Generalised additive models to investigate environmental drivers of Antarctic minke whale (*Balaenoptera bonaerensis*) spatial density in austral summer

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ABSTRACT

There is a need to characterise the physical environment associated with Antarctic minke whale density in order to understand long-term changes in minke whale distribution and density in open waters of the Southern Ocean during austral summer months. To investigate environmental drivers of Antarctic minke whale density, generalised additive models (GAMs) were developed, based on line transect data collected for the International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programmes. The GAMs were fitted independently by survey year. Explained deviances ranged from 14.9% to 35.1%. Most models included covariates related to transition zones, such as distances to the continental shelf break and sea ice edge, both of which showed a predominantly negative relationship with whale density. This study suggests high variability in the relationships between Antarctic minke whale density and the environment. None of the selected covariates had a consistent qualitative relationship with density at either the circumantarctic or the regional scale. This in part may be explained by the changing ice-related boundaries of the surveys between years and hence differences in survey region. Another possible reason is that in absence of better data, most of the covariates considered were derived from remote sensing data. More localised surveys with comparable survey area conducted across the Southern Ocean, where whale sightings data are collected simultaneously with *in situ* non-biotic and prey data, are likely to provide a better assessment of the environmental determinants of whale density.

KEYWORDS: ANTARCTIC MINKE WHALE; SOUTHERN OCEAN; DISTRIBUTION; ICE; MODELLING; SOWER

INTRODUCTION

The Southern Ocean is the most important feeding ground for Antarctic minke whales (*Balaenoptera bonaerensis*). Mainly during the austral summer months, these whales predominantly feed on krill (Kawamura, 1994) and are observed both within the pack ice region (e.g. Ensor, 1989; Ribic *et al.*, 1991; Thiele *et al.*, 2002; 2005; Thiele and Gill, 1999; van Franeker, 1992) and in the open ocean (Friedlaender *et al.*, 2006; Kasamatsu *et al.*, 1988; 2000; Murase *et al.*, 2002; Thiele *et al.*, 2000).

The Antarctic minke whale is currently the most abundant baleen whale species in the Southern Ocean, and is likely to be a major consumer of krill. During the austral summer, several hundred thousand Antarctic minke whales inhabit the Southern Ocean (Branch, 2006), although Antarctic minke whale abundance estimates are currently under major review (IWC, 2009; Zerbini *et al.*, 2008). Estimates of annual circumpolar krill consumption by Antarctic minke whales are important to understand the role of minke whales in marine ecosystems, including interactions with potential competitors (e.g. Ainley *et al.*, 2006). Estimates of krill consumption by minke whales range between 35.5 (± 6.2) million tonnes per year (Armstrong and Siegfried, 1991) and 75 million tonnes per year (Everson, 2000). However, they are based on historic Antarctic minke whale abundance estimates. Understanding how the changing environment affects minke whales and their prey is important to map changes in whale abundance and trends.

Several studies have reported regional trends in sea surface temperature and sea ice extent attributed to climate change in the Southern Ocean in the second half of the 20th century. This is especially true for the Bellingshausen-Amundsen Seas sector, with a marked increase in sea surface temperature (Meredith and King, 2005) and a strongly negative trend in sea ice extent (Stammerjohn *et al.*, 2008; Zwally *et al.*, 2002). The environmental variability may underlie long-term changes in Antarctic minke whale density. For a better understanding of these long-term changes the physical environment associated with Antarctic minke whale density dynamics needs to be characterised.

From large-scale independent studies (e.g. Kasamatsu *et al.*, 1988; 2000; Murase *et al.*, 2002; Thiele *et al.*, 2000), it is not clear which environmental variables determine the circumantarctic variability in Antarctic minke whale summer distribution and density. Only recently, studies on Antarctic minke whale distribution have been conducted at a smaller scale, and these indicate potentially complex spatial relationships between Antarctic minke whales and their prey (Friedlaender *et al.*, 2006; 2009).

The International Whaling Commission (IWC) has conducted visual cetacean surveys in the Southern Ocean for almost 30 years under the IDCR (International Decade of Cetacean Research) and SOWER (Southern Ocean Whale and Ecosystem Research) programmes. These have resulted

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in three circumpolar sets of surveys, which were specifically designed for the visual detection of cetaceans, with an emphasis on Antarctic minke whales and the environment. This is in contrast with multidisciplinary surveys, such as the CCAMLR 2000 (Commission for the Conservation of Antarctic Marine Living Resources – Reilly *et al.*, 2004) and SO GLOBEC surveys (Southern Ocean Global Ocean Ecosystem Dynamics – Friedlaender *et al.*, 2006; Thiele *et al.*, 2004), which targeted specific study areas.

The IWC/IDCR-SOWER dataset is thus the only circumantarctic whale sightings dataset for the Southern Ocean that allows for a long-term large-scale analysis of spatio-temporal variability in minke whale density. To determine the environmental drivers of whale density, the data were analysed with the spatial modelling methodology developed by Hedley *et al.* (1999), and simple generalised additive models (GAMs) (Wood, 2006). Input variables were derived from remote sensing data that are related to transition zones in the Southern Ocean. These zones are characterised by their enhanced productivity, such as the marginal ice zone (e.g. Arrigo *et al.*, 1998; Moore and Abbott, 2000; Smith and Nelson, 1986) and frontal zones (e.g. Moore and Abbott, 2000). Bathymetric variables, sea surface temperature, chlorophyll a concentration and latitude were also considered as inputs for the spatial models.

With this analysis, predictive spatial models were developed for Antarctic minke whale summer density in open waters of the Southern Ocean at the regional scale, which is defined as the area surveyed during a specific season. In recent years, improved models have been developed to estimate Antarctic minke whale summer abundance in the Southern Ocean (recently developed models are presented in Bravington and Hedley (2009), Cooke (2009) and Okamura and Kitakado (2009)). However, the models presented in this paper were not used for derivation of summer abundance estimates. Instead, the aim of the models was to identify aspects of the environment that underlie Antarctic minke whale density distribution at the regional scale, and to characterise the various relationships between minke whale density and the environment. Furthermore, whether these relationships held at the circumantarctic scale was also investigated.

MATERIALS AND METHODS

Study area and effort

The IWC/IDCR-SOWER programme has completed three circumpolar (CP) sets of cetacean sighting surveys in the Southern Ocean, namely CPI (1978/79–1983/84), CPII (1985/86–1990/91) and CPIII (1991/92–2003/04). The IWC has divided the Southern Ocean into six Management Areas (Fig. 1) (Donovan, 1991; Mackintosh, 1942), and Table 1 shows general information about the surveys analysed in this study in the context of the Management Areas. Coverage of most surveys was restricted to one Management Area, and some surveys covered sections of two Management Areas. Almost all open waters within the full latitudinal range from below 60°S to the sea ice edge were surveyed in CPIII. In contrast, the surveyed strata covered only about 65% and 81% of the ranges in CPI and CPII, respectively (Branch and Butterworth, 2001), with northern boundaries of the surveyed

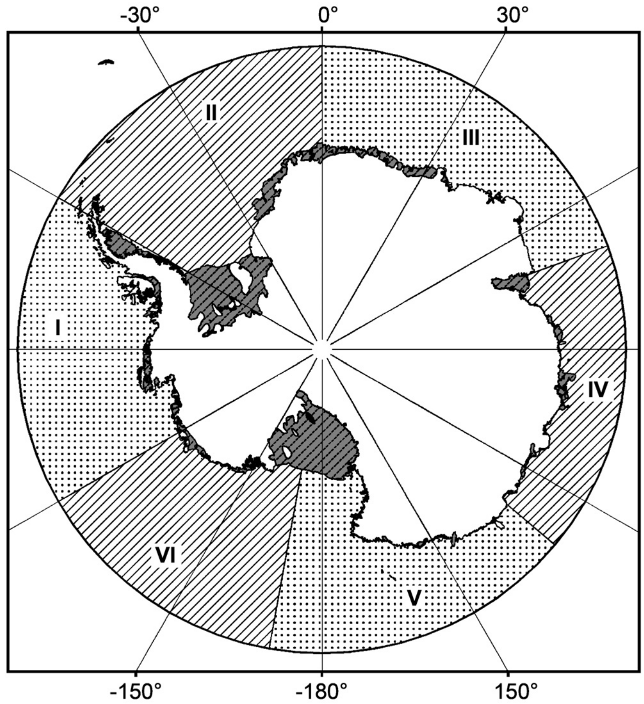


Fig. 1. IWC Management Areas in the Southern Ocean (Mackintosh, 1942; Donovan, 1991). Ice shelves are represented by the grey striped areas. See Branch and Butterworth (2001) and Branch (2006) for detailed maps of the strata surveyed during the IDCR/SOWER programme.

strata often at latitudes south of 60°S. During each survey, 2–4 vessels covered the open waters of the Southern Ocean, thereby excluding the pack ice region and polynyas (enclosed or semi-enclosed areas of open water) within this region. The surveys varied in timing and duration, but were always conducted during austral summer, within a period from the end of December to the beginning of March of each season.

Primary search effort, i.e. effort made when a vessel is in searching mode, was exclusively in closing mode for the surveys conducted between 1978/79 and 1984/85 and alternated between effort in closing mode and Independent Observer (IO) mode for surveys since 1985/86. In IO mode, the vessel stays on the track line after a sighting, with the two observer teams on the primary and secondary platforms on full search effort. Meanwhile, the observers on the upper bridge track and identify the sighting. In contrast, in closing mode the survey vessel leaves the track line and approaches the sighted group(s) of whales for better school size estimation and species identification (Branch and Butterworth, 2001). See Branch and Butterworth (2001) and Branch (2006) for a more detailed description of the IWC/IDCR-SOWER surveys, including maps of the surveyed strata.

The first surveys (1978/79–1980/81) were not considered because of the lack of environmental data from the satellite record needed to develop spatial models. Thus, spatial models were developed with line transect data from the 1981/82–2004/05 surveys. Total survey area ranged from 0.690 million km^2 (2001/02 survey) to 3.305 million km^2 (1985/86 survey). The lowest level of primary effort was 2,842km (2000/2001 survey), while a maximum of 15,645km primary effort was obtained during the survey in 1985/86. Table 1 summarises Antarctic minke whale

Table 1

Survey and Antarctic minke whale sighting information, grouped per IWC Management Area, south of 60°S. Sighting information refers to sightings made during primary effort and Independent Observer (IO) modes. Schools and sightings are standardised per unit primary effort and are given before truncation.

IWC Area[1]	Survey season	Survey period	Area size (10^6 km^2)	Primary effort (km)	IO effort (km)	Number of schools	Schools/ effort	Number of whales	Whales/ effort
Area I	1982/83	01 Jan.–18 Feb. 1983	1.099	8,938	n/a	616	0.069	1,546	0.173
(120–60°W)	1989/90	28 Dec. 1989–15 Feb. 1990	1.473	10,192	5,635	608	0.060	1,208	0.119
	1993/94	29 Dec. 1993–13 Feb. 1994	2.290	9,002	4,601	314	0.035	608	0.068
	1999/2000	12 Jan. 1999–14 Feb. 2000	0.776	3,409	1,887	53	0.016	95	0.028
Area II	1981/82	26 Dec. 1981–08 Feb. 1982	1.078	11,503	n/a	505	0.044	1,418	0.123
(60°W–0)	1986/87	25 Dec. 1986–09 Feb. 1987	1.699	13,503	6,988	791	0.059	2,621	0.194
	1996/97	13 Jan.–17 Feb. 1997	1.479	6,235	3,303	214	0.034	404	0.065
	1997/98	16 Jan.–15 Feb. 1998	1.053	5,699	3,133	199	0.035	370	0.065
Area III	1987/88	20 Dec. 1987–27 Jan. 1988	1.645	8,204	4,314	365	0.044	807	0.098
(0–70°E)	1992/93	25 Dec. 1992–02 Feb. 1993	1.527	10,126	5,298	388	0.038	870	0.086
	1994/95	12 Jan.–27 Feb. 1995	1.470	8,017	4,201	277	0.035	498	0.062
	2004/05	10 Jan.–27 Feb. 2005	0.720	4,843	2,318	162	0.033	333	0.069
Area IV	1984/85	28 Dec.1984–21 Feb. 1985	1.105	11,436	n/a	370	0.032	904	0.079
(70–130°E)	1988/89	28 Dec. 1988–12 Feb. 1989	1.622	12,957	4,767	476	0.037	1,361	0.105
	1998/99	20 Jan.–23 Feb. 1999	1.329	7,288	3,933	186	0.026	432	0.059
Area V	1985/86	22 Dec. 1985–20 Feb. 1986	3.305	15,645	8,101	1,184	0.076	2,752	0.176
(130°E–170°W)	1991/92	27 Dec. 1991–12 Feb. 1992	1.522	6,872	3,834	637	0.093	1,491	0.217
	2001/02	25 Dec. 2001–13 Feb. 2002	0.690	3,397	1,879	136	0.040	392	0.115
	2002/03	22 Dec. 2002–26 Feb. 2003	1.653	7,332	3,892	265	0.036	580	0.079
	2003/04	21 Dec. 2002–1 Mar. 2003	1.446	7,333	3,845	704	0.096	2,136	0.291
Area VI	1983/84	03 Jan.–18 Feb. 1984	2.516	7,701	n/a	194	0.025	431	0.056
(170–120°W)	1990/91	02 Jan.–13 Feb. 1991	1.912	6,734	4,020	187	0.028	357	0.053
	1995/96	10 Jan.–24 Feb. 1996	1.531	6,298	3,222	227	0.036	379	0.060
	2000/01	08 Jan.–22 Feb. 2001	1.553	6,046	2,842	207	0.034	490	0.081

[1]In this table, as in subsequent tables, only the Management Areas were listed that were predominantly surveyed during a season. During most seasons, (part of) only one Management Area was surveyed. Three surveys were conducted in two Management Areas, namely the 1999/2000 survey (80–55°W, Areas I + II), 1994/95 survey (40–80°E, Areas III + IV) and 1995/96 survey (140–110°W, Areas VI + I).

sightings data under primary effort. The number of Antarctic minke whale schools per km ranged from 0.016 (Area I, 1999/2000 survey) to 0.096 (Area V, 2003/04 survey). The number of sighted Antarctic minke whales per km ranged from 0.028 (Area I, 1999/2000 survey) to 0.291 (Area V, 2003/04 survey).

Whale sightings and detection probabilities

Following recommendations in Branch and Ensor (2001), Branch and Butterworth (2001) and Branch (2006), sightings coded as 04, 91 and 92 (all classified as 'definitely minke whale') and 39 ('like minke whale') were extracted from the DESS (IWC Database-Estimation Software System) V3.52 database package (Strindberg and Burt, 2004), under the assumption that these sightings represented Antarctic minke whales. Dwarf minke whales, so far an unnamed subspecies of the common minke whale (*Balaenoptera acutorostrata*), also inhabit the Southern Ocean, and may be confused with Antarctic minke whales during shipboard surveys. However, probably less than 1% of minke whales in the Southern Ocean are dwarf minke whales (Zerbini *et al.*, 2008). Sightings used for this analysis were obtained in both closing and IO mode.

Some whale schools were sighted two or three times from different platforms during the survey and recorded as duplicates or triplicates, respectively. Each duplicate/ triplicate was marked as either 'definite', 'possible', 'remotely possible' or 'uncertain'. Only the first sighting of a duplicate/triplicate marked as 'definite' was included. All other duplicates/triplicates were treated as distinct schools (Branch and Butterworth, 2001). Only sightings with activity codes considered suitable as defined in Table 3 of Branch (2006) were included in this analysis. Radial distances and angles were smeared using Method II of Buckland and Anganuzzi (1988). Selected sightings were further filtered by truncation of perpendicular distances at 1.5 nautical miles (nmi), after smearing (Branch and Butterworth, 2001).

Detection probabilities were estimated using Mark Recapture Distance Sampling (MRDS) methods implemented in Distance V5.0 release 2 (Thomas *et al.*, 2006) and the MRDS package (V1.2.9) of Program R, V2.9.2 (R Development Core Team, 2008), which is part of Distance.

An MRDS detection function can be written as (Laake and Borchers, 2004):

$$p.(x, \underline{z}) = p.(0, \underline{z})g.(x, \underline{z}) \quad (1)$$

where: $p.(x, \underline{z})$ = the probability that at least one of the observers detects a whale group at perpendicular distance x from the track line, given the vector of $\underline{z}$ sighting covariates (school size, sea state, etc);

$p.(0, \underline{z})$ = the probability that at least one of the observers detects a whale group on the track line (with perpendicular distance x = 0), given the covariate vector $\underline{z}$. The mark recapture (MR) component of the MRDS model is needed to estimate this probability;

$g.(x, \underline{z})$ = the probability that at least one of the observers detects a whale group at perpendicular distance x from the track line, given the covariate vector $\underline{z}$ and under the assumption that $g.(0, \underline{z}) = 1$. The distance sampling (DS) component of the MRDS model is needed to estimate this probability.

$p.(x, \underline{z})$ is derived from the individual detection functions in the following way (Laake and Borchers, 2004):

$$p.(x, \underline{z}) = p_1(x, \underline{z}) + p_2(x, \underline{z})\,[1 - p_{1|2}(x, \underline{z})] \qquad (2)$$

where: $p_j(x, \underline{z})$ = the probability that observer j detects a whale group at perpendicular distance x from the track line, given the covariate vector $\underline{z}$, for j = 1 or 2;
$p_{1|2}(x, \underline{z})$ = the conditional probability that observer 1 detects a whale group at perpendicular distance x from the track line, given that observer 2 detects the animal, for covariate vector $\underline{z}$.

To model the DS component, the half-normal and hazard-rate key functions without any adjustment terms were considered (see Buckland *et al.* [2001] for the formulae of these functions). The MR component as implemented in the MRDS package is the logistic model:

$$p_{j|3-j}(x, \underline{z}) = \frac{\exp(\beta_0 + \beta_1 z_1 + \ldots + \beta_q z_q)}{1 + \exp(\beta_0 + \beta_1 z_1 + \ldots + \beta_q z_q)} \qquad (3)$$

where: $p_{j|3-j}(x, \underline{z})$ = the conditional probability that observer j detects a whale group at perpendicular distance x from the track line, given that observer (3–j) also detects the group, for sighting covariates $z_1 \ldots, z_q$;
$\beta_0, \ldots, \beta_q$ = parameters to be estimated, with q = total number of covariates.

School size, sightability and sea state were considered as covariates for the detection-function models. All covariates were fitted as factor variables, with five levels for school size (i.e. 1, 2, 3–4, 5–9, 10+), four levels for sightability (2, 3, 4 and 5) and two levels for sea state (0 = Beaufort 0–2; 1 = Beaufort 3+) (Bravington and Hedley, 2009; Okamura and Kitakado, 2009). Model selection was based on Akaike's Information Criterion (AIC) (Akaike, 1973).

Only Antarctic minke whale sightings collected during double platform effort in IO mode were used to model MR detection functions with the assumption of 'point independence'. This means that the individual detection probabilities $p_1(x, \underline{z})$ and $p_2(x, \underline{z})$ are independent at $x = 0$, but not necessarily elsewhere (Laake and Borchers, 2004). The $p.(0, \underline{z})$ values were only estimated for surveys since the 1985/86 season, which collected IO data, but not previously. Models for $p.(x, \underline{z})$ were fitted using all IO data pooled over the following Area(s): Areas I + II, Areas III + IV + VI and Area V. Pooling was necessary to meet the recommendation of having at least 60 duplicate sightings, which is desirable for a good detection-function model (Buckland *et al.*, 2001; Hedley *et al.*, 2001). Detection-function models were fitted per vessel when sample size was appropriate.

The estimated $p.(0, \underline{z})$ values were smaller than 1 for all surveys conducted since 1985/86. Therefore, the $p.(0, \underline{z}) = 1$ assumption was also relaxed for the surveys between 1981/82 and 1984/85, for which IO data were not available. For these surveys, $g.(x, \underline{z})$ values were estimated by fitting detection functions to data collected under closing mode. As every vessel collected more than 60 sightings during each survey, detection-function models for $g.(x, \underline{z})$ were fitted per vessel and season. Values of $p.(0, \underline{z})$ were predicted with the detection-function models fitted to IO data in the same Areas. For instance, the detection-function model based on IO data pooled over Areas I + II was used to predict $p.(0, \underline{z})$ values for the 1982/83 survey, which was conducted in Area I. Estimates of $p.(x, \underline{z})$ for the early surveys were then derived from the individual components using equation (1). In this way, although IO data were not available for these surveys, sightings and covariate information collected during these surveys were used to determine the shape of the detection function.

Remote sensing data

The IWC/IDCR-SOWER surveys were specifically designed to detect cetaceans and relatively few non-biotic data were collected when compared to cruises under multi-disciplinary programmes such as SO GLOBEC and CCAMLR 2000. No observations were made on krill during the IWC/IDCR-SOWER cruises and *in situ* biotic data are not available. Instead, remote sensing datasets were used for the derivation of potential environmental covariates needed to study the relationships between Antarctic minke whale density and their environment. Ocean depth and continental shelf break locations were obtained from the General Bathymetric Chart of the Oceans (GEBCO) dataset, at one lat-lon minute resolution (IOC *et al.*, 2003). Sea ice concentrations were estimated from weekly passive microwave remote sensing data, derived from measurements obtained by the Scanning Multichannel Microwave Radiometer (SMMR) onboard the Nimbus-7 satellite and by the Special Sensor Microwave Imagers (SSM/I) onboard Defense Meteorological Satellite Program (DMSP) satellites F8, F11 and F13. Version 2 of the sea ice concentration data were used, released in September 2007, which had a 0.2° × 0.2° resolution (Cavalieri *et al.*, 1996, updated 2006). Weekly 0.083° × 0.083° gridded chlorophyll a concentration data were derived from the NASA Sea-viewing Wide Field-of-view Sensor (SeaWiFS) dataset (*http://oceancolor.gsfc.nasa.gov/SeaWiFS*). For sea surface temperature, Optimum Interpolation version 2 Sea Surface Temperature (hereafter called OISST) data (Reynolds *et al.*, 2002; Reynolds and Smith, 1994) were used, provided on an approximately 7 day interval one-degree latitude-longitude grid (*http://www.cdc.noaa.gov/data/gridded/data.noaa.oisst.v2.html*). Frontal zone locations were obtained from two sources: firstly, positions were used of the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC) as identified by Orsi *et al.* (1995), based on long-term datasets; secondly, sea surface velocities (SSV), a proxy for frontal zone location, were derived from absolute geostrophic velocities from AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) on a weekly 1/3° × 1/3° Mercator grid based on altimetry instruments onboard the Topex/Poseidon, Jason-1, ERS and ENVISAT satellites.

Spatial models and potential covariates

Antarctic minke whale sightings were used in spatial models based on line transect data using GAMs from Wood (2006), as implemented in the R software library *mgcv (*V1.5–5). The count method developed by Hedley *et al*. (1999) was applied for which the transect line was divided into equal segments of ten nautical miles.

The number of Antarctic minke whales per segment area, N_i, was obtained using the following Horvitz-Thompson-like (Horvitz and Thompson, 1952) estimator:

$$\hat{N}_i = \Sigma_j \frac{n_{i,j}}{\hat{p}(x, \underline{z})_{i,j}} \qquad (4)$$

where: $n_{i,j}$ = the number of minke whales within group j in segment i;
$\hat{p}.(x, \underline{z})_{i,j}$ = the estimated probability that at least one of the observers detects the jth group in segment i, at perpendicular distance x from the track line, given the covariate vector $\underline{z}$.

$\hat{N}$ was then used as the response variable for GAMs that assumed a logarithmic link-function and a Tweedie error distribution. Tweedie distributions are characterised by a variance that is proportional to the power θ of the mean (Peel *et al.*, 2008). Within the package *mgcv* (Wood, 2006), the best value of θ was selected where $1<\theta<2$, based on the best possible fit according to standard diagnostic plots. Furthermore, the quasi-Poisson and simple Poisson error distributions were considered, which are special cases of the more general Tweedie distribution (Peel *et al.*, 2008).

The following GAM-model (Hedley *et al.*, 1999) was used with the natural logarithm of the segment area as an offset variable:

$$E(\hat{N}_i) = \exp[1\mathrm{n}(A_i) + \theta_0 + \Sigma_r f_r(k_{i,r})] \qquad (5)$$

where: A_i = segment area, equal to 2 l_i w (l_i = segment length, with w = 1.5 nmi);
θ_0 = intercept;
$k_{i,r}$ = value of covariate r for segment i;
f_r = smoothed function ('smoother') of covariate r.

Two different smoother function types were considered, namely isotropic smoothers and tensor product smoothers.

Potential covariates used in the spatial models were: closest distance to the sea ice edge, defined at 15% sea ice concentration (Tynan and Thiele, 2003), bathymetric depth and nearest distance to the continental shelf break, defined as the 1000m depth contour, SSV and closest distances to the SACCF and SBACC, OISST, chlorophyll a, latitude and longitude (latter two covariates both in degrees). The GAMs were fitted independently by survey year. Although the package *mgcv* can be used for automated model selection (Wood, 2008), a somewhat *ad hoc* selection procedure was used, as the primary aim was to identify important whale density – environment relationships with this study, instead of maximising explained deviance. Also, covariate interaction terms were not considered in this study. Model selection was based on minimisation of the Generalised Cross Validation (GCV) score, while excluding GAMs that generated extreme minke whale density values.

To avoid overfitting, the degree of covariate smoothing was constrained by setting the argument gamma to 1.4 within the function 'gam' of package *mgcv* (Wood, 2006, p.256). Forward selection was used as a selection procedure: in each step, covariates were considered which had correlation coefficients smaller than 0.7 with the covariates that were already selected in the previous steps. In each step, the covariate was selected for which inclusion showed the largest increase in explained deviance. A new covariate was only retained if it was significant, lowered the GCV score, and increased the amount of explained deviance by at least 4% (Southwell *et al.*, 2008).

Predicted density maps

Spatial models were used to generate Antarctic minke whale density surfaces for each Area and year, in regions encompassed by the surveyed strata. Density maps were used to examine the predictions of the selected models, e.g. to identify extreme predicted density values, if present. Antarctic minke whale densities were only predicted for the surveyed strata, which were all in open waters of the Southern Ocean. Predicted density maps on a 0.2-degree latitude-longitude grid were plotted with ESRI ArcMap V9.2 (ESRI, 2006).

In order to compare the results between different surveys, whale density, $\hat{D}_v$, was defined as $\hat{N}_v/A_v$, the number of Antarctic minke whales per km^2 for grid cell v. The segment area per grid cell, A_v, was calculated using the South Pole Lambert Azimuthal Equal Area polar projection within ArcMap. As surveys within a specific Area took place over weeks throughout the year, covariate values were estimated for the middle date of the overlapping survey period for surveys conducted within the same Area.

RESULTS

Whale sightings and detection probabilities

Tables 2 and 3 summarise the selected detection-function models and derived detection probability estimates (also Figs 2 and 3). To illustrate the model selection process, Tables 4 and 5 list the detection-function model fits of the models that were successfully fitted. The $\bar{g}.(x)$ estimates for the surveys between 1981/82 and 1984/85 ranged from 0.392 (SE = 0.048, vessel K27, 1983/84 survey) to 0.576 (SE = 0.022, vessel SM2, 1982/83 survey). For these surveys, sea state data were only available for the 1984/85 survey. School size was the only sighting covariate apart from perpendicular distance that was frequently included in the models (Table 2), even though sightability and sea state were also considered as sighting covariates in some of the surveys (Table 4). The estimated $\bar{p}.(0)$ values for surveys conducted

Table 2

Summary of selected detection function models and derived $\hat{\bar{g}}.(x)$ estimates for surveys between 1981/82 and 1984/85. $\hat{\bar{g}}.(x)$ is the estimated average detection probability derived from the detection function model which assumed $g(0)$ = 1. Detection function models were fitted per survey year and vessel. Abbreviations: hn = half-normal model, hr = hazard-rate model, x = perpendicular distance, s = school size.

Survey season	Area	Vessel	Number of sightings	Selected model	$\hat{\bar{g}}.(x)$ ± SE
1981/82	II	SM1	268	hn ($x + s$)	0.480 ± 0.021
		SM2	198	hn ($x + s$)	0.455 ± 0.022
1982/83	I	SM1	179	hn ($x + s$)	0.558 ± 0.032
		SM2	393	hn ($x + s$)	0.576 ± 0.022
1983/84	VI	SM1	120	hr ($x + s$)	0.492 ± 0.054
		SM2	165	hn (x)	0.410 ± 0.019
		K27	95	hr ($x + s$)	0.392 ± 0.048
1984/85	IV	SM1	73	hn (x)	0.438 ± 0.035
		SM2	162	hr ($x + s$)	0.565 ± 0.057
		K27	79	hn ($x + s$)	0.565 ± 0.047

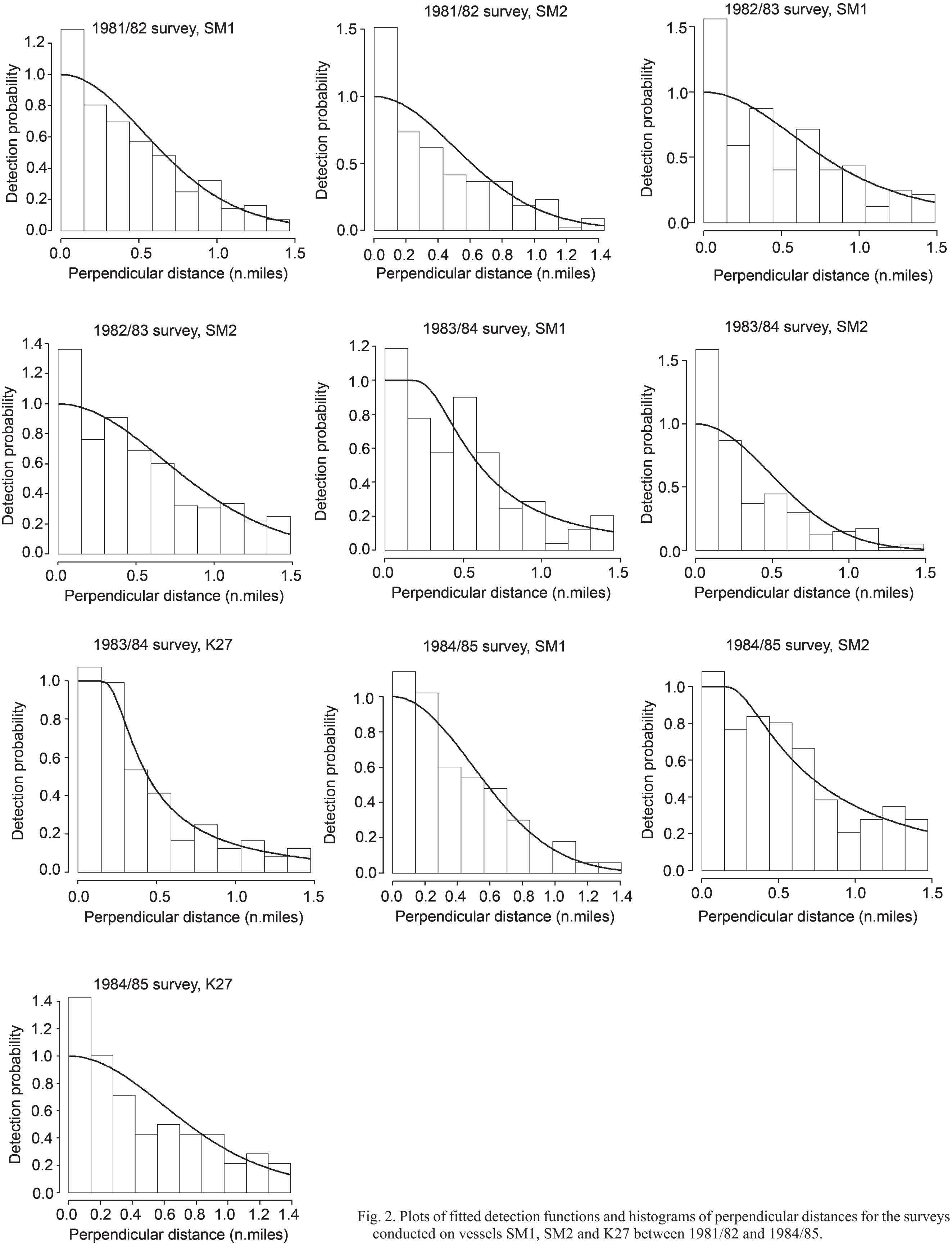


Fig. 2. Plots of fitted detection functions and histograms of perpendicular distances for the surveys conducted on vessels SM1, SM2 and K27 between 1981/82 and 1984/85.

between 1985/86 and 2003/04 ranged from 0.561 (SE = 0.027, vessels SM1 + K27, Area V) to 0.724 (SE = 0.031, vessel SM1, Areas III+IV+VI). Estimated $\overline{p}.(x)$ values ranged from 0.182 (SE = 0.021, vessel SM2, Area V) to 0.338 (SE = 0.019, vessels SM1 + K27, Areas I + II). Group size was always selected in the models (Table 3). The MR component of some models included sea state as well, but sightability never improved model fit (Table 5).

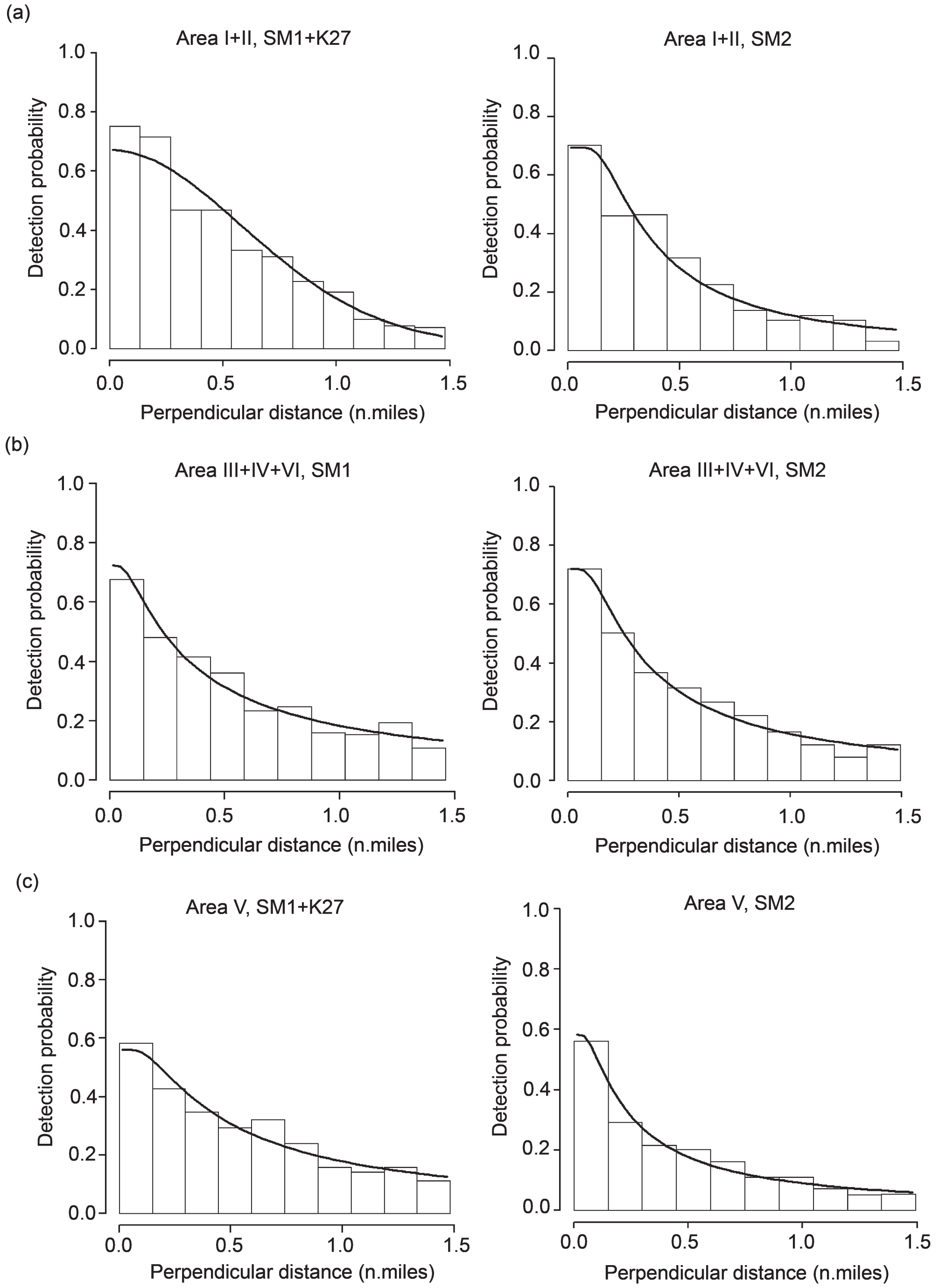


Fig. 3. Plots of fitted detection functions and histograms of perpendicular distances for the surveys conducted on vessels SM1, SM2 and K27 between 1985/86 and 2004/05. Detection function models were fitted with independent observer (IO) sightings data from all surveys conducted in the following (sets of) Area(s): (a) Areas I+II; (b) Areas III, IV and VI; (c) Area V.

Table 3

Summary of selected detection function models and derived detection probability estimates for surveys between 1985/86 and 2003/04. Detection function models were fitted with Independent Observer (IO) sightings data from all surveys conducted in the following (sets of) Area(s): (a) Areas I + II; (b) Areas III, IV and VI; and (c) Area V. $\hat{p}.(0)$ is the estimated average probability of sighting an Antarctic minke whale group on the survey line, derived from the mark recapture (MR) model. All MR models assumed point independence. $\hat{g}.(x)$ is the estimated average detection probability derived from the distance sampling (DS) model which assumed $g(0) = 1$. $\hat{p}.(x)$ is the estimated average detection probability from the mark recapture distance sampling (MRDS) model. Abbreviations: hn = half-normal model, hr = hazard-rate model, x = perpendicular distance, s = school size, ss = sea state.

Area	Vessel	Number of duplicate sightings	Selected model	$\hat{p}.(0) \pm SE$	$\hat{g}.(x) \pm$ SE	$\hat{p}.(x) \pm$ SE
I + II	SM1 + K27	119	hn (DS: $x + s$, MR: $x + s$)	0.672 ± 0.030	0.503 ± 0.017	0.338 ± 0.019
	SM2	135	hr (DS: $x + s$, MR: $x + s$)	0.696 ± 0.029	0.384 ± 0.028	0.267 ± 0.023
III + IV + VI	SM1	127	hr (DS: $x + s$, MR: $x + s + ss$)	0.724 ± 0.031	0.418 ± 0.045	0.303 ± 0.036
	SM2	167	hr (DS: x, MR: $x + s$)	0.721 ± 0.025	0.400 ± 0.034	0.289 ± 0.027
V	SM1 + K27	234	hr (DS: $x + s$, MR: $x + s + ss$)	0.561 ± 0.027	0.496 ± 0.034	0.278 ± 0.024
	SM2	152	hr (DS: $x + s$, MR: $x + s + ss$)	0.584 ± 0.031	0.313 ± 0.031	0.182 ± 0.021

Table 4

Detection-function model fits with AIC and ΔAIC for the surveys conducted between 1981/82 and 1984/85. Abbreviations: hn = half-normal model, hr = hazard-rate model, *x* = perpendicular distance, *s* = school size, *sg* = sightability, *ss* = sea state. Selected models are in bold. Only models with good fits are listed.

Survey season	Area	Vessel	Model	AIC	ΔAIC
1981/82	II	SM1	**hn (*x*+*s*)**	**60.8**	**0**
			hn (*x*+*sg*)	73.1	12.3
			hn (*x*)	74.9	14.1
		SM2	**hn (*x*+*s*)**	**22.6**	**0**
			hn (*x*)	28.8	6.2
			hn (*x*+*sg*)	30.5	7.9
			hn (*x*+*s*+*sg*)	21.0	8.4
1982/83	I	SM1	**hn (*x*+*s*)**	**79.8**	**0**
			hn (*x*+*s*+*sg*)	81.9	2.1
			hn (*x*)	94.6	14.8
			hn (*x*+*sg*)	94.7	14.9
		SM2	**hn (*x* + *s*)**	**194.2**	**0**
			hn (*x* + *sg*)	197.0	2.8
			hn (*x* + *s* + *sg*)	199.6	5.4
			hn (*x*)	204.2	10.0
1983/84	VI	SM1	**hr (*x* + *s*)**	**38.8**	**0**
			hr (*x*)	39.4	0.6
			hn (*x*)	40.5	1.7
			hr (*x* + *sg*)	41.2	2.4
			hr (*x* + *s*)	41.7	2.9
		SM2	**hn (*x*)**	**– 0.14**	**0**
			hn (*x* + *sg*)	1.81	2.0
			hn (*x* + *s*)	1.86	2.0
		K27	**hr (*x* + *s*)**	**5.1**	**0**
			hr (*x* + *s* + *sg*)	9.0	3.9
			hr (*x* + *s*)	11.7	6.6
			hr (*x*)	12.2	7.1
			hn (*x*)	21.6	16.5
1984/85	IV	SM1	**hn (*x*)**	**1.5**	**0**
			hn (*x* + *s*)	2.1	0.6
			hr (*x*)	3.1	1.6
			hn (*x* + *sg*)	3.4	1.9
			hn (*x* + *ss*)	3.5	2.0
		SM2	**hr (*x* + *s*)**	**78.9**	**0**
			hr (*x*)	94.1	15.2
			hn (*x*)	95.6	16.7
			hr (*x* + *ss*)	95.8	16.9
			hr (*x* + *sg*)	96.1	17.2
		K27	**hn (*x* + *s*)**	**29.3**	**0**
			hn (*x*)	31.0	1.7
			hn (*x* + *ss*)	31.9	2.6
			hn (*x* + *sg*)	32.3	3.0

Table 5

Detection-function model fits with AIC and ΔAIC for the surveys conducted between 1985/86 and 2003/04. Abbreviations: hn = half-normal model, hr = hazard-rate model, DS = Distance Sampling model, MR = Mark Recapture model, *x* = perpendicular distance, *s* = school size, *sg* = sightability, *ss* = sea state, *v* = vessel. Selected models are in bold. Only models with good fits are listed.

Area	Vessel	Model	AIC	ΔAIC
I+II	SM1+K27	**hn (DS: *x* + *s*, MR: *x*+ *s*)**	**1,242.9**	**0**
		hn (DS: *x* + *s* + *ss*, MR: *x* + *s*)	1,245.9	3.0
		hn (DS: *x* + *s* + *sg*, MR: *x* + *s*)	1,248.0	5.1
		hn (DS: *x* + *sg*, MR: *x* + *s*)	1,250.1	7.2
		hn (DS: *x* + *ss*, MR: *x* + *s*)	1,251.5	8.6
		hn (DS: *x*, MR: *x* + *s*)	1,255.9	13
		hn (DS: *x*, MR: *x* + *s* + *ss*)	1,257.0	14.1
		hn (DS: *x*, MR: *x* + *s* + *v*)	1,257.7	14.8
		hn (DS: *x*, MR: *x* + *s* + *sg*)	1,259.2	16.3
		hr (DS: *x*, MR: *x* + *s*)	1,259.4	16.5
		hn (DS: *x*, MR: *x* + *ss*)	1,291.6	48.7
		hn (DS: *x*, MR: *x*)	1,291.7	48.8
		hn (DS: *x*, MR: *x* + *v*)	1,292.6	49.7
		hn (DS: *x*, MR: *x* + *sg*)	1,296.1	53.2
	SM2	**hr (DS: *x* + *s*, MR: *x* + *s*)**	**1,176.9**	**0**
		hr (DS: *x* + *sg*, MR: *x* + *s*)	1,180.2	3.3
		hr (DS: *x*, MR: *x* + *s*)	1,180.3	3.4
		hr (DS: *x* + *ss*, MR: *x* + *s*)	1,182.3	5.4
		hn (DS: *x*, MR: *x* + *s*)	1,191.1	14.2
		hn (DS: *x*, MR: *x* + *s* + *ss*)	1,191.1	14.2
		hn (DS: *x*, MR: *x*)	1,201.1	24.2
		hn (DS: *x*, MR: *x* + *ss*)	1,202.0	25.1
III+IV+VI	SM1	**hr (DS: *x* + *s*, MR: *x* + *s* + *ss*)**	**1,188.4**	**0**
		hr (DS: *x*, MR: *x* + *s* + *ss*)	1,191.7	3.3
		hr (DS: *x* + *sg*, MR: *x* + *s* + *ss*)	1,193.0	4.6
		hr (DS: *x* + *ss*, MR: *x* + *s* + *ss*)	1,193.2	4.8
		hn (DS: *x*, MR: *x* + *s* + *ss*)	1,206.3	17.9
		hn (DS: *x*, MR: *x* + *s*)	1,213.3	24.9
		hn (DS: *x*, MR: *x* + *s* + *sg*)	1,215.3	26.9
		hn (DS: *x*, MR: *x* + *ss*)	1,216.0	27.6
		hn (DS: *x*, MR: *x*)	1,222.8	34.4
		hn (DS: *x*, MR: *x* + *sg*)	1,224.2	35.8
III+IV+VI	SM2	**hr (DS: *x*, MR: *x* + *s*)**	**1,588.4**	**0**
		hr (DS: *x* + *s*, MR: *x* + *s*)	1,588.7	0.3
		hr (DS: *x* + *sg*, MR: *x* + *s*)	1,590.4	2.0
		hr (DS: *x* + *ss*, MR: *x* + *s*)	1,590.4	2.0
		hn (DS: *x*, MR: *x* + *s*)	1,614.3	25.9
		hn (DS: *x*, MR: *x* + *s* + *ss*)	1,615.3	26.9
		hn (DS: *x*, MR: *x* + *ss*)	1,618.9	30.5
		hn (DS: *x*, MR: *x* + *s* + *sg*)	1,621.1	32.7
		hn (DS: *x*, MR: *x*)	1,624.8	36.4
		hn (DS: *x*, MR: *x* + *sg*)	1,631.1	42.7
V	SM1 + K27	**hr (DS: *x* + *s*, MR: *x* + *s* + *ss*)**	**2,373.6**	**0**
		hr (DS: *x*, MR: *x* + *s* + *ss*)	2,380.6	7.0
		hr (DS: *x* + *sg*, MR: *x* + *s* + *ss*)	2,391.2	17.6
		hr (DS: *x* + *ss*, MR: *x* + *s* + *ss*)	2,392.2	18.6
		hn (DS: *x*, MR: *x* + *s* + *ss*)	2,396.3	22.7
		hn (DS: *x*, MR: *x* + *ss*)	2,445.3	71.7
		hn (DS: *x*, MR: *x* + *s*)	2,447.3	73.7
		hn (DS: *x*, MR: *x* + *s* + *sg*)	2,449.9	76.3
		hn (DS: *x*, MR: *x*)	2,466.6	93.0
		hn (DS: *x*, MR: *x* + *sg*)	2,468.1	94.5
	SM2	**hr (DS: *x* + *s*, MR: *x* + *s* + *ss*)**	**1,291.9**	**0**
		hr (DS: *x* + *sg*, MR: *x* + *s* + *ss*)	1,294.3	2.4
		hr (DS: *x*, MR: *x* + *s* + *ss*)	1,296.9	5.0
		hr (DS: *x* + *ss*, MR: *x* + *s* + *ss*)	1,298.5	6.6
		hn (DS: *x*, MR: *x* + *s* + *ss*)	1,339.0	47.1
		hn (DS: *x*, MR: *x* + *s*)	1,342.3	50.4
		hn (DS: *x*, MR: *x* + *ss*)	1,361.9	70.0
		hn (DS: *x*, MR: *x*)	1,365.4	73.5

Spatial models and selected covariates

To illustrate goodness-of-fit, Fig. 4 shows standard diagnostic plots for a fitted GAM using the gam.check function in package *mgcv*. Plots correspond to data collected during the 1981/82 survey and show patterns common to the majority of models fitted in this study. For instance, the QQ-plot (upper left panel) has a convex shape and the histogram of residuals (lower left panel) is right-skewed. Nevertheless, the distribution of predicted Antarctic minke whale density for the 1981/82 survey corresponded broadly with the sightings distribution (Fig. 5). The moderate model fit is the result of the high proportion of segments for which no schools were sighted: this proportion was often in excess of 70% for the various survey years. Methods specifically devised for zero-inflated data (R package *COZIGAM* 2.0–2, Liu and Chan, 2009) could not improve the results, due to non-convergence issues during the iteration process of model fitting.

GAM model descriptions are given in Table 6. It was not possible to select a good model, based on spatial covariates which were the main focus of this analysis, for the 1995/96 and 2001/02 surveys. Seven out of ten potential covariates were included at least once in the selected GAMs; only SSV, chlorophyll a concentration and latitude were never selected.

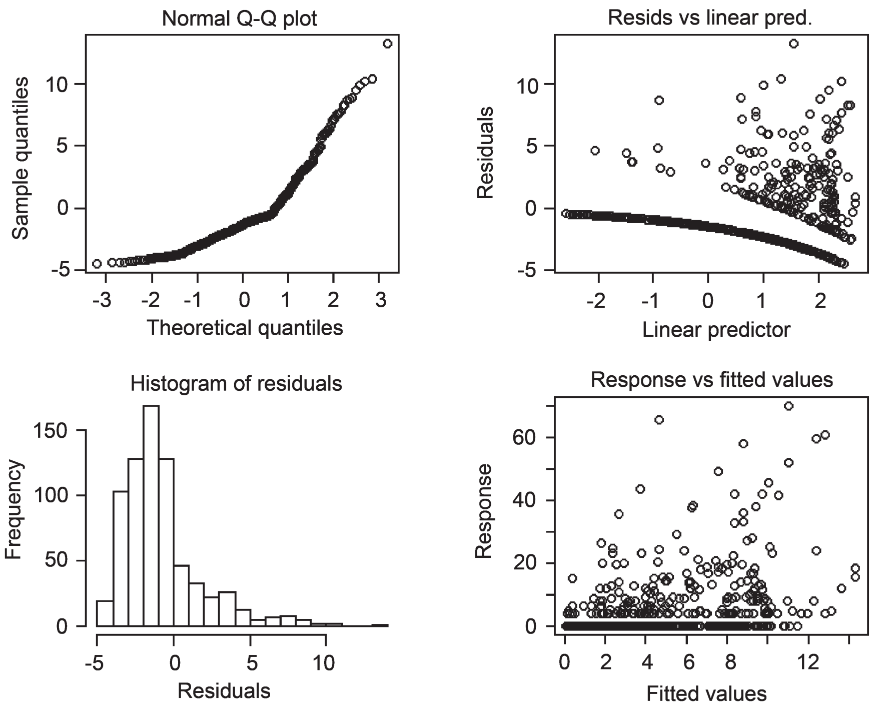


Fig. 4. Standard diagnostic plots for the model based on the 1981/82 survey.

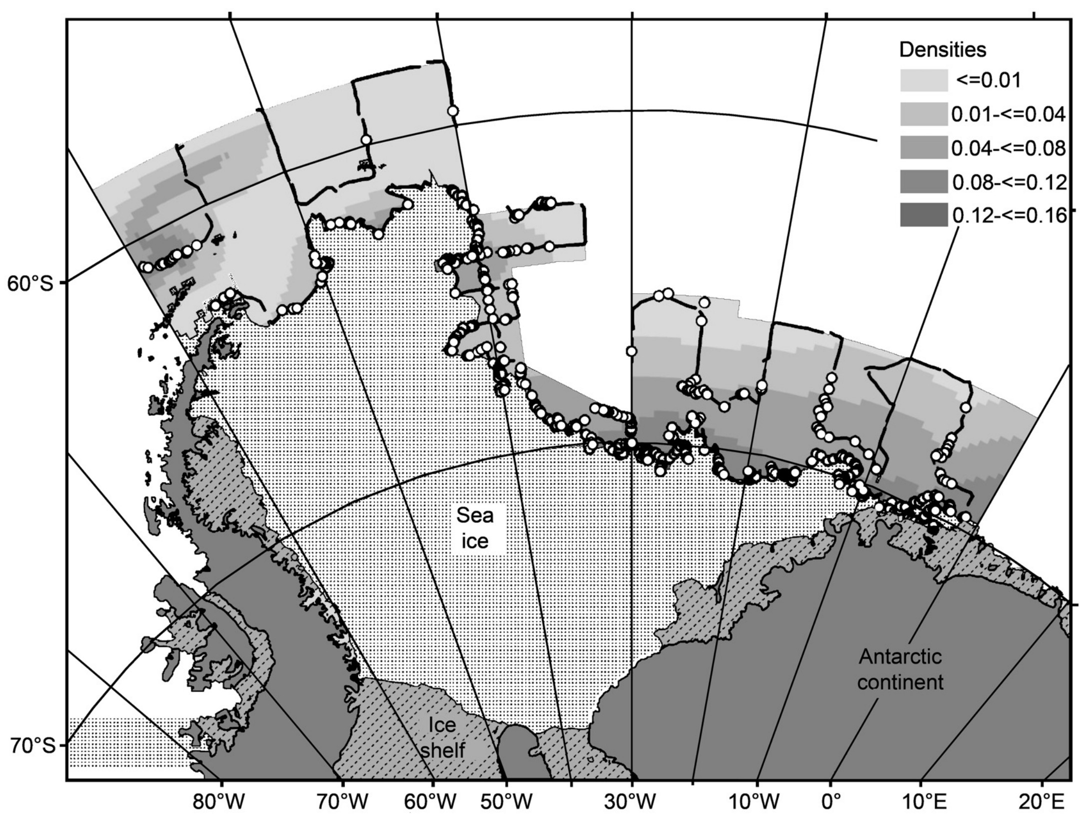
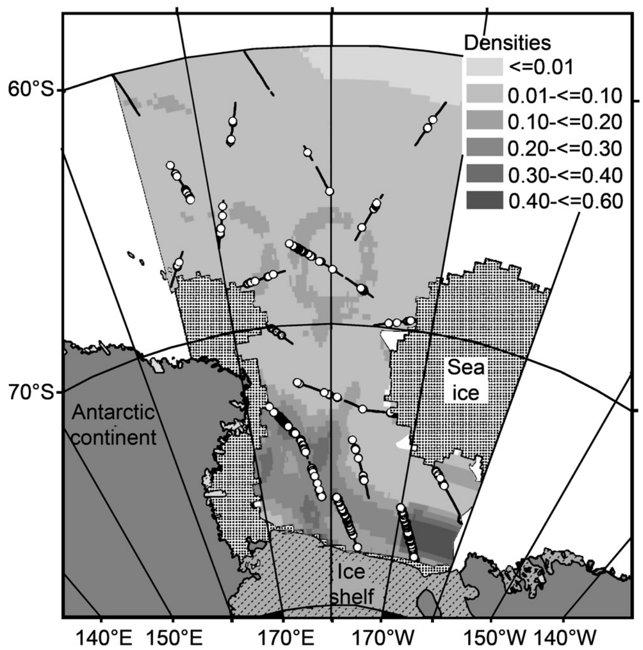


Fig. 5. Prediction plot of Antarctic minke whale density in the Weddell Sea sector (Area II) for the 1981/82 survey. Density, expressed in number of whales per km^2, was only predicted for surveyed strata. Sightings are represented by circles; survey effort is displayed by thick solid lines. The overlapping period for surveys conducted in Area II was 16 January – 8 February.

Of the environmental covariates, closest distance to the continental shelf break (1000m-dist), sea ice edge (icedist) and SACCF (SACCFdist) were most often included in the models. Table 7 shows selected model output. Explained deviances ranged from 14.9% to 35.1%, with a mean explained deviance of 25.3%.

Table 7 highlights the highly variable nature of the relationships between whale density and the environment. Firstly, none of the covariates showed a consistent qualitative relationship with its effect on Antarctic minke whale density. However, three covariates (1,000m-dist, icedist and OISST) had a predominantly negative relationship with density. No



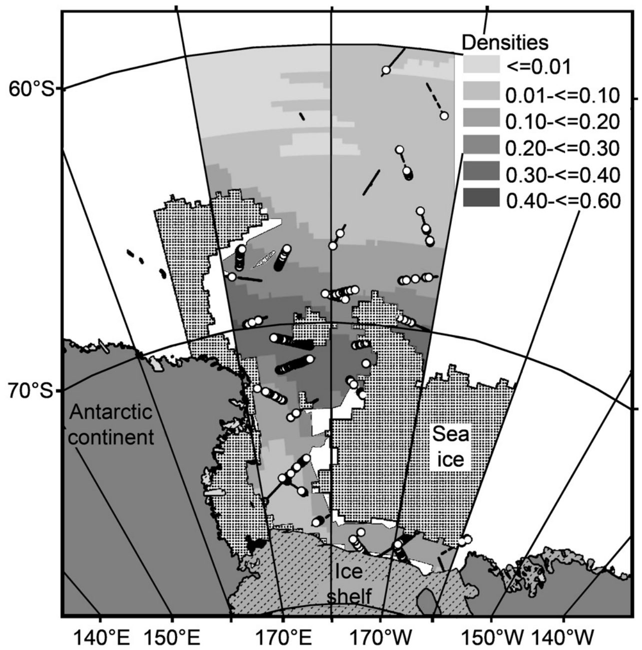


Fig. 6. Prediction plots of Antarctic minke whale density in the Ross Sea sector (Area V) for the 1985/86 survey (a) and 2003/04 survey (b). Density, expressed in number of whales per km^2, was only predicted for surveyed strata. Sightings in independent observer (IO) mode are represented by circles; survey effort in IO mode is displayed by thick solid lines. The overlapping period for surveys conducted in Area V was 27 December – 8 February.

dominant qualitative relationships were found for longitude, depth, SACCFdist or SBACCdist. Secondly, the selected models for every Management Area had variable sets of covariates. None of the covariates were selected in all surveys conducted in the same Management Area. Icedist was most often selected in models based on surveys in the Weddell Sea sector (Area II), a sector characterised by strong seasonal ice melt. Furthermore, icedist was non-significant for all models based on surveys in regions within the Bellingshausen/Amundsen Seas (Area I) and Indian Ocean sector (Area III). Areas I and III were characterised by relatively small sea ice coverage throughout the survey period. 1000m-dist was most often selected in models based on surveys conducted in Area III.

Table 6

Descriptions of selected models per area and survey year. Numbers between brackets in the 'selected model' column refer to the covariate-specific number of degrees of freedom. Numbers between brackets in the error distribution column refer to the selected θ-value for the Tweedie error distribution. Abbreviations of the smoothers: s = isotropic smoother, te = tensor product smoother. Abbreviations of the covariates: *icedist* = closest distance to the sea ice edge (defined at 15% sea ice concentration), *OISST* = Optimally Interpolated Sea Surface Temperature, *1000m-dist* = closest distance to the continental shelf edge (defined at 1000m depth), *SACCFdist* = closest distance to the Southern Antarctic Circumpolar Current Front (SACCF), *SBACCdist* = closest distance to the Southern Boundary of the Antarctic Circumpolar Current (SBACC). Model descriptions are given as fitted with the R software library *mgcv* (V1.5–5). All models included an offset variable which consisted of the natural logarithm of the segment area.

Area	Survey season	Selected model	Error distribution
I	1982/83	s(*longitude*, 2.6) + s(*1000m-dist*, 8.4)	Tweedie (1.3)
	1989/90	s(*OISST*, 3.0) + s(*SACCFdist*, 4.8)	Tweedie (1.4)
	1993/94	s(*longitude*, 8.7) + s(*1000m-dist*, 2.0)	Tweedie (1.2)
	1999/2000	s(*longitude*, 4.5) + s(*1000m-dist*, 1.0)	Tweedie (1.3)
II	1981/82	s(*icedist*, 3.0) + s(*SACCFdist*, 7.8)	Tweedie (1.1)
	1986/87	s(*longitude*, 7.2) + s(*depth*, 4.0)	Tweedie (1.3)
	1996/97	s(*longitude*, 4.0) + s(*icedist*, 3.0)	Tweedie (1.1)
	1997/98	s(*icedist*, 2.1) + s(*1000m-dist*, 4.0)	quasi-Poisson
III	1987/88	s(*longitude*, 8.4) + te(*1000m-dist*, 1.0)	Tweedie (1.1)
	1992/93	s(*longitude*, 4.0) + s(*1000m-dist*, 4.9)	Tweedie (1.1)
	1994/95	s(*OISST*, 6.1) + s(*1000m-dist*, 1.0) + te(*SACCFdist*, 1.8)	quasi-Poisson
	2004/05	s(*OISST*, 1.0) + s(*depth*, 4.0)	Tweedie (1.3)
IV	1984/85	s(*longitude*, 8.0) + te(*OISST*, 2.2) + s(*SBACCdist*, 5.0)	Tweedie (1.1)
	1988/89	s(*longitude*, 4.0) + s(*icedist*, 2.0)	Tweedie (1.3)
	1998/99	s(*longitude*, 4.0) + s(*1000m-dist*, 1.6)	Tweedie (1.3)
V	1985/86	s(*depth*, 4.0) + s(*1000m-dist*, 4.0)	Tweedie (1.2)
	1991/92	s(*1000m-dist*, 1.0) + s(*SACCFdist*, 7.0)	Tweedie (1.3)
	2002/03	s(*longitude*, 6.3) + s(*icedist*, 1.0)	Tweedie (1.1)
	2003/04	s(*OISST*, 4.0) + s(*SACCFdist*, 2.7)	Tweedie (1.2)
VI	1983/84	s(*longitude*, 2.5) + s(*1000m-dist*, 7.4)	Tweedie (1.2)
	1990/91	s(*icedist*, 2.0) + te(*SACCFdist*, 3.4)	quasi-Poisson
	2000/2001	s(*longitude*, 8.4) + s(*icedist*, 1.4)	quasi-Poisson

Table 7

Model output for the various surveys, grouped per IWC Area. The covariate columns show the relationships between a specific covariate and the effect of the specific covariate on Antarctic minke whale density. Abbreviations of the covariates: *icedist* = closest distance to the sea ice edge (defined at 15% sea ice concentration), *OISST* = Optimally Interpolated Sea Surface Temperature, *1000m-dist* = closest distance to the continental shelf edge (defined at 1,000m depth), *SACCFdist* = closest distance to the Southern Antarctic Circumpolar Current Front (SACCF), *SBACCdist* = closest distance to the Southern Boundary of the Antarctic Circumpolar Current (SBACC). Legend for the relationship characterisations: — = negative, + = positive, ∪ = minimum effect on density in middle of covariate range, ∩ = maximum effect on density in middle of covariate range, NL = complex non-linear relationship.

			Covariates						
IWC Area	Survey season	Explained deviance (%)	*Longitude*	*Icedist*	*OISST*	*Depth*	*1000m-dist*	*SACCF-dist*	*SBACC-dist*
Area I	1982/83	21.5	∩				—		
(120–60°W)	1989/90	22.0			—			∪	
	1993/94	30.5	NL				—		
	1999/2000	32.8	+				—		
Area II	1981/82	27.3		—				NL	
(60°W–0)	1986/87	26.4	NL			—			
	1996/97	23.7	—	∪					
	1997/98	35.1		—			+		
Area III	1987/88	33.4	NL				—		
(0–70°E)	1992/93	31.2	—				—		
	1994/95	33.5			—		—	—	
	2004/05	30.8			—	NL			
Area IV	1984/85	17.0	NL		—				NL
(70–130°E)	1988/89	28.2	∪	—					
	1998/99	20.9	NL				—		
Area V	1985/86	19.5				—	∩		
(130°E–170°W)	1991/92	14.9					—	NL	
	2002/03	17.4	NL	—					
	2003/04	24.8			—			∩	
Area VI	1983/84	23.6	—				NL		
(170–120°W)	1990/91	15.5		—				∪	
	2000/2001	27.3	NL	—					

Density distributions

The Antarctic minke whale density distribution plots generated with the spatial models showed changes in whale density distribution throughout the years. As an example, Fig. 6 shows the predicted density distributions within the Ross Sea sector (165°E–170°W) for the 1985/86 and 2003/04 surveys. For both surveys, relatively high minke whale densities were predicted on or near the continental shelf. However, minke whale densities higher than 0.2 whale per km^2 were exclusively predicted below 72°S for the 1985/86 survey (Fig. 6a), whereas these densities were predicted within the 68°–72°S band for the 2003/04 survey (Fig. 6b). These results suggest an important spatial and temporal heterogeneity in Antarctic minke whale density and distribution.

DISCUSSION

Detection probabilities

Detection probability estimates as reported by Bravington and Hedley (2009) were closest to independent estimates reported by Burt *et al*. (2009), based on Buckland-Turnock (BT) mode experiments conducted during 2005/06–2007/08 (IWC, 2009). Therefore, the detection probability estimates in this study were compared with those reported by Bravington and Hedley (2009); the estimates in Burt *et al.* (2009) were derived from a different dataset. As $\overline{p}.(0)$ estimates in Bravington and Hedley (2009) were only provided for the individual platforms, the estimates for $\overline{p}.(x)$ were compared with each other (Table 8). For the majority of CPII sightings, $\overline{p}.(x)$ estimates reported by the two studies were similar. Furthermore, $\overline{p}.(x)$ estimates were also similar for the two largest classes of CPIII sightings. These two classes contained only sightings of one-animal schools, and had sightability values of 3 and 4+, respectively. For almost all other classes of CPIII sightings, $\overline{p}.(x)$ estimates in this study were lower than those reported by Bravington and Hedley (2009). The exception was sightings of individual whales seen with sightability 2, which had a higher $\overline{p}.(x)$ estimate in this study.

The discrepancies in $\overline{p}.(x)$ estimates for various classes may be partly attributed to the different ways in which the two studies pooled IO sightings data. Furthermore, Bravington and Hedley (2009) developed a more sophisticated method for estimating detection probabilities, which takes school size errors into account. The possibility that discrepancies in $\overline{p}.(x)$ estimates could affect presented model output was assessed by comparing the output of the models presented in this paper with models in which the $\overline{p}.(x)$ estimates reported by Bravington and Hedley (2009) were incorporated. It was found that the model output in terms of covariate inclusion and the qualitative nature of covariate- whale density relationships remained the same. However, explained deviance was often somewhat lower for the models that incorporated the $\overline{p}.(x)$ estimates reported by Bravington and Hedley (2009). The aim of this study was to examine the relationships between whale density and the environment; the detection probability estimates were not used for whale abundance estimation. Therefore, the detection probability estimates reported in this paper are sufficient for the purpose of this study.

Table 8

Comparison of estimates $\bar{p}.(x)$ for in this study, $\hat{p}.(x)_{BE}$, with those reported by Bravington and Hedley (2009), $\hat{p}.(x)_{BR}$. $\hat{p}.(x)_{BR}$ is defined as $\widehat{ESW}_{BR}$ / 1.5 (truncation distance = 1.5 nmi), with $\widehat{ESW}_{BR}$ = estimated effective strip half-width as reported in Bravington and Hedley (2009). CP = circumpolar set, n = number of sightings in specific class. $\hat{p}.(x)_{DIFF}$ = $\hat{p}.(x)_{BE}$ minus $\hat{p}.(x)_{BR}$. ESW_{BR} estimates are given for classes defined by sea state for CPII surveys, and for classes defined by sightability for CPIII surveys.

Sea state	Sightability	School size	n	$\hat{p}.(x)_{BE}$	$\widehat{ESW}_{BR}$	$\hat{p}.(x)_{BR}$	$\hat{p}.(x)_{DIFF}$
CPII							
0–2		1	90	0.24	0.33	0.22	+0.02
		2	27	0.38	0.69	0.46	–0.08
		3–4	14	0.48	0.89	0.59	–0.11
		5–9	7	0.47	1.03	0.69	–0.22
		10+	3	0.71	1.30	0.87	–0.16
3+		1	812	0.23	0.29	0.19	+0.04
		2	323	0.35	0.46	0.31	+0.04
		3–4	208	0.43	0.65	0.43	0
		5–9	73	0.44	0.69	0.46	–0.02
		10+	25	0.64	1.04	0.69	–0.05
CPIII							
	4+	1	513	0.29	0.52	0.35	–0.06
		2	179	0.38	0.78	0.52	–0.14
		3–4	98	0.43	0.99	0.66	–0.23
		5–9	43	0.46	1.02	0.68	–0.22
		10+	17	0.50	1.38	0.92	–0.42
	3	1	521	0.24	0.41	0.27	–0.03
		2	176	0.33	0.64	0.43	–0.10
		3–4	121	0.40	0.85	0.57	–0.17
		5–9	44	0.42	0.91	0.61	–0.19
		10+	21	0.51	1.33	0.89	–0.38
	2	1	86	0.23	0.16	0.11	+0.12
		2	30	0.28	0.62	0.41	–0.13
		3–4	10	0.30	0.76	0.51	–0.21
		5–9	2	0.37	0.81	0.54	–0.17
		10+	1	0.63	0.98	0.65	–0.02

Exclusion of covariates in the GAMs

Most covariates considered for model selection were retained by the best models in various combinations (Table 6). Only SSV, chlorophyll a concentration and latitude were never selected in the best models. For the first two covariates, this may have been due to limitations of the available remote sensing datasets: SSV data were not available for a wide band along the sea ice edge, which made it harder to detect a signal across the survey region, if indeed there was any signal present; and chlorophyll a data were missing in a large proportion of the weekly grids due to cloud cover. The chlorophyll a range was also very small for some Areas (e.g. Area IV), which made it hard to detect any signal if present. Thus, it is not clear if a better spatial coverage of this covariate would improve the explanatory value of the models. Latitude was often highly correlated with other covariates, especially with icedist and OISST, and thus was often dropped in later steps of the model selection process.

Relationships with the environment

Covariates related to transition zones, such as 1,000m-dist, icedist and SACCFdist, were most often selected in the models. As transition zones often show enhanced productivity, the expected effect of these covariates on whale density would be smaller or more negative at greater distances to the boundaries of the zones (Kasamatsu *et al.*, 2000; Tynan, 1998). In agreement, the covariate-density effect relationships for 1,000m-dist and icedist were predominantly negative. This suggested that Antarctic minke whale density tended to be higher in regions closer to the continental shelf break and/or sea ice edge, often in colder waters (as icedist and OISST were often highly correlated, a selected model never included both icedist and OISST, with icedist having a clearer signal in more models). However, the covariate-density effect relationship for SACCFdist was often difficult to interpret, suggesting that the Antarctic Circumpolar Current may not be as important for Antarctic minke whales as it has been reported to be for larger baleen whales (Tynan, 1998).

This study suggests that relationships between minke whales and their environment are best explored at a regional scale; spatial models did not show consistent relationships between the covariates and their effects on density at the circumantarctic scale. Circumantarctic relationships between minke whale density and their environment may be non-significant, while those relationships are significant at a regional scale.

Even within Management Areas, it was not possible to detect consistent qualitative relationships between minke whale density and environment over the various survey years. This in part may be explained by the changing ice-related boundaries of the surveys between years and hence differences in survey regions. Another possible reason may be that only a limited number of environmental variables could be considered for this study. Other aspects of the environment that interact with the selected covariates, for which data were not available, may have changed throughout the years. In conjunction with this, the IWC/IDCR-SOWER surveys did not cover the pack ice region. Changes in the extent and heterogeneity of the pack ice may influence the Antarctic minke whale distribution in the pack ice region (Thiele *et al.*, 2005). The pack ice quantity and quality may affect the minke whale density distribution in open waters close to the sea ice edge as well. For instance, in years when the pack ice is more diverse in quality, shows more cracks, or encloses polynyas relatively in the proximity of the sea ice edge, Antarctic minke whales may move more easily into the pack ice region. In years when the pack ice close to the sea ice edge is more solid, the whales may be restricted in their movements into the pack ice region and stay in open waters close to the sea ice edge. In those years, the relationship between closest distance to the sea ice edge and its effect on Antarctic minke whale density in open waters may be (more) negative. In order to have a better understanding of the relationship between minke whale density and its environment in the various sectors of the Southern Ocean, more aerial and shipboard surveys within the pack ice region are needed, ideally in combination with shipboard surveys in open waters in the same sector of the Southern Ocean (Hedley *et al.*, 2007; Kelly *et al.*, 2009).

Performance and application of spatial models

Most spatial models for Antarctic minke whale density had moderate value for explained deviance. This was in part the result of the conservative selection method used in this study. The flexibility of the GAMs potentially leads to overfitting of the data (Forney, 2000; Hastie *et al.*, 2005). While overfitting is not critical for prediction purposes, it did not improve the ability to describe the physical environment underlying minke whale distribution, which was the main objective of this analysis. In order to prevent overfitting, a covariate was only selected if it contributed at least 4% to the explained deviance of the model. Alternatively, Principal Components Analysis can be used to reduce the number of intercorrelated variables, and then the principal components can be interpreted as synthetic climatic covariates (Grosbois *et al.*, 2008). However, this interpretation necessarily provides less fine-scale resolution when explaining the specific relationships whale-environment, and may not work well for covariate data sets with poor spatial resolution.

The performance of the models used in this study was probably also limited by the nature of the available environmental datasets from which covariates were derived. At this spatial scale, only remote sensing data and long-term frontal positions could be considered as covariate input for our models. Explained deviance of the models would probably increase if covariates could be included that more accurately reflect the environment, such as *in situ* data or remote sensing data at a higher resolution. For instance, explained deviances were 63.1% and higher for spatial models of baleen whales near the Western Antarctic Peninsula that included covariates derived from *in situ* chlorophyll a and acoustic zooplankton data (Friedlaender *et al.*, 2006). In order to obtain a better understanding of the relationship between whale density and the environment, more localised surveys can be conducted during which whale sightings data will be collected simultaneously with *in situ* non-biotic and biotic (prey) data.

Nevertheless, given the limited possibilities for including environmental information in our models, model performance was satisfactory. Furthermore, models could be developed for surveys under considerably different environmental conditions, such as sea ice distribution and coverage, for the same time period (Fig. 6). The predicted density maps (Figs 5 and 6) show both spatial and temporal variability in Antarctic minke whale density. Further investigation is planned on the temporal variability in density at a regional scale across the Southern Ocean by focusing on regional environmental features that were not captured by the models. Examples are regional sea ice extent during the survey and the degree of seasonal change therein. A better understanding of the temporal variability in whale density is needed for any scenario analysis of Antarctic minke whale density in the Southern Ocean under various climate regimes.

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REFERENCES

Ainley, D.G., Ballard, G. and Dugger, K.M. 2006. Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87(8): 2080–93.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp.267–81. *In*: Petran, B.N. and Csaáki, F. (eds). *International Symposium on Information Theory*. Akademia Kiado, Budapest, Hungary. 451pp.

Armstrong, A.J. and Siegfried, W.R. 1991. Consumption of Antarctic krill by minke whales. *Antarct. Sci.* 3(1): 13–18.

Arrigo, K.R., Worthen, D., Schnell, A. and Lizotte, M.P. 1998. Primary production in Southern Ocean waters. *J. Geophys. Res.* 103(C8): 15,587–15,600.

Branch, T.A. 2006. Abundance estimates for Antarctic minke whales from three completed circumpolar sets of surveys. Paper SC/58/IA18 presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies (unpublished). 28pp. [Paper available from the Office of this Journal].

Branch, T.A. and Butterworth, D.S. 2001. Southern Hemisphere minke whales: standardised abundance estimates from the 1978/79 to 1997/98 IDCR-SOWER surveys. *J. Cetacean Res. Manage.* 3(2): 143–74.

Branch, T.A. and Ensor, P. 2001. Report of the Scientific Committee. Annex G. Report of the sub-committee on the Comprehensive Assessment of whale stocks – In-depth Assessments. Appendix 8. Recommended species code changes for minke and blue whale sightings, for analysis of IDCR-SOWER surveys. *J. Cetacean Res. Manage. (Suppl.)* 3: 200–03.

Bravington, M.V. and Hedley, S.L. 2009. Antarctic minke whale abundance estimates from the second and third circumpolar IDCR/SOWER surveys using the SPLINTR model. Paper SC/61/IA14 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 25pp. [Paper available from the Office of this Journal].

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. vi + xv + 432pp.

Buckland, S.T. and Anganuzzi, A.A. 1988. Comparison of smearing methods in the analysis of minke sightings data from IWC/IDCR Antarctic cruises. *Rep. int. Whal. Commn* 38: 257–63.

Burt, M.L., Ensor, P. and Borchers, D.L. 2009. Detection probability of Antarctic minke whales: analyses of the BT mode experiments conducted on the IWC-SOWER cruises 2005/06–2007/08. Paper SC/61/IA18 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 14pp. [Paper available from the Office of this Journal].

Cavalieri, D.J., Parkinson, C.L., Gloersen, P. and Zwally, H.J. 1996, updated 2006. Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/1 passive microwave data. Boulder, Colorado, USA: National Snow and Ice data Center. [Digital media]

Cooke, J.G. 2009. An integrated method for analysis of IDCR/SOWER data and TRANSIM simulated data sets. Paper SC/A09/AE6 presented to the Workshop on minke whale abundance estimates using IWC/SOWER data, 7–10 April 2009, St. Andrews, UK (unpublished). 11pp. [Paper available from the Office of this Journal].

Donovan, G.P. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn (special issue)* 13: 39–68.

Ensor, P.H. 1989. Minke whales in the pack ice zone, East Antarctica, during the period of maximum annual ice extent. *Rep. int. Whal. Commn* 39: 219–25.

ESRI. 2006. Arcmap 9.2. Environmental Systems Resource Institute, Redlands, California.

Everson, I. 2000. Role of krill in marine food webs – The Southern Ocean. *In*: Everson, I. (eds). *Krill: biology, ecology and fisheries.* Blackwell Science, Oxford, UK. 384pp.

Forney, K.A. 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. *Conserv. Biol.* 14(5): 1271–86.

Friedlaender, A.S., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D. and Read, A.J. 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the western Antarctic peninsula shelf waters. *Mar. Ecol. Prog. Ser.* 317: 297–310.

Friedlaender, A.S., Lawson, G.L. and Halpin, P.N. 2009. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Mar. Mammal Sci.* 25(2): 402–15.

Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P. and Weimerskirch, H. 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.* 83: 357–99.

Hastie, G.D., Swift, R.J., Slesser, G., Thompson, P.M. and Turrell, W.R. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. *ICES J. Mar. Sci* 62: 760–70.

Hedley, S.L., Bravington, M., Gales, N., Kelly, N. and Peel, D. 2007. Aerial survey for minke whales off eastern Antarctica. 47pp. Paper SC/59/IA2 presented to the IWC Scientific Committee, May 2007, Anchorage, USA (unpublished). 47pp. [Paper available from the Office of this Journal]

Hedley, S., Buckland, S.T. and Borchers, D.L. 1999. Spatial modelling from line transect data. *J. Cetacean Res. Manage.* 1(3): 255–64.

Hedley, S., Reilly, S., Borberg, J., Holland, R., Hewitt, R., Watkins, J., Naganobu, M. and Sushin, V. 2001. Modelling whale distribution: a preliminary analysis of data collected on the CCAMLR-IWC krill synoptic survey, 2000. Paper SC/53/E9 presented to the IWC Scientific Committee, July 2001, London (unpublished). 38pp. [Paper available from the Office of this Journal].

Horvitz, D.G. and Thompson, D.J. 1952. A generalisation of sampling without replacement from a finite universe. *J. Am. Stat. Assoc.* 47: 663–85.

IOC, IHO and BODC. 2003. Centenary edition of the GEBCO Digital Atlas. [Published on CD-rom on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans, British Oceanographic Data Centre, Liverpool, UK.

International Whaling Commission. 2009. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 11:1–74.

Kasamatsu, F., Hembree, D., Joyce, G., Tsunoda, L., Rowlett, R. and Nakano, T. 1988. Distribution of cetacean sightings in the Antarctic: results obtained from the IWC/IDCR minke whale assessment cruises, 1978/79 to 1983/84. *Rep. int. Whal. Commn* 38: 449–87.

Kasamatsu, F., Matsuoka, K. and Hakamada, T. 2000. Interspecific relationships in density among the whale community in the Antarctic. *Polar Biol.* 23: 466–73.

Kawamura, A. 1994. A review of baleen whale feeding in the Southern Ocean. *Rep. int. Whal. Commn* 44: 261–71.

Kelly, N., Peel, D., Pike, D., Bravington, M.V. and Gales, N. 2009. An aerial survey for Antarctic minke whales in sea ice off east Antarctica: a pilot study. Paper SC/61/IA3 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 14pp. [Paper available from the Office of this Journal].

Laake, J.L. and Borchers, D.L. 2004. Methods for incomplete detection at distance zero. pp.108–89. *In*: Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. (eds). *Advanced Distance Sampling*. Oxford University Press, Oxford. 416pp.

Liu, H. and Chan, K-S. 2009. COZIGAM: constrained and unconstrained zero-inflated generaised additive models with model selection criterion. R package version 2.0–2.

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22: 197–300.

Meredith, M.P. and King, J.C. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett.* 32((L19604)): 5pp.

Moore, J.K. and Abbott, M.R. 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. *J. Geophys Res.* 105(C12): 28,709–722.

Murase, H., Matsuoka, K., Ichii, T. and Nishiwaki, S. 2002. Relationship between the distribution of euphausiids and baleen whales in the Antarctic (35°E–145°W). *Polar Biol.* 25: 135–45.

Okamura, H. and Kitakado, T. 2009. Abundance estimates and diagnostics of Antarctic minke whales from the historical IDCR/SOWER survey data using the OK method. Paper SC/61/IA6 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 58pp. [Paper available from the Office of this Journal].

Orsi, A.H., Whitworth, T., III and Nowlin, W.D., Jr. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res. I* 42: 641–73.

Peel, D., Kelly, N., Bravington, M.V. and Hedley, S. 2008. IWC 2008 title: Design of future SOWER voyages: an update. 11pp. Paper SC/60/IA5 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 11pp. [Paper available from the Office of this Journal].

Reilly, S., Hedley, S., Borberg, J., Hewitt, R., Thiele, D., Watkins, J. and Naganobu, M. 2004. Biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean. *Deep-Sea Res. II* 51(12–13): 1,397–1,409.

Reynolds, R.W., Rayner, N.A., Smith, T.M., Stokes, D.C. and Wang, W. 2002. An improved in situ and satellite SST analysis for climate. *J. Clim.* 15: 1,609–25.

Reynolds, R.W. and Smith, T.M. 1994. Improved global sea surface temperature analyses using optimum interpolation. *J. Clim.* 7: 929–48.

Ribic, C.A., Ainley, D.G. and Fraser, W.R. 1991. Habitat selection by marine mammals in the marginal ice zone. *Antarct. Sci.* 3(2): 181–86.

Smith, W.O., Jr and Nelson, D.M. 1986. Importance of ice edge phytoplankton production in the Southern Ocean. *Biosci.* 36: 251–57.

Southwell, C.J., Paxton, C.G.M., Borchers, D.L., Boveng, P.L., Nordøy, E.S., Blix, A.S. and De la Mare, W.K. 2008. Estimating population status under conditions of uncertainty: the Ross seal in East Antarctica. *Antarct. Sci.* 20(2): 123–33.

Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Yuan, X. and Rind, D. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño – Southern Oscillation and Southern Annular Mode variability. *J. Geophys Res.* CO3S90: 20pp.

Strindberg, S. and Burt, M.L. 2004. *IWC Database-Estimation System Software (DESS) User Manual*. Research Unit for Wildlife Population Assessment, Mathematical Institute, University of St Andrews, St Andrews. 300pp. [Paper available from the Office of this Journal].

Thiele, D., Chester, E. and Friedlaender, A. 2002. Antarctic sea-ice habitat for minke whales (*Balaenoptera acutorostrata* sp.). Results of a line transect survey in East Antarctica. Paper SC/54/IA6 presented to the IWC Scientific Committee, April 2002, Shimonoseki, Japan (unpublished). [Paper available from the Office of this Journal].

Thiele, D., Chester, E.T. and Asmus, K. 2005. Antarctic sea ice: measuring habitat complexity, and seasonal and regional variability in habitat use for minke whales (unpublished). 21pp. Paper SC/57/E1 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea. [Paper available from the Office of this Journal].

Thiele, D., Chester, E.T. and Gill, P.C. 2000. Cetacean distribution off Eastern Antarctica (80–150°E) during the austral summer of 1995/96. *Deep-Sea Res. II* 47 (12–13): 2543–72.

Thiele, D., Chester, E.T., Moore, S.E., Sirovic, A., Hildebrand, J.A. and Friedlander, A.S. 2004. Seasonal variability in whale encounters in the western Antarctic Peninsula. *Deep-Sea Res. II* 51(17–19): 2311–25.

Thiele, D. and Gill, P.C. 1999. Cetacean observations during a winter voyage into Antarctic sea ice south of Australia. *Antarct. Sci.* 11(1): 48–53.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment, University of St Andrews, UK. [Available from: *http://www.ruwpa.st-and.ac.uk/distance/*].

Tynan, C. and Thiele, D. 2003. Report on Antarctic ice edge definition by the ad hoc Working Group on ice data collection in the Antarctic. Paper SC/55/E19 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 1pp [Paper available from the Office of this Journal].

Tynan, C.T. 1998. Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. *Nature* 392: 708–10.

van Franeker, J.A. 1992. Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia seas, Antarctica, November 1988 to January 1989 (EPOS Leg 2). *Polar Biol.* 12: 93–102.

Wood, S.N. 2006. *Generalized Additive Models: an introduction with R*. Chapman and Hall, Boca Raton, Florida. 391pp.

Wood, S.N. 2008. Fast stable direct fitting and smoothness selection for generalised additive models. *J.R. Statist. Soc.* B70(3): 495–518.

Zerbini, A., Bannister, J.L., Branch, T., Clapham, P.J., Donovan, G.P., Leaper, R. and Reilly, S. 2008. A review of abundance, trends and foraging parameters of baleen whales in the Southern Hemisphere. 29pp. Paper SC/60/EM3 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 29pp. [Paper available from the Office of this Journal].

Zwally, H.J., Comiso, J.C., Parkinson, C.L., Cavalieri, D.J. and Gloersen, P. 2002. Variability of Antarctic sea ice 1979–1998. *J. Geophys Res.* 107(C5): 3041.

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