ABUNDANCE AND DISTRIBUTION OF LONG-FINNED PILOT WHALES, WHITE-BEAKED DOLPHINS AND HARBOUR PORPOISES IN WEST GREENLAND

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WHITE-BEAKED DOLPHINS

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ABSTRACT

Data on abundance and spatial distribution of species are increasingly being used for environmental impact assessments and for adjusting exploitation of species to sustainable levels. When monitoring population sizes and trends especially in large areas with somewhat hostile environments such as West Greenland, counting data is the essential component. But cetaceans spend a substantial part of their time submerged, hence undetectable for observers, adding to the difficulty of obtaining data and estimating true abundance and distribution patterns. Furthermore, the complexity of the marine environment makes it difficult to sample, interpret and understand the underlying mechanisms determining species distribution.

In this thesis the relative and absolute abundance estimates for long-finned pilot whales, white-beaked dolphins and harbour porpoises in West Greenland were produced from the data collected at an aerial survey targeting baleen whales in summer 2007. Results show that reliable estimates can be produced even though the design of the survey was not intended for small cetaceans. The spatial trends of abundance for each species was examined by means of a geographic information system and by density surface modelling of physical geographical variables obtained for the area. For the distribution, an actual examination of the significance of these variables explaining relationships between the presence and absence of whales still needs to be produced but the response curves found in this study indicate a clear segregation in habitat preference between the three species.

Improvements in data collection for future aerial surveys would be lowering the target altitude to ensure detection of small cetaceans and measure exact altitudes for each observation to obtain exact distances. Few observations were made of pilot whales which seemed to have a clumped distribution. Increased effort in this area by adaptive distance sampling would probably increase the number of observations and lower the variance caused by the encounter rate. For harbour porpoises, a greater sample effort in the fjords would probably increase the number of observations. The placement of acoustic dataloggers in strategic high density areas would also add to the knowledge of the annual abundance as well as the species' behaviour in the water column.

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INTRODUCTION

Abundance and distribution of species are important information in management biology when assessing status and risk of populations that are subject to any level of anthropogenic impacts (*Caughley and Sinclair 1994*). Data on abundance and spatial distribution are increasingly being used for environmental impact assessment and for adjusting exploitation to sustainable levels. For cetaceans, which are often sparsely dispersed over a large area, estimation of indirect or relative abundance acquires special techniques like distance sampling, photo studies with mark-recaptured animals or acoustic surveys. Distribution can sometimes be assessed based on opportunistic data, such as historical information or local knowledge but these data usually lack information on observer effort and are often biased towards the behaviour of the observers (*Teilmann and Dietz 1998*). In addition, most cetaceans are seasonal migrants, and their habitat preferences and seasonal occurrence in remote offshore areas can be difficult to establish (*Redfern et al 2006*). When managing whale stocks, it is of particular interest to know whether whales observed in different areas belong to one or several populations, but survey areas are typically determined by management goals rather than natural population boundaries (*Perrin et al 2002*). Obtaining a sufficiently large sample size of individual sightings is another concern, and this can be particularly difficult to obtain in cases of endangered or small subpopulations (*Williams and Thomas 2009*). Difficulties related to environmental factors, i.e. weather or logistical concerns not to mention the political and financial aspects are also to be taken into account when planning surveys for cetaceans. However when successful, large-scale offshore surveys of cetaceans can, under optimal conditions and with good analytical techniques provide both reliable abundance estimates and an unbiased picture of the distribution of species at a given time.

Development of techniques for surveying both small and large cetaceans has received a lot of attention and funding over the past 20 years (*nammco.no, iwcoffice.org*), and large cetaceans are managed under intense international supervision by the International Whaling Commission (IWC). No international agreement exists for small species of cetaceans inhabiting Greenlandic waters but Greenland has a need for assessing the sustainability of their harvest and to document the status of their living resources. Especially the exploitation of whale resources has been a subject of considerable controversy (*IWCoffice.org*). For these reasons, it has been the practise in Greenland for some years now to perform aerial surveys at regular intervals, aiming at obtaining abundance estimates of cetaceans based on various modification of line transect or distance sampling (*Buckland et al 2008*). The allocation of survey effort is largely based on local knowledge of hunters and previously obtained (sometimes opportunistic) data on distribution of whales.

Small cetaceans in Greenland

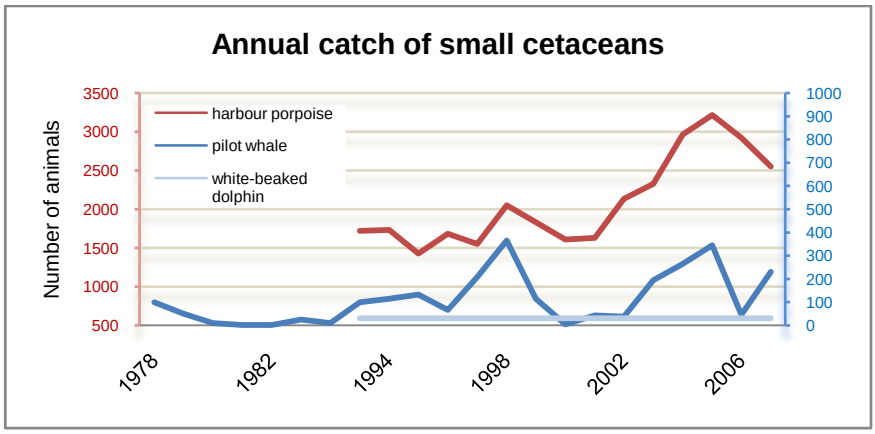
Estimating abundance of small cetaceans in Greenland has so far been concentrated on belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) because of management concerns since these two species are of high priority for the Inuit subsistence hunting (*Hertz and Kapel 1986*). The quotas set by the Home Ruling in Greenland rely, in theory, on the recommendations from the North Atlantic Marine Mammal Commission (NAMMCO) based on various elements of research where especially surveys conducted by the Greenland Institute of Natural Resources have played an important role.

Long-finned pilot whales (*Globicephala melas)*, white-beaked dolphins (*Lagenorhynchus albirostris)* and harbour porpoises (*Phocoena phocoena*) are hunted by locals for food consumption in Greenland but

nothing is known about stuck structure or abundance of these species in Greenlandic waters. Because of the active hunt, monitoring is necessary in order to evaluate safe catch limits. The three species migrate over longer distances and they are believed to visit West Greenland for shorter (or for harbour porpoises longer) periods mainly during spring-autumn. The rest of the year they are assumed to be part of larger populations in the North Atlantic (*Bloch et al 2003*). To assess the impact of hunting the removal of animals, rate of population growth and the approximate abundance are used to model different scenarios in order to evaluate the need for quotas to sustain the harvest (*Witting and Born 2005*).

Catch statistics of small cetaceans are based on historic archives, previous research and the Greenlandic Home Rule's report system which started proper registration in the early 1990s (Figure 1, *Teilmann and Dietz 1998, Ugarte F, Piniarneq 2010*). Since 1993 when proper registration began, approximately 150 pilot whales have been taken every year mainly between May and October from Qaqortoq in the south to Upernavik (72˚N) in the midwest. In contrast, little data for white-beaked dolphins exists but it is estimated that the annual catch is about 30 whales, taken mainly in South Greenland during summer (*Piniarneq 2010*). For harbour porpoises, catch statistics from 1900 to 1993 indicate an overall increase with an annual average take of 668 harbour porpoises (*Teilmann and Dietz 1998*), which for the last 10 years has increased to an average of 2200 animals, with 99% taken in West Greenland (*Piniarneq 2010*). Harbour porpoises are taken year round with a peak between April and November. In Greenland there is no system for reporting by-catches which should be counted as catches, although this is not mandatory (*NAMMCO 2008a*). The annual loss must therefore be considered as a minimum and the large magnitude of the harvest needs to be assessed in terms of its potential effects on the affected populations (Figure 1).

Figure 1



Annual catch of pilot whale, white-beaked dolphin and harbour porpoise from west Greenland during 1978 through 2007 (Piniarneq 2010)

Abundance and distribution of pilot whales, white-beaked dolphins and harbour porpoises in the North Atlantic

Long-finned pilot whale is an oceanic species that has its main distribution in offshore areas far away from land but it can also be found in coastal areas (picture 1). They live in groups of 10s to 100s, composed of individuals with close matrilineal associations, and they are widely distributed throughout the North and European Atlantic (*Buckland et al 1993, Perrin et al 2002, Carwadine 1995)*. There is no information whether pilot whales undertake extensive systematic seasonal migrations; however their distribution does change on a seasonal basis, correlating with movements of their principle prey squid (*Payne and Heinemann 1993*, *Gannon et al 1997*). While some reside permanently in- or offshore, others make inshore (summer and autumn) to offshore (winter and spring) migrations (*Carwadine 1995*). Around the Faroe Islands pilot whales occur all year round with a peak in abundance in July-September and tracking studies show a preference for the border of the continental shelf (*Bloch et al 2003*). Pilot whales have been the subject of a lot of research in the Faroese and the North-eastern Atlantic pilot whale subpopulation was estimated to 778,000 animals in 1993 (*Buckland et al 1993*). In Canada, an aerial survey in eastern Newfoundland and Labrador waters was conducted in 1980, estimating the relative abundance to 13,200 individuals (*Hay 1982*). Pilot whales are also abundant in the offshore waters of the north-eastern USA (*Nelson and Lien 1996*), where a sighting survey in 1995 gave an estimated abundance of 8,200 pilot whales in that area. In West Greenland, pilot whales sightings and catches are reported along the coast from Upernavik in Northwest to Qaqortoq in South Greenland between May and October (*Piniarneq 2010*).

White-beaked dolphin is the largest and most northerly member of the genus *Lagenorhynchus*, found throughout the North Atlantic in offshore waters distributed broadly between 40-70˚N from Canada to Norway (picture 2) (*Perrin et al 2002, Carwadine 1995*). In some areas, white-beaked dolphins make inshore-offshore or north-south movements with the seasons with summer residence mainly in inshore and northern areas of their distribution range. In other areas, such as Great Britain, they seem to be present all year round (but with seasonal peaks of abundance in coastal waters) (*Carwadine 1995*). A survey in the European Atlantic in 2005 provided an estimate of 22,600 white-beaked dolphins (*Hammond et al 2006*), but no current population estimates for the North Atlantic stock exists. The magnitude of the estimated abundance throughout its entire range is in the 100,000 animals (*Carwadine 1995*). In West Greenland, individuals are sighted year round along the coast from Disko Bay (limited by the ice edge) to the southern tip, but they are primarily caught during summer where there seems to be a peak in the abundance of sightings (*Piniarneq 2010*).

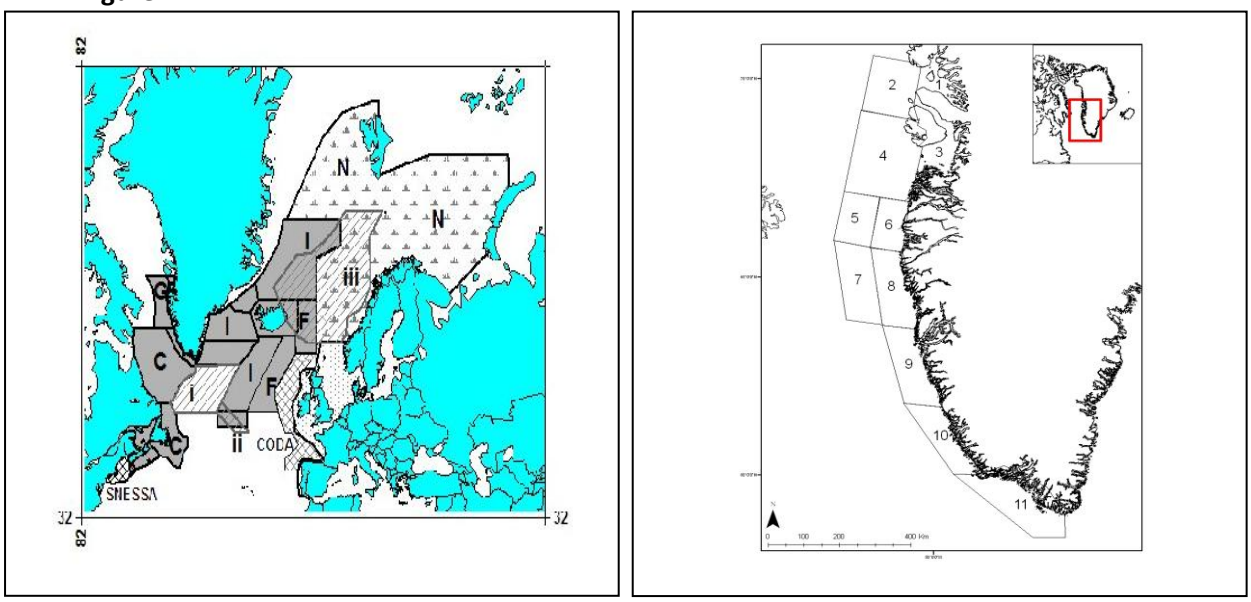
Harbour porpoises are among the smallest cetaceans in the world and they are widely distributed in coastal and continental shelf waters from Svalbard to Portugal across the North Atlantic (picture 3) (*Bjørge and Øien 1995, Andersen 2003, Jørgensen 2007, Hammond et*

al 2008). Movement across the Atlantic appears only to occur at a low level (*Rosel 1999*). Throughout their distribution, harbour porpoises are vulnerable to mortality in commercial gillnet fisheries and has been the subject of management initiatives in a number of areas (*Stenson 2003)*. The relative abundance has been estimated for selected portions of the region and at least 700,000 individuals are recognised as the likely magnitude of the North Atlantic population (*Hammond et al 2006, Angliss and Outlaw 2008, Stenson 2003, Waring et al 2009, Bjørge and Øien 1995*). In West Greenland they are abundantly found along the coast and fjord systems and are hunted throughout the year *(Teilmann and Dietz 1999, Piniarneq 2010*).

Objective

This thesis represents the first attempt to derive the summer abundance estimates and specify the distribution and habitat preferences of pilot whales, white-beaked dolphins and harbour porpoises in West Greenland. The data used was collected during a large-scale aerial line transect survey of cetaceans in August and September 2007 by the Greenland Institute of Natural Resources. This was the largest systematic effort to provide coverage for the West Greenland shelf area and the first survey that covered the entire coast from Midwest (69˚N) to South Greenland (59˚N) during the summer season (Figure 2b). The survey was a component of the multinational trans-North Atlantic Sighting Survey (T-NASS) organized by NAMMCO, providing a synoptic coverage of the whole North Atlantic from Canada to Norway between 40˚N and 80˚N (Figure 2a) (*NAMMCO* 2008b). Although the objective of the survey was to perform a precise count of the number of minke-, humpback- and fin whales off the banks in West Greenland, all sightings, including small cetaceans, were recorded. In the following two manuscripts I will develop abundance estimates for pilot whales, white-beaked dolphins and harbour porpoises (manuscript 1) and look at their spatial distribution and the variables that predict habitat preferences for these three species (manuscript 2).

Figure 2

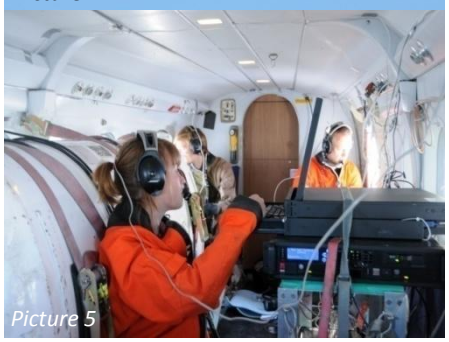


The planned Trans-North Atlantic Sighting Survey area (nammco.no) and the Greenlandic survey effort

Survey effort

The survey area was designed to cover the banks along the coast of West Greenland covering the area between the coast and offshore waters crossing the shelf break, i.e. the 200m contour line. The area was divided into 11 offshore strata from the coast to the shelf break (200 m depth curve) and 10 inshore strata covering 3 main fjord systems from 59N to 71N (Figure 2b), covering a total area of 200,900 km^2. The demarcations were designed based on sampling strategy to increase the chance of good weather in at least some strata during the survey period as well as the feasibility of covering the area. The boundaries of the strata were chosen to cover difference in bathymetry and a possible north-south gradient. Track lines in the offshore strata were oriented perpendicular to the shoreline and to the depth contour in an east-west direction except for strata 11 where the transect lines were north-south directed but still perpendicular to the depth contour. Ten track lines were set at 10 nautical miles apart to ensure a sufficient sample within each stratum and to avoid double counting of whales moving between transects. The track lines in the fjord systems were surveyed in a zigzag design. Due to the limited time (5 weeks) to cover this large area it was decided to collect the data by doing an aerial survey. Whales uses late summer in West Greenland to feed and movement must be considered random during the time of this survey. It was therefore assumed that during this period, the in- and outflux of animals on transects were constant across the survey area and that no directional movement would introduce a bias in the sampling design. Essentially, this implies that the probability of an animal moving towards a transect line is the same as the probability of an animal moving away from it.

Picture 4


Picture 5

The survey platform was a Twin Otter plane operated by Air Greenland flying at a target altitude of 700 feet (213 m) travelling at an average speed of 170 km per hour. The plane was equipped with two observation platforms, one in the front and one in the rear of the plane. Observations for cetaceans were conducted from bubble windows and were recorded and georeferenced onto a Redhen msDVRs system that also allowed for continuous video recording of the trackline as well as vertical digital photographic recordings. This made it possible for four observers to independently observe the track line at the same time. Survey conditions were recorded at the start of the transect lines and whenever a change in sea state, horizontal visibility and glare occurred, making it possible to extract the part of the track line lengths that had optimal survey conditions. A sighting was defined as an observation of one animal or a group of animals. An animal or group of animals was defined as an independent sighting if there were at least three full body lengths between the individuals. Declination angles to sightings (centre of groups) were recorded with Suunto inclinometers when the animals became abeam and the exact angles noted. To diminish observer fatigue, each observed transect line was followed by a ten minute break. The audio and video channels were subsequently analyzed each night using the software program Mediamapper (*redhensystems.com*) and sightings and effort collected and stored.

ABUNDANCE OF LONG-FINNED PILOT WHALES (*GLOBICEPHALA MELAS*), WHITE-BEAKED DOLPHINS (*LAGENORHYNCHUS ALBIROSTRIS*) AND HARBOUR PORPOISES (*PHOCOENA PHOCOENA*) IN WEST GREENLAND

Abstract

An aerial line transect survey conducted off West Greenland during summer 2007 was used to estimate the abundance of long-finned pilot whales (*Globicephala melas*), white-beaked dolphins (*Lagenorhynchus albirostris*) and harbour porpoises (*Phocoena phocoena*). A total of 17, 62 and 35 sightings respectively were collected during 9,433 km of survey effort in sea states <5. Based on conventional and mark-recapture techniques correcting for perception bias, an abundance estimate for each species was found. To accommodate the negative bias for submerged animals during passage of the plane, an availability correction factor for time spend at the surface was applied. This increased the abundance for long-finned pilot whales to 7,440 animals (95% CI 3,014-18,367), white-beaked dolphins to 11,801 animals (95% CI 7,562-18,416) and harbour porpoises to 33,271 animals (95% CI 15,939-69,450). These abundance estimates are the first obtained from West Greenland.

Introduction

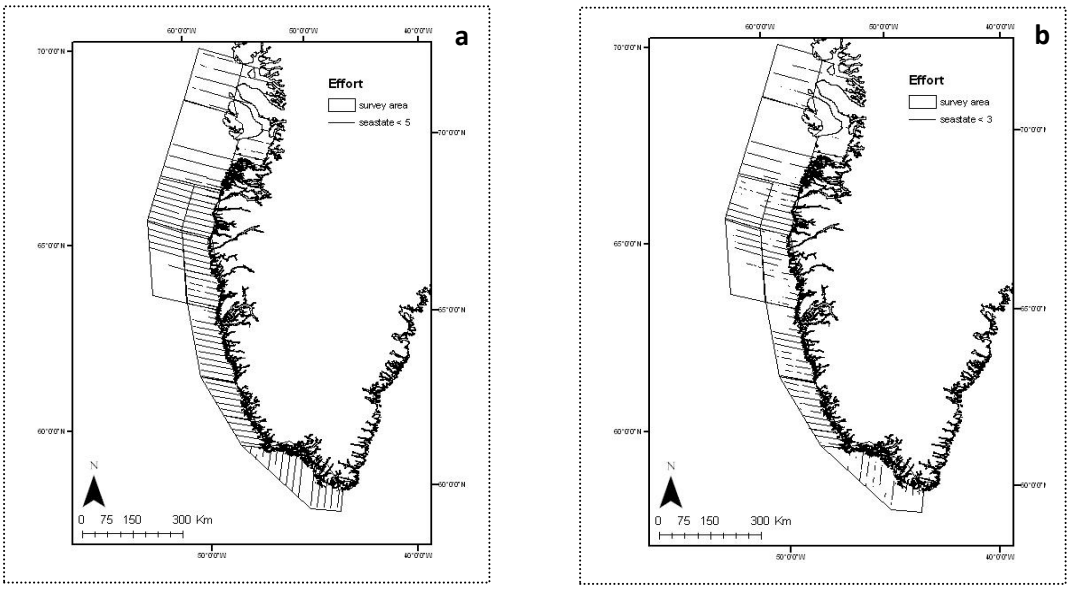
Obtaining abundance estimates of sparsely distributed and migrating cetaceans can be a challenge. In West Greenland, where feeding areas for cetaceans are scattered along and several hundred kilometres off the coast, the total area that needs to be sampled in order to obtain robust abundance estimates is very large. Distance line-transect sampling is at present the most widely used technique for estimating the abundance of cetaceans (*Buckland et al 2008*). It answers the question: given the detection of *n* animals, how many animals are estimated to occur within the sampled area (*N*). In practice, a set of randomly placed (regularly spaced) transect lines are established representing a random sample of all habitat area in the survey area. Because lines are assumed to be placed at random with respect to the location of animals, one can avoid the assumption that animals are uniformly distributed throughout the area. These lines are then traversed by one or more observers, who collect exact perpendicular distances from the track line to the animals. The theory assumes 100% detection on or very close to the track line but allows for detectability to decrease with increasing distance from the transect line and for some objects to go undetected. The key to distance sampling analyses is then to fit a detection function to the observed distances, and use this fitted function to estimate the proportion of animals missed by the observer. From this, estimates of density and abundance of animals in the survey area can be obtained (*Buckland et al 2008*). The development of the software program "Distance" has made it user-friendly for biologist around the world to design and analyze distance sampling surveys in a standardized way in order to obtain reliable density and robust abundance estimates (*Thomas et al 2010*). The advantages of distance sampling for cetaceans are among others that estimates can be generated on a relatively small sample size and the direction and magnitude of biases can be quantified. Therefore, distance sampling is a particularly appropriate tool since the basic assumptions

(that animals are distributed independently of the line and that all animals on the line are detected) can be met when doing ship or aerial surveys covering large areas (*Buckland et al 2008*).

Analysis methods

The search method for cetaceans used an independent observer configuration where platform 1 (front seat observers) and 2 (rear seat observers) acted independently (both visually and audible) of each other. Detections of animals by platform 1 served as a set of binary trials in which a success (duplicate) corresponded to a detection of the same animal or group by platform 2 and vice versa (*Buckland et al 2007*). Analysis of the detection histories using logistic regression allows for 'the probability that an animal on the track line is detected by an observer' to be estimated. Thus, abundance can be estimated without the assumption that all animals on the track line are detected (assumption of $g(0)= 1$) (*Buckland et al 2007, Borchers et al 2006, Laake et al 2007*). The declination angles were converted to perpendicular distance of the animal from the track line. Together with the altitude of the plane, these distances were used to model the detection probability and the encounter rate, i.e. the expected number of animals detected per linear kilometre (*Buckland et al 2008*). Animals or groups of animals seen by both platforms (called duplicates) were determined by the coincidence of timing, distance from trackline and group size. If there was a difference in recorded measurements, the average distance and/or group size was used. It should be noted that the average flying altitude and not the altitude at each individual sighting was used to calculate the distances to the animals. This might introduce a bias and violate one of the three main rules in distance sampling – that distances should be measured accurately. The estimated density of animals in the region was found by the estimated encounter rate divided by the estimated detection probability, scaled appropriately by the surveyed areas (*Buckland et al 2008*). To stratify the estimated densities, the geographic areas (strata) were used since it was assumed that there were similar densities on lines surveyed and lines not surveyed within each stratum (Figure 2 and 3).

Figure 3



*The realized survey effort from the 2007 West Greenland aerial survey showing strata 1-11 and lines flown in Beaufort sea state less than 5 (**a**) and sea state less than 3 (**b**)*

Perception bias

The survey design allowed for multiple-covariate conventional distance sampling (MCDS), where it is assumed that animals directly on the track line are detected with certainty and that detection probability decreases smoothly as distance increases, due to heterogeneity in the sighting process. Covariates that introduce this heterogeneity include distance from trackline, sea state, glare, group size and observer performance. This survey approach also allowed for mark-recapture distance sampling (MRDS), which relaxes the assumption of certain detection at zero distance (*Buckland et al 2007*). Both methods are design based as the abundance estimates from them rely on the survey design to provide a representative sample (equal coverage probability) within each stratum. Global detection functions for the three species' full data sets were used. Whenever data allowed, estimates of abundance were calculated for each stratum with the correction for animals missed by the observers using MRDS methods, i.e. the perception bias could be calculated. MRDS methods require an adequate sample size of duplicate sightings for fitting a detection function and for some species there were too few duplicate sightings. Instead data from both platforms were combined, one of each duplicate sighting removed, to create a dataset of unique sightings. These data were then analysed using MCDS methods. All data were analysed by Distance Software 6.0 (*Thomas et al 2010*).

Availability bias

A complication associated with sampling of cetacean populations is that they spend some of their time under water invisible to observers. Depending on the species, a proportion of the whales are submerged during the passage of the plane, reducing the probability of detection. In order to account for this negative bias, the derived abundance estimates were corrected for availability bias using known surface times obtained from telemetry studies of the three species (Table 1) (*Heide-Jørgensen et al 2002, Rasmussen M et al 2007, Teilmann et al 2007*). A corrected abundance (denoted by the subscript 'c') was estimated by

$$\widehat{N}_c = \widehat{N} / \hat{\alpha} \qquad \text{[Formula 1]}$$

where $\hat{\alpha}$ is the availability correction factor i.e. proportion of time an animal is potentially available at the surface to be seen by the observers. The coefficient of variation (*cv*) calculated as the standard error in proportion to the mean is then (*Heide-Jørgensen pers.comm.*)

$$cv(\widehat{N}_c) = \sqrt{cv(\widehat{N})^2 + cv(\hat{\alpha})^2} \qquad \text{[Formula 2]}$$

The log-normal 95% confidence intervals are subsequently recalculated as
Lower confidence interval limit= *N/C*
Upper confidence interval limit= *N*C*

$$\text{Where } C = exp[z_\alpha * \sqrt{1 + \left\{log_e \left(\frac{varN}{N^2}\right)\right\}}] \qquad \text{[Formula 3]}$$

Table 1

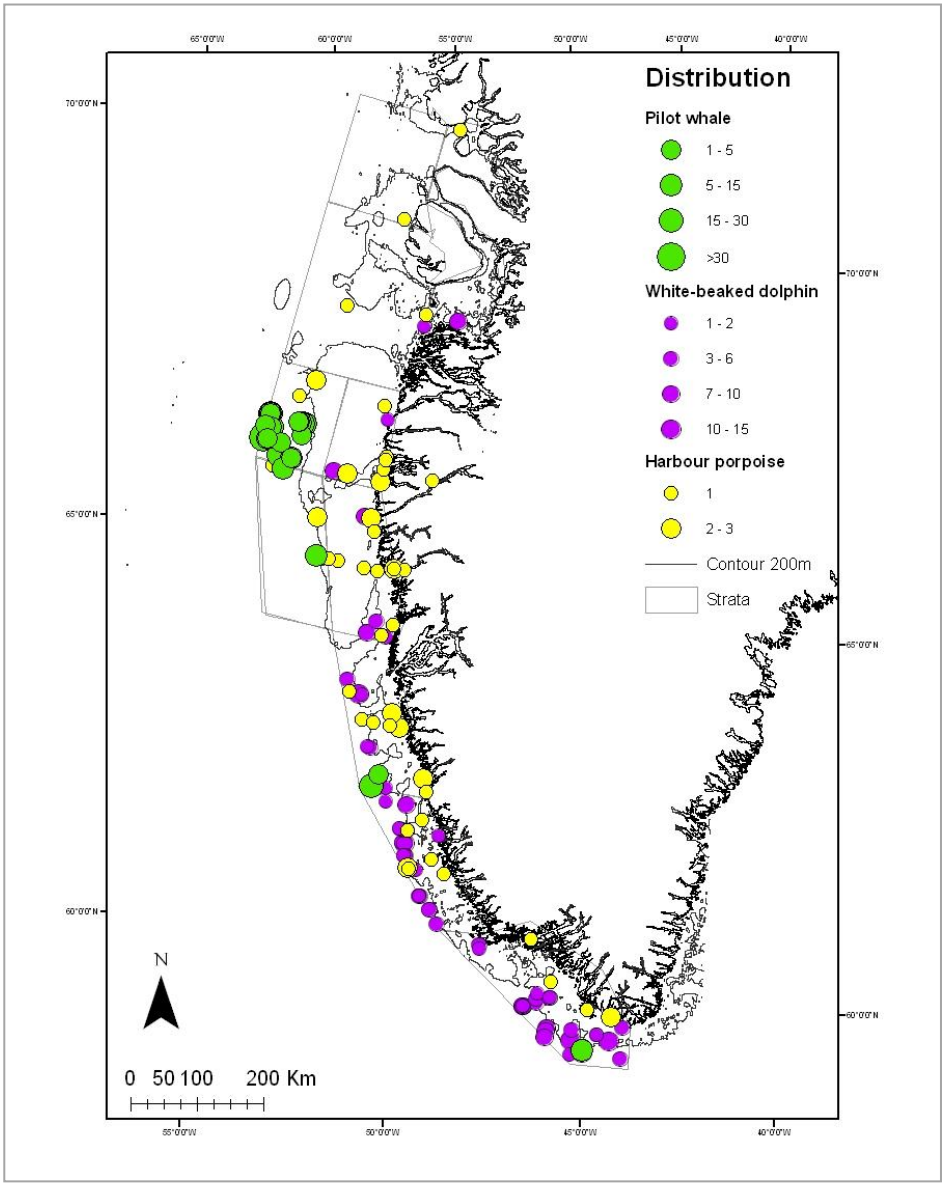
Species	Geographic area of instrumentation	Number of animals	Percentage of time spend at surface [cv]	Submerged in water column (meter)
Pilot whale	Faroe Islands	3	40 [0.15]	0-7
White-beaked dolphin	Iceland	1	82 [-]	0-2
Harbour porpoise	Denmark	3	31 [0.17]	0-1

Geographic areas where animals have been instrumented with satellite transmitters showing the average time spend at the surface during daytime. Coefficient of variation in brackets.

Results

Nine cetacean species were recorded during the survey, including long-finned pilot whale, white-beaked dolphin and harbour porpoise. The survey region and track lines are shown in figure 3 and the distribution and group sizes of animals in figure 4. The search effort is given in appendix 1. A total of 9,433 km of track lines were flown (8,631 km offshore and 802 km inshore) in Beaufort sea states less than 5 and of these 6,098 km were flown in sea states less than 3. The total search time was 56 hours. Weather conditions during the summer of 2007 were generally good, except for the northern area around Disko Island (strata 1-4) and stratum 11 in South Greenland which had relatively poor conditions, reducing the time available for surveying. Nevertheless, 9,433 km of survey effort was achieved, enabling abundance estimates to be calculated. For pilot whale and white-beaked dolphin data collected during sea state 0-4 were used whereas only data for sea state 0-2 were used for harbour porpoise. The reduced effort for harbour porpoises was chosen because the visual detection can only reliably be maintained in fairly calm waters (*Hammond et al 2006*). All sightings of pilot whales and white-beaked dolphins were in strata 5 to 11, with pilot whales primarily detected in offshore areas and white-beaked dolphins on the banks in south Greenland. Harbour porpoises were widely distributed throughout the covered area including several fjords (Appendix 1). In total there were 17, 62 and 35 individual sightings of pilot whale, white-beaked dolphin and harbour porpoise respectively to be used in the analysis. Both single and double platform analyses were carried out for all three species using MCDS and MRDS methods. For all models, it was decided to stratify the data by the same geographic region as used in the survey design thus estimating the encounter rate and density, and hence the abundance per strata. Truncation of perpendicular distance was necessary for white-beaked dolphins and harbour porpoise in order to fit a reliable detection function in the MCDS models. Several explanatory covariates were explored in addition to perpendicular distance for all three species.

Figure 4



Distribution of pilot whales, white-beaked dolphin and harbour porpoise in survey area showing the 200 m depth curve indicating the start of the shelf edge

Detection functions for the MCDS and MRDS analyses

To fit the MCDS detection functions both hazard rate, half normal and uniform functional forms with various number of cosine adjustment were considered. The explanatory variables available to include in both MCDS and MRDS models were, in addition to perpendicular distance, pod size and Beaufort sea state (as a factor variable with 3 levels for pilot whales and white-beaked dolphins; 2 levels for harbour porpoise), side of plane and observer platform (2 levels). The final models were chosen on the basis of goodness of fit tests as well as the overall variance of object density and finally weighted using Akaike's information criteria (AIC). For the MRDS models, the estimates of the probability of detecting an animal on the track line g(0) by each observer and both platforms combined are given in Table 2.

Table 2

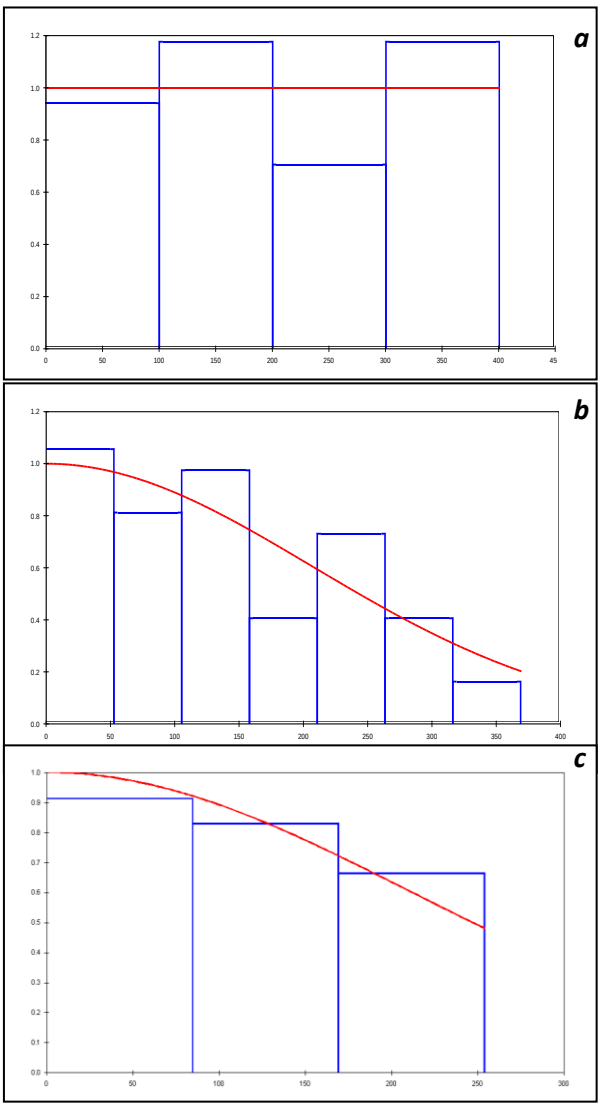
Species	Observer 1	Observer 2	Combined
Pilot whale	0.90 [0.11]	0.90 [0.11]	0.99 [0.02]
White-beaked dolphin	0.88 [0.09]	0.79 [0.10]	0.98 [0.02]
Harbour porpoise	0.35 [0.28]	0.35 [0.28]	0.57 [0.23]

Estimates of the probability of detection on the trackline g(0) by each observer platform and platforms combined. The estimates are obtained using the best MRDS model for each species. The coefficients of variation are given in brackets

For pilot whales, both the MCDS model and the MRDS model were fitted to the data without truncation (17 sightings – 12 duplicates) and they both show the detection probability being constant out to a perpendicular distance of 400 m. The final MCDS model chosen was a uniform function and hence the data was treated as a strip census with an equal probability of detection in an effective strip width of 400 m (Figure 5a). In the overall variance for density, the encounter rate accounted for 81%, probability of detection for 12% and group size for 7%. For the MRDS model, different explanatory variables were tested both in the MR and DS model but based on goodness of fit tests and lowest AIC the simplest (uniform) model was chosen (Figure 6a and Appendix 2).

For white-beaked dolphin, the distance data were truncated at 10% (370 m) for the conventional DS analysis which left 56 sightings for analysis. The final MCDS model included a term for side, indicating that observers on the left side of the plane had a more uniform distribution of perpendicular distances from the track line. Including side as a factor resulted in only a small reduction in AIC compared to the simpler model of perpendicular distance only, and so the simpler model (with a halfnormal key) was chosen (Figure 5b). The biggest component in the variance of density was the encounter rate (78%) whereas the probability of detection and cluster size each contributed 11%. In the MRDS analysis, the data were not truncated (62 sightings – 35 duplicates). The final MRDS model included a term for observer in the MR model (Figure 6b and Appendix 2). This indicated that platform 2 had

Figure 5

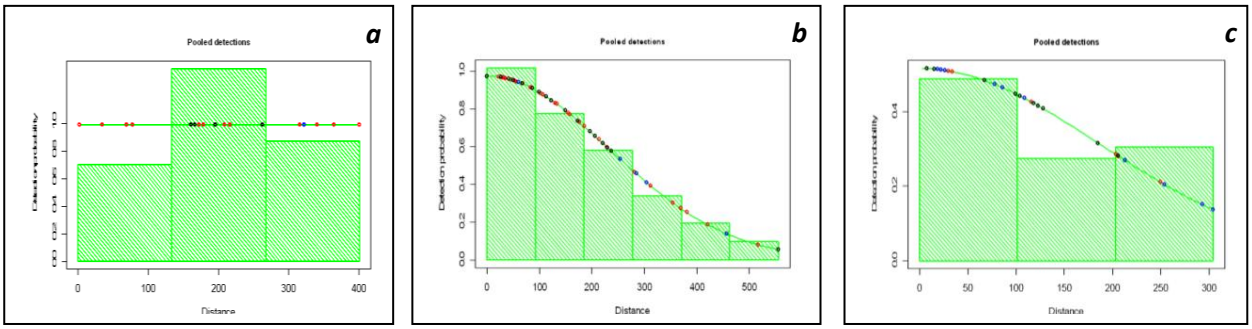


*Perpendicular distance distribution (blue bars) and fitted detection probability model (red line) fitted using CDS methodology for pilot whale (**a**), white-beaked dolphin (**b**) and harbour porpoise (**c**). Perpendicular distance (m) is plotted on the x-axis and probability of detection on the y-axis*

a smaller probability of detection on the track line than platform 1.

Harbour porpoise is a difficult animal to detect, but two of the observers, both sitting in the same side of the plane, were specially trained for harbour porpoise surveys. This was evident in the data, since this observer team shared almost all detections between them. When using only data from this side, the effort was halved and 31 sightings (7 duplicates) were left for analysis. In the MCDS model, the simplest halfnormal key model gave the best fit (figure 5c), with the encounter rate contributing 95%, probability of detection and group size with 4% and 1% respectively to the variance of density. Post-stratifying per sea state was also considered but yielded similar results as the stratification per geographic stratum, and the latter was then chosen for making comparison with the other two species possible. For harbour porpoise, the detection probability on the track line was well below one (Table 2) and so the probability of 1/*g*(0)= 1/0.57 (*cv*= 0.23) = 1.75 was used to correct the abundance estimate for the perception bias by $D_{Corrected}$= D*1.75 (Table 3). The corrected coefficient of variation was estimated by using Formula 2. For the MRDS model, different explanatory variables were tested both in the MR and DS model. Based on goodness of fit tests and AIC the best model took group size into account, indicating that the larger the group, the easier it was to detect. The difference in AIC between this and the simplest model was below 2, and therefore the simplest model (half normal key) was chosen (Figure 6c and Appendix 2).

Figure 6



*Pooled detection function plots for the MRDS analyses for pilot whale (**a**), white-beaked dolphin (**b**) and harbour porpoise (**c**). The points are the probability of detection for each sighting given its perpendicular distance; the line is a smooth function fitted to the points. Perpendicular distance in meters is plotted on the x-axis and probability of detection on the y-axis.*

Density and abundance estimates

A key assumption of conventional distance sampling (CDS) methodology is that observers detect all animals occurring on the track line (denoted as *g*(0)= 1). In this survey the mark-recapture approach was used to design the survey. Because of the double platform design, detection on the track line could be estimated, implying that abundance could be estimated without assuming that *g*(0)= 1 (Table 2). However, this method of analysis depends on obtaining a sufficient number of duplicate sightings to allow for estimation of the parameters in the fitted models. The present survey had few sightings from all three species, but both MCDS and the MRDS estimates are presented. Due to low sample size of pilot whales and the fact that *g*(0) can be assumed close to one the DS estimate is chosen. For white-beaked dolphin, *g*(0) is also close to one. Because the MR model included a term for side, the DS estimate was chosen, since this model takes pooling robustness into account (*Buckland et al 2007*). For harbour porpoise, *g*(0) was well below one and

therefore only the MRDS estimate was chosen even though the number of duplicates was low. When comparing the MCDS estimate corrected for perception bias, these two are in the same order of magnitude. Estimates of density and abundance obtained using both MCDS and MRDS methods are given in Table 3.

Table 3

Method	*Species*	*Esw (meter)*	*N_G Pod*	*n/L (pods/km)*	*E[s] pod size*	*D_G, (pods/km2)*	*D (animals/km2)*	*N (animals)*
MRDS	Pilot whale		462.9 [0.41]		7.03	0.002 [0.41]	0.015 [0.38]	3,253 [0.38]
	White-beaked dolphin		2096 [0.18]		4.69	0.009 [0.18]	0.044 [0.19]	9,827 [0.19]
	Harbour porpoise		7843 [0.35]		1.32	0.036 [0.35]	0.047 [0.35]	10,314 [0.35]
MCDS	Pilot whale	400 [0.27]		0.0051 [0.74]	6.5 [0.21]	0.002 [0.49]	0.013 [0.54]	2,976 [0.54]
	White-beaked dolphin	240 [0.12]		0.0135 [0.44]	4.53 [0.10]	0.009 [0.20]	0.044 [0.23]	9,677 [0.23]
	Harbour porpoise	203 [0.17]		0.0414 [0.84]	1.31	0.021 [0.28]	0.027 [0.29]	6,043 [0.29]
	Harbour porpoise $_{Corrected}$							10,602 [0.37]

Abundance estimates using DS and MRDS methodology showing the effective strip width (esw), encounter rate (n/L) and estimates for pod abundance N_G, pod size E[s], pod density D_G, animal density D and animal abundance N. Note that (n/L) and D_G is an average for only the strata where animals were seen. The coefficients of variation (cv) are given in brackets

Point estimates corrected for availability bias

For pilot whales, the at-surface abundance was estimated to 3,253 animals (*cv*= 0.38) using MRDS methods. When ignoring the 1% bias for *g*(0) of 0.99 derived from the MRDS model. The more robust MCDS model of 2,976 animals (*cv*= 0.46) was chosen. By using formula 1-3, the correction of the at-surface abundance with the availability factor (40%, *cv*= 0.15) increases the absolute abundance of pilot whales to 7,440 animals (*cv*= 0.49) (Table 4).

For white-beaked dolphin, the at-surface abundance was estimated to 9,827 animals (*cv*= 0.19) using MRDS methods. Again, the 3% bias for *g*(0) of 0.97 derived from the MRDS model was ignored, and the abundance estimate from the MCDS model of 9,677 animals (*cv*= 0.23) was used. Correction of the at-surface abundance with the availability factor (82%, *cv*= 0) increased the absolute abundance of white-beaked dolphins to 11,801 animals (*cv*= 0.23) (Table 4).

For harbour porpoise, the density per square kilometre in the inshore strata (fjord systems) was much higher (*D*= 0.19) than the offshore strata (*D*= 0.042). The total density of the strata where animals were present was 0.047 animals and so the total surface abundance was estimated to 10,314 animals (*cv*= 0.35).

Table 4

Species	Relative abundance		Absolute abundance	
	CDS	MRDS	Corrected	95% $CI_{corrected}$
Pilot whale	2,976 [0.46]	3,253 [0.38]	7,440 [0.49]	3,014 – 18,367
White-beaked dolphin	9,677 [0.23]	9,827 [0.19]	11,801 [0.23]	7,562 – 18,416
Harbour porpoise	10,602 [0.29]	10,314 [0.35]	33,271 [0.39]	15,939 – 69,450

Abundance estimates using DS and MRDS methodology corrected for availability bias with the associated 95% confidence intervals (CI). The coefficient of variation (cv) is shown in brackets. Numbers in black are the estimates used for the availability correction

Correction of the at-surface abundance with the availability factor (31%, cv= 0.17) increased the absolute abundance of harbour porpoises to 33,271 animals (*cv*= 0.39) (Table 4).

Discussion

The marine environment in West Greenland is a heterogeneous, three-dimensional environment that is influenced by numerous factors including topography, sea ice cover and nutrient availability. These factors vary not only in space but also in time over short and long terms, setting the boundaries for cetaceans' habitat utilization. Hunting statistics indicate that pilot whales, white-beaked dolphins and harbour porpoises are most abundant throughout the summer although this could also be due to a change in the hunters' behaviour, not the animals'. Still, what is known of the seasonal and even daily movement of these species from different other parts of the Atlantic, they would likely be encountered at different rates throughout the year if one were to survey the covered area in different seasons (*Bloch et al 2003, Rasmussen et al 2007, Hammond et al 2006, Teilmann et al 2007*).

Densities and relative abundance estimates exist for some of the species in parts of the North Atlantic but this thesis represents the first attempt to derive summer abundance estimates from West Greenland. Prior to this study only limited information was available regarding the distribution and abundance of these species in Greenlandic waters. The present survey indicates that the three species were not uniformly distributed throughout the region during the summer of 2007 and that they use some areas more than others. This patchiness has interesting implications both in regard to the biology and ecology of West Greenlandic subpopulations and to the management of assigning quotas to the different districts.

Pilot whales

From the surveys conducted in the Eastern North Atlantic in 1987-89, a density of 0.066 (*cv*= 0.36) (1987) and 0.35 (*cv*= 0.359) (1989) animals/km^2 were found (*Buckland et al 1993*). In West Greenland, the density for pilot whales was 0.015 (*cv*= 0.38) and somewhat lower than the density found around Iceland and the Faroese in summer. This indicates that the eastern North Atlantic subpopulation might congregate at higher densities at the feeding areas. But, the West Greenland survey did not cover the entire summer distribution range of pilot whales as the surveys in Eastern North Atlantic did and the topographical coverage was also different between the two survey areas. The coverage in the East Atlantic surveys was largely over deep waters and over the continental shelf around Iceland and the Faroese, a habitat that is believed to be preferred by pilot whales (*Payne and Heinemann 1993, Heide-Jørgensen et al 2002*). In this survey, western boundaries were approximately the 500 m depth curve, and so just on the outer side of the major slopes. That these outer bounds of the off shore areas are preferred habitat for pilot whales was evident from the many observations both on and off effort between transects at the western border of the strata (Figure 4). Also several observations were made in this area in a dedicated seabird survey from September 2009 covering Baffin Bay from Greenland to Canada (Figure 4, Appendix 3, pers.obs.). This indicates, that the density and hence abundance, might reveal more accurate estimates if waters further west were included or if an adaptive distance sampling approach was implemented.

The relative abundance estimate was corrected for availability bias to an absolute abundance of 7,440 animals (*cv*= 0.49, 95% CI: 3,014-18,367). Using diving times from areas outside of Greenland and for only

three animals is of course not ideal, but it may not necessarily change the abundance significantly since the large variance from the corrections applied should cover the biological range of correction factors. For pilot whales the surface time from the three individuals was used to correct the availability of pods/groups (i.e. the detection unit), assuming a high degree of diving synchrony within the pods. Since all sightings were groups of more than one individual, this might cause an overestimation of the availability correction factor. This assumption is, however, somehow alleviated by using a surface layer of 6 m below which the entire pod is likely to be submerged.

White-beaked dolphin

The density found in West Greenland is 0.044 animals/km^2 (*cv*= 0.23) compared to the density of 0.023 (*cv*= 0.42) in the European Atlantic (*Hammond et al 2006*). The density for West Greenland is somewhat higher but still within the same range. The only white-beaked dolphin ever to be tagged with a satellite transmitter is from an experiment conducted in Icelandic waters (*Rasmussen et al 2007*). Since there is no variation in the dive patterns, it makes the availability correction factor of 82% a bit uncertain. Other studies of dolphins with similar habitat preferences show average times spend at surface between 89% (spotted dolphin (*Baird et al 2000*)) and 99% (risso's dolphin (*Wells et al 2009*)). Compared to these studies as well as personal conversations with white-beaked dolphin researchers, the at-surface time of 82% seems reasonable (*Lawson J and Rasmussen M*).

Harbour porpoise

There was a significantly higher density of animals in inshore areas compared to offshore strata (between 0 and 0.19 animals/km^2), which is similar, although somewhat lower compared to estimates reported from the coast of California-Washington ranging from 0.03 to 2.8 animals/km^2 (*Barlow 1988*) and 0.009 to 1.016 animals/km^2 in the Baltic Sea (*Scheidat et al 2008*). Harbour porpoises are small, with no visible conspicuous blow or splash, and occur in groups of only a few animals (mean group size 1.32; 1.29 from *Hammond et al 2006*). This makes harbour porpoises a difficult animal to survey, both from plane and ship (*Hammond et al 2006, Barlow 1988*), which is also evident in the number of animals missed on the trackline by the observers – 33% in this study (Table 2, Appendix 2), and similar probability is found in other studies (*Barlow 1988*). Because this survey made it possible to analyse the data with MRDS methods, it was possible to correct for the perception bias in the MCDS model. The estimate of abundance in West Greenland was 10,602 [*cv*= 0.29] from the MCDS analysis compared to 10,314 [*cv*= 0.35] from the MRDS and not significantly different. Because one of the three main assumptions in distance sampling is 100% detection of animals on the track line, the MRDS estimate was chosen so not to violate this assumption. The relative abundance estimate was 10,314 (*cv*= 0.35) animals, and this number was about 10 times smaller than what was found in an aerial survey from the European Atlantic (area 1.5 times larger) (*Hammond et al 2006*). A reason for this lower density and abundance in West Greenland could be the difference in design. Where this survey in West Greenland covers the waters over the continental shelf or app. out to 1000 m depth, the survey mentioned only covered the immediate offshore waters from the coastlines. Since harbour porpoise are mainly found over relatively shallow depths, the survey in West Greenland was likely to yield more accurate estimates of density and abundance, if the survey concentrated more on the inshore and immediate off shore areas. But this survey seemed to cover the northern distribution of this species, and hence the animals would occur at lower density than in the centre of this subpopulation's distribution range. The availability correction factor was not from Greenlandic waters, and the transmitters were applied to animals using a shallow water habitat in Denmark (*Teilmann*

et al 2007). Since harbour porpoises are also found over deep waters in West Greenland, they might spend more time diving to the bottom for feeding. The availability correction factor then might be too low and the absolute abundance estimate of 33,271 animals (*cv*= 0.39, 95% CI: 15,939-69,450) would then be an underestimation.

Conclusion

Aerial surveys are very effective regarding coverage of large areas, but not ideal in areas of low density. Instead, shipboard surveys might yield more accurate estimates of density and abundance since they allow for using additional acoustic devices such as towed hydrophones which will increase the chance of detecting (submerged) cetaceans. Since this survey only gives a snapshot of the abundance and distribution of the three species it would be interesting to perform additional research at other times of the year so as to investigate any seasonal changes. This could be achieved by passive acoustic monitoring which provide a more continuous record of animals over long periods of time. Behavioural and satellite tracking studies would also increase the understanding of the animals' biology and ecology at different times during the day and the season. This would all help to increase the understanding of the temporal and spatial use of Greenlandic waters for these species and to provide a better platform for future survey design. Better data from the time and area where the survey was conducted is of course preferable, although hard (and expensive) to obtain. The MCDS and MRDS models provided estimates of abundance for predetermined survey strata with equal coverage probability but provided no information on density at a finer spatial resolution. For this, one would have to define covariates for predicting density in the surveyed strips and extend that to the whole survey area.

Although this survey was primarily designed for baleen whales, it still covered the peak season for the hunting and occurrence of pilot whales, white-beaked dolphins and harbour porpoises. It did however not cover the entire distribution of these whales in Greenlandic waters as some areas off Disko Bay, believed to be suitable habitat for pilot whales, were not surveyed due to bad weather. Also, some areas in mid-west Greenland were only surveyed in sea states between 3 and 5 which are unsuitable conditions for detecting harbour porpoises (Figure 3). Furthermore, the waters adjacent to West Greenlandic waters were not surveyed and for pilot whales, that live primarily in deeper waters, this survey design did not cover the outer boundaries for the species range. The fjord systems (inshore waters) were a low priority in this survey, but actually the fjords are places where the hunters catch a substantial part of the annual take of harbour porpoises. The target altitude of 700 feet was perhaps above the preferred altitude for small cetaceans and especially for a specific harbour porpoise survey (*Hammond et al 2006*). In the case of estimating group size, only baleen whales encountered in groups were further investigated, and so the group size estimates made by the observers for small cetaceans might be biased. Therefore the average group size estimates for duplicate sightings was used instead of using the group size from either individual observer. Although it could be argued that in some sightings one observer might have sighted the group far ahead and had more time to investigate it, the majority of sightings were made shortly before the animals became abeam. For these reasons, the densities and abundance estimates presented here must be considered minimum estimates. To assess the current impact of hunting, the abundance estimates derived from this thesis is a first step but more information on population dynamics, life history, distribution and preference habitat is needed.

DISTRIBUTION AND SPATIAL TRENDS IN THE ABUNDANCE OF LONG-FINNED PILOT WHALES (*GLOBICEPHALA MELAS*), WHITE-BEAKED DOLPHINS (*LAGENORHYNCHUS ALBIROSTRIS*) AND HARBOUR PORPOISES (*PHOCOENA PHOCOENA*) IN WEST GREENLAND

Abstract

An aerial line transect survey conducted off West Greenland during summer 2007 was used to produce spatial models fitted to the line transect data. Based on density surface modelling methods, a count model with a generalized additive model (GAM) formulation was used to relate the abundance of long-finned pilot whales (*Globicephala melas*), white-beaked dolphins (*Lagenorhynchus albirostris*) and harbour porpoises (*Phocoena phocoena*) to spatial variables obtained by a geographic information system (GIS). The variables used to describe patterns in the distribution and spatial trends in the abundance were latitude, distance to the nearest coastline, depth and slope. Response curves indicated that the preferred habitats were deep water offshore areas in Northwest Greenland for pilot whales, deep water over steep seabed slope areas in South Greenland for white-beaked dolphins and relatively shallow inshore waters in Midwest-South Greenland for harbour porpoises. Kruskal-Wallis tests showed significant differences in distribution for all species with respect to depth and distance to coast. The results presented here are to be used in producing prediction maps of density for the whole survey area and in further investigations into variables affecting the species' presence and absence in West Greenland.

Introduction

The shelves of the Arctic contain some of the most productive and tightly connected physical-biological systems in the marine environment (*Laidre et al 2010*). In West Greenland, these domains are shallow and they play an important role in inflow and outflow from the Arctic Ocean and in energy transfer through the ecosystem (*Carmack and Wassmann 2006*). This is based partly upon continuous biomass advection as well as high nutrient content of Atlantic waters causing large biomass concentrations (*Laidre et al 2004*). When the annual sea ice cover retreats in spring it triggers an enormous bloom of primary production on the shelves, attracting high densities of lower trophic level forage fish and zooplankton (*Heide-Jørgensen et al 2007*). Ultimately this culminates in large numbers of top marine predators. Among the cetacean species moving in from the Atlantic Ocean are the pilot whale and white-beaked dolphin while harbour porpoise can be found and are caught by local hunters throughout the year although they might occur in larger numbers during summer (*Carwadine 1995, Piniarneq 2010*).

Mammals often choose habitats that offer the greatest fitness and consequently habitat utilization is often assumed to reflect the quality and abundance of resources in an area (*Gregr and Trites 2001*). It is interesting to quantify the relationship between habitat features and habitat use of top predators for greater insight into the processes characterizing important foraging regions. Seasonal and annual variation in prey densities might play a role in the aggregation and foraging success of pilot whales, white-beaked

dolphins and harbour porpoises in West Greenland. Of the three species, only harbour porpoises have been the subject of research in Greenland and prey species targeted by pilot whales and white-beaked dolphin in the North Atlantic are known only for the Faroese Islands and Great Britain, respectively (*Teilmann and Dietz 1998, Desportes and Mouritsen 1993, Canning et al 2008*). In addition, few data are available on the densities and spatial forage fish in West Greenland presumably targeted by these species. With little knowledge of the prey distribution, environmental factors such as water temperature, depth and slope can be used instead as proxies for prey distribution. Then presence of whales associated with these variables might indicate the quality and abundance of these prey resources.

Ideally quantifying habitat selection should require knowledge of both an individual's location in space and time and a measure of the individual's activity (*Laidre et al 2004*). The spatial and temporal distributions of pilot whales, white-beaked dolphins and harbour porpoises in West Greenland have not been subject to dedicated research in the past and the annual hunting records give only an indication of the species' temporal distribution along the coast (Piniarneq 2010). No behavioural studies have been carried out in West Greenland with regards to the three species and this survey offers only a snapshot of the distribution of individuals. Since this survey was carried out at a time of year where the whales are believed to feed in the area, critical habitat could be expected to include feeding areas and not necessarily migration routes.

Regression is one of the most commonly used techniques to model the relationship between cetacean distribution and one or more variables (*Gregr and Trites 2001, Redfern et al 2006, Laidre et al 2004 among others*). Generalized linear models (GLMs) and generalized additive models (GAMs) can be used to examine covariate trends by modelling the probability of animal occurrence as a function of environmental variables. These models are widely used for species distribution models and have proven to be robust in understanding species presence and absence patterns (*Weir et al 2007, Redfern et al 2006*). Methods for modelling zero inflated data (data that has a larger proportion of zeros than expected from pure count data) usually model the data in two steps (*Barry and Welsh 2002*). First modelling the association between the presence and absence of a species and the available covariates and second modelling the relationship between density and the covariates, conditional on the organism being present. GLMs are typically used to examine the relationship between cetacean presence/absence and environmental variables. Relationships between cetacean density (given presence) and environmental variables are often examined by the use of GLMs or GAMs (*Canning et al 1008, Laidre et al 2010*).

The aim of this part of the thesis was partly to establish baseline data on the distribution of the three species in West Greenland by inspection using GIS and to relate the abundance of whales to spatial variables reflecting habitat preferences. The wish to explain the patterns of distribution and abundance of the three species were examined by spatial modelling of the line transect data. Several methods have been developed for fitting spatial models to line transect data and these methods are a different way to obtain density estimates and model the spatial variation of density instead of the usual two step model approach (*Buckland et al 2007, Redfern et al 2006*). The next step would be to use the data obtained here to produce prediction maps of the modelled response (abundance) over the entire survey area to get a graphical map of the densities and potential hot spot areas for the three species.

Analysis methods

Spatial analysis

It is not a simple task to isolate a single variable affecting prey aggregation or predator fidelity because marine trophic interactions are often complex and interwoven (*Laidre et al 2004*). Therefore, physical habitat features such as depth or distance from coast are often used by necessity as alternative for the distribution of prey resources. A geographic information system GIS (*ArcView 3.2*) was used to divide the surveyed area and to integrate sighting data with a set of environmental characteristics. The geographic coordinate system and coastline data for Greenland were a part of the World Vector Shoreline (WSG) called WSG1984 and projected as standard UTM Zone 24N (in meters). The sighting effort was measured by computing the length of the transect lines in sea states 4 or less for pilot whale and white-beaked dolphin and sea states 2 or less for harbour porpoise. Then a 1 km flat buffer on each side of the transect lines was added. The length, 1 km, was chosen to be sure that the effective strip width for all three species was covered so abundance could be estimated for all three species in each segment. The lines were then cut in segments of 2 km so that each square measured 4 km^2 producing 4454 and 3130 squares for sea states ≤4 and ≤2 respectively. The response variables were the abundance of each species in each square. The centre point of each segment was assigned the explanatory variables latitude, longitude, distance from coast and distance from the 200 m contour line. Spatial bathymetric data were extracted as a raster file from a terrain model from The General Bathymetric Chart of the Oceans which had a 30 arc-second spatial resolution (*GEBCO.net*). The bathymetry was then reclassified to only get the negative (depth) values and the 200 m contour line (shelf break) consequently identified. Depth was treated as a continuous variable and the slope in degrees was subsequently calculated as the rise in degree between adjacent points using spatial analysis software (*ArcView 3.2*). Both depth and slope were calculated as an average for each square using zonal statistics.

The five explanatory predictor variables (latitude, depth, seabed slope, distance from coast and 200 m contour line) were chosen to explain the spatial trends in abundance for the three species. To describe the geographical distribution an interaction between latitude and longitude was considered as a two-dimensional term but to keep the model simple and easy to interpret, only latitude was included in order to describe a possible north-south gradient. To produce the following prediction map, this latitude-longitude interaction term would probably be included in the final model. Pearson correlations were made in order to test for correlation relationship among variables, which was found between distance to coast and distance to the 200m contour line. Therefore only the variable 'distance to coast' was used, since the 200m contour line lies implicitly in the depth variable and an attraction or avoidance should therefore be detected in the response to depth. The variables were first extracted for each species to examine the relationship graphically to see if there were any apparent differences. First and foremost, the geographic range (latitude) was examined as a possible explanation for whale abundance. Distance from coast (as a measure of coastal or pelagic tendency) and depth were chosen on the basis of presumably presence of preferred prey species. Lastly, slope was chosen as a possible explanatory variable since it might play a role in topographically induced up-welling of nutrients and increased primary production (*Gregr and Trites 2001*).

Statistical analysis

Several methods have been developed for fitting spatial models to line transect data (*Weir et al 2007, Hammond et al 2006*). These allow animal abundance or animal density to be related to topographical, environmental, habitat, and other spatial variables, helping wildlife managers to identify the factors that affect abundance. They also enable estimation of abundance for any subarea of interest within the surveyed region and for prediction maps to be drawn. The 'count model' proposed by Hedley *et al.* was applied to model the trend in spatial distribution of the three species (*Hedley et al 1999, Hammond et al 2006*). To model the relationship between abundance and the explanatory variables associated with each segment, species abundance was estimated for each segment by using the Horvitz-Thompson estimator in Distance 6.0 (*Buckland et al 2007, Thomas et al 2010*). No cetaceans were encountered in many of the surveyed segments and so a large proportion of the segments had zero abundance. Poisson regression are usually used to model count values (abundance of animals in each segment) and the Poisson distribution is also employed for modelling systems where the probability of an event occurring is very low, but the number of opportunities for such occurrence is very high (*Gregr and Trites 2000, Redfern et al 2006*). To model the response as a function of covariates, GAMs were produced for each species.

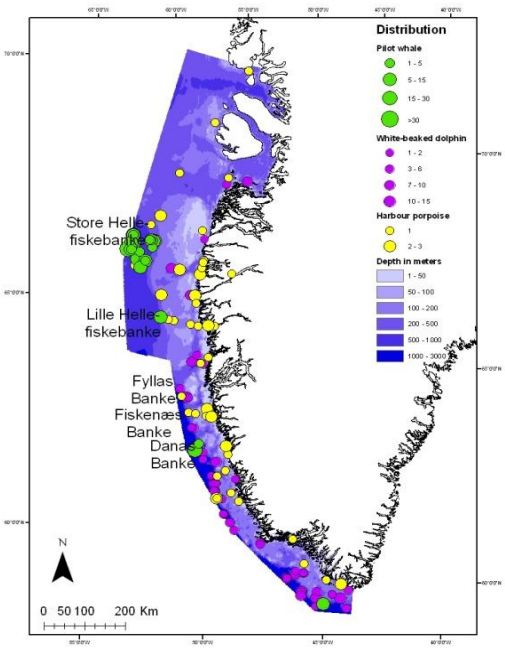
Generalized additive models (GAMs) are very flexible, and can provide a good fit in the presence of nonlinear relationships (*Forney K 2000, Weir et al 2007*). They consist of a random component, an additive component and a link function relating these two components. Because of the allowance for a link between the function and the expected value of the response value, GAMs allow for an alternative distribution for underlying random variation besides the normal distribution. They also allow a smooth function (here a cubic spline scatterplot smoother) to be fitted to the explanatory variables and no assumption of monotonicity is needed. GAMs provide the nearest fit to the data (by smoothing) and are often used to describe trends but can also be used to evaluate the response of abundance or density. GAMs have little power in testing as they are explanatory models which rather provide information about the shape of effects to be tested further by for example GLMs or GAMs to test for presence/absence.

To model the abundance of whales as a function of the explanatory variables, GAMs were developed using the open-source statistical package R (function gam from the mgcv packages, *R Development Core Team 2009*). GAMs with logarithmic links were fitted using all explanatory variables assuming a Poisson form of the error distribution. Failure to correct for over dispersion could result in standard error estimates that are too small and for too much confidence in the results. Therefore an overdispersed Poisson distribution was used where a scaling parameter estimated from the data multiplied with the variance equalled the mean (*Barry and Walsh 2002, Redfern et al 2006*). The response variable was modelled as the abundance of animals as a function of the covariates and the area of the segment was treated as an offset. Latitude, depth, slope and distance to coast were included as smoothing spline terms with the maximum number of degrees of freedom chosen on the basis of the generalized cross-validation score (GCV) and visual inspection of residual plots (the default number was 10 *df*). For each smoothing effect in the model, an F-test comparing the deviance between the full model and the model without the variable was computed. For each GAM, a t-test was used to test the null hypothesis H_0: $\alpha = 0$ (i.e. intercept= 0). To identify the most parsimonious model for each species, each variable was left out in return and the GCV score and residual plots used to determine whether the variable should be included in the final model.

Results

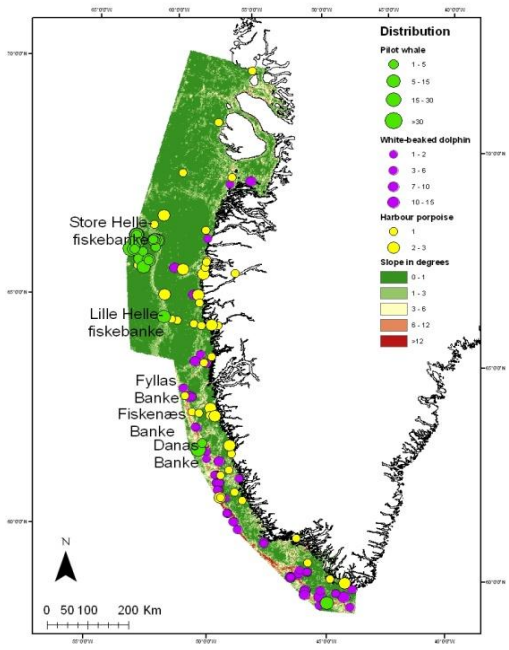
The distribution of long-finned pilot whale, white-beaked dolphin and harbour porpoise in relation to depth and slope can be viewed graphically in figure 7 and 8.

Figure 7



Distribution of pilot whales, white-beaked dolphin and harbour porpoise in survey area showing categorised depths

Figure 8



Distribution of pilot whales, white-beaked dolphin and harbour porpoise in survey area showing seabed slope measured in degrees

Spatial models

Spatial models were fitted to the line transect data. Each variable was visually inspected through the construction of diagnostic plots of residuals and the smoothness of the function was limited by setting the degrees of freedom to a maximum to avoid over-fitting and unrealistic predictions. If the maximum number of degrees of freedom was set to 5, the function was allowed 4 knots for smoothing. The terms included in the final model was based on significance of each smooth term. The approximate significance of smooth terms were found on the basis of an F-test, where the p-value was calculated to test whether the coefficients associated with the smooth functions were equal to zero (all p-values <0.001). Finally, general cross validation (GCV) score was used to find the best model (Table 1).

Table 1

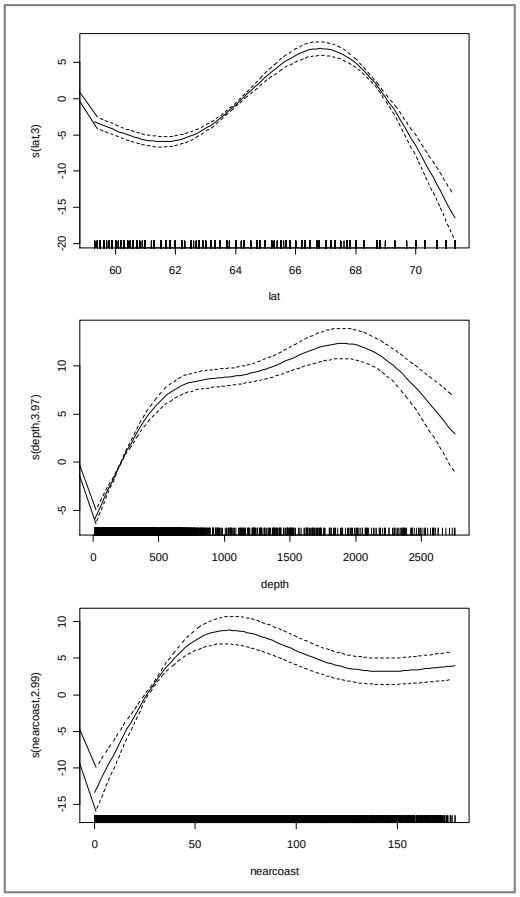
Species	Model	% Deviance
Pilot whale	*s(lat, 2.99, k=4) + s(depth, 3.97, k=5) + s(near.coast, 3.0, k=4)*	42.6
White-beaked dolphin	*S(lat, 3.89, k=5) + s(depth, 4.92, k=6) + s(slope, 2.78, k=4) + s(near.coast, 2.9, k=4)*	24.8
Harbour porpoise	*s(lat, 3.79, k=5) + s(depth, 1.0, k=4) + s(near.coast, 3.24, k=5)*	6.8

GAMs. The term s(covariate, df) represents a smooth function of the explanatory variable covariate with df degrees of freedom. The expression k=n means that the function has been limited to fitting a smooth function up to a maximum of n degrees of freedom. %Deviance is the percentage of deviance explained by the model

Response curves suggested that pilot whale abundance was positive correlated to the distance from the coast (Figure 9). They were present at deep offshore waters with a preference between 300-2000m depth, at least 30 km from land, indicating that pilot whales, whether travelling or foraging are not found on the Greenlandic shelf, but only in the deeper waters passed the shelf/fish banks (indicated by the 200m contour line) towards deeper waters. Slope was not an important predictor for pilot whales, probably because they are found at the edge of the shelf where the slope varies greatly. The spatial variable, latitude, show a preference for the area between 65-68˚N (north of survey area).

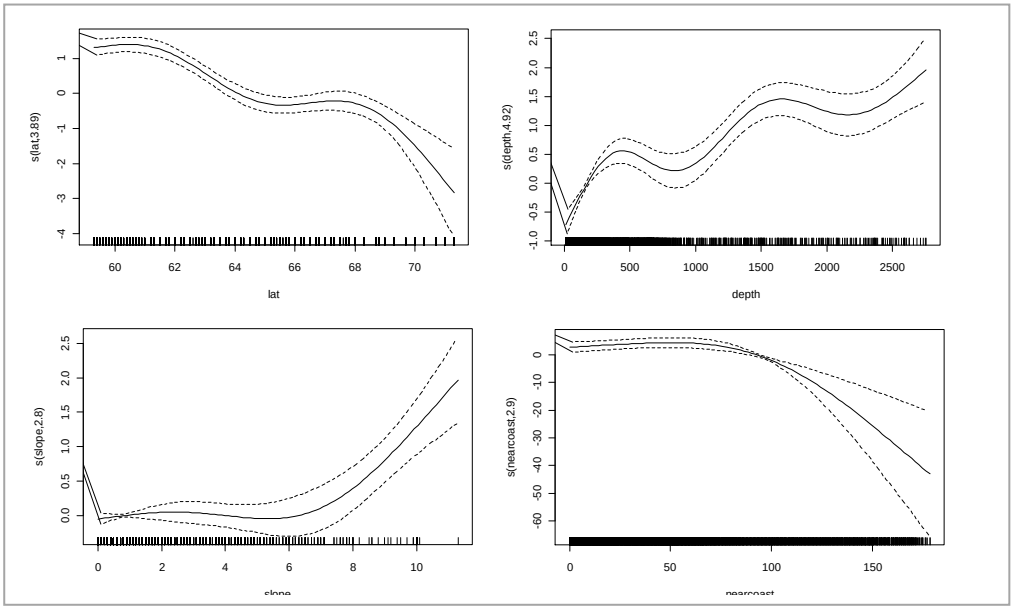
Response curves suggested that white-beaked dolphins are positive correlated with depth and slope with more dolphins at deeper depths and steeper slopes (Figure 10). They are present between the coastline and approximately 90 km off the coast. When modelling group size instead of the abundance as the response variable, the associated response curve suggested that only small groups (1-4 animals) were present over deeper water and larger groups tended to be associated with depths between 300-1000m (plot not shown but see figure 13). The presence at steep slopes was based on only a few observations so caution concerning interpretation should be made. Abundance seemed to be inversely correlated with latitude with higher abundance in South Greenland (low latitudes).

Figure 9



Plot of the estimated smooth functions from the final model for pilot whales. The dashed lines are 95% confidence limits and the location of the variables is indicated along the bottom of the x-axes

Figure 10

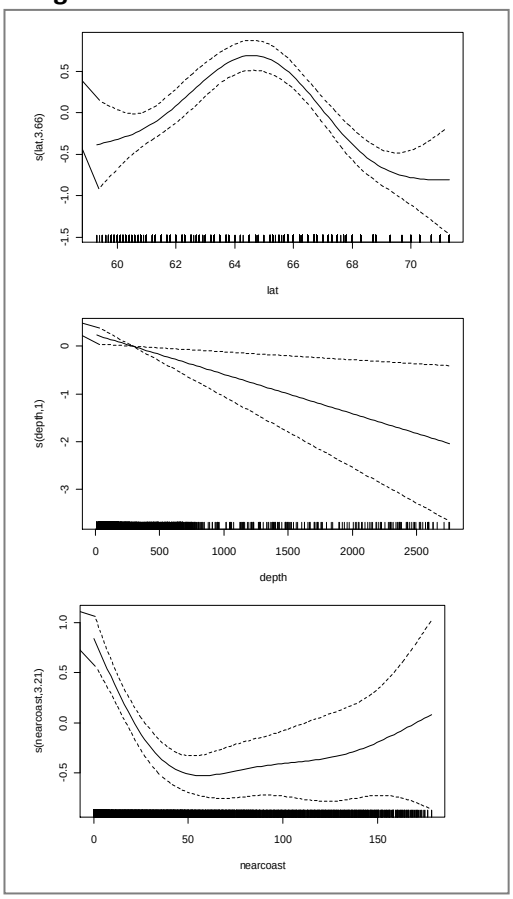


Plot of the estimated smooth functions from the final model for white-beaked dolphins. The dashed lines are 95% confidence limits and the location of t variables is indicated along the bottom of the x-axes

Response curves suggested harbour porpoise presence between 62-67˚N (figure 11). Additional plots show that there is a tendency for harbour porpoise to avoid deep waters and that they are inversely correlated to the distance from coast with more harbour porpoise close to the coast. They were the also the only of the three species present in the fjord systems. Slope was not an important predictor for presence or absence and was left out of the model. Even though harbour porpoise are found in off shore shallow waters close to the coast they are also encountered at deeper waters. The shelf edge starts it drop at around 200m and there is great variability in the slope of the shelf edge from very steep escarpments to gently sloping planes (Figure 8). Since harbour porpoises are found over both low and steep slope which might explain why slope was not an important contributor to the final model.

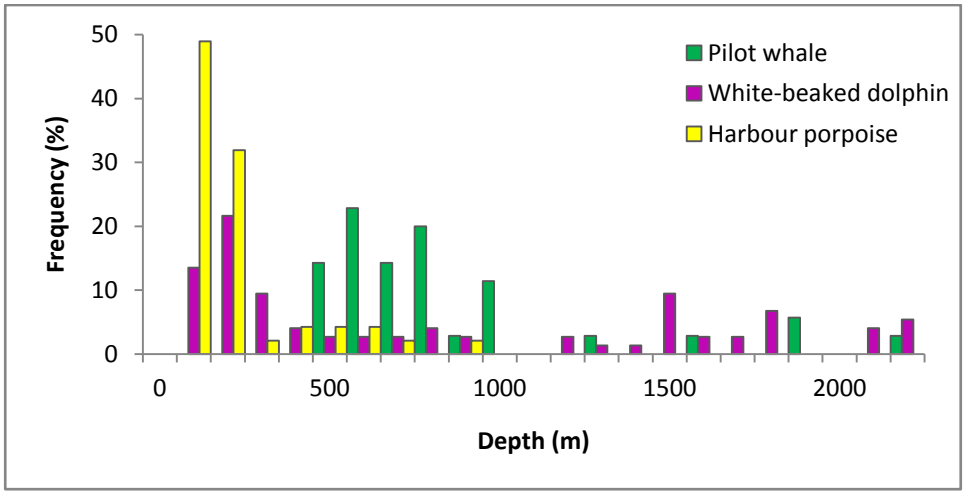
Depth and distance to coast explained the spatial trend in the abundance of all three species. Depth is considered to be a reliable explanatory proxy for prey distribution, and a Kruskal Wallis test showed highly significant difference between the distribution of the three species (*k= 55.42, p<0.0001*). The distance from the coast also varied significantly between species (*k= 77.8, p<0.0001*).

Figure 11



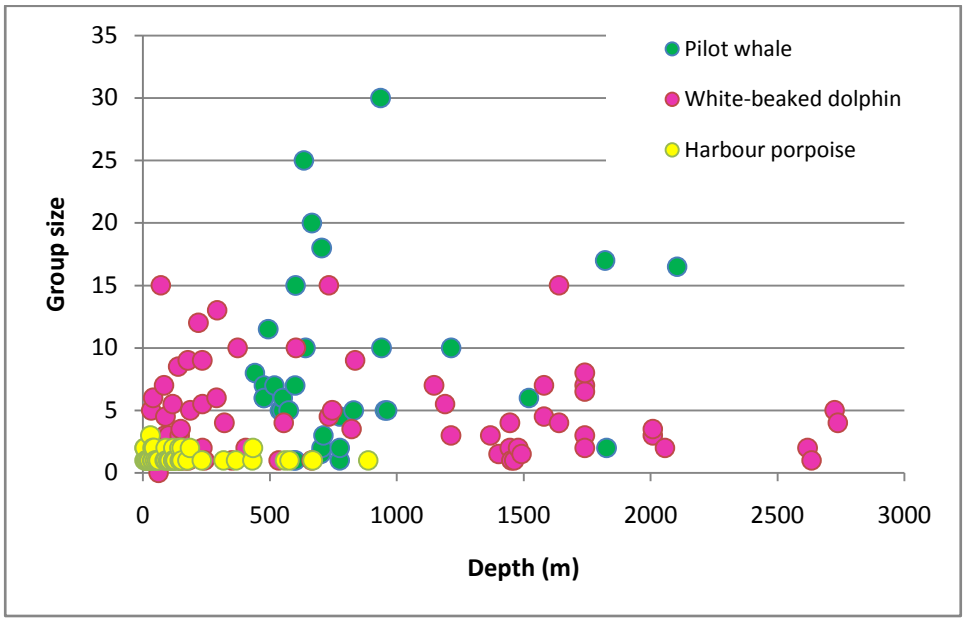
Plot of the estimated smooth functions from the final model for harbour porpoises. The dashed lines are 95% confidence limits and the location of the variables is indicated along the bottom of the x-axes

Figure 12



Bathymetry frequency distribution of pilot whale, white-beaked dolphin and harbour porpoise

Figure 13



Bathymetry group size distribution of pilot whale, white-beaked dolphin and harbour porpoise

DISCUSSION

When analyzing data from surveys of animal populations, it has been common in the past to ignore important factors such as variation in animal detection probabilities across space, and spatial dependence in animal density. This study aimed at fitting multidimensional response surfaces to the line transect data so the response curve of each variable could be investigated. However exploring the response of each variable separately may be of limited use in a multiple variable context where interactions between predictors can modify the shape of the response curve. The interpretation of the results may be relatively simple, at least graphically (response curves and residual plots), but hypothesis tests can be somewhat problematic. Results indicated that physical geography can play a role in the distribution of pilot whales, white-beaked dolphins and harbour porpoises in West Greenland. In the case of benthic prey species physical geography can limit the distribution directly by depth or substrate or for pelagic fish indirectly through mechanisms such as upwelling of nutrients in steep slope areas. Depth was the variable with the strongest influence, although the distance to the nearest coastline also played a role in the distribution of the three species. The difference in distribution relating depth and distance to the coast indicated that the three species target different prey in West Greenland. Only static physical covariates were used for this study and it might be expected that biological features of the environment, particularly related to prey distribution, would be better predictors of the distribution and abundance.

Pilot whales

Three major areas of high krill density was identified in West Greenland for the summer of 2005, and although these areas might change from year to year they still give an indication of high productivity areas,

and hence feeding areas for cetaceans in West Greenland (*Laidre et al 2010*). One of these areas is called Store Hellefiske banke and is known to be a highly productive area, that arctic marine mammals utilize in winter and migrating cetaceans during spring and summer (Figure 7, *Heide-Jørgensen et al 2007, Laidre et al 2010*). Pilot whales were found over deep waters far from the coast indicating a pelagic behaviour. They are believed to prey mainly on *Gonatus spp*. which live in the deep waters off the continental shelf (*Piatkowski and Wieland 1993,Gannon et al 1997*), but they can diversify their diet according to prey availability and so will take medium-sized fish when available (*Desportes and Mouritsen 1993, Gannon et al 1997*). They seem to utilize the area adjacent to Store Hellefiske banke more than other areas which might indicate a high density of their preferred prey *Gonatus spp*. But they might also target Greenland halibut (*Reinhardtius hippoglossoides*) that are found in high densities in the shallower waters at Store Hellefiske banke (*Piniarneq 2010*). Pilot whales sightings and catches are reported along the coast from Upernavik down to Qaqortoq in the south between May and October and so there seems to be a summer-winter movement following the spring bloom of primary production and subsequently increase in fish and squid abundance in West Greenland (*Piniarneq 2010*).

White-beaked dolphin

White-beaked dolphins were found throughout the survey area but at a higher density in South Greenland and this survey seemed to cover the northern range of the species distribution. As found in another study, white-beaked dolphins were observed over deep waters (*Canning et al 2008*) and over a seabed with steep slopes. Although white-beaked dolphins spend the majority of time close to the surface the water column down to considerable depths is believed to be exploited during foraging events. White-beaked dolphin travel in small groups (1-5) and feed in larger numbers (*Rasmussen pers. comm.*) and the observations of small groups off the shelf at very deep waters are probably animals travelling. This might have influenced the distribution pattern relating depth so that depth was not only a proxy for prey distribution and hence preferred habitat but also included animals travelling, making interpretation more difficult. White-beaked dolphins feed primarily on small, pelagic schooling fish (95%) and a study in UK found haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and cod (*Gadus sp.*) dominating the stomach content of stranded animals (*Canning et al 2008*). In West Greenland, fish species such as capelin (*Mallotus villosus*), sandeel (*Ammodytes sp*) and haddock could be components in the main diet of white-beaked dolphins. These species are distributed in shelf waters on the banks which are indicated as the area from the coast out to the 200 m contour line (Figure 4) overlapping some of the areas where white-beaked dolphins are found in high numbers (*Friis-Rødel and Kanneworff 2002, Simonsen et al 2006, Heide-Jørgensen pers.comm., ICES.org*).

Harbour porpoise

As with other studies, I found that the frequency of sighting of harbour porpoise decreased (linearly) with increasing depth beyond 3-400m (Figure 12, *Barlow 1988, Hammond et al 2006*). They are found most often in shallow waters, however, they were not absent from deep water regions in West Greenland. This was not unexpected; although harbour porpoise usually occur in shallow habitats, the topography in West Greenland can change rapidly and the locations of transect lines might have crossed some of the deep channels in West Greenland. Harbour porpoise sightings were common close to the coast and the area between 62-67˚N. Maniitsoq at 65˚N is the settlement in Greenland that has the highest annual catch of harbour porpoises, corresponding well to the high abundance of harbour porpoise in that area. Throughout the range of harbour porpoise pelagic and benthic fish species dominate the diet. Harbour porpoises from

West Greenland feed primarily on capelin (*Mallotus villosus*), Greenland halibut (*Reinharditus hippoglossoides*), polar cod (*Boreogadus saida*), squid sp. (*Gonatus sp.*) and Norway haddock (*Sebastes marinus*) (*Teilmann and Dietz 1998, Iversen pers.comm.*). Species that are associated with the fish banks as well as the fjord systems (*Siegstad 2006*). Previous studies in West Greenland have indicated high densities of capelin in shallow waters, the species which is the main component of harbour porpoise stomach content from the area around Maniitsoq (*Friis-Rødel and Kanneworff 2002, Laidre et al 2010, Iversen pers.comm.*).

Laidre et al found that the presence (but not the density given presence) of baleen whales in West Greenland was correlated with high density of krill in three main feeding areas (*Laidre et al 2010*). But this was only the case when the observations of whales were collected at the same time (same vessel) as the krill abundance was measured. This indicated that the spatial and temporal distribution of krill can change rapidly and is an example of why modelling cetacean distribution in relation to prey densities is a real challenge. Even though the primary influence of the physical environment over cetacean distribution is probably the aggregation of prey species, the possibility of defining habitat by physiographic terms provided valuable information in this study. The selected covariates did explain a reasonable amount of the model deviance for pilot whale and white-beaked dolphin but little for harbour porpoise. In order to predict the density distribution for the whole survey area, the inclusion of an interaction term between latitude and longitude would probably increase the amount of deviance explained by the models. Reliable measures of sea surface temperature and salinity might also help as indicators for prey distribution and might add further insight into the distribution patterns found here.

Conclusion

The movement of prey may explain the temporal distribution of pilot whales, white-beaked dolphins and harbour porpoises since they feed upon a wide range of prey species that may vary in occurrence both spatially and temporally. Whether the movement of pilot whales and white-beaked dolphins are related to inshore-offshore movements of preferred prey species of if they migrate south during autumn/winter remains unclear. But in any case an increased energetic demand is needed for seasonal migration. Harbour porpoises might prefer habitat utilization of sheltered waters close to the coast during calving season and an increase in energetic demand relating to calving and lactation is needed. The increased abundance during summer might be the result of a combination of factors including the distribution of prey species, increased energetic demands or simply insufficient information on the abundance and distribution from other times of the year.

The data obtained for this study provided only a snapshot of the spatial distribution of pilot-whales, white-beaked dolphins and harbour porpoises in West Greenland. But it is the first study into the distribution of these species in West Greenland and will work as a stepping stone into further examination of the relationship between their distribution and variables working as proxies for prey distribution. The next step is to develop regression models (GLMs or GAMs) relating these variables to the presence, absence and density of the whales.

RECOMMENDATIONS FOR FUTURE MANAGEMENT OF LONG-FINNED PILOT WHALES, WHITE-BEAKED DOLPHINS AND HARBOUR PORPOISES IN WEST GREENLAND

This study aimed at producing abundance estimates of pilot whales, white-beaked dolphins and harbour porpoises in West Greenland and to fit multidimensional response surfaces to the line transect data so that the response curve of possible predictor variables for the abundance could be investigated. The abundance estimates obtained here could be used as a parameter in assessment models, especially for harbour porpoises that are caught in high numbers without any information on the sustainability of the exploitation. It is also suggested to obtain altitude measurements for each observation at future aerial surveys to calculate exact distances. Training of observers should also continually be carried out since the results indicated different detection function forms between trained and untrained observers.

As for the distribution of the species, it is suggested to first incorporate the response surfaces found here into a GIS and produce density maps over the whole survey area. Secondly it would be valuable to use the exploratory step in this thesis to evaluate whether parameters to model the presence and absence of whales should be fitted parametrically (as in GLMs) or non-parametrically (as in GAMs). The spatial autocorrelation in GLM residuals that might occur by incorrect specification of functional form of species response curve (i.e. using a linear function to fit a non-linear species response) should be avoided by examining the response curve forms obtained here.

Further insight into the spatial and temporal trends in abundance and distribution of pilot whales, white-beaked dolphins and harbour porpoises could be obtained by using passive acoustic techniques such as acoustic dataloggers which can be anchored and transmit for months at a time. This would provide information on the abundance of animals throughout the year by measuring encounters and intensities of clicks made by the animals. This could also provide insight into the diving behaviour of the animals and give a perspective on the 3D nature of foraging behaviour.

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Appendix 1

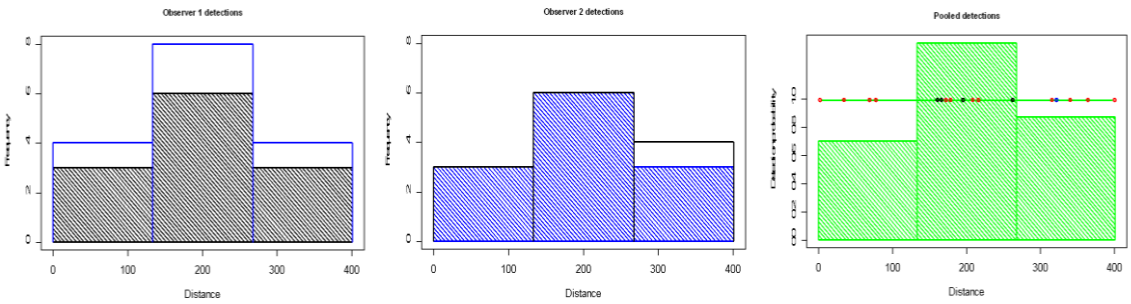
Summary of strata information; size of strata, number of transects (k), total length of transects and total number of sightings for each species

Stratum		*Area (km²)*	*k ss<5*	*Length (km) ss<5*	*Pilot whale*	*White-beaked dolphin*	*k ss<3*	*Length (km) ss<3*	*Harbour porpoise*
	1	8403.5	3	191.0	0	0	3	151.9	1
O	2	22630.6	5	507.9	0	0	5	282.6	2
F	3	14653.1	9	531.8	0	0	8	363.4	0
F	4	34272.0	4	544.7	0	0	3	452.8	1
	5	16226.2	9	862.5	12	0	9	548.6	2
S	6	14901.9	9	972.8	0	0	9	701.8	3
H	7	22084.9	6	551.2	2	0	6	439.4	2
O	8	20263.8	12	1344.8	0	1	12	574.7	4
R	9	20333.9	12	998.3	2	9	12	690.8	6
E	10	15950.2	10	931.9	0	27	9	704.4	4
	11	24085.2	16	1194.2	1	25	11	579.6	2
	12	329.6	4	49.9			4	35.4	2
I	13	92.0	3	29.2			2	17.7	1
N	14	189.3	6	44.9			3	15.0	1
	16	286.5	7	85.2			6	80.1	0
S	17	1041.8	4	48.4			4	39.0	1
H	18	348.4	3	13.8			3	13.8	1
O	19	2731.4	50	325.3			46	258.2	0
R	23	579.2	6	78.0			4	21.6	1
E	30	286.4	6	49.3			6	49.0	0
	31	1233.9	11	78.2			11	78.2	1
Total		**200923.7**	**195**	**9433.3**	**17**	**62**	**176**	**6098.1**	**35**

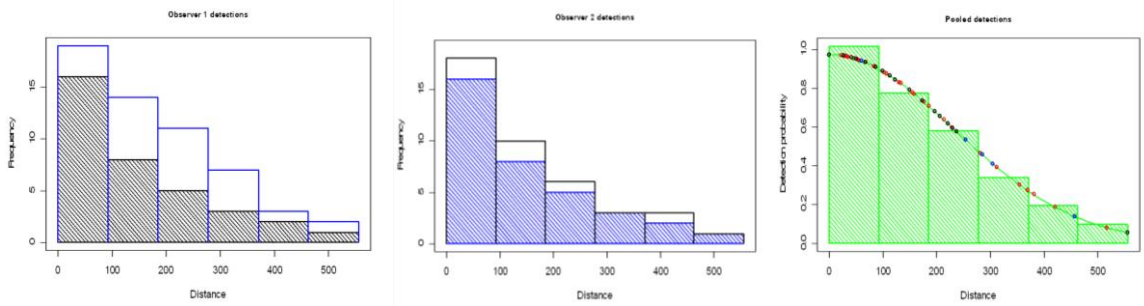
Appendix 2

Plots from the MRDS analysis showing the frequency of distances for observer 1 and observer 2 (blue bars) where duplicate detections are indicated as a number in the shaded areas. In the pooled detection plot (green bars), the points are the probability of detection for each sighting given its perpendicular distance; the line is a smooth function fitted to the points.

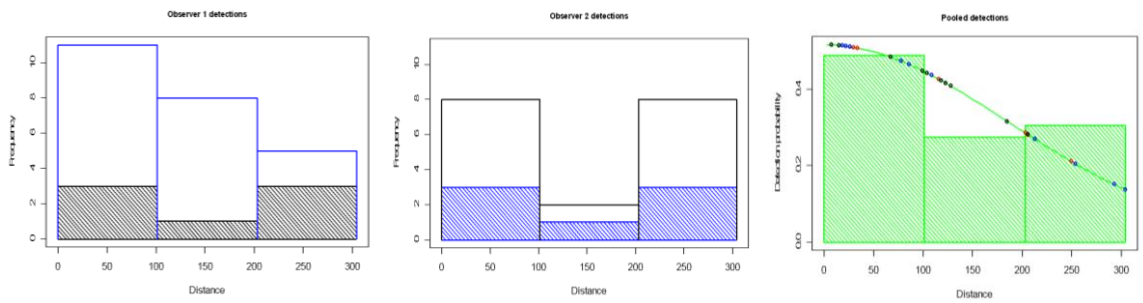
Pilot whale:

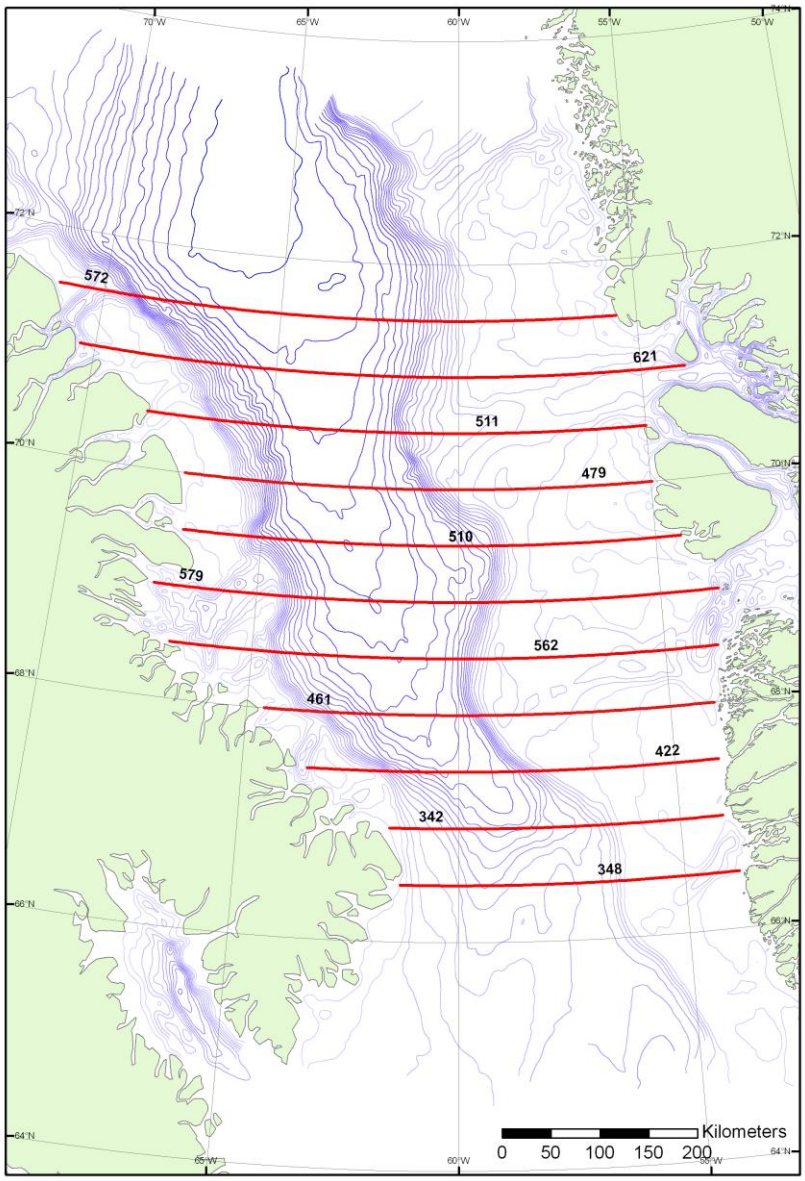


White-beaked dolphin:



Harbour porpoise:



Appendix 3

Survey area for the seabird survey conducted in September 2009 from the National Environmental Research Institute (NERI)