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Spatial trends in abundance of long-finned pilot whales, white-beaked dolphins and harbour porpoises in West Greenland

Rikke Guldborg Hansen · Mads Peter Heide-Jørgensen

Abstract Data from an aerial line transect survey conducted off West Greenland during August–September 2007 were used to estimate the abundance of long-finned pilot whales (*Globicephala melas*), white-beaked dolphins (*Lagenorhynchus albirostris*) and harbour porpoises (*Phocoena phocoena*). The abundance of each species was estimated using mark-recapture distance sampling techniques to correct for perception bias, and correction factors for time spent at the surface were applied. The fully corrected abundance estimates were 8,133 long-finned pilot whales, 11,984 white-beaked dolphins and 33,271 harbour porpoises. Based on density surface modelling methods, a count model with a generalised additive model formulation was used to relate abundance to spatial variables. Response curves indicated that the preferred habitats were deep offshore areas in Midwest Greenland for pilot whales, deep water over steep seabed slopes in South Greenland for white-beaked dolphins and relatively shallow inshore waters in Midwest–South Greenland for harbour porpoises. The abundance estimates and spatial trends for the three species are the first obtained from Greenland.

Introduction

Obtaining abundance estimates of cetaceans that have clumped or sparse distributions can be a challenge. In West Greenland, where feeding areas for cetaceans are scattered along the coast and offshore to several hundred kilometres from the coast, the total area that needs to be sampled in order to obtain robust abundance estimates is both large and remote, making monitoring both financially and logistically challenging. In addition, most cetaceans are seasonal migrants, and their habitat preferences and seasonal occurrence in remote offshore areas can be difficult to establish.

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 relatively 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). When the annual sea ice cover retreats in spring, it triggers an enormous bloom of primary production on the shelves where high nutrient content of Atlantic waters support large biomass concentrations (Laidre et al. 2004; Heide-Jørgensen et al. 2007). The bloom will attract high densities of lower trophic level forage fish and zooplankton ultimately culminating in large numbers of top marine predators. Among the cetacean species moving in from the Atlantic Ocean are long-finned pilot whales (*Globicephala melas*) (hereafter referred to as pilot whale) and white-beaked dolphins (*Lagenorhynchus albirostris*), while harbour porpoises (*Phocoena phocoena*) are present throughout the year although they might occur in larger numbers during the summer (Piniarneq 2010; Heide-Jørgensen et al. 2011).

Mammals often choose habitat that offers the greatest fitness, and consequently habitat utilisation is often assumed to reflect the quality and abundance of resources in an area (Gregr and Trites 2001). Seasonal and annual variation in prey densities likely plays a role in the aggregative behaviour and foraging success of pilot

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whales, white-beaked dolphins and harbour porpoises in West Greenland. In the North Atlantic, the diet of harbour porpoises has been investigated in Greenland, while prey species of white-beaked dolphins are known only for Great Britain (Teilmann and Dietz 1998; Canning et al. 2008; Heide-Jørgensen et al. 2011) and around the Faroe Islands and the west coast of USA for pilot whales (Desportes and Mouritsen 1993; Gannon et al. 1997a, b). With little knowledge of prey distribution, environmental factors such as depth and slope can serve as proxies for prey distribution (Cañadas et al. 2002). 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 (Piniarneq 2010) give only an indication of the species' temporal distribution along the coast. The three species migrate over long distances, and they are believed to visit West Greenland for short (or for harbour porpoises relatively long) periods mainly during spring–autumn. Here, we present the first abundance estimates of pilot whales, white-beaked dolphins and harbour porpoises in West Greenland. To elucidate patterns of distribution and density of the three species, we applied spatial modelling to the line transect data.

Methods

Aerial survey

A large-scale multi-species aerial line transect survey was conducted over the West Greenland shelf area covering the coast from 69°N to 59°N and crossing the shelf break, i.e., the 200-m contour line, during August and September 2007. Whales spend the late summer in West Greenland to feed, and their movements can be considered random during the time of the survey. It was therefore assumed that during this period, the in- and out-flux of animals on track lines was constant across the survey area and that no directional movement would have introduced a bias to the sampling design. Essentially, this implies that the probability of an animal moving towards a track line is the same as the probability of an animal moving away from it. The area was divided into 11 offshore strata from the coast to the shelf break and 10 inshore strata covering 3 main fjord systems from 71°N to 59°N, covering a total area of 200,900 km². The demarcations were based partly on sampling strategy, partly on optimising the chances of good weather in the different strata during the survey period and partly on the feasibility of covering the area. The boundaries of the strata were chosen to provide proportional coverage of the different depth contours. Track lines in the offshore strata were oriented in an east–west direction perpendicular to the shoreline and thus also roughly perpendicular to the depth contour lines, except for the southernmost strata where the track lines were north–south directed but still perpendicular to the depth contours. 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 track lines. The fjord systems were surveyed in a zigzag transect design. To reduce observer fatigue, each observed track line was followed by a 5–10 min break.

The survey platform was a high-winged Twin Otter aircraft equipped with a long-range fuel tank, operated by Air Greenland. The plane was flown at a target altitude of 700 feet (213 m) which was a compromise between target altitudes for both small (harbour porpoise) and large cetaceans (fin whales *Balaenoptera physalus*). The target altitude for harbour porpoise surveys is usually 600 feet. Two experienced harbour porpoise observers sat in the same side of the plane making later analysis more precise. On effort, the plane travelled at an average speed of 170 km per hour. The plane had two observation platforms, one in the front and one in the rear, making it possible for four observers to observe the track line independently at the same time. This arrangement allowed the survey to be conducted as a double-platform experiment with the four observers being both visually and acoustically isolated. Survey conditions were recorded at the start of the track lines and whenever a change in sea state, horizontal visibility or glare occurred, making it possible to select the parts of the track lines that had optimal survey conditions. A sighting was defined as an observation of one animal or a group of animals, and an observation 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. The declination angles recorded by the observers were converted to the perpendicular distances from the sightings to the track lines (distance = altitude*tan (90-angle)). Observations were made through bubble windows and were recorded and georeferenced onto a four-channel Redhen sDVRms system (www.redhensystems.com) that also allowed for continuous video recording of the track line. Vertical digital photographic recordings were also collected. The audio and video channels were subsequently analysed using the software program Mediamapper (redhensystems.com).

Abundance estimation

Perception bias

The survey approach allowed for mark-recapture distance sampling (MRDS), which relaxes the assumption of certain detection at zero distance (Buckland et al. 2007). Animals or groups of animals seen by both platforms (called duplicates) were determined by the coincidence of timing, distance from track line and group size. If there was a difference in recorded measurements, the average distance and/or group size was used. Both methods are design based as the abundance estimates obtained 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 estimated. The investigated covariates which might introduce heterogeneity were distance from track line, sea state, glare, group size and observer performance. 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 the animals spend some of their time underwater and invisible to observers (i.e. unavailable for detection). Depending on the species, a proportion of the animals 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 (Heide-Jørgensen et al. 2002; Rasmussen et al. 2013; Teilmann et al. 2007). A corrected abundance (denoted by the subscript 'c') was estimated by:

$$\hat{N}_c = \hat{N}/\hat{\alpha} \tag{1}$$

where $\hat{\alpha}$ is the availability correction factor, i.e., proportion of time an animal is available at the surface and potentially seen by the observers. The coefficient of variation (cv) calculated as the standard error in proportion to the mean (Laidre and Heide-Jørgensen 2011) is given by:

$$\mathrm{cv}\,(\hat{N}_c) = \sqrt{\mathrm{cv}(\hat{N})^2 + \mathrm{cv}(\hat{\alpha})^2} \tag{2}$$

The log-normal 95 % confidence intervals are subsequently recalculated as

Lower confidence interval limit $= N/C$

Upper confidence interval limit $= N * C$

by using:

$$C = \exp\left[z_\alpha * \sqrt{1 + \left\{ \log_e\left(\frac{\mathrm{var}N}{N^2} \right) \right\}} \right] \tag{3}$$

Density estimates

There were 17, 62 and 35 individual sightings of pilot whales, white-beaked dolphins and harbour porpoises, respectively, to be used in the analysis. Several explanatory covariates were used in addition to perpendicular distances for all three species. The density of animals in the region was estimated as the encounter rate divided by the detection probability, scaled appropriately to the surveyed areas (Buckland et al. 2008). To stratify the estimated densities, the geographic areas (strata) were used, and it was assumed that densities were similar on lines surveyed and lines not surveyed within each stratum.

Spatial trends in abundance

Environmental data

Physical habitat features such as depth or distance from coast are often used, out of necessity, as proxies for the distribution of prey resources and hence prey aggregations or predator site fidelity (Cañadas et al. 2002; Laidre et al. 2010). A geographic information system (GIS: ArcView 3.2) was used to divide the surveyed area and to integrate sighting data with a set of physical 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 24 N (in metres). The five explanatory predictor variables (latitude, depth, seabed slope and distance from coast and 200-m contour line) were chosen to explain the spatial trends in abundance for the three species. To describe the geographic 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. Pearson's correlations were made in order to test for correlations among variables, and these were found between distance from coast and distance to the 200-m contour. Therefore, only the variable 'distance from coast' was used, since the 200-m contour is implicitly subsumed within the depth variable, and 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 whether there were any apparent differences. First and foremost, the geographic range (latitude) was examined as a possible explanation for animal abundance. Distance from coast (as a measure of coastal or pelagic tendency) and depth were chosen on the basis of presumed presence of preferred prey species. Lastly, seabed 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). To investigate spatial trends in abundance, sighting effort was measured by computing the length of the track lines surveyed in sea states 4 or less for pilot whales and white-beaked dolphins and sea states 2 or less for harbour porpoises. Then, a 1-km flat buffer on each side of the track lines was added. This buffer width was chosen to be sure that the effective strip width for all three species was covered and therefore that abundance could be estimated for all three species in each segment. The lines were then cut in segments of 2 km so that each segment measured 4 km^2 producing 4,454 and 3,130 segments for sea states ≤4 and ≤2, respectively. The response variable for the spatial modelling was the abundance of each species in each segment. The centre point of each segment was assigned the explanatory variables latitude, longitude, distance from coast and distance from the 200-m contour. 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*). 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.

Statistical analysis

Several methods have been developed for fitting spatial models to track line data (Cañadas and Hammond 2006; Hammond et al. 2006; Weir et al. 2007). These allow animal abundance or animal density to be related to topographic, environmental, habitat and other spatial variables, helping wildlife managers to identify factors affecting abundance. They also enable estimation of abundance for any subarea of interest within the surveyed region. 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). By using the open-source statistical package R (function gam from the mgcv packages *R Development Core Team* 2009), generalised additive models (GAMs) with a logarithmic link function were used to model the abundance of animals as a function of covariates (Forney 2000; Cañadas and Hammond 2006; Weir et al. 2007). GAMs provide the nearest fit to the data (here with a cubic spline scatterplot smoother) and are often used to describe trends but can also be used to evaluate the response of abundance or density. Due to over-dispersion in the data (a large proportion of segments had zero encounters), a quasi-Poisson error distribution was used (Barry and Welsh 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 from coast were included as smoothing spline terms with the maximum number of degrees of freedom chosen on the basis of the generalised 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 turn and the GCV score and residual plots were used to determine whether the variable should be included in the final model.

Results

Abundance

The search effort is given in Table 1. A total of 9,433 km of track lines were flown (8,631 km offshore and 802 km inshore) in Beaufort sea states <5, and of these, 6,098 km were flown in sea states <3. The total search time was 56 h and the distribution and group sizes of animals are shown in Table 1 and Fig. 1. Weather conditions during August and September 2007 were generally good, except for the northern area around Disko Island and in South Greenland which had relatively poor conditions, reducing the time available for surveying. For pilot whales and white-beaked dolphins, data collected during sea state 0–4 were used for analysis, whereas only data for sea state 0–2 were used for harbour porpoises. The stricter cut-off criteria applied to harbour porpoises reflect the fact that they can be reliably detected visually only in fairly calm waters. Pilot whales were detected primarily in offshore areas and white-beaked dolphins primarily on the banks in South Greenland. Harbour porpoises were widely distributed throughout the surveyed area, including several fjords.

Table 1 Stratum area, number of transects (k), effort in Beaufort seastate <3 and <5, and number of sightings for each species

Stratum	Area (km²)	k ss <5	Effort (km) ss <5	Pilot whale	White-beaked dolphin	k ss <3	Effort (km) ss <3	Harbour porpoise
Offshore								
1	84,045	3	191	0	0	3	152	1
2	22,631	5	508	0	0	5	283	2
3	14,653	9	532	0	0	8	363	0
4	34,272	4	545	0	0	3	453	1
5	16,226	9	863	12	0	9	549	2
6	14,902	9	973	0	0	9	702	3
7	22,085	6	551	2	0	6	439	2
8	20,264	12	1,345	0	1	12	575	4
9	20,334	12	998	2	9	12	691	6
10	15,950	10	932	0	27	9	704	4
11	24,085	16	1,194	1	25	11	580	2
Inshore								
12	330	4	50	–	–	4	35	2
13	92	3	29	–	–	2	18	1
14	189	6	45	–	–	3	15	1
16	287	7	85	–	–	6	80	0
17	1,042	4	48	–	–	4	39	1
18	348	3	14	–	–	3	14	1
19	2,731	50	325	–	–	46	258	0
23	579	6	78	–	–	4	22	1
30	286	6	49	–	–	6	49	0
31	1,234	11	78	–	–	11	78	1
Sum	220,925	195	9,433	17	62	176	6,098	35

Because of the double-platform design, detection on the track line could be estimated, implying that abundance could be estimated without assuming that $g(0) = 1$, and MRDS estimates were produced for all three species. Estimates of density and abundance are given in Table 3. The explanatory variables available to include in both the 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 and 2 levels for harbour porpoises), 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).

Pilot whales

A MRDS model was fitted to the data without truncation (17 sightings—12 duplicates), revealing constant detection probability to a perpendicular distance of 400 m (Fig. 2). The final model included no explanatory variables, and the total estimate of abundance (uncorrected) was 3,253 pilot whales (cv = 0.38). By using formulas 1–3, the correction of the at-surface abundance with the availability factor

(40 %, cv = 0.15) increased the absolute abundance of pilot whales to 8,133 (cv = 0.41) (Tables 2 and 3).

White-beaked dolphins

The final MRDS model included no explanatory variables and was fitted to the data without truncation (62 sightings—35 duplicates). The uncorrected abundance estimate of white-beaked dolphins was 9,827 (cv = 0.19). Correction of the at-surface abundance with the availability factor (82 %, cv = 0; only one white-beaked dolphin has been tagged) increased the absolute abundance to 11,984 white-beaked dolphins (cv = 0.19) (Tables 2 and 3).

Harbour porpoises

Small cetaceans can be difficult to detect, and the target altitude of 700 feet was perhaps above the optimal altitude for a harbour porpoise survey (Hammond et al. 2006). Two of the four observers were specially trained for harbour porpoise surveys. This was evident in the data, since this pair of observers accounted for almost all of the porpoise detections. They were positioned on the same side of the aircraft, and when using only their observations, the

Fig. 1 Realised survey effort with *lines* flown in Beaufort sea state <5 (*grey*) and sea state <3 (*black*). Distribution of pilot whales, white-beaked dolphins and harbour porpoises in relation to depth
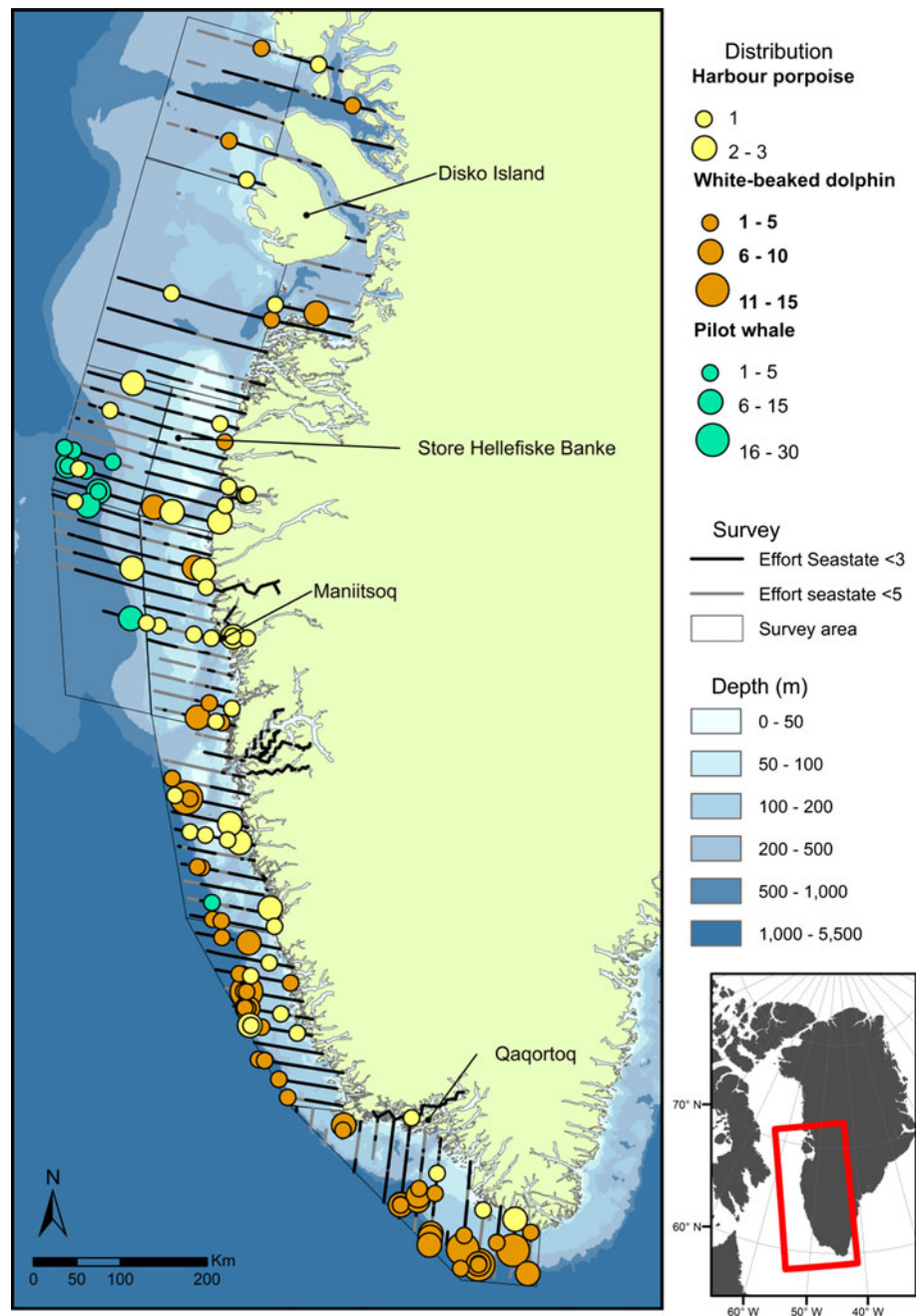
effort was halved and 31 observations (7 duplicates) were left. The combined $g(0)$ for harbour porpoises was well below one ($g(0) = 0.57$).

For the MRDS model, different explanatory variables were tested in both the MR and DS models. 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 <2, and therefore, the simplest model was chosen (Fig. 2). For harbour porpoises, the density (animals/km^2) in the inshore strata (fjord systems) was higher ($D = 0.19$) than in the offshore strata ($D = 0.042$). The MRDS model (where perception bias is implicit) gave a total density of 0.047 harbour porpoises/km^2 and the total estimate of abundance was 10,314 (cv = 0.35) (Table 3).

Correction of the at-surface abundance with the availability factor (31 %, cv = 0.17) increased the absolute abundance of harbour porpoises to 33,271 (cv = 0.39) (Tables 2 and 3).

Spatial trends in abundance

Spatial models were fitted to the track line data. Each variable was visually inspected through the construction of diagnostic plots of residuals, and the smoothness of the
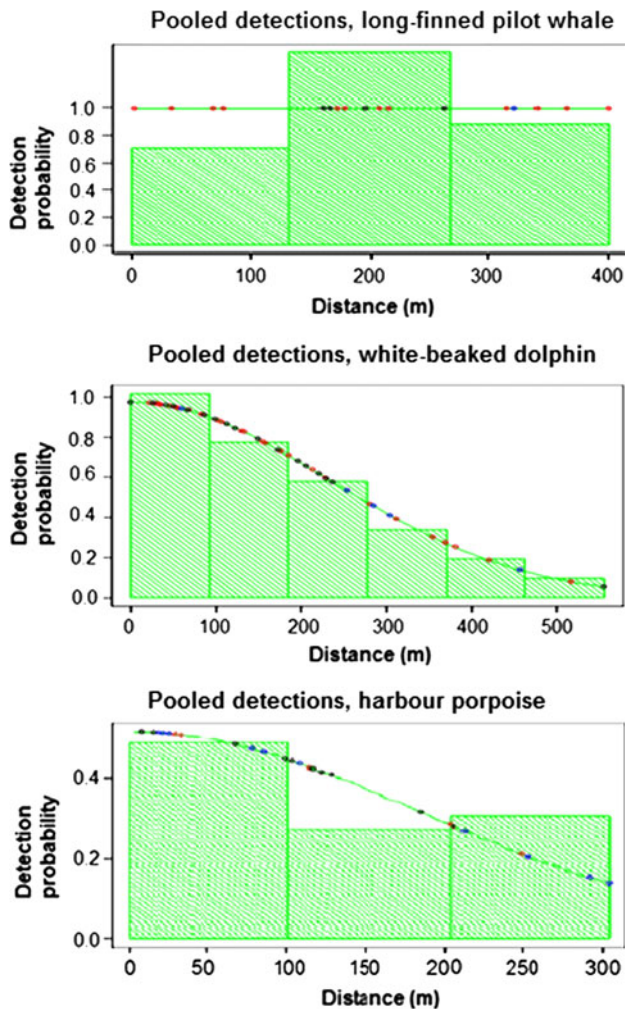

Fig. 2 Pooled detection function plots showing the perpendicular distance distribution and detection probability model fitted using MRDS methodology for pilot whales, white-beaked dolphins and harbour porpoises. Perpendicular distance in metres is plotted on the *x* axis and probability of detection on the *y* axis. Individual sightings are indicated by different *coloured circles*

function was limited by setting the degrees of freedom to a maximum to avoid over-fitting and unrealistic predictions. The maximum number of degrees of freedom was set to 10. The terms included in the final model were based on significance of each smooth term. General cross-validation (GCV) scoring was used to find the best model (Table 4).

Pilot whales

Pilot whales were present in deep offshore waters with a preference for depths between 300 and 2,000 m, at least 30 km from land (Fig. 3). This indicates that pilot whales, whether travelling or foraging, are usually not found on the Greenlandic shelf, but primarily in the deeper waters beyond the shelf. 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 showed that pilot whales preferred the area between 65°N and 68°N (northern part of survey area).

White-beaked dolphins

White-beaked dolphin abundance is correlated with depth and slope, with more dolphins occurring in deep water with steep bottom slopes (Fig. 3). They were present between the coastline and approximately 90 km from the coast (Fig. 3). The response curve when modelling group size suggested that only small groups (1–4 animals) were present over deeper water and that larger groups tended to be associated with depths of between 300 and 1,000 m (plot not shown but see Fig. 1). The tendency of white-beaked dolphins to occur in areas with steep slopes was based on only a few observations so this finding needs to be interpreted with caution. Abundance also seemed to be correlated with latitude, with higher abundance in South Greenland (low latitudes).

Harbour porpoises

Harbour porpoises occur primarily in latitudes between 62°N and 67°N (Fig. 1). Of the three species, only harbour porpoises were present in the fjord systems. Additional

Table 2 Geographic areas where animals have been instrumented with satellite transmitters showing the average percentage of time spent at the surface during daytime

Species	Geographic area of instrumentation	Number of animals	Percentage of time spent at surface (cv)	Submerged in water column (m)
Pilot whale	Faroe Islands	3	40 (0.15)	0–7
White-beaked dolphin	Iceland	1	82 (–)	0–2
Harbour porpoise	Denmark	3	69 (0.17)	0–1

Coefficients of variation are shown in brackets. Only one white-beaked dolphin has been tagged and therefore no variance was available

Table 3 Abundance estimates using MRDS methodology showing pod size E[s], pod density D_G, animal density D, animal abundance N and abundance corrected for availability $N_{corrected}$ with the associated 95 % confidence intervals (CI$_{corrected}$)

Species	E[s] pod size	D_G (pods/km^2)	D (animals/km^2)	N (animals)	$N_{corrected}$	95 % CI$_{corrected}$
Pilot whale	7.03	0.002 (0.41)	0.015 (0.38)	3,253 (0.38)	8,133 (0.41)	3,765–17,565
White-beaked dolphin	4.69	0.009 (0.18)	0.044 (0.19)	9,827 (0.19)	11,984 (0.19)	8,285–17,334
Harbour porpoise	1.32	0.036 (0.35)	0.047 (0.35)	10,314 (0.35)	33,271 (0.39)	15,939–69,450

The coefficients of variation (cv) are given in brackets

Table 4 General additive models of cetacean sightings and physiographic parameters

Species	Model	% Deviance
Pilot whale	$s(lat, 2.99, k = 4) + s(dep, 3.97, k = 5) + s(dist, 3.0, k = 4)$	42.6
White-beaked dolphin	$S(lat, 3.89, k = 5) + s(dep, 4.92, k = 6) + s(slop, 2.78, k = 4) + s(dist, 2.9, k = 4)$	24.8
Harbour porpoise	$s(lat, 3.79, k = 5) + s(dep, 1.0, k = 4) + s(dist, 3.24, k = 5)$	6.8

The terms (covariate, degrees of freedom) represent a smooth function of the explanatory variable covariate with 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 (10) degrees of freedom. %Deviance is the percentage of deviance explained by the model

Lat latitude, *dep* depth, *slop* slope, *dist* distance from coast

plots showed a tendency for harbour porpoises to avoid deep waters and that their abundance is correlated with distance to the coast, with more animals close to the coast. Bottom slope was not an important predictor for presence or absence and was left out of the model. Even though harbour porpoises are found in shallow waters close to the coast, they also occur in deeper waters. The shelf edge starts at around 200 m depth, and there is great variability in the bottom slope there, from very steep escarpments to gently sloping plains. Since harbour porpoises are found over both shallow and steep slopes, this could explain why slope was not an important contributor to the final model.

Water depth and distance to the coast explained the spatial trend in the abundance of all three species (Fig. 1). Depth is considered to be a reliable explanatory proxy for prey distribution, and a Kruskal–Wallis test showed highly significant differences between the distribution of the three cetacean species ($k = 55.42$, $p < 0.0001$). The distance from the coast also varied significantly between the species ($k = 77.8$, $p < 0.0001$).

Discussion

The marine environment off West Greenland is heterogeneous influenced as it is 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 habitat utilisation by cetaceans. Hunting statistics suggest that pilot whales, white-beaked dolphins and harbour porpoises are most abundant off West Greenland throughout the summer

although this could be a biased impression since conditions for hunting (weather, day length, etc.) are more favourable in summer than in other seasons. Evidence from other parts of the North Atlantic that have been surveyed indicates that the distribution of these three species is likely to change greatly on a seasonal and even daily basis (Bloch et al. 2003; Mate et al. 2005; Hammond et al. 2006; Rasmussen et al. 2013; Teilmann et al. 2007).

The abundance estimates and trends in abundance presented here are the first for pilot whales, white-beaked dolphins and harbour porpoises in West Greenland. Prior to this study only limited information was available regarding the distribution and abundance of these species in Greenlandic waters, and even though more observations would be desirable, this information serves as a good baseline. Our survey results indicate that the three species were not uniformly distributed throughout the region during the summer of 2007 and that they used some areas more than others. This patchiness has interesting implications both in regard to the biology and ecology of the population that summer in West Greenland and in regard to resource management.

This study also fitted multidimensional response surfaces to the track line 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 multivariate context where interactions between predictors can modify the shape of the response curves. Interpretation of the results may be relatively simple, at least graphically (response curves and residual plots), but hypothesis testing can be problematic. The results indicated that physical geography might play a role in the
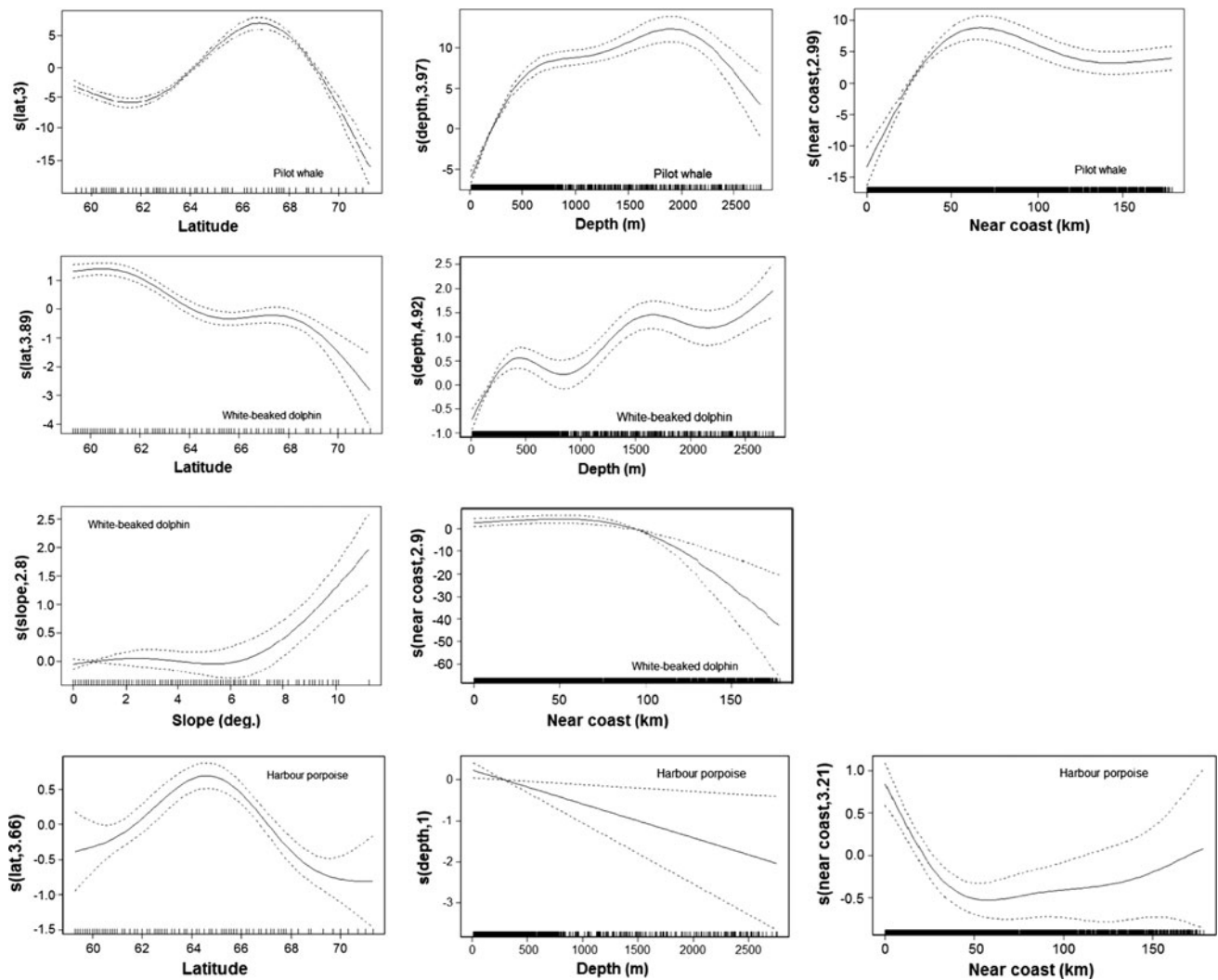
Fig. 3 Shapes of the functional forms for the smoothed covariates used in the GAMs for pilot whales (three *upper panels*), white-beaked dolphin (four *middle panels*) and harbour porpoise (three *lower panels*). Zero on the *vertical axes* corresponds to no effect of the covariate on the estimated response. The *dashed lines* represent the 95 % confidence limits. The locations of the observations are plotted as ticks along the *horizontal axes*

distribution of pilot whales, white-beaked dolphins and harbour porpoises in West Greenland. In the case of benthic prey species, physical geography can limit distribution directly by depth or substrate, and in the case of pelagic fish, it can limit distribution indirectly through mechanisms such as upwelling of nutrients in steep slope areas (Cañadas et al. 2002). Depth was the variable with the strongest influence, although distance from the coast also played a role in determining the distribution of the three species. The differences among the species in regard to trends in depth and distance to the coast indicated that they target different prey in West Greenland. Only static physical covariates were used for this study and it is expected that biologic features of the environment, particularly related to prey distribution and abundance, would be better predictors of both cetacean distribution and cetacean abundance.

Pilot whales

From surveys conducted in the eastern North Atlantic during summer 1987–1989, density estimates were 0.066 (cv = 0.36) (1987) and 0.35 (cv = 0.36) (1989) animals/km^2 (Buckland et al. 1993). In West Greenland, the density of pilot whales was 0.015 (cv = 0.38) somewhat lower than the densities around Iceland and the Faroe Islands (Buckland et al. 1993). The present survey did not cover the entire summer range of pilot whales off West Greenland (as evident from off-effort observations at the western boundaries of the offshore strata) as did the surveys in Iceland and the Faroe Islands. The coverage in the northeast Atlantic surveys was largely over deep waters 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 at the 500-m-depth curve. The density, and hence abundance estimates, might be more accurate if waters further west had been included in the survey or if an adaptive distance sampling approach had been implemented.

For pilot whales, the surface time from three individuals was used to correct for the availability of pods (i.e. the detection unit), assuming a high degree of diving synchrony within pods. Since all sightings were of groups of more than one individual, the availability correction factor may have been overestimated. Any positive bias, however, would have been at least partly offset by our use of a surface layer of 6 m depth below which the entire pod was considered likely to be undetectable. As the sighting process is not instantaneous, the length of time that a sighting is potentially in view of an observer could cause a positively biased abundance estimates. For this survey, the time in view for pilot whales was on average 1.6 s (<1 s for white-beaked dolphin and harbour porpoise), and if area-specific times for surfacing and diving events existed, this combined could be used to estimate the availability bias more accurately (Laake et al. 1997). Using dive times from only three whales from areas outside of Greenland to produce a correction factor for availability bias is not ideal. However, the large variance of the correction factors applied should cover the biologic range of diving behaviour.

Three areas of high krill density were identified off West Greenland in the summer of 2005, and although these areas might change from year to year, they can be considered indicative of highly productivity areas, and hence of feeding areas for cetaceans (Laidre et al. 2010). One of these areas, called Store Hellefiske banke, is known to be highly productive, and it is used by arctic marine mammals in winter and migrating cetaceans in spring and summer (Fig. 1; Heide-Jørgensen et al. 2007; Laidre et al. 2010). The majority of pilot whale sightings were in deep water west of Store Hellefiske Bank. Pilot whales are known to prey mainly on Gonatus spp. that live in the deep waters off the continental shelf (Piatkowski and Wieland 1993; Gannon et al. 1997a, b), but they can diversify their diet according to prey availability and will take medium-sized fish when available (Desportes and Mouritsen 1993; Gannon et al. 1997a, b). They seem to use the area adjacent to Store Hellefiske Bank more than other areas, and this might indicate that high densities of Gonatus spp. occur there. However, pilot whales might also target Greenland halibut (Reinhardtius hippoglossoides) that are found in high densities in the shallower waters of Store Hellefiske Bank (Piniarneq 2010). Pilot whale sightings and catches are reported along the coast of Greenland from Qaqortoq in the south to Upernavik in the north between May and October, which suggests a summer–winter movement following the

spring bloom of primary production and subsequent pulses in fish and squid abundance.

White-beaked dolphins

The density of 0.044 white-beaked dolphins/km^2 (cv = 0.19) in West Greenland can be 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 that has been tagged with a satellite transmitter was in Icelandic waters (Rasmussen et al. 2013). Since no variance was associated with the dive patterns described for that individual, the derived availability correction factor of 82 % must be considered uncertain. Studies of other dolphin species have shown average times spent at the surface of between 89 % (spotted dolphin, Stenella attenuate) (Baird et al. 2001) and 99 % (Risso's dolphin, Grampus griseus) (Wells et al. 2009). Compared to those studies, the at-surface time of 82 % seems reasonable.

White-beaked dolphins were found throughout the whole survey area, but densities were higher in South Greenland, and it appeared as though this survey covered the northern areas of the species' range in this part of the North Atlantic. As found in another study (Canning et al. 2008), white-beaked dolphins were observed in deep water and over a seabed with steep slopes. Although white-beaked dolphins spend the majority of time close to the surface, they are believed to forage in the water column down to considerable depths. White-beaked dolphins travel in small groups (1–5) and congregate in larger numbers in good feeding areas; observations of small groups off the shelf in very deep waters are considered to be travelling. This might have confounded the distribution pattern relating depth, as depth would then represent not only a proxy for prey distribution but also for movement corridors between foraging areas. White-beaked dolphins feed primarily on small, pelagic schooling fish (95 %), and a study in the UK found haddock (Melanogrammus aeglefinus), whiting (Merlangius merlangus) and cod (Gadus sp.) as the predominant species in the stomachs 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 (Friis-Rødel and Kanneworff 2002, Simonsen et al. 2006), some of the areas where white-beaked dolphins were observed in large numbers.

Harbour porpoises

There were significantly higher densities of porpoises in inshore strata than in offshore strata (between 0 and 0.19

animals/km^2), a trend also found in the Baltic Sea, 0.009–1.016 animals/km^2 (Scheidat et al. 2008). Harbour porpoises are small animals, with no visible or conspicuous blow or splash, and they occur in groups of only a few individuals (mean group size 1.32). This makes harbour porpoises difficult to survey, both from aircraft and ships (Barlow 1988, Hammond et al. 2006). The proportion of animals seen by both experienced observers (combined $g(0) = 0.57$) was somewhat lower compared to other studies (Laake et al. 1997). The relative abundance estimate from the MRDS model was 10,314 (cv = 0.35), and this number is about 10 times smaller than what was found in an aerial survey from the European Atlantic (an area 1.5 times larger) (Hammond et al. 2006). Since harbour porpoises are mainly found over relatively shallow depths, the survey in West Greenland would likely have yielded more accurate estimates of density and abundance if it had concentrated more on the inshore and immediately offshore areas. As was true for white-beaked dolphins, the survey seems to have covered the northern extent of the distribution of harbour porpoises in this part of the Atlantic, and hence, it might be expected that the animals would occur here in lower densities than in the centre of their range. The availability correction factor was not derived from data collected in Greenlandic waters; instead, the at-surface data were collected from 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 when feeding compared to porpoises in Denmark. Thus, the availability correction factor might be too low and the absolute abundance estimate of 33,271 (cv = 0.39, 95 % CI 15,939–69,450) would be an underestimate. On the other hand, the main prey of harbour porpoises in West Greenland during summer are pelagic species compared to Danish waters where they feed more on demersal species (Heide-Jørgensen et al. 2011; Sveegaard et al. 2012). Despite the large physiographic differences in the two types of habitat, it is assumed that the time spent at the surface is comparable.

As is the case with other studies, the frequency of harbour porpoise observations decreased (linearly) with increasing depth beyond 300–400 m (Barlow 1988; Hammond et al. 2006). They were most frequently found in shallow waters, however, they were not absent from deep water regions off West Greenland. This was not unexpected; although harbour porpoises usually occur in shallow habitat, the bathymetry in West Greenland varies considerably and the track lines crossed some of the deep channels in West Greenland. Harbour porpoise sightings were common close to the coast in latitudes between 62°N and 67°N. Maniitsoq at 65°N is the settlement in Greenland

with the highest annual catch of harbour porpoises, corresponding well to the relatively high abundance of harbour porpoises in that area. Throughout their range, harbour porpoises prey on both pelagic and demersal fish species. Those off West Greenland feed primarily on capelin (*M. villosus*), polar cod (*Boreogadus saida*), Atlantic cod (*Gadus morhua*) and squid sp. (*Gonatus sp.*) (Teilmann and Dietz 1998; Heide-Jørgensen et al. 2011), 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. During summer, massive schools migrate along the coast seeking food in the highly productive areas there, on the fish banks and in the fjords. This is consistent with the findings of Heide-Jørgensen et al. (2011) where the main component of harbour porpoise stomach contents from the area around Maniitsoq was indeed capelin (Friis-Rødel and Kanneworff 2002; Laidre et al. 2010; Heide-Jørgensen et al. 2011).

Conclusions

This study aimed at producing abundance estimates of pilot whales, white-beaked dolphins and harbour porpoises in West Greenland and fitting two-dimensional response surfaces to the track line data in order to examine the response curve of possible predictor variables for abundance. The movements of prey may explain the trends in 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 movements of pilot whales and white-beaked dolphins are related to inshore–offshore movements of preferred prey species or instead these cetaceans migrate south during autumn/winter remains unclear although the latter seems more reasonable due to the formation of sea ice in Baffin Bay during autumn. In any case, seasonal migration increases the demand for energy to be obtained in the high-latitude feeding grounds. Harbour porpoises might prefer 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. Even though the primary influence of the physical environment over cetacean distribution is probably the aggregation of prey species, the effort to define habitat in physiographic terms was a useful aspect of this study. The selected covariates explained a reasonable amount of the model deviance for pilot whales and white-beaked dolphins but little for harbour porpoises.

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