ABUNDANCE AND TRENDS IN ABUNDANCE OF THE ATLANTIC WALRUS (*ODOBENUS ROSMARUS ROSMARUS*) IN CENTRAL WEST GREENLAND

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ABSTRACT

Atlantic walrus (*Odobenus rosmarus rosmarus*) are exploited for subsistence purposes in Central West Greenland. However, current information about the abundance of walruses subject to exploitation in this area is lacking yet necessaryfor sustainable catch levels. Between 21 March and 19 April 2006 and between 3 and 12 April 2008, two visual aerial surveys were conducted to estimate the number of walruses on two disjunct Central West Greenland wintering grounds: the southern wintering ground between ca. 66º 30' and the northern wintering ground between ca. 68º15' N and 69º15' and 70º 30' N, respectively. The surveys resulted in abundance estimates that were corrected for (1) the availability of walruses on sea ice based on data collected simultaneously with the aerial surveys, (2) walruses submerged below a detectability threshold, and (3) walruses that were missed by the observers. Two methods of calculating abundance were utilized: Method I applied separate adjustments for walruses detected on ice and walruses detected in water. The fully corrected estimates of abundance were 3,162 (95% CI: 3,101-3,225) for 2006 and 1,625 (1,363-1,938) for 2008. A weighted average of the estimates from the two years suggests that the West Greenland wintering stock of walruses numbers 3,008 (2,245-4,029). Method II corrected all detections for walruses that were not hauled out. The estimates of abundance were 3,041 (1,128-8,196) for 2006 and 3,240 (863-12,170) for 2008 with a weighted average of 2,978 (2,597-3,415). Trends in abundance since the early 1980s were reflected in sighting rates (i.e. weighted estimates of density of walruses observed per linear km flown) during 11 aerial surveys conducted in Central West Greenland in 1981, 1982, 1984, 1990, 1991, 1993, 1994, 1998, 1999, 2006 and 2008. The sighting rate (n=11 years) in the southern walrus´ wintering area fluctuated between

0.004 and 0.018 walrus per km, and showed no statistically significant trend between 1981 and 2008. In contrast, the sighting rate dropped significantly in the northern wintering grounds (n=8 years) from 0.05 to 0.003 walrus per km during the same period. The mechanism behind these apparent different trends is not fully understood but they may reflect changing ice conditions in the northern area since the early 1990s.

Key words: walrus, *Odobenus rosmarus*, aerial survey, abundance, West Greenland

INTRODUCTION

Atlantic walruses (*Odobenus rosmarus rosmarus*) have been hunted for subsistence purpose in Central West Greenland for centuries (Born et al. 1994). However, historical and current exploitation rates are relatively high and have been noted to be unsustainable over the long term (Born et al. 1994, 1995, Witting & Born 2005, NAMMCO 2006, COSEWIC 2006). Thus, obtaining current estimates of abundance are critical establishing sustainable catch levels in West Greenland.

Based on various information on distribution, migration and genetics, walruses in the Baffin Bay-Davis Strait region are thought to represent at least three separate stocks or sub-populations: (1) The North Hudson Bay-Hudson Strait-North Labrador-South-eastern Baffin Island stock (Born et al. 1995, NAMMCO 1995, denoted HBDS, Hudson Bay-Davis Strait in Stewart 2008), (2) the Central West Greenland stock, and (3) the North Water or N Baffin Bay stock (Andersen & Born 2000, Born et al. 2001, Stewart 2008, Andersen et al. 2009).

This categorization follows Stewart (2008) and adopts Secor´s (2005) definition that a stock is a specific part of a population impacted by human activity in a way that affects population productivity, with Ricker´s (1975) caveat to include potential utilization.

In Central West Greenland walruses winter at two distinct nearshore foraging grounds: the southern wintering ground in the Sisimiut-Aasiat area (66º 30' and 68º 15 N) and the northern wintering ground off the west coast of Disko Island/Qeqertarsuaq (69º 15' and 70º 30' N). Their occurrence in these areas is due to the availability of shallow water (<100 m) with suitable benthic prey densities and ideal ice for hauling out. Walruses are generally absent from the entrance to Disko Bay where water depths exceed 200 m (Born et al. 1994).

Walruses occur in Central West Greenland between the fall until sometime in May when the sea ice starts melting and gradually disappears (Born et al. 1994, 1995).

In the early part of the 20th century, walruses were abundant in Central West Greenland where many hundreds used several terrestrial haul-outs (*uglit*) during fall and early winter (Born et al. 1994, 1995). However, from 1911 the hunt was intensified and by the late 1930s walruses apparently had permanently abandoned all *uglit*. Until ca. 1940 the catch of walruses increased rapidly, reaching a maximum of more than 600 animals reported in the catch in both 1938 and 1940. A rapid drop in the annual catch followed, likely reflecting a decrease in the number of walruses wintering in Central West Greenland due to overharvest. Currently, the number of walruses in West Greenland is much lower than indicated by historical records (Born et al. 1995 and references therein).

Walruses are still exploited for subsistence in West Greenland. In Greenland, quotas for the catch of walrus were introduced in 2006 (Anon. 2006a). The quotas for Central West Greenland took effect beginning in spring 2007 (Anon. 2006b). The annual quota for the landed catch in this area in 2007, 2008 and 2009 was 80, 65 and 50 animals, respectively (Anon. 2006b).

The quotas set for Central West Greenland were based on incomplete information on abundance (cf. NAMMCO 2006) due to lack of data in some important areas. However, to be able to determine sustainable levels of exploitation in West Greenland it is crucial to provide an updated estimate of the number of walruses in the area.

For most of the year walruses are widely dispersed over vast areas where they usually occur at relatively low densities (e.g. Fay 1982, Born et al. 1995 and references therein). Hence, the only reasonable way of obtaining estimates of abundance are by means of aerial surveys (e.g. Estes and Gilbert 1978, Gilbert 1989, 1999, Fay et al. 1997, Udevitz et al. 2001). Seven systematic aerial surveys conducted between 1981 and 1994 showed that walruses still occupy their former wintering range in the margin of the Davis Strait pack ice (i.e. “The West Ice”) (McLaren and Davis 1981, 1983, Born et al. 1994, Heide-Jørgensen and Born 1995).

In this paper we report on the abundance of walruses at their Central West Greenland wintering grounds based on aerial surveys conducted during March-April 2006 and 2008. Using data on activity obtained from satellite-linked transmitters (SLTs) that were deployed on walruses at their Central West Greenland wintering grounds during the survey periods we applied a correction factor to the estimates of walruses at the surface. In order to detect trends in abundance in West Greenland the recent estimates of sighting rates (walrus per linear km flown) reflecting relative abundance were compared to a time series of sighting rates obtained from 11 aerial surveys conducted over the walruses´ West Greenland wintering grounds (11 and 8 surveys on the southern and the northern grounds, respectively) during spring 1981-2008.

METHODS

Aerial surveys in 2006 and 2008

Visual aerial line-transect surveys were conducted in West Greenland between 21 March and 19 April 2006 and between 3 and 12 April 2008. The 2006 survey was a multi-species marine mammal survey with the main purpose of determining the abundance of beluga, *Delphinapterus leucas* (Heide-Jørgensen et al. in press). The survey covered the coastal areas between 65º40' N and 74º N including the two main wintering areas for walrus (Fig. 1). The 2008 survey specifically targeted obtaining an abundance estimate for walrus in West Greenland. Hence, this survey concentrated on the walruses´ main wintering grounds between 66º30' N and 70º 45' N but also included an offshore stratum for documentation of the distribution of narwhal, *Monodon monoceros,* in Central Davis Strait (Fig. 2).

The survey design utilized systematically placed east-west going transects (Figs 1 and 2). In both years, the realized effort was slightly less than originally planned due to unfavorable weather conditions with sea states >3 and horizontal visibility <1 km.

Both surveys were conducted as a sight-resight experiment with two independent observation platforms on each side of the survey plane (a DeHavilland Twin Otter equipped with four bubble windows). In both years target altitude and speed was ca. 213 m (700 feet) and 167 km $*$ h^{-1} (90 knots), respectively. Of the six observers that participated in 2006, three also participated in 2008 in addition to two new observers who, however, also had experience from previous aerial surveys of marine mammals. In each observation of a walrus or a group of walruses the declination angle was measured to the observation using a Suunto inclinometer. Each observer recorded his or her observations independently by speaking to a microphone. During the 2006 survey, data were consecutively stored *en route* on four independent tape recorders with time stamps from a Garmin 100 GPS that also downloaded positions at 1 sec intervals to a computer. During the 2008 survey a Redhen msDVRs (www.redhensystems.com) four channel audio and video computerized recording system was used for the same purposes.

During the 2006 survey sea ice coverage of the trackline was recorded on a Hi-8 tape recorder with superimposed continuous GPS stamp. During the 2008 survey sea ice along the track line was recorded with a High Definition digital video recorder on the msDVRs system together with the GPS recordings stored in a separate file. Both video systems had a swept rectangle below the aircraft of 40 $*$ 60 m at the target altitude of 213 m as measured during overpass of the airstrip in Kangerlussuaq/Søndre Strømfjord. Later examination of the video recordings utilized the GPS recordings to estimate the start of sea ice coverage defined as a full screen of sea ice and end of sea ice defined as a full screen of water. This provided a 40 m resolution of the sea ice and no further classification of sea ice types were attempted. In addition to the video camera that monitored the track line a separater video camera was mounted at an oblique angle to cover the area ahead of the plane in order to detect walruses that were disturbed by the plane before being detected by the observers. Theoretically the system would be able to detect hauled out walruses up to ca. 150 m ahead of the aircraft.

Instrumentation and data collection from walruses

In order to obtain estimates of the true walrus abundance (i.e. not only the visible portion of the population), correction factors were developed to account for walruses that were not available to be detected by the observers. A two-step correction factor for detection availability was necessary because the walruses were either hauled-out on ice floes or were submerged below a sightability threshold in the water column.

Information on “haul-out” and “at surface time” was obtained from activity measurements from the saltwater switch (SWS) of satellite-linked transmitters that were deployed on walruses in the survey area (67º30' - 68º00' N and 54º45' - 56º00' W; i.e. 75-100 km NW of the town of Sisimiut) in 2006 and 2008 (Dietz et al. in prep., Table 1). During 19-26 March 2006, SLTs (“post tags” cf. Jay et al. 2006; ST-24, Telonics, Mesa, Arizona, USA) were applied to the skin of five walruses using a compound crossbow (PSE Wiper Mojave 185 pd.) following the methods described in Jay et al. 2006). On 2 and 4 April 2008, ten 60 g SPOT-5 “match box” transmitters (Wildlife Computers, Redmond, Washington, USA) were attached to walruses using a CO_2-powered rifle from DanInject (www.dan-inject.com) or a hand held harpoon. Seven of these transmitters provided activity data that were included in the analysis (Table 1). All tags were attached to the tough skin of the animals using a 6.5 cm long harpoon head-like stainless steel anchor developed by Mikkels Vaerksted (www.mikkelvillum.com).

In the field, experienced walrus researchers and Greenlandic hunters determined the sex and age category of the tagged walruses based on their general physical appearance and approximate tusk lengths (for criteria cf. e.g. Fay 1982); Table 1.

The "post tags" measured the conductivity of the SWS every second. The percentage of dry measurements that occurred during a given 30-min interval was recorded using one of two percentage classes (0-90%, and >90%). Hence, if the recordings during a 30 min interval indicated that the SWS was dry for more than 90% of the time the animal was considered to be hauled out during the entire period. Each satellite transmission contained data of the most recent 240 30-min intervals (cf. Jay et al. 2006).

All SPOT 5 transmitters had a transmission rate of 45 s in water and 90 s when the walrus was hauled out and were programmed to transmit up to 150 uplinks between 11 and 22 GMT (i.e. 3 h in advance of local W Greenland time). To extend the daily monitoring period , transmission was suspended after 2 hours of continuous haul-out. The tags were programmed to transmit every day in March and April and then every 4th day after 1 May.

The internal system of all transmitters continuously checked the status of the SWS ("dry" vs. "wet") every 0.25 sec and recorded the activity of the SWS in 1 h increments. This information was stored in "timelines" (TIM) showing the percentage of the hour the SWS was dry. Percentage of "dry"-time/h was given in a total of thirteen increments ranging from "0%" (every measurement was wet) to "100%" (every measurement was dry). Two increments ranged 5% (i.e. 0-5%; 95-100%) and nine increments between 5% and 95% SWS dry ranged 10%. Each TIM with information on haul-out activity during 24 h was transmitted during 12 days (Wildlife Computers 2006).

To account for walruses that were submerged below a certain detectability threshold (2 m) during the aerial surveys, a correction factor was developed from data obtained from an adult male walrus monitored with a satellite-linked dive recorder (SLDR) during winter (November-January) in NE Greenland (Born et al. 2005 and unpublished data), Table 2.

Construction of correction factors for walruses not available to be detected by the observers

Correction for walruses that are hauled-out on ice floes

All data lines with voltage error message were deleted during the analysis of the time-line data for haul-out periods collected from five walruses instrumented in West Greenland in March 2006. Incomplete data series for the 1st day after deployment were also deleted. Data were converted to binary format and aligned in 24 hr columns with day as row for each transmitter. The fraction of time in water was calculated for all half hour intervals for all walruses. The mean fraction of time in water for each walrus was calculated before a mean with variance of the five walruses was calculated

The mean (i) hourly, (ii) daily and (iii) diurnal (i.e. between 10h-18h local time) haul-out time was calculated for seven walruses tracked with SPOT5 transmitters in 2008 in West Greenland. Six individuals were successfully tracked during the aerial survey period in April 2008 and the mean diurnal haul-out time within this period was calculated. For all individuals, we tested the relationship between the haul-out pattern and (1) the time of the day, and (2) the wind chill situation. The wind chill index (W) was calculated from:

$$W = 13.12 + 0.6215T - 11.37(V^{0.16}) + 0.3965T(V^{0.16})$$

where T is the temperature in °C and V is the wind speed in $km * h^{-1}$ recorded in the town of Sisimiut at 12:00 local time. The wind chill index is only defined for wind speeds above 4.8 $km * h^{-1}$, i.e. 1.3 m/s (NOAA 2008).

Correction for animals diving below a certain threshold

An unknown proportion of walruses are in the water diving below a certain threshold and are therefore are not available for detection during the aerial surveys. Information on surface:subsurface time was not available from the study area but has been collected either from direct observations of walruses (Fay 1982, Fay et al. 1984, Miller & Bonness 1983, Born & Knutsen 1997) or during studies involving the use of SLDRs (Born & Knutsen 1997, Gjertz et al. 2001) and/or time-depth recorders – TDR (Wiig et al. 1993, Gjertz et al. 2001, Acquarone et al. 2006). Direct observations of walrus "at surface" times likely do not represent an unbiased sample of all types of walrus swimming and diving behaviours because the observations have tended to focus on "stationary" walruses that were foraging in a local area for a short period of time (cf. Fay 1982 and Born & Knutsen 1997 and references in these sources). Furthermore, direct observations have been made from relatively low altitudes (ships or cliffs) and information on surface:subsurface ratios obtained from observation studies are not readily comparable to such ratios relevant to aerial surveys where animals sometimes can be seen also to a certain depth below the surface. Comparison with information from TDRs and SLDRs indicates that corrections based on information on surfacing time from direct information (e.g. Fay et al. 1997) will be positively biased. Hence, correction factors to be applied in aerial surveys to account for the fraction of walruses below a certain visibility threshold must be established on Time-at-Depth (TAD) data obtained from SLDRs or TDRs.

Their generally light brownish colour and the presence of tusks together with their large size and powerful way of swimming make it possible to detect and identify walruses from a low-flying aircraft down to ca. 2 m depths (Born personal observation). Hence, relevant to the present study was time spent between 0 and 2 m depths - and deeper.

In this study a correction factor was developed based on the winter diving behaviour of walruses obtained from the activity of a single adult male walrus tracked by satellite (SSC3, Wildlife Computer, Redland, USA) in NE Greenland between November 2000 and January 2001 (Born et al. 2005). The unit had a maximum depth limit of ca. 250 m. The SLDR recorded time at surface and at different depths. TAD data were extracted and analyzed according to methods described in Born et al. (2005 and references therein).

Survey analysis

Angles to sightings were converted to perpendicular distances based on a formula for earth curvature (Buckland et al. 2001). Distributions of perpendicular distances were fitted by conventional distance sampling methods (Distance ver. 5.1, http://www.ruwpa.st-and.ac.uk/distance/) to a suite of models in order to estimate detection functions.

The abundance in each stratum was estimated as the product of the density, the mean group size, and the area of the stratum. Total abundance was the sum of the abundance in the individual strata and the variance of the total abundance was the sum of the variance in the individual strata.

A simple estimate of perception bias can be derived by the mark-recapture method from Magnusson et al. (1978) assuming that all walruses have the same probability of being detected or not detected, i.e. the probability that a walrus is being seen by one observer is the same as it being seen by the other observer. Variance of the perception bias was estimated by a Jackknife procedure.

Confidence limits were calculated based on the assumption of log-normal distribution with lower limit=N/V and upper limit=N∗V and
V=exp(z ∗ sqrt(ln(1+varN/N^2))) (Buckland et al. 2001); where N is the abundance of walruses and the factor *z* varied with the desired confidence limits (90 or 95%) and the degrees of freedom.

Analysis of trends in abundance

Previous surveys of walruses wintering in Central West Greenland date back to 1981 (cf. Born et al. 1994). However, a direct comparison with previous abundance estimates are confounded by differences in (1) airplanes and survey methods, (2) types of corrections for the surveys and (3) intensity and distribution of survey effort. Only the surveys in 2006 and 2008 provide abundance estimates which are fully corrected for both perception and availability biases. However all surveys covered the walrus core wintering areas in West Greenland and a comparison of sighting rates weighted by the survey effort (in linear km) is a feasible method for detecting trends and variations in relative abundance (i.e. uncorrected for biases in detection process and in availability) across the entire available time series (1981 through 2008). Between 1981 and 2008, eight surveys were conducted over the northern wintering ground west of Disko Island and 11 were conducted over the southern ground (cf. Table 7).

RESULTS

Fraction of time hauled out on ice

Twelve walruses were monitored during the aerial surveys in 2006 and 2008 for haul-out activity. Eight were males and three were females (1 sex not identified). Seven walruses were categorized as being adults, three as sub-adults and two as 2-3 year old calves (Table 1).

The five walruses instrumented in 2006 provided a total of 65 days (range: 6-22 d/animal) of data on haul-out patterns in March-April (Table 1). The mean haulout time weighted by the days with available data during the 2006 survey (21 March -19 April 2006 between10.00 to 18.00 local time when the survey was conducted) was 36.5% (cv=0.23).

The seven walruses that were instrumented in 2008 provided haul-out data for 170 days in April (range: 21-28 d/animal). The six animals that provided data during the survey period (3 April – 12 April 2008) spent on average 24.7% (cv=0.18) of their day time (10.00-18.00 local time) hauled out (Table 1).

Although the fraction of haul-out time was higher during the aerial survey in 2006 than in 2008, the fraction of time spent out of the water did not differ significantly between years (t-test, $p>0.05$).

In 2006 there was a clear peak in the fraction of walruses hauled-out around noon local time (Fig. 3). During 2007 and 2008 the haul-out pattern varied significantly with the time of the day (Kruskal-Wallis test, $H_{23,3696} = 49.14$, $p < 0.01$, Fig. 4 upper panel). Haul-out time was significantly higher between 14:00 pm-02:00 am local time than between 02:00 am-14:00 pm based on six four hour classes (Kruskal-Wallis test followed by a post-hoc Bonferroni test; Fig. 4 lower panel).

Fraction of submerged walruses

The fraction of time spent below a certain observation threshold was estimated from activity data from one adult male walrus (#4347) monitored in NE Greenland with a SLDR. This walrus spent an average of 73% of the time below 2 m depths between August 2000 and January 2001 (Table 2). During winter (November-January), an average of 9.2% of the time was spent at the surface (sd=1.8, range of monthly surface time: 7.2-10.7%) and an average of 23.9% of the time was spent between 0 and 2 m (sd=8.1, range: 16.3-32.3%). Hence the animal spent 76.1% of time deeper than 2 m and not detectable (Born et al. 2005, this study).

Therefore if a walrus, on average, spends 23.9% (95% CI 0.13-0.46) of the time at the surface (0-2 m) during winter the total number of animals in the water is about 4.2 times the number present at the surface. A correction factor of 4.2 (cv=0.34) was therefore applied to the aerial survey results for walruses swimming at the surface to account for those that were diving and not detectable during the passage of the aircraft.

Distribution of sightings

In 2006, 21 sightings were made on 75 transect lines covering 11642 linear km, or 6552 km over strata with walrus sightings (Fig. 1). The sightings were distributed with 9 groups on ice floes and 12 groups in water. The mean group size for all strata was 1.86 (se=0.27). In 2006, almost half of the sightings were in stratum 4 that had good coverage obtained over three days (1, 6 and 7 April) where there was almost no ice cover: Despite the relatively small area in stratum 4 it contributes more than 50% of the total abundance estimate (see later).

The survey in 2008 also resulted in 21 sightings but because it specifically focused on prime walrus habitat only 38 transects were flown covering 3236 linear km (Fig. 2). Seven sightings were walruses in the water and the remaining 14 were walruses hauled out on ice. The mean group size for all strata was 1.28 (se=0.22).

In both years walruses were mainly found in shallow water (<200 m) on the Store Hellefiske Bank between 66^{o} 30' N and 68^{o} 15' N and on the bank west of Qeqertarsuaq/Disko Island. However, in 2006 when a larger area was covered, and when ice conditions generally were lighter than in 2008, a few additional walruses were detected north and south of these main concentration areas (Fig. 1).

The percentage of sea ice on transects covered in 2006 over the northern wintering ground (i.e. stratum 9) was ca. 88% compared to ca. 77% in 2008. In 2006 the southern wintering ground on Store Hellefiske Bank (walrus strata 3 and 4) had an average of ca. 9% sea ice cover on the transect lines compared to ca. 38% in 2008 (Table 3).

Detection of walruses

None of the years had sufficient number of sightings to allow independent estimation of detection probabilities in the two habitat categories (ice and water). However, since the surveys used similar methods with a large overlap in observers pooling the detections from both years is justified.

The double platform experiment resulted in the following distribution of the 42 sightings: 6 animals were seen by both platforms, 14 were seen by the front platform only, 22 were seen by the rear platform only (Table 4). As indicated it is necessary to distinguish between detection on ice and in the water and the perception bias is therefore calculated separately for the two substrates but pooling the data from the two years.

In 2008 two walruses were recorded by the forward looking video system and none responded to the plane by escaping into the water. However, one dropped into the water after passage of the plane. Hence we did not apply any corrections for walruses that escaped into the water before the passing of the airplane reducing their chance of being detected.

Estimation of abundance

Detection of walruses in the water is a different process than detecting walruses on the sea ice. Essentially walruses at the surface in the water can rarely be seen far from the track line (>500 m) whereas walruses that are hauled-out on sea ice can be detected at long distances (Estes & Gilbert 1978, Born et al. 1994). During our surveys walruses in the water were usually not detected beyond 350 m from the track line which was slightly more than half the detection distance for walruses on the sea ice (Fig. 5).

Attempts to fit a monotonically decreasing detection function to the distribution of distances to the sightings did not provide an improved fit over a simple uniform (flat detection) model that included 95% of the sightings. Therefore the density of walruses was estimated on the basis of a flat detection function essentially meaning using strip census methods with a half strip width of 350 m for walruses in the water and 600 m for walruses on sea ice.

Two methods were used to calculate fully corrected abundance estimates. Method I applied separate correction factors for detections of walruses on ice and walruses in the water by calculating two estimates: (1) one based on walruses that were hauled out corrected for the fraction theoretically present in the water, and (2) one based on walruses that were hauled out plus those detected at the water surface corrected for the fraction theoretically submerged below the 2 m detection threshold (Table 2). In strata where there walruses were only in one type of habitat the estimate from that type was used in both estimates. In 2006, the combined corrected estimate of the two approaches was 3162 walruses (cv=0.01) being almost twice the combined estimate of 1625 walruses (cv=0.09) attained in 2008, but in both years the two abundance estimates were similar and not statistically different. The combined weighted (weight =1/cv) averages for 2006 and 2008 were 2178 walruses (cv=0.38, 95%CI: 1,060-4.474) for the first approach (correction for fraction not hauled-out) and 2467 (cv=0.27, 95%CI: 1,467-4,149) for the second approach (correction for submerged walruses). A weighted average of the estimates from the two years suggests that the West Greenland wintering stock of walruses numbers 3,008 (95%CI: 2,245- 4,029).

Method II corrects all detections for walruses that are not hauled out independent if they were detected on ice or in the water (Table 5). In order to allow for a simple mark-recapture correction of perception bias all detections were truncated at 350m from the trackline. The estimates of abundance from this method were 2,791 (95% CI: 1,036-7,522) for 2006 and 3,240 (95%CI: 863-12,170) for 2008 with a weighted average of 2,978 (cv=0.07, 2,597-3,415).

All estimates did not differ significantly indicating that the point estimate of the fully corrected abundance of walruses wintering in Central West Greenland in 2006-08 is around 3,000 animals.

Age and gender

Only in few cases were walruses identified to size category during the aerial surveys - and in none of the cases to gender. However, during the ship-based tagging operations in spring 2005-2008 in the study area records were kept of gender and estimated age of walruses that were tagged and other walruses seen in the area. All age categories except newborn were observed. Of 44 animals identified by sex, 45% were males (Table 6). Hence, the population estimated during the aerial surveys comprised both gender and all age groups except newborn.

Trends in abundance

A comparison of the sighting rates (i.e. weighted estimates of density of walruses per linear km) from the surveys conducted between 1981 and 2008 (Table 7) reveals no significant trend ($p>0.05$) in the southern wintering area (Store Hellefiske Bank, Fig. 6) whereas there is a significant decline ($p=0.0058$) in the northern wintering area west of Disko Island (Fig. 6). However, this latter trend is, to a large extent, driven by the surveys in 2006 and 2008 that had a thorough coverage of that area compared to previous years.

There is a weak but non-significant decline in sighting rates if both areas are combined (again weighted by effort; Fig. 7). The low sighting rate in the northern area is negatively correlated with the high sighting rates in the southern area (Fig. 7), which may indicate a connection between walruses occurring in the two areas.

The mechanism behind the fluctuating occurrence of walruses in the northern area can be examined relative to the sea ice extent index for March in West Greenland (Fig. 8, see Stern and Heide-Jørgensen 2003 for definition of these analysis areas). The sighting rate of walruses west of Disko Island was positively correlated with the sea ice extent in the ‘medium area’ (Fig. 9). This may indicate that extent of sea ice in this area is a mechanism behind the abundance of walruses in the northern wintering ground and that walruses abandon or avoid the northern area in years with less sea ice. In contrast, no significant relationship between sea ice extent and walrus abundance was detected in the southern area (Fig. 9). This area, however, may not be as reliably covered with sea ice and walruses may use the region regardless of expected or realized sea ice conditions.

DISCUSSION

There are a number of well-known difficulties associated with estimation of abundance of marine mammals and walruses are clearly among the more difficult to survey. The difficulties include clumped distribution, occurrence in two habitats (sea ice and water) with different detection probabilities, pod sizes and availability correction factors. Surveys of walruses notoriously suffer from large variances of sighting rates, unknown proportions of the population diving or in open water and therefore unavailable to be counted during surveys, and large annual variations in sea ice distribution and extent (Estes & Gilbert 1978, Gilbert 1989, 1999, Udevitz et al. 2001). Inevitably all these factors influenced the surveys of walruses in Central West Greenland in 2006 and 2008.

Ice conditions, sighting rates and stock delineation

Ice conditions in 2006 were markedly lighter than in 2008. This meant that a higher proportion of walruses were detected in water in 2006 than that in 2008 when the major southern walrus wintering area had about four times more drift ice for hauling out compared to 2006.

Sighting rate in the southern wintering ground was slightly higher (significantly?) in 2008 than in 2006, whereas the opposite was seen on the northern wintering ground. If change in sighting rate over time is an expression of change in abundance, then the abundance of walrus in the southern area has remained unchanged since the early 1980s whereas the abundance at the wintering ground west of Disko Island has decreased significantly. However, there was a tendency for an inverse relationship in sighting rates in the two areas: High sighting rates in the north were usually associated with low sighting rates in the south. Furthermore, in years with relatively dense ice conditions in eastern Baffin Bay (the “medium area” defined in Stern and Heide-Jørgensen 2003) sighting rates were relatively high in the northern area. This indicates that ice conditions may have influenced the number of walruses wintering on the foraging banks at western Disko Island whereas such a relationship could not be detected on the southern wintering ground. Since ca. 1990 the sea ice has decreased in eastern Davis Strait and Baffin Bay

(Stirling & Parkinson 2006) although 2007 and 2008 were heavy ice years (Heide-Jørgensen et al. in press). It is possible lighter ice conditions may have caused some walruses to emigrate earlier, having otherwise wintered off Disko Island further north and/or walruses wintering at Disko Island. This suggestion is supported by the observatoin of walruses in Upernavik in 2006 when ice conditions were light (this study). The same area was not covered in 2008 with heavy ice conditions and no conclusion can be made.

Movements of walruses equipped with SLTs on the southern wintering ground during March-April 2005, 2006, 2007 and 2008 have demonstrated that some walruses move from Store Hellefiske Bank north to Disko Island and some move to SE Baffin Island from Central West Greenland during spring (Dietz et al. in prep.).

The mean group size in 2006 of 1.86 walrus (se=0.27) and in 2008 of 1.28 (se=0.22) did not differ from mean group sized observed during previous aerial surveys in West Greenland during 1981-1991, where mean group size ranged between 1.55 and 1.77 walrus (cf. Born et al. 1994). Furthremore maximum group sizes recorded during 2006 and 2008 (8 and 6, respectively) did not differ from maximum group sizes (ranging between 3 and 8 animals) in previous surveys. Walruses have a tendency to be highly gregarious (e.g. Fay 1982). We suggest that the small group sizes in combination with the scattered distribution of groups indicate that walruses still occur in relatively low numbers in West Greenland.

Haul-out time

Studies of the haul-out activity of free ranging walruses have mainly been conducted during summer. They have, however, shown a remarkable consistency in mean fraction of time spent out of the water of between ca. 23-25% (Jay et al. 2001, Lydersen et al. 2008) and ca. 30-35% (Hills 1992, Born & Knutsen 1997, Acquarone et al. 2006, Born & Acquarone 2007). Walruses studied in captivity were hauled out for ca. 25% of the time (Pryaslova & Lyamin 2006). This consistency in daily haul-out time indicates that the haul-out pattern of walruses is basically governed by fundamental physiological requirements rather than the weather regime as suggested by Born & Knutsen (1997).

During the aerial surveys, the instrumented walruses hauled out for an average of ca. 34% of the time in 2006 and ca. 25% of the time in 2008 with no statistically significant difference between years. This is comparable to a monthly haul-out time ranging between 19% and 30% of an adult walrus monitored during winter (November-December) in NE Greenland (Born et al. 2005) and is similar to haul-out times observed in other studies of walruses at other times of the year (e.g. Fay et al. 1997, Lydersen et al. 2008). The difference in haul-out time and patterns between 2006 and 2008 emphasizes the importance of collecting activity data simultaneous with the surveys, as also recommended by Gilbert (1999). The fact that walruses were present in some areas despite the lack of sea ice for hauling out also stresses the importance of the Central West Greenland wintering grounds as feeding ground for walruses in the Davis Strait-Baffin Bay region. The West Greenland shelf is shallow (<200 m) and highly productive (among the most productive in the Arctic, Heide-Jørgensen and Laidre 2004, Laidre et al. 2008) and offers walruses unsurpassed feeding habitat during winter and spring.

Submerged walruses

Walruses feed on their wintering grounds in Central West Greenland and are therefore expected to dive intensively (Born et al. 1994). Presumably they also spend time travelling between localized feeding areas and areas with suitable ice for hauling-out. Examination of walrus stomachs from the hunt at Store Hellefiske Banke and faecal stains frequently detected on ice floes where walruses hauled out indicated that they were engaged in feeding. Direct observations indicate that during travelling and feeding walruses are submerged between 76% and 89% of the time (Fay 1982, Born & Knutsen 1997 and references therein). Based on data from direct observations Fay et al. (1999) applied a correction factor to aerial surveys in the Bering Strait region of 6.2 (i.e. the number of walruses seen at the surface must be multiplied by 6.2 to account for those theoretically submerged and therefore not visible) to adjust for walruses in the water but not seen. In this study we have used a similar correction of 4.2.

Most data on walrus diving behavior have been collected during summer and for obvious reasons information on time submerged by walruses during winter is scarce. We applied a correction factor of ca. 24% visible at surface down to 2 m assuming that a walrus can be detected down to ca. 2 m depth (i.e. total:surface ratio 4.2). Despite that the correction factor used was based on only one individual sampled in a different area (East Greenland) it was in general agreement with other studies involving SLDRs and its variance (cv=0.34) is sufficiently large to cover the population variability.

In a study of an adult male walrus monitored with a TDR at Svalbard during summer, Wiig et al. 1993 found that about 24% of the time was spent between 0 and 2 m. In contrast, Jay et al. (2001) found that four Pacific walruses in the Bering Sea equipped with TDRs when at sea spent ca. 39.7% of the time between 0 and 2 m during summer (total:surface ratio 2.5). Using TDRs and SLDRs to study walrus activity during late July-August at Svalbard, Gjertz et al. (2001) found that nine walruses spent ca. 83% of their time in water of which 39% was spent between 0 and 2 m depth, and 44% of the time below 2 m (i.e. total:surface ratio 2.1) (*Ibid*.). It is far more reasonable to use a surface availability correction factor derived from winter-time to correct the late winter surveys in Central West Greenland for walruses that theoretically were submerged and remained undetected.

Diurnal haul-out rhythm

We found that walruses in 2008 showed a variation in haul-out rhythm across a diel cycle. The greatest proportion of time was spent out of the water during late afternoon and early evening – with a clear increase during the survey period between 10:00 and 18:00 h local time. This pattern is in accordance with studies of haul-out behavior of walruses during summer in Alaska (Hills 1992), the Canadian High Arctic (Salter 1979) and NE Greenland (Born & Knutsen 1997) indicating that walruses prefer to haul out during day time hours with a tendency of a peak during late afternoon and evening (Born & Knutsen 1997) with most sunlight.

Studies conducted during summer have revealed that generally walrus haul out is influenced by weather conditions. In particular it is negatively affected by low temperature, high wind speeds (wind chill effect) and precipitation (Salter 1979, Pankratov 1982, Hills 1992, Born & Knutsen 1997). In contrast, at Svalbard Lydersen et al. (2008) did not find any relationship during summer between haul-out activity of walruses instrumented with transmitters and wind chill. In this study we were not able to detect any relationship between wind chill and walrus haul out pattern. However, this may have been influenced by the fact that our weather data were collected at a land station 100-200 km from the actual walrus grounds. Weather conditions at a land-based station may be markedly different from those found offshore among drift ice at sea level where the walruseswere located. However, lack of *in situ* weather data prevents us from pursuing this issue further.

Age and gender

Age and sex of the walruses can be difficult if not impossible to determine during aerial surveys – perhaps except in cases of adult females with small calves. However, other information indicates that the population of walruses estimated during the present study comprises all age groups (except newborn) and both genders. Females constituted ca. 55% of the observations. The genetically identified sex composition of a sample of walruses (n=127) obtained from the catch in the Sisimiut-Attu area (1988-2007) was 59% females and 41% males (Andersen et al. 2008 in prep.). Born *et al.* (1994) also found indications that walruses wintering in West Greenland constitute adults, sub-adults and 1+-year old calves of both genders. Hence, our estimates address both genders and all age groups – except newborn.

Abundance estimates

The survey in 2006 covered a wider area and was conducted a little earlier in the season than the 2008 survey. Despite earlier timing the 2006 survey also had less severe ice conditions than the 2008 survey (Heide-Jørgensen and Stern unpubl.). This is also reflected by the sightings where 12 out of 21 were of walruses in water in 2006 compared to 7 out of 21 in 2008. When choosing the estimates with the lowest variance the fully corrected abundance in 2006 from Method I was 3245 (95% CI: 1078-9772) walruses and 1505 in 2008 (95% CI: 695-3259). Part of the reason for the larger estimate in 2006 is the wider coverage including stratum 6 and 13 but the main reason is the effect of the corrections applied to the walruses in the water this year. As stated more walruses were detected in the water in 2006; and in particular stratum 4, which had no walruses on ice, made a large contribution to the abundance estimates in 2006.

The correction factor for availability in water used in Method I was not derived from the study area, and, although its associated variance is large, it was still based on only one walrus. Hence, it appears scientifically sound to put more emphasis on the abundance estimates that rely less on the correction for detection availability in water (i.e. to rely more on the 2008 estimates and the average estimate based on both years).

The results from Method II are more consistent between years and depend on fewer corrections but still maintain a high variance due to the low number of sightings involved in the calculations. However, Method II avoids the use of the correction for walruses that are submerged that is based on observations from one walrus instrumented in Northeast Greenland.

Trends in abundance

A construction of a compatible time series of relative abundance of walruses in Central West Greenland can be made with some reservations because during the years at least four different airplanes, 3 different methods, as well asdifferent altitudes, and different timing and observers were involved. The most simple time series is just an index of walruses (in water or on ice) per linear kilometer flown covering 11 years between 1981 and 2008. This index assumes that observation efficiency and local weather conditions that may influence walrus behavior and detectability were essentially the same during all surveys.

The 1999 sighting rate estimate is positively biased because only a small proportion of the entire survey was included in the sighting rate determination. No walruses were seen outside the area included thus a lower sighting rate would be anticipated if a larger effort was included. The 2006 sighting rate estimate is negatively biased because walruses were detected in areas north of the previous surveys but they were not included in the estimate.

Comparison with previous estimates of abundance

Previous estimates of abundance of walruses in Central West Greenland based on aerial surveys only addressed the number of animals at the surface and due to lack of information of walrus activity from SLDRs and TDRs. These surveys did not attempt to make corrections for animals not available to be seen or those missed by the observers (Born et al. 1994). However, using the estimates of walruses at the surface obtained from line-transect aerial surveys conducted in Central West Greenland in early spring of 1990 and 1991(Born et al. 1994), Witting and Born (1995) included a correction based on data on haul-out percentage and diving activity obtained from SLDRs deployed on walruses in Northeast Greenland. The total number of walruses wintering off Central West Greenland was estimated at ca. 1000 (cv=0.48) (Witting & Born 2005). The estimates from the present study include corrections for the availability of walruses on sea ice based on data collected simultaneously with the aerial surveys, corrections for walruses submerged below detectability and a correction for walruses that were missed by the observers. However, although the point estimates of abundance in either year in the present study are higher than that in Witting & Born (2005) they do not differ statistically from the estimates offered by these researchers.

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Table 1. Summary of estimated age and gender of 12 walruses equipped with satellite-transmitters that generated data on haul-out time during aerial surveys, conducted during 21, 23, 24 March and 1, 6, 7, 9-11 and 15-19 April 2006 and during 3-4 and 10-12 April 2008 in Central West Greenland. Values are expressed as mean ± s.d. * = individuals successfully tracked (i.e. with recorded data) during the periods of aerial surveys. Suffixes a and b indicates that the same transmitter ID number was used on different animals in different years.

ID no.	Date tagged	Sex	Age (estimated)	No. of days with activity data	Mean daily haulout time % (sd)	Mean diurnal haulout time (10-18 local h local time) % (sd)	Mean fraction of walruses hauled out during the aerial surveys % (sd) (days)
17763 *	19-03-2006	M	Adult	6	36.3 (18.7)	36.3 (20.6)	45.1 (20.2) (3)
17765 *	19-03-2006	M	2-3 yr.	19	22.4 (8.4)	22.4 (9.8)	22.8 (14.1) (8)
56570a *	21-03-2006	F	Adult	7	57.1 (18.4)	57.1 (16.8)	76.5 (25.7) (2)
56571a *	22-03-2006	M	Subadult	22	23.5 (6.9)	23.5 (5.8)	25.9 (7.0) (9)
56574a *	26-03-2006	M	Adult	11	28.9 (9.8)	28.9 (9.2)	52.9 (16.9) (6)
56570b *	02-04-2008	F	Adult	21	21.5 (27.6)	21.3 (34.1)	31.0 (47.4) (4)
56571b *	02-04-2008	M	Adult	22	18.8 (19.9)	14.2 (27.7)	0.0 (0.0) (1)
56572 *	02-04-2008	?	2-3 yr.	25	20.4 (23.6)	21.7 (31.7)	15.1 (14.5) (5)
56573 *	04-04-2008	F	Adult	24	15.4 (21.5)	22.2 (33.2)	40.0 (42.1) (3)
56574b *	02-04-2008	M	Subadult	28	8.1 (12.3)	10.9 (18.3)	23.6 (33.4) (2)
57101	04-04-2008	M	Adult	25	23.5 (26.6)	21.1 (28.7)	-
57100 *	04-04-2008	M	Subadult	25	14.9 (18.7)	18.5 (26.5)	26.0 (31.3) (4)

Table 2. Percentage of time spent in the upper 2 m of the water column by an adult male walrus (#4347) during August-December 2000 and January 2001. The percentage of time at the surface (= salt water switch dry) and the number of days and time blocks (6 hr periods) monitored are shown. Time = all blocks except those with all 6 hours dry at the surface (= hauled out). Data from Born et al. 2005 and unpublished.

Month	% time	Percentage time in different depth intervals (m)						Days	Time
	at surface	0-2	0-6	6-18	18-42	42-90	> 90		blocks
Aug	7.9	36.8	47.5	47.1	3.3	1.4	0.8	12	30
Sep	14.3	28.1	33.6	60.3	4.9	0.9	0.4	27	81
Oct	10.3	25.3	33.7	44.7	20.1	1.5	0.01	16	42
Nov	7.2	32.4	38.2	40.4	13.4	5.6	2.5	26	61
Dec	10.7	16.3	22.8	45.7	6.5	16.2	8.9	25	68
Jan	9.8	23.1	35.7	38.9	5.3	19.7	0.4	24	55
Mean	10.0	27.0	35.3	46.2	8.9	7.6	2.2		
SD	2.5	7.2	8.0	7.6	6.5	8.3	3.4		

Table 3. Stratum size (km^2), effort (linear km), observations of walruses on ice and in water, and uncorrected and corrected estimates of abundance of walruses in Central West Greenland, 2006 and 2008. Detections were truncated at 350 m for sightings in water and 600 m for sightings on ice.

			Observations		Uncorrected abundance				Perception bias on ice		Perception bias in water		Availability bias on ice		Availability bias in water		Corrected abundance		Corrected abundance	
Stratum	Area	L (km)	On ice	In water	On ice $\hat{N}_{ice}$	cv	In water $\hat{N}_{water}$	cv	$\hat{p}_{ice}$	cv	$\hat{p}_{water}$	cv	$\hat{a}_{ice}$	cv	$\hat{a}_{water}$	cv	$\hat{N}^*=(\hat{N}_{ice}/\hat{p}_{ice})/\hat{a}_{ice}$	cv	$\hat{N}^*=\hat{N}_{ice}/\hat{p}_{ice}+\hat{N}_{water}/\hat{p}_{water}/\hat{a}_{water}$	cv
2006: 1	1496	137	0	0																
2006: 2	9669	1329	2	0	10	1.06			0.57	0.26			0.37	0.23			49	1.11	49	1.11
2006: 3	8613	837	6	1	87	0.70	23	1.02	0.57	0.26	0.49	0.37	0.37	0.23	0.24	0.34	418	0.78	349	0.33
2006: 4	6376	420	0	9			270	0.66			0.49	0.37			0.24	0.34	2321	0.83	2321	0.83
2006: 5	8041	434	0	0																
2006: 6	5935	1091	0	1			12	1.05			0.49	0.37			0.24	0.34	104	1.06	104	1.06
2006: 7	8205	1076	0	0																
2006: 9	5792	491	0	1			26	1.07			0.49	0.37			0.24	0.34	225	1.18	225	1.18
2006: 10	10779	523	0	0																
2006: 12	3612	306	0	0																
2006: 13	27544	2384	1	0	16	1.03			0.57	0.26			0.37	0.23			78	1.09	78	1.09
2006: 14	14168	1296	0	0																
2006: 15	13256	712	0	0																
2006: 16	2148	138	0	0																
2006: 17	2312	468	0	0																
2006: Sum	127946	11642	9	12	113	0.57	331	0.55									3196	0.62	3127	0.62
Stratum	Area	L (km)	On ice	In water	On ice $\hat{N}_{ice}$	cv	In water $\hat{N}_{water}$	cv	$\hat{p}_{ice}$	cv	$\hat{p}_{water}$	cv	$\hat{a}_{ice}$	cv	$\hat{a}_{water}$	cv	$\hat{N}^*=(\hat{N}_{ice}/\hat{p}_{ice})/\hat{a}_{ice}$	cv	$\hat{N}^*=\hat{N}_{ice}/\hat{p}_{ice}+\hat{N}_{water}/\hat{p}_{water}/\hat{a}_{water}$	cv
2008: North	11778	1151	2	1	29	0.71	23	1.06	0.57	0.26	0.49	0.37	0.25	0.18	0.24	0.34	205	0.78	246	0.95
2008: South	22554	2085	12	6	182	0.33	144	0.72	0.57	0.26	0.49	0.37	0.25	0.18	0.24	0.34	1300	0.46	1560	0.70
2008: Sum	34332	3236	14	7	211	0.30	167	0.64									1505	0.41	1806	0.62

Table 4. Distribution of walrus sightings by platform (front or rear) and habitats (ice or water) for the 2006 and 2008 surveys in Central West Greenland.

	Total number of sightings	On ice	In water	Front	Rear	Both	Platform	Ice	Water
							front	8	5
2006	21	9	12	9	9	3	rear	11	12
2008	21	14	7	5	13	3	both	4	2
Sum	42	23	19	14	22	6		23	19

Table 5. Stratum size (km^2), effort (linear km), combined observations of walruses on ice and in water, and uncorrected and corrected estimates of abundance of walruses in Central West Greenland, 2006 and 2008. Correction of the availability bias is based on the fraction of time walruses are hauled out ($\hat{a}_{ice}$). Detections were truncated at a distance of 350m from the track-line.

			Observations	Uncorrected abundance		Perception bias		Availability bias		Corrected abundance	
Stratum	Area	L (km)	On ice or in water	$\hat{N}_{both}$	cv	$\hat{p}_{both}$	cv	$\hat{a}_{ice}$	cv	$\hat{N}^{*}_{both} = (\hat{N}_{both} / \hat{p}_{both}) / \hat{a}_{ice}$	cv
2006: 3	8613	837	4	122	0.61	0.56	0.35	0.37	0.23	602	0.74
2006: 4	6376	420	8	359	0.68	0.56	0.35	0.37	0.23	1770	0.80
2006: 6	5935	1091	1	16	1.06	0.56	0.35	0.37	0.23	79	1.14
2006: 9	5792	491	1	35	1.09	0.56	0.35	0.37	0.23	173	1.17
2006: 13	27544	2384	1	34	1.12	0.56	0.35	0.37	0.23	168	1.20
Sum	54260	5223	15	566	0.51					2791	0.54
2008: North	11778	1151	2	40	0.41	0.42	0.47	0.25	0.18	385	0.65
2008: South	22554	2085	14	297	0.70	0.42	0.47	0.25	0.18	2856	0.86
Sum	34332	3236	16	337	0.39					3240	0.76

Table 6. Sex and age category of walruses that were either tagged with satellite-transmitters or observed during ship-based tagging operations (March-April 2005-2008) in Central West Greenland in the area covered by the aerial surveys in 2006 and 2008. Unid.=unidentified.

	Males		Females		Calves	Unid.
Year	Adult	Subadults	Adult	Subadults	<= 2-3 yr.	
Tag 2005	2	0	1	0	0	0
Obs. 2005						
Tag 2006	2	1	1	0	1	0
Obs. 2006	4	0	11	1	9	5
Tag 2007	2	4	3	1	0	0
Obs. 2007			2		2	1
Tag 2008	2	3	3	1	1	0
Obs. 2008						
Total	12	8	21	3	13	6
% of identified	21.4	14.3	37.5	5.4	23.2	

Table 7. Construction of a sighting rate time series. N and S denote the northern and the southern walrus concentration area respectively, group is mean group size, nL is sighting rate (walrus per linear km flown on transect), and cv is coefficient of variation.

	Northern wintering ground					Southern wintering ground					Both areas combined	
Year	N_n	N_{group}	N_{Effort} km	$N_{n/L}$	N_{cv}	S_n	S_{group}	S_{Effort} km	$S_{n/L}$	S_{cv}	$\frac{N_n + S_n}{N_{Effort} + S_{Effort}}$	$N_{Effort} + S_{Effort}$ km
1981	1		137	0.0073		14		1228	0.0114	0.75	0.011	1365
1982	17		342	0.0496		12		2967	0.004	0.41	0.009	3309
1984	6		160	0.0375	0.56	5		1273	0.0039	0.32	0.008	1433
1990	3	1.33	156	0.0192	0.33	9	2.11	721	0.0125	0.4	0.014	877
1991	4	1.75	156	0.0256	0.41	25	1.44	1377	0.0182	0.21	0.019	1533
1993	5	1	192	0.026	0.55	23	1.39	4169	0.0055	0.27	0.006	4361
1994	.		.	.		25	1.56	5233	0.0048	0.26	.	.
1998	.		.	.		23	1.44	1621	0.0142	0.21	.	.
1999	.		.	.		5	1.4	1169	0.0043	0.37	.	.
2006	2	1	491	0.0041	1.06	18	1.61	2585	0.007	0.43	0.007	3076
2008	3	1	1151	0.0027	0.59	18	1.35	2085	0.0088	0.35	0.0065	3236

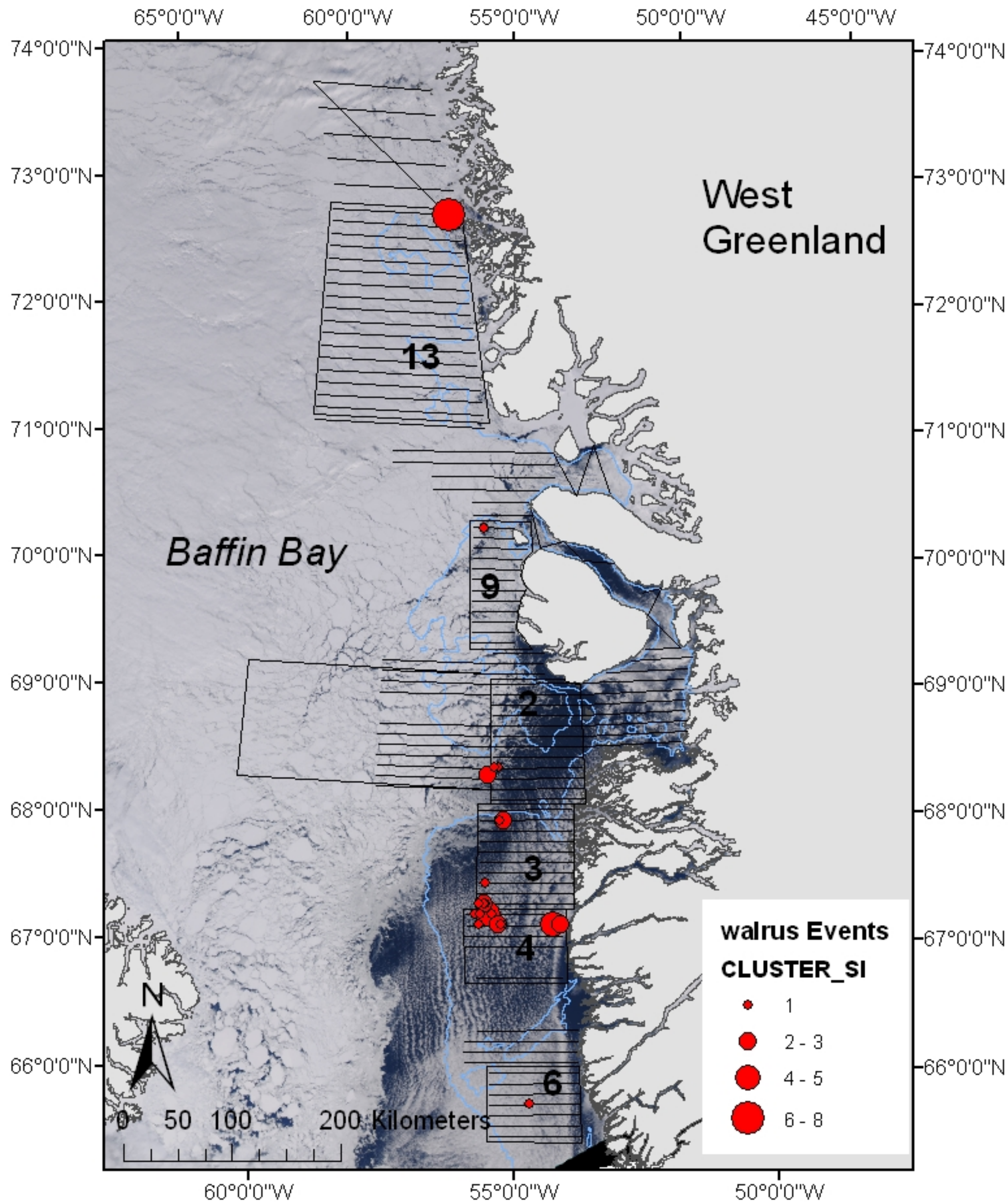

Fig. 1. Realized survey effort and sightings of walruses in West Greenland in 2006 in the different strata. The left map show the ice coverage in the surveyed areas (Modis satellite image from 3 April 2006). Dots indicate group size.

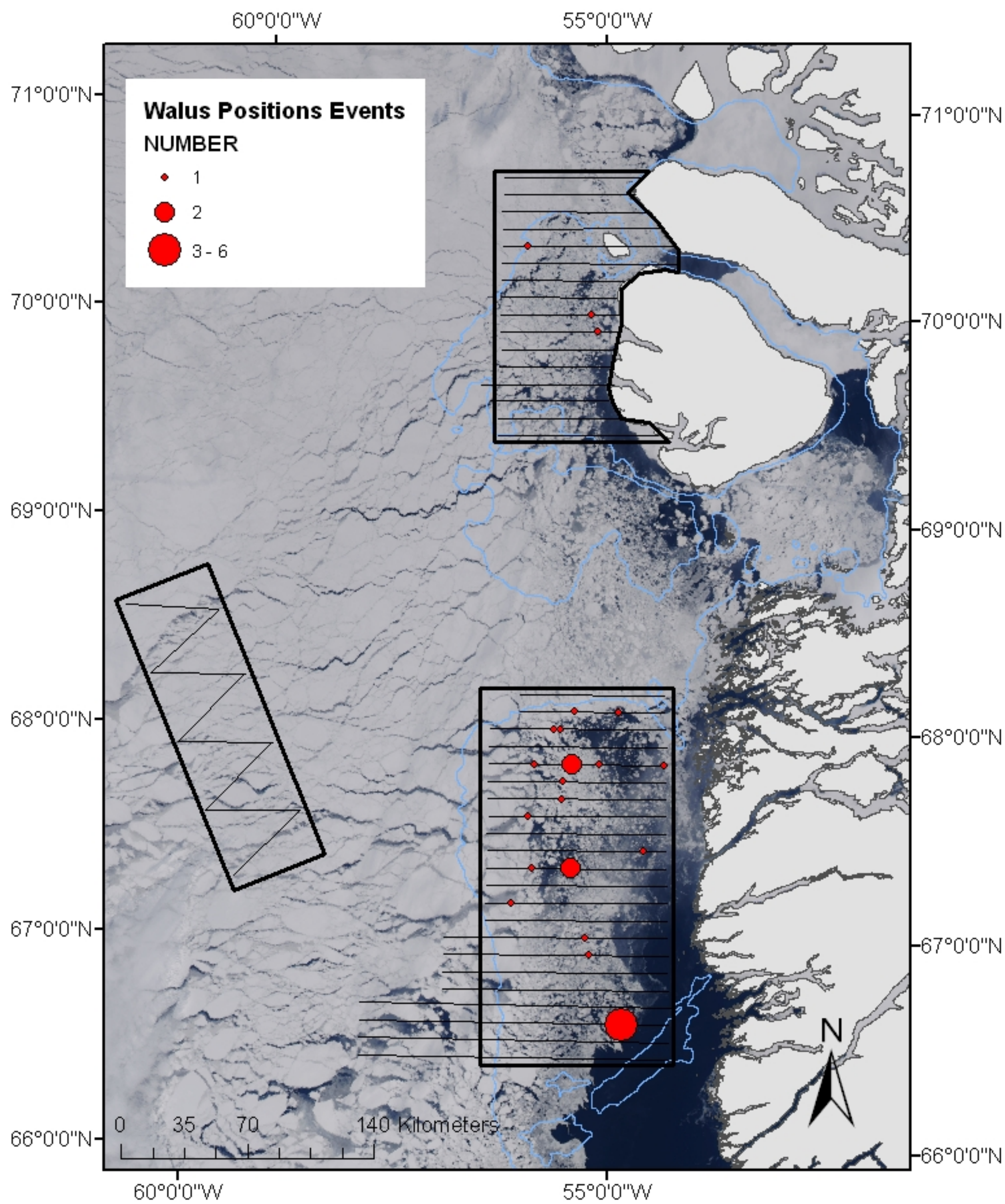

Fig. 2. Realized survey effort and sightings of walruses in two strata in West Greenland in 2008. The offshore stratum was covered for other purposes (see Material and methods) but is included here for the documentation. The left map show the ice coverage in the surveyed areas (Modis satellite image from 3 April 2008). Dots indicate group size.

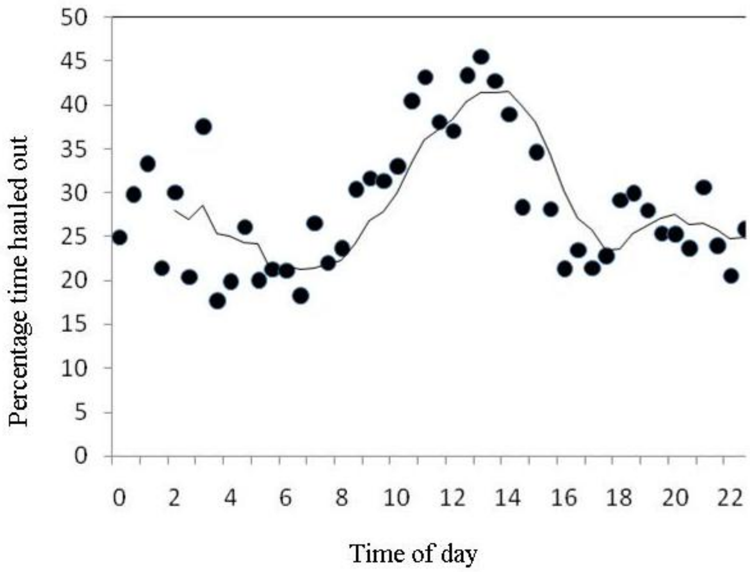

Fig. 3. Half-hourly diurnal variation of mean haul-out time of 5 walruses that were tracked by use of satellite transmitters in Central West Greenland in 2006.

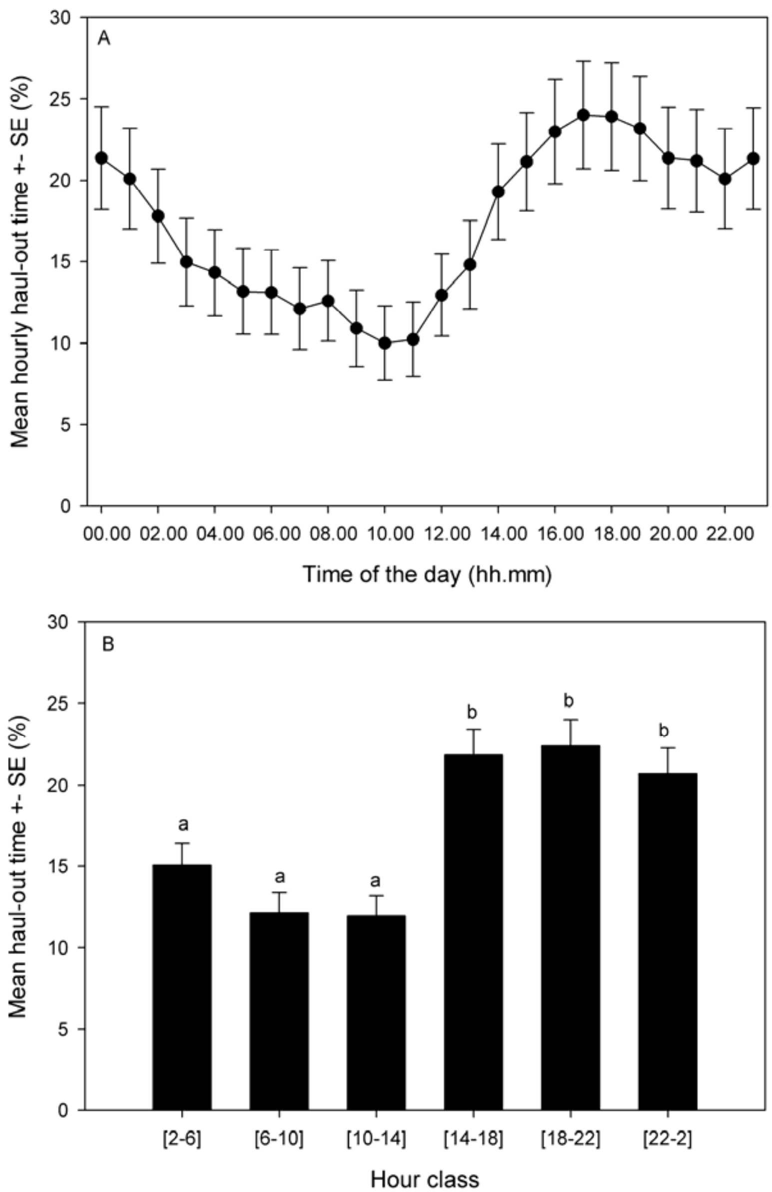

Fig. 4. Upper panel: Hourly variation of mean haul-out time of seven walruses that were tracked by use of satellite transmitters in West Greenland in 2008. Lower panel: Mean haul-out time in relation to the time of the day in seven walruses satellite-tracked in West Greenland in 2008. Differences in means were tested statistically using a Kruskal–Wallis test followed by a *post-hoc* Bonferroni test (n = 6 hour classes). Different letters (a, b) indicate significant (P < 0·05) differences among hour classes.

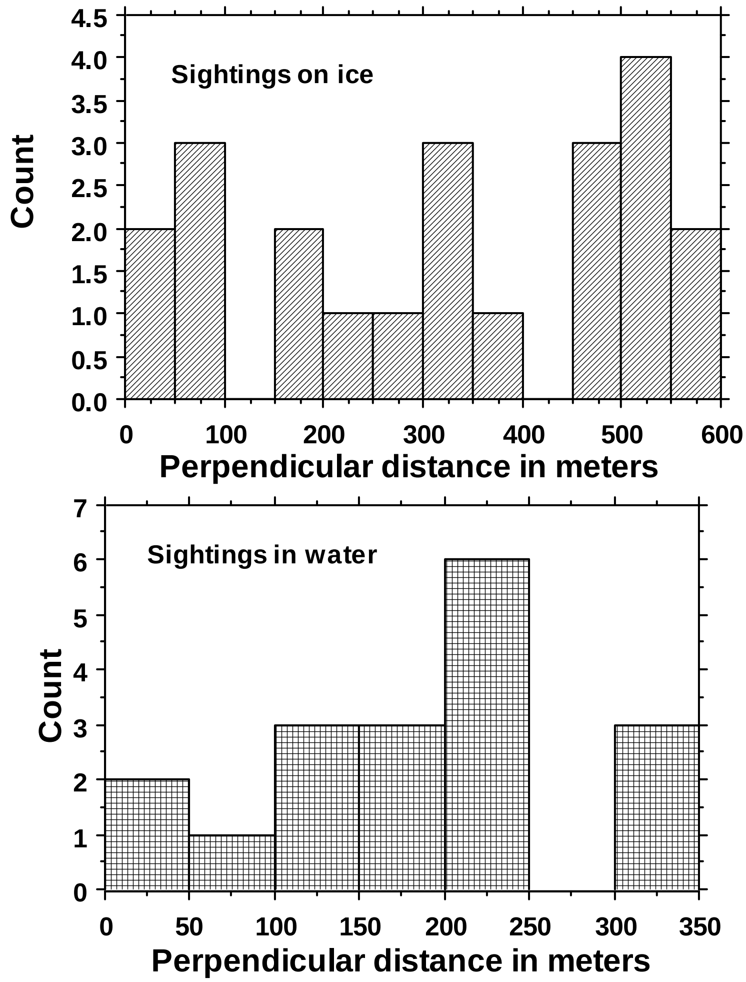

Fig. 5. Distribution of perpendicular distances to sightings of walruses during aerial surveys of walruses in Central West Greenland during March 2006 and April 2008. Thee upper panel shows sightings of walruses in the water, lower panel shows sightings on ice for both years combined. The upper panel displays the distribution of 18 out of 19 sightings of walruses in the water and the lower panel displays 22 out of 23 sightings of walruses on ice.

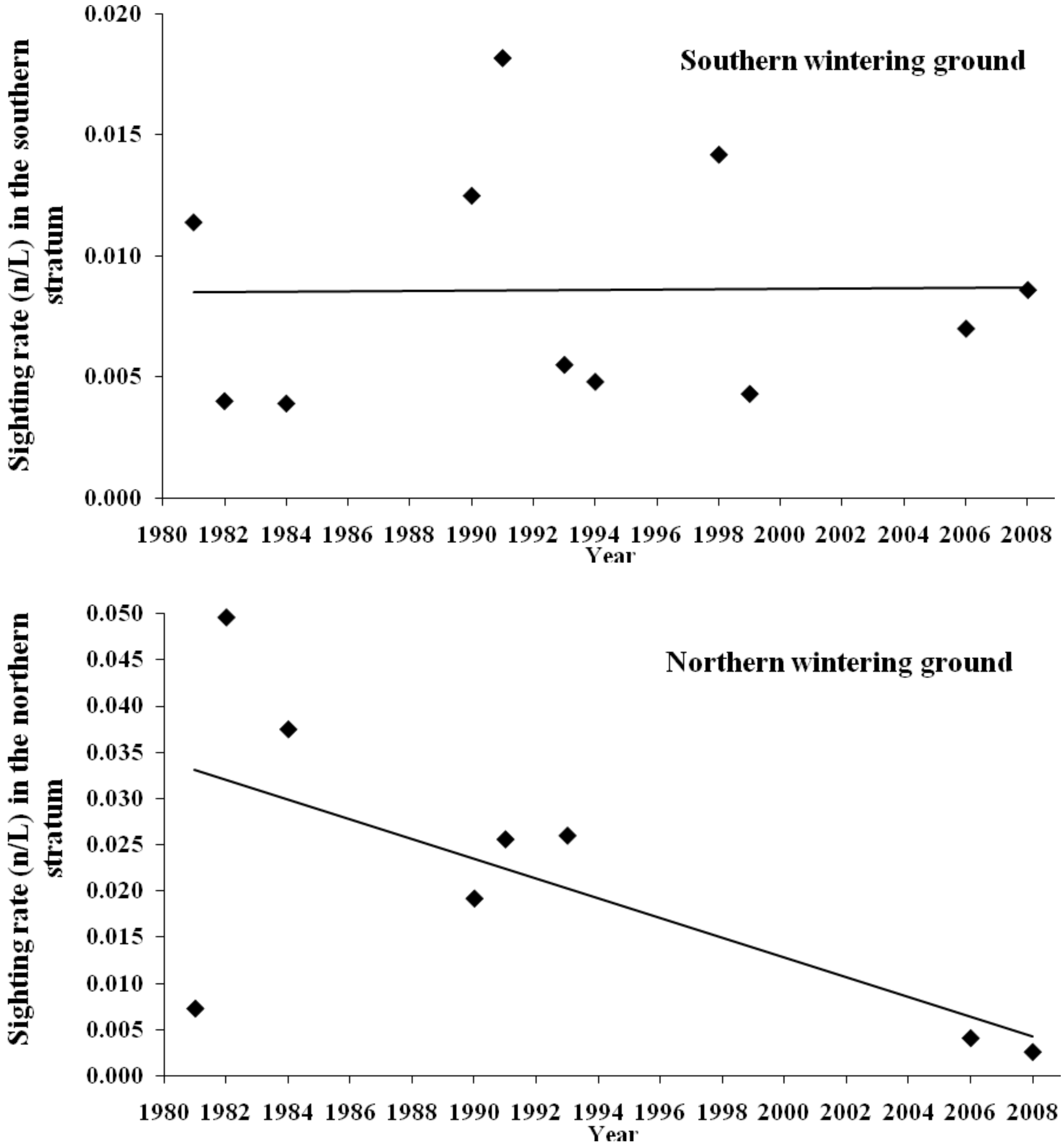

Fig. 6. Linear fit of trends in sighting rates, $S_{n/L}$ (walrus * km^{-1}) in the southern and northen walrus wintering grounds in Central West Greenland weighted by effort (linear km flown) during 1981-2008. The trendline is non-significant for the southern wintering ground. The trendline for the northern wintering ground ($N_{n/L}$ = 2.15 - 0.0011*Year) is significant (p=0.0058).

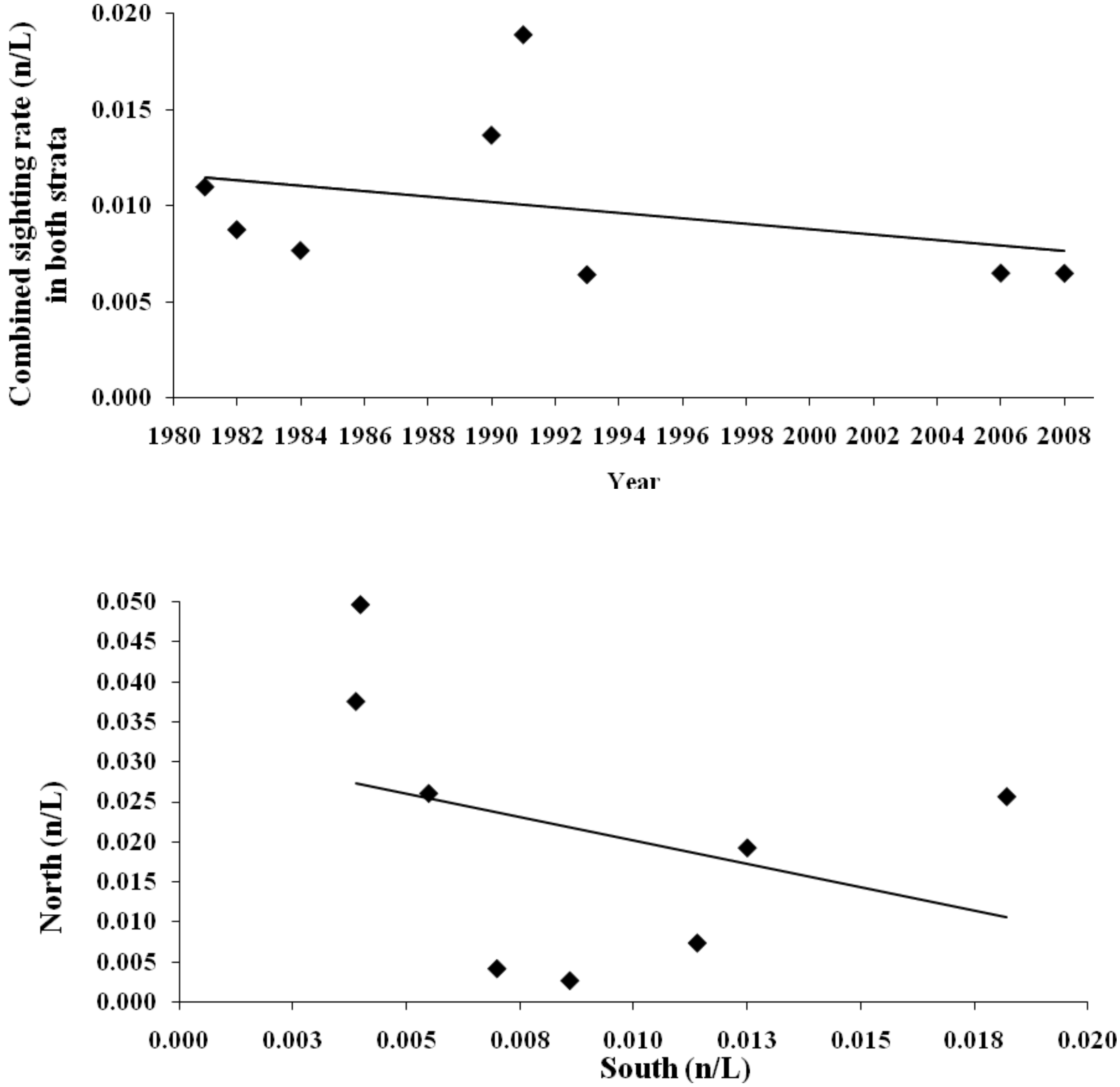

Fig. 7. Upper panel: The relation between sighting rate of walruses in the northern and southern wintering ground in Central West Greenland combined weighted by the effort in both areas. The linear fit $S_{n/L}+N_{n/L}$ = 0,29 - 0,0001 Year is not significant.

Lower panel: The relation between sighting rate of walruses during eight aerial surveys conducted in the northern and southern wintering ground in Central West Greenland during 1981-2008.

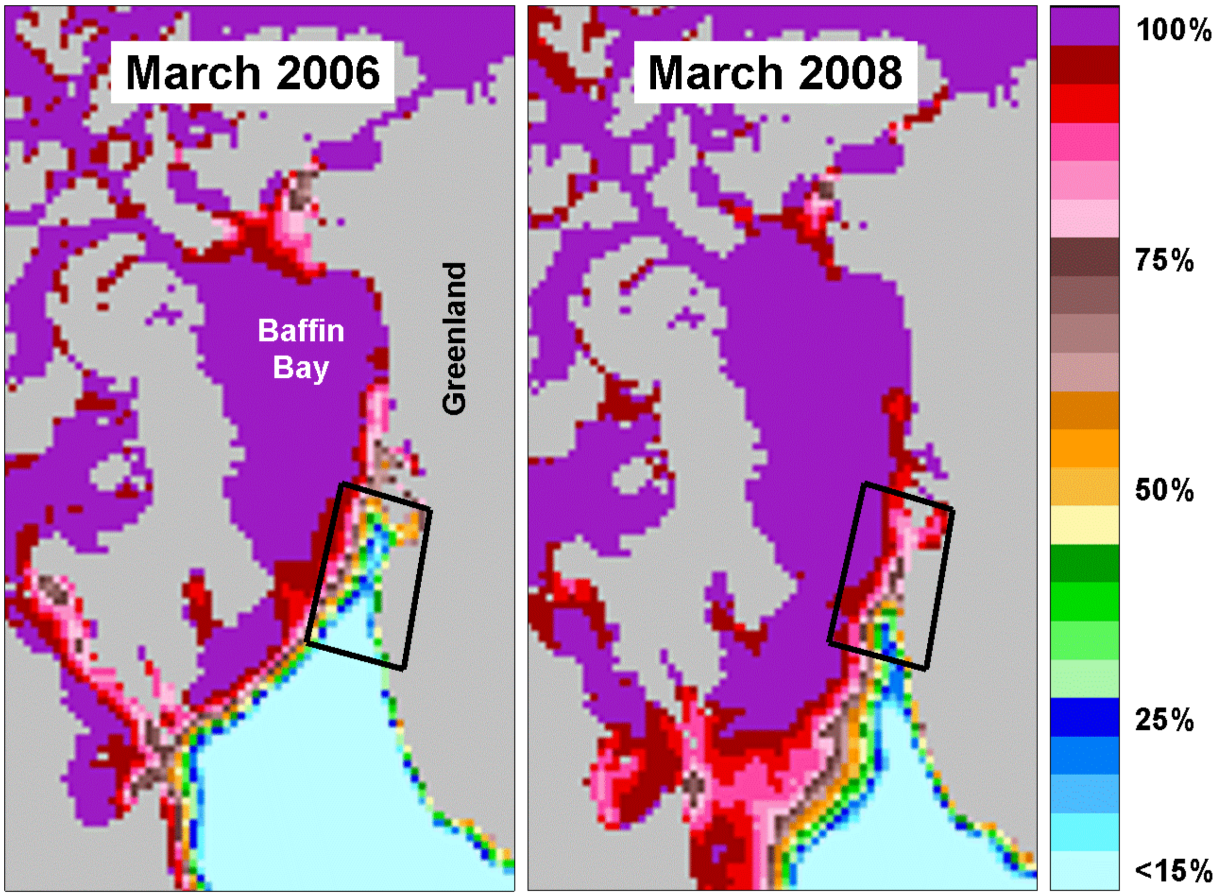

Fig. 8. Left panel: Sea ice areas in West Greenland used for the comparison with the walrus sighting rates. The red box indicate the ‘medium area’ used here. Right panel: Sea ice concentrations in Baffin Bay 2006 and 2008 based on SSMI (NSIDC).

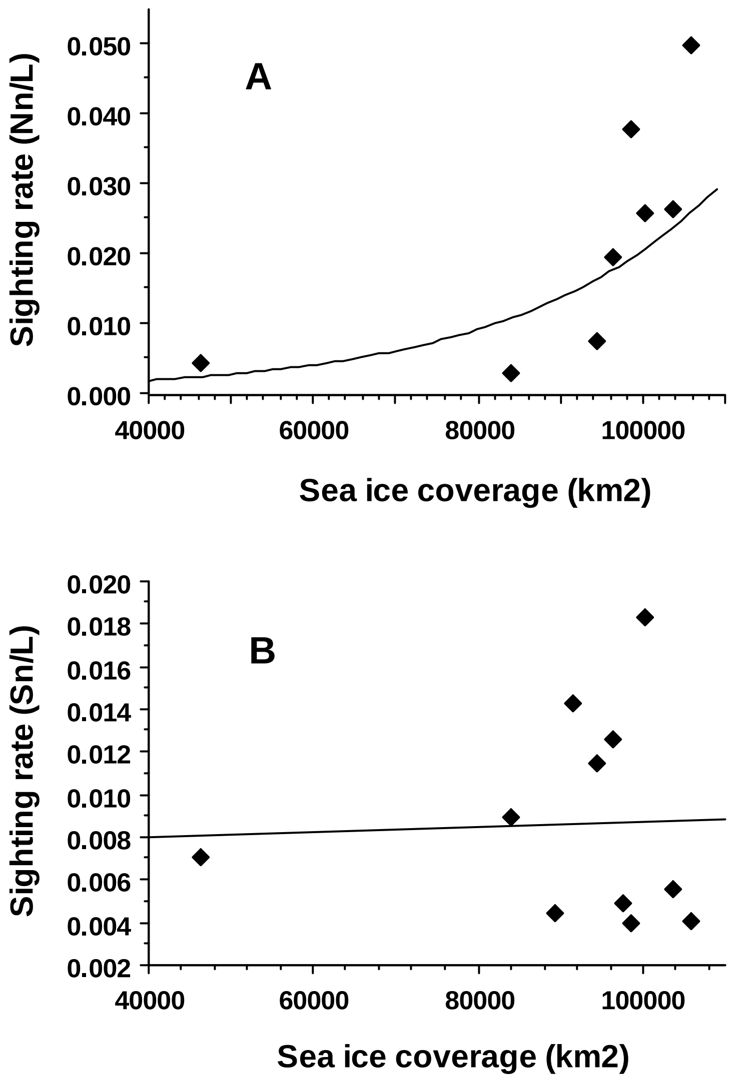

Fig. 9. Sighting rates of walrus in A: the northern wintering ground (west of Disko) (ANOVA p=0.08).and B: the southern wintering ground (ANOVA p=0.90), in relation to the ice extent in the west part of Baffin Bay (i.e. the "medium area" in Stern and Heide-Jørgensen (2003) during 1981-2008.