depth was estimated to be 0.21 ($CV = 0.09$) for the summer season in Melville Bay and Inglefield Bredning. The uncorrected (for availability) individual abundance estimate for Melville Bay was 1,265 ($CV = 0.85$, Table 6). The corrected individual abundance estimate for Melville Bay was 6,024 ($CV = 0.86$; 95% *CI* 1,403–25,860). The uncorrected individual abundance estimate for Inglefield Bredning was 1,757 ($CV = 0.23$) and the corrected individual abundance was 8,368 ($CV = 0.25$; 95% *CI* 5,209–13,442). The time between when a group of whales was first seen and when it passed abeam was 1 s ($SD = 2.83$) in Melville Bay and 0.85 s ($SD = 2.0$) in Inglefield Bredning, and because of the small interval, probably due to the high density of whales, no corrections were made for the noninstantaneous sighting process.

Survey of East Greenland in 2008.—The surveyed region included the Scoresby Sound fjord system and tributaries, the Blosseville Coast with most of the fjords including Kangerlussuaq, the coastal areas south of Kangerlussuaq with the major fjord systems of Sermiligaaq, Kulusuk, and Sermilik and tributary fjords, and the glacial area south to 65°N. The region of interest (Figs. 4–6) was divided into 20 strata, and 2,376 km of track line were searched. A total of 71 unique

TABLE 6.—List of fjords along the Blosseville Coast with approximate latitudinal position. Effort in each fjord, the number of sightings, and narwhal information from other sources is shown. Data obtained during bird surveys in 2008 were provided by (a) Flemming Merkel (Greenland Institute of Natural Resources), and (b) http://www2.dmu.dk/Pub/FR721.pdf.

Fjord	Latitude	Presence and activity of glacier	Survey effort Transects: km	Narwhal sightings	Sightings from other sources
Sfinx Glacier	70.00	Glacier	-	-	
Kap Graham	69.58	Glacier	-	-	
Steward Isle N	69.57	Glacier	1: 3.08	0	Hunting area, Dietz et al. (1994)
Steward Isle S	69.56	Glacier	1: 3.82	0	Hunting area, Dietz et al. (1994)
Akinarteqita	69.52	No ice, no glacier	1: 4.69	0	
Deichmann Fjord	69.49	Glacier	3: 7.45	0	
Turner Sound	69.45	No ice, no glacier	1: 1.70	0	Hunting area, Dietz et al. (1994)
Rømer Fjord	69.40	No ice, no glacier	1: 6.83	0	Hunting area
Aqilegita	69.36	No glacier	-	-	
Bartholin Bræ	69.35	Glacier	-	-	
Uunartaqartikajip kangertiva	69.33	Glacier	-	-	
Kap Dalton–Kap Ewart	69.25	No glacier	-	-	
Knighton Fjord	69.22	Glacier	-	-	100–150 animals; 23 June (a)
Barclay Bugt	69.15	Active glacier, lots of ice	3: 15.45	2	
No name 1	69.07	Little ice, no active glacier	1: 1.84	1	
No name 2	69.05	No ice, no glacial activity	3: 6.63	1	
d'Aunay Bugt	69.03	No glacier, no ice	4: 17.78	0	5 animals; 26 July (b)
de Reste Bugt	68.57	Active glacier, lots of ice	3: 8.50	0	Dietz et al. (1994)
Storbrae	68.50	Lots of ice, active glacier	1: 3.72	2 off effort	
Johan Petersen Bugt	68.45	Glacial edge but inactive, no ice	2: 5.86	2 off effort	7 groups; 25 June (a)
Søkongen Bugt	68.41	No glacier	-	-	2 animals; 25 June (a)
No name fjord ved Kap Daussy	68.40	No glacier	-	-	
Sortebrae	68.38	Lots of ice, active glacier	1: 4.84	0	
Savary Fjord	68.37	Inactive glacier edge, little ice	3: 11.97	1	1 group; 25 June (a)
Grivel Bugt	68.33	Driftwood, inactive glacier, no ice	3: 16.13	0	
Vedel Fjord	68.30	Active glacier	4: 16.57	5	
Wiedeman Fjord	68.28	Inactive glacier edge, little ice	4: 15.94	0	Some; 25 June (a)
Ravn Fjord	68.25	Inactive glacier edge, little ice	2: 8.21	0	
Stephensen Fjord	68.22	Active glacier, lots of ice	2: 5.76	0	
Kap Rink–Kap Normann	68.20	2 inactive and 1 active glacier	4: 8.89	1	
Kivioq Fjord	68.20	2 inactive and 1 active glacier	4: 26.16	0	
Kap Garde–Kap Nansen	68.18	4 inactive glaciers, little ice	4: 12.82	0	
Nansen Fjord	68.18	Active glacier, lots of ice	5: 40.43	1	7 groups; 25 June (a)
J. A. D. Jensens Fjord	68.12	Glacier, little ice	3: 9.27	0	Dietz et al. (1994)
Ryberg Fjord	68.10	Ice, active glacier	13: 49.93	0	Dietz et al. (1994)
JC Jacobsens Fjord	68.07	No ice, only icebergs from other glaciers, inactive glacier	3: 9.27	0	Dietz et al. (1994)
Mikis Fjord	68.06	No glacier	-	-	Dietz et al. (1994)

sightings of narwhal groups was recorded in 8 strata, with more than half of the sightings occurring in the Scoresby Sound region, primarily in the tributary of Fønfjord (Table 5). This fjord was surveyed repeatedly to augment the sample size for estimating detection probability. Scattered sightings were collected in Hall Bredning and at Nordvestfjord. Of the 37 fjords along the Blosseville Coast, a random sample of 27 was surveyed and narwhals were detected in 9 (2 off effort detections) of these. Other information suggests that narwhals occur in an additional 13 fjords, and with the present survey at least of 22 of 37 fjords along the Blosseville Coast have reports of narwhals (Table 6). On the basis of this wide distribution of narwhals in the fjords along the Blosseville Coast, we decided to treat the Blosseville Coast as 1 stratum. South of Kangerlussuaq narwhals were present only in certain fjords that were treated as separate strata.

Differences in duplicate sightings for perpendicular distances were examined (Fig. 9), and again no systematic patterns were apparent. Observers recorded different group sizes for 4 duplicate sightings. In 3 of these cases 1 observer had recorded a group size of 1 and the other had recorded a group size of 2. In the remaining case the group sizes were 12 and 15 animals. The majority of sightings were of single animals, and the largest groups (group size $\geq$5) all were recorded in Kangerlussuaq and Nordvestfjord strata (Table 5).

Detection functions for East Greenland survey.—Observer 1 made fewer detections $\leq$50 m from the track line than $>$50 m, suggesting that detection was difficult below the plane (Fig. 7). This did not occur with observer 2, and because of small sample sizes the data were not left-truncated. However, the data were right-truncated at 800 m to avoid small detection probabilities occurring in the tail of the distribution.

The available explanatory variables were group size, side of plane (left and right), region (see below), and observer (used only in the MR model). Group size was included either as a continuous variable or as a factor variable with 2 levels (to

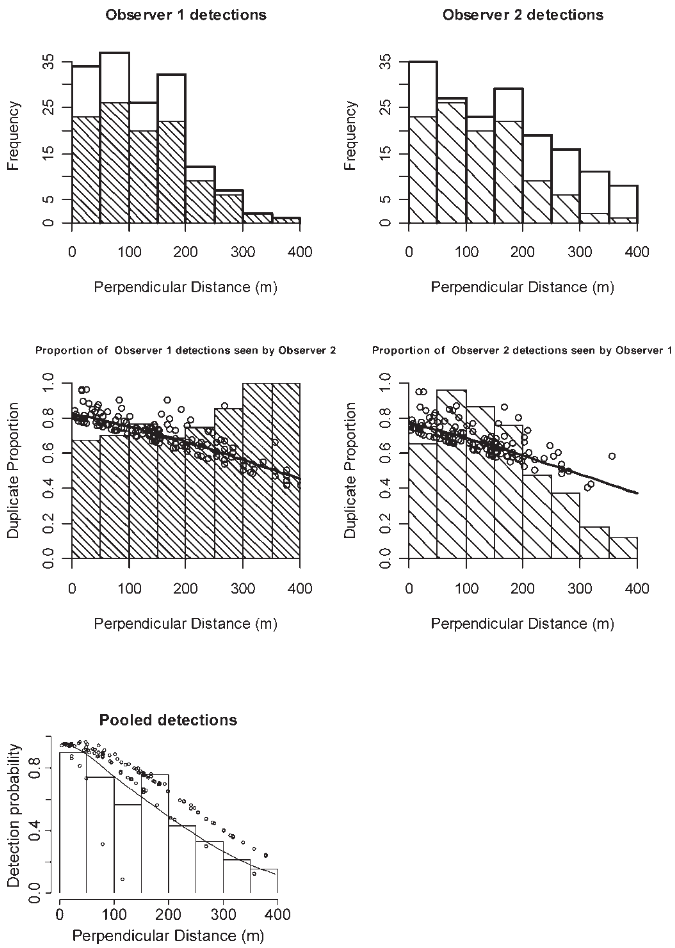

Fig. 10.—Detection function plots after left-truncation for the survey in Inglefield Bredning and Melville Bay 2007. Duplicate detections are indicated in the shaded areas—as a number in the top plots and as a proportion in the middle plots. Points (circles) are the probability of detection for each sighting given its perpendicular distance and other covariate values. Lines are the fitted models. In the pooled detection plot (bottom) the line is a smooth function fitted to the points.

represent group sizes of 1 and >1). Strata could not be used directly as an explanatory variable as too few sightings were made in some strata. Thus, a region variable was created that consisted of 2 levels corresponding to stratum Fønfjord as 1 level and all other strata combined as the second level.

The various models fitted are given in Table 4. For the DS model, region and side of plane were the most important explanatory variables. For the MR model, group size (as a factor variable) and side of plane were the most important explanatory variables. The estimated detection function plots are shown in Fig. 11. The probability of detection on the track line for each observer was estimated to be 0.61 (*CV* = 0.15) and for the observers combined was 0.81 (*CV* = 0.10).

Abundance estimates from East Greenland survey.—No information on time at the surface exists for narwhals in East Greenland so any correction for availability must be based on data from other regions. Here, the surface time for the 2 whales tracked in Melville Bay in August and September 2007 and 2008 (Table 1), which had a mean availability of 0.21 (*CV* = 0.09) down to 2 m, was used to correct the abundance from East Greenland. No attempts were made to correct for the noninstantaneous sighting process because all sightings were within 1 s from passing abeam.

Table 7.—Abundance of narwhals in Inglefield Bredning in 1985, 1986, 2001, and 2002 (data from Born et al. 1994 and Heide-Jørgensen 2004). Estimates are based on daily line-transect surveys, which are uncorrected for submerged whales but corrected for perception bias in 2001, 2002, and 2007 but not in 1985–1986. The weighted average (and associated variance) is weighted by the area covered during the survey. AB indicates surveys that included Academy Bay (see Fig. 1).

Survey date	Effort in linear km	Effort (km^2)	Abundance of narwhals (*CV*)	Mean group size
1985				
27 August—AB	233	249	847 (0.49)	
28 August	104	111	932 (0.41)	
29 August—AB	306	327	1,366 (0.24)	
3 September—AB	94	101	979 (0.62)	
Weighted average abundance 1985: 1,091 (*CV* = 0.12); 95% *CI*: 825–1,358				
1986				
9 August I	179	169	4,369 (0.40)	
9 August II	167	158	2,683 (0.38)	
10 August	114	163	1,894 (0.37)	
Weighted average abundance 1986: 3,002 (*CV* = 0.25); 95% *CI*: 1,558–4,446				
2001				
19–22 August—AB		840	873 (0.35)	1.76 (0.08)
2002				
7–29 August—AB		9,788	562 (0.24)	2.49 (0.06)
2007				
13–24 August—AB	1,840		1,757 (0.23)	3.31 (0.06)

The uncorrected individual abundance estimate was 1,353 animals (*CV* = 0.50, Table 5). The corrected individual abundance estimate was 6,444 (*CV* =0.51; 95% *CI*: 2,504–16,575). The highest densities of whales were found in Nordvestfjord and Fønfjord in the Scoresby Sound fjord complex and in the Kangerlussuaq and Tasiilaq fjords (Table 5).

Discussion

The survey protocol and analytical methods used in these surveys took advantage of recent methodological advancements to address the bias that has comprised many previous surveys of cetaceans. Despite the costs, the Twin Otter with bubble windows is an optimal platform for this type of survey in Arctic conditions, and the survey coverage was as intensive as possible while still assuming a near-instantaneous coverage (i.e., no migrations in and out of the strata) over the large areas.

The abundance estimates of narwhals in West Greenland are exceptional because they are the first to cover the wintering ground in eastern Baffin Bay. They represent the first successful survey of the Melville Bay summering ground.

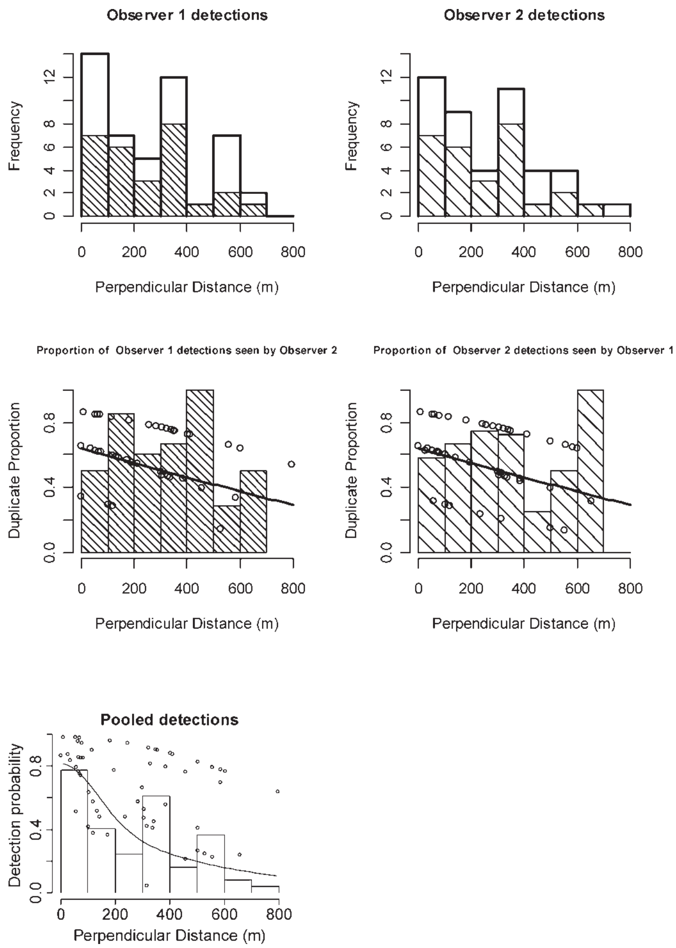

FIG. 11.—Detection function plots for the final model for East Greenland in 2008. Duplicate detections are indicated in the shaded areas—as a number in the top plots and as a proportion in the middle plots. Points (circles) are the probability of detection for each sighting given its perpendicular distance and other covariate values. Lines are the fitted models. In the pooled detection plot the line is a smooth function fitted to the points.

In East Greenland the abundance estimates are the first ever produced for the hunting grounds. Furthermore, the abundance estimate in Inglefield Bredning is a considerable improvement over previous surveys and documents the largest abundance ever detected in that area. The estimates, together with the catch history and estimates of maximum rates of sustainable yield, should be used directly for setting catch limits that ensure adequate conservation of narwhal stocks in both East and West Greenland. The distribution of whales and their abundance, together with data on changes of sea ice and prey production, also will provide a baseline for examining the effects of climate change on the abundance and distribution of narwhals.

The West Greenland wintering ground.—The encounter rate in strata 1, 2, and 3 was below what has been obtained in previous surveys of the same area. Previous surveys also have documented considerable offshore concentrations of narwhals throughout Baffin Bay and Davis Strait, and it seems probable that fewer narwhals were available in the coastal strata 1–3 in 2006. These strata are at the margin of the core distribution of narwhals in Baffin Bay, and slight alterations in occurrence always will have a larger impact on the margins of the distribution (Heide-Jørgensen et al. 1993).

The abundance estimate obtained in this survey is below estimates from previous surveys for comparable strata. The survey in 1998 and 1999 estimated that 2,861 narwhals (95% *CI*: 954–8,578) were present in the Disko Bay area in strata 1–3 (Heide-Jørgensen and Acquarone 2002). The comparable estimate from this survey is 148 narwhals (95% *CI*: 52–420). If stratum 14 is included, this results in 299 narwhals (95% *CI*: 82–516). The difference in perception bias correction factors from 0.50 in 1998–1999 (video surveillance of track line) to ~0.80 (MRDS model) cannot explain the observed difference. It is possible that the later timing of the 2006 survey (1 month later) allowed for some northward movement of whales out of the area (whales that would have been encountered in the Disko Bay area in the previous surveys). This could explain some but not all of the sightings in strata 10, 13, and 15 in Uummannaq and Upernavik.

If it is assumed that the estimate from all surveyed areas in April 2006 is compatible with the survey in 1998–1999 (covering strata 1–3 in late March), the estimates from the 2 surveys are not statistically different. However, this may not be in agreement with what is known about the movement patterns of these whales. Most narwhals from the Melville Bay stock winter outside the surveyed areas in March but by April head north toward their summering ground in Melville Bay. At least some of the sightings in strata 13 and 15 could be narwhals migrating toward Melville Bay, and because they are unlikely to be found within the surveyed area in March, inclusion of these sightings is incompatible with the 1998–1999 and earlier surveys.

The abundance of animals corrected for availability from the West Greenland winter survey in 2006 was about half of the total 2007 summering ground estimate of 14,392 (CV = 0.39) narwhals. The uncorrected abundance estimate for the winter survey in 2006 was 1,407 (CV = 0.30) animals, which is approximately half of the uncorrected abundance estimate from 2007 in Melville Bay and Inglefield Bredning summering grounds (3,022; CV = 0.38). Although the difference in the availability correction factor explains some of the difference in the estimates, it does not explain everything. The main difference is probably in the encounter rate. In 2006 only 66 groups were detected with twice the amount of search effort used in 2007. In 2006 the encounter rate was 0.0046 groups/km (0.20) compared with 0.0390 groups/km (0.28) in 2007. Although the winter survey in 2006 covered a large area of the eastern part of Baffin Bay, it is still possible that not all narwhals that summer in Melville Bay and Inglefield Bredning were inside the surveyed area.

Melville Bay.—Surveys have been attempted previously in Melville Bay, but no narwhals were detected, probably because survey coverage was allocated mostly to offshore areas (M. P. Heide-Jørgensen, in litt.) where whales were absent. The 2007 survey demonstrated that narwhals are detected primarily close to the coast in Melville Bay and that they seem to prefer to spend the summer in front of the glaciers in the bay. The abundance estimate of 6,024 (95% *CI*: 1,403–25,860) narwhals in Melville Bay in 2007 is the first estimate from this locality, and no information on trends exists for this locality.

Inglefield Bredning.—Several surveys using various, and not directly comparable, methods have been used in Inglefield Bredning since 1984. The distribution of narwhals in Inglefield Bredning is in good agreement with what was documented during aerial surveys in 1985–1986 and 2001–2002 (Born et al. 1994; Heide-Jørgensen 2004). In all years a major part of the whale population was found in the eastern part of the fjord, with only a few whales seen in the western part, contributing marginally to the overall results. The average group size was higher in 2007 than in previous surveys (Born et al. 1994, Heide-Jørgensen 2004).

Born et al. (1994) reported on 4 visual line-transect surveys uncorrected for perception bias conducted in Inglefield Bredning on 27–29 August and 3 September 1985. The weighted average of these 4 surveys was 1,091 whales (95% *CI*: 925–1,358; Table 7). In 1986 3 surveys were conducted on 9 and 10 August, and the weighted average was 3,002 (95% *CI*: 1,558–4,446). Heide-Jørgensen (2004) reported on a photographic survey conducted in 2001 and 2002, which covered a larger area of Inglefield Bredning than was covered in the previous surveys. The abundance of animals within 2 m of the surface in 2001 and 2002 was lower than the values for 1985 and 1986 (Table 7) despite the absence of any perception bias affecting the photographic surveys. The surface abundance in 2007 was definitely larger than the estimates from 2001 and 2002 but smaller than the abundance in 1986. Information from local hunters indicated that the abundance of narwhals in Inglefield Bredning in 2007 (and 2008) was higher than they had experienced previously. This also was in agreement with observations from the land-based narwhal study site that has been maintained in Inglefield Bredning every August since 2002 (M. P. Heide-Jørgensen, pers. obs.). This observation point is located on the southern shore of the middle of the bay, and for the years 2002–2006 the maximum numbers of narwhals counted have not exceeded 1,500 animals. In 2007 a massive immigration of narwhals into the bay was observed that resembled the situation in August 1984 where about 4,000 narwhals were counted from shore in the eastern part of the bay (Born 1986). The abundance of narwhals in the area undergoes large annual fluctuations that are difficult to capture with surveys that only cover a snapshot in time of Inglefield Bredning. Areas farther north in Smith Sound also are used as summering grounds for narwhals, but the abundance here is unknown. Recent reductions in sea ice coverage and increased use of fast dinghies on hunting trips have caused an increase in catches in those areas (Nielsen 2009).

East Greenland.—The abundance estimates developed for East Greenland are the first estimates in the Scoresby Sound fjord system south to Sermilik. A previous aerial survey conducted in 1983 and 1984 in Scoresby Sound and adjacent fjords is not comparable with the present survey because it was conducted later in the season (September) and it did not account for sightings missed by the observers or for whales that were submerged during the survey (Larsen et al. 1994).

Narwhals were detected in low numbers all along the Blosseville Coast in several fjords. When the sightings from this survey were combined with observations from other surveys, hunting reports, and historical information on distribution, it appears that narwhals occur in a continuum between Scoresby Sound and Kangerlussuaq. Of the 37 fjords along the Blosseville Coast, narwhals were detected in at least 22 (Table 6). About half the glaciers in the fjords along the Blosseville Coast are active (16), and the narwhals seem to be equally distributed between active (10) and inactive (12) glaciers; thus no delineation or stratification can be based on this habitat classification.

South of Kangerlussuaq narwhals were detected in several major fjords; however, narwhals were not seen along the glacial front between Kangerlussuaq and Kangertigtivatsiaq. No narwhals were seen in Sermiligaaq where they are hunted at other seasons, but both Sermilik and Tasiilaq fjords had scattered sightings. South of Sermilik narwhals have been reported to occur down to Umivik (Dietz et al. 1994), but no sightings were made along the glacial front area from Sermilik to Umivik. Information on movement patterns and seasonal shifts in occurrence is necessary to assess whether narwhals between Scoresby Sound and Sermilik constitute a single stock and the degree of exchange between the two areas. On the basis of the continuous distribution along the Blosseville Coast, it seems likely that narwhals in Kangerlussuaq, along the Blosseville Coast, and in Scoresby Sound and adjacent fjords belong to the same stock. South of Kangerlussuaq narwhals were detected only in small numbers, and only a fraction of the abundance of narwhals in these areas was covered by the survey. The abundance estimates from these areas in summer are too low to support the local harvest of 50 narwhals/year, and presumably the narwhals supplying the hunt south of Kangerlussuaq are part of the abundance from the northern areas that moves south seasonally.

Availability correction factors.—The sample size of the surfacing time data from only 2 narwhals is too low for developing a reliable correction factor. However, for logistical reasons it is difficult to obtain survey-specific availability correction factors, and thus it is necessary to use values obtained from other areas and other years. However, over time, more observations of narwhal surfacing time will be accumulated, and a better understanding of the range of values under different seasons and in different water depths will be attained. Heide-Jørgensen and Acquarone (2002) were the first to correct a narwhal abundance estimate with the time narwhals are submerged and, on the basis of SLTDR, applied an availability correction of 0.35, similar to that for belugas. They assumed that narwhals can be detected down to 5-m depth during winter in West Greenland. Because of unrealistic low *SE*s from the SLTDR recordings achieved from whales tracked to central and eastern Baffin Bay in January and

February, they assumed that a *CV* of 0.23 would realistically represent the population variability. The availability correction was applied to video surveillance of the track line, together with data on perception bias, to derive a $g(0)$ for the visual line-transect survey. The large variance of the availability correction chosen by Heide-Jørgensen and Acquarone (2002) covered the range of the later more specific correction factors used in other surveys. Richard et al. (1994) and Heide-Jørgensen (2004) demonstrated that narwhal-like figures can be detected reliably only down to 2-m depth, and availability was subsequently adjusted to that depth range.

Heide-Jørgensen et al. (2001) observed that the surface time declined during fall for narwhals tracked from the Canadian high Arctic to central Baffin Bay, and a similar change seems to be evident for the 2 whales tracked from Melville Bay to central Baffin Bay in this study. It is therefore important to give priority to season in the selection of values for correction factors. Innes et al. (2002) used short-term data from retrievable time–depth recorders (TDR) used on 3 whales in the Canadian high Arctic (Laidre et al. 2002) to develop a correction factor of 0.38 ($CV = 0.38$) for whales available between 0- and 2-m depth during a survey in approximately the same habitat and season. However, these were collected in different years. Data from the same 3 whales were used by Heide-Jørgensen (2004), in combination with a *CV* of 0.06 derived from 6 different whales (Heide-Jørgensen et al. 2001), as an availability correction factor for a photographic survey of narwhals in Inglefield Bredning in 2001 and 2002.

Richard et al. (2010) used a combination of data from 4 narwhals instrumented with SLTDRs in Hudson Bay, the 3 TDR data sets mentioned above, plus an extra later TDR deployment covering a total of 4 localities in the Canadian high Arctic to derive an overall availability correction factor of 0.32 ($CV = 0.05$) that covered the timing of the survey and had some data sets that were specific to the surveyed area.

For this study priority was given to data collected in the same area and season for the availability correction factor developed here. This came from only 2 narwhals tracked with SLTDRs in Melville Bay in 2007. The time at surface (0–2 m) was considerably lower than in other areas, both in the coastal summering grounds and in the offshore winter habitat. This could be an effect of the whales being in a much deeper habitat compared with the Canadian high Arctic at least in summer, but it could also be a behavioral feature of the Melville Bay population. Both East Greenland and Inglefield Bredning had similar deep fjords with glaciers as Melville Bay, which is different from the Canadian summering grounds; thus we decided not to include surfacing data from the Canadian Arctic.

The summarized daily SLTDR recordings provide a much larger sample (several months) from the behavior of each whale compared with the TDR data (few hours) and the long-term data confirmed the lower time spent at the surface for these 2 whales. The SLTDR data from Melville Bay are corroborated further by 2 whales tracked in August–September in 1993–1994 with an earlier generation of SLTDR instruments, which spent an average of 22% of their time between 0–1-m depth ($CV = 0.09$—Heide-Jørgensen and Dietz 1995). The threshold depth for defining an animal as available was 1 m shallower for these data than for the 2 whales tracked in 2007–2008. If data from these whales are included, the average availability correction is the same as the 2007–2008 whales but the *CV* is slightly lower (0.04 compared with 0.09). No site-specific corrections were available for Inglefield Bredning, and instead, data from the 2 Melville Bay whales were used. No information on diving behavior of narwhals exists in East Greenland, and the correction factor from the same season in Melville Bay was used. Until site-specific data on surfacing time in East Greenland become available, it seems reasonable to use the correction factor from Melville Bay. Considering the impact that the availability correction factor has on the abundance estimates, it is unsatisfactory to derive these corrections on the basis of data from few individuals collected in different areas and seasons. However, it is a logistically and technically complex operation to collect dive data from narwhals, and the only feasible approach may be to accumulate a large amount of data over time to compose a better, more complete picture of the range of values and their variances. To ensure compatibility with previous surveys this will also require recalculation of past abundance estimates as new data in support of the availability corrections emerge.

Conclusion.—The surveys presented here provide the first narwhal abundance estimates from Melville Bay and the coast of East Greenland south of Scoresby Sound. The surveys also add larger and more reliable estimates from the hunting grounds in Inglefield Bredning and the wintering ground in West Greenland. The estimates should, together with the catch history and estimates of maximum sustainable yield rates, be used directly for setting catch limits that ensure adequate conservation of narwhal stocks in both East and West Greenland. The distribution of whales and their abundance, together with data on changes of sea ice and prey distribution and production, also will provide a baseline for examining the effects of climate change on narwhal abundances.

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