Antartic minke whale (*Balaenoptera bonaerensis*) density distributions in the Southern Ocean: a preliminary analysis.

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ABSTRACT

There is a need to characterise the physical environment associated with minke whale density in order to understand long-term changes in Antarctic minke whale distribution and density in the Southern Ocean in austral summer months. We developed spatial models for Antarctic minke whale densities using generalised additive models (GAMs) based on line transect data collected for the IDCR (International Decade of Cetacean Research) and SOWER (Southern Ocean Whale Ecosystem Research) programmes. The GAMs were fitted independently by survey year. Selected GAMs included combinations of the following covariates: distance from the sea ice edge, bathymetric depth and distance from the shelf edge, distances from the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC), Optimally Interpolated Sea Surface Temperature (OISST) and latitude. Explained deviances ranged between 24.5% and 66.8%. The spatial models did not show consistent relationships between the covariates and their effect on densities, although in most models Antarctic minke whale densities tended to be higher close to the sea ice edge and/or in colder surface waters. Predicted mean densities were in most regions lowest for the most recent surveys. In four out of ten regions, this coincided with a change in the relationship between at least one year-specific covariate and its effect on Antarctic minke whale density, with those relationships becoming non-significant over time. These changes in ecological relationships may reflect changes in the sea ice environment, which are not captured by the covariates we considered for the spatial models. Further work will investigate the variability in relationships between covariates and their effect on minke whale densities by focusing on overall environmental features that characterised the surveyed regions, such as changes in sea ice extent.

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

INTRODUCTION

The Southern Ocean is the most important feeding ground for Antarctic minke whales. Mainly during 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, 1991; van Franeker, 1992; Thiele and Gill, 1999; Thiele *et al.*, 2002, 2005) and in the open ocean (e.g. Kasamatsu et al., 1988, 2000; Thiele, 2000; Murase *et al.*, 2002; Friedlaender, 2006). Most studies on Antarctic minke whale distribution have associated encounter rates or sighting densities with environmental variables. For instance, Kasamatsu *et al.* (1988) found that Antarctic minke whales were seen more frequently near the sea ice edge at a circumpolar scale, with gradually decreasing densities for lower latitudes. Similarly, Kasamatsu *et al.* (2000) reported a significant negative correlation between Antarctic minke whale encounter rates and distance from the sea ice edge. Antarctic minke whale encounter rates also showed a gradient in this study along the different sea floor-slope types, with highest encounter rates coinciding with the continental shelf. The relationship between Antarctic minke whale encounter rates and sea surface temperature (SST) was non-significant.

During an austral summer survey in the waters off Eastern Antarctica, Antarctic minke whales were more frequently sighted close to the sea ice edge and the Southern Boundary of the Antarctic Circumpolar Current (SBACC) (Thiele *et al.* 2000). In a study by Murase *et al.* (2002), Antarctic minke whale sightings were concentrated in areas where the sea ice edge and continental slope coincided within the 35ºE-145ºW region during the 1998/1999 and 1999/2000 seasons. These areas were also populated by large krill aggregations. However, the authors concluded that Antarctic minke whale habitat selection was not primarily influenced by krill distribution, as only a few Antarctic minke whales were sighted in offshore areas containing large krill aggregations. From these independent studies, it is not clear what determines the variability in Antarctic minke whale distribution and density during the austral summer. Therefore, there is a need to characterise the physical environment associated with minke whale density in order to understand long-term changes in minke whale density associated with the environment.

In recent years, spatial models have been developed for baleen whale distributions in several parts of the Southern Ocean. Spatial models based on line transect data were developed by Hedley *et al.* (1999) and applied to survey data in the 0-40ºE region of the Southern Ocean. However, only distance from the sea ice edge was used as an explanatory environmental variable, together with latitude and longitude. Friedlaender *et al.* (2006) developed spatial models based on pooled humpback and Antarctic minke whale sightings in waters off the Western Antarctic Peninsula, collected during surveys in the autumn of 2001 and 2002. All spatial models suggested that whale distribution was influenced by zooplankton acoustic volume between 25-100m, distance from the sea ice edge and bathymetric slope.

To our knowledge, spatial models have not been developed for baleen whales at a circumpolar scale. 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. This has resulted in three circumpolar sets of surveys. The IWC/IDCR-SOWER surveys were specifically designed for the visual detection of cetaceans, with an emphasis on Antarctic minke whales. This is in contrast with surveys during which baleen whale sightings and krill acoustics data were simultaneously sampled, such as during the CCAMLR2000 (Commission for the Conservation of Antarctic Marine Living Resources, Reilly *et al.*, 2004) and SO GLOBEC surveys (Southern Ocean Global Ocean Ecosystem Dynamics, Thiele *et al.*, 2004; Friedlaender *et al.*, 2006).

The IWC/IDCR-SOWER dataset is thus the only circumpolar whale sightings dataset for the Southern Ocean that allows for a long-term circumpolar analysis of variability in minke whale density. We applied the spatial model methodology developed by Hedley *et al.* (1999) to analyse this dataset. We hypothesised that Antarctic minke whale distribution was determined by the distribution of its main prey. However, as krill density and other biological variables were not sampled during the IWC/IDCR-SOWER cruises, we used remote sensing variables which are likely to be related to krill distribution. Examples are variables related to sea ice (Nicol *et al.*, 2006), bathymetry (Pauly *et al.*, 2000, Atkinson *et al.*, *in press*), sea surface temperature (Pauly *et al.*, 2000) and fronts associated with the Antarctic Circumpolar Current (ACC) (Murphy *et al.*, 2004). With this analysis we provide for the first time a large-scale and long-term perspective of the variability in minke whale density and distribution associated with the physical environment.

MATERIALS AND METHODS

Study area and effort

The IWC/IDCR-SOWER programme has already resulted in three circumpolar sets of cetacean sighting surveys in the Southern Ocean. We decided not to use data from the first few surveys (1978/79 – 1980/81), as there were not enough environmental data to produce reliable spatial models. We developed spatial models based on line transect data from the 1981/82-2004/05 IWC/IDCR-SOWER surveys. Each year, one of six IWC management Areas was surveyed. Sometimes Areas were revisited, if the Area could not be surveyed completely in the previous year. Table 1 shows general information about the surveys used in this study. Total area covered 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

4,991km (2000/2001 survey), while a maximum of 32,678km primary effort was obtained during the 1985/86 survey.

Whale sightings and g(0) estimation

For this analysis, we selected sightings coded as “04”, definitely Antarctic minke whale according to IWC classification rules, obtained during primary effort mode, both closing and passing mode. From these, only the first sighting of a pair/triplet of non-simultaneous “definite” (“D”) duplicates was included in the analysis. Duplicates marked as possible duplicate (“P”), remotely possible duplicate (“R”) and “uncertain” (“U”) were treated as separate sightings.

We estimated g(0), the probability that a whale group on the transect line was sighted, using Mark Recapture Distance Sampling (MRDS) methods as implemented in Distance V5.0 release 2 (Thomas *et al.*, 2006). Only Antarctic minke whale sightings collected during Independent Observer (IO) mode served as input for detection functions that assumed point independence (Laake and Borchers, 2004). The g(0) values could be estimated for surveys undertaken since the 1985/86 season, as IO sightings data have only been collected during these surveys. The g(0) values were estimated per vessel for each survey season. IO sightings data were pooled over several surveys in the same Area if the number of IO sightings for a vessel was too low (i.e. under 60, Buckland *et al.*, 2001, p. 240) or if the detection function did not provide a good fit based on data collected only on the particular vessel. As the estimated g(0) values were clearly smaller than 1 for the surveys conducted since 1985/86, we also abandoned the g(0) = 1 assumption for the surveys between 1981/82 and 1984/85, for which IO data were not available. Instead, for the vessels that also took part in later surveys (labelled as “SM1” and “SM2”), we fitted detection functions using all IO sightings data that had been collected during the 1985/86-2004/05 surveys in the particular Area. Vessels which had only been used in the 1981/82 – 1984/85 seasons (i.e. for which none of the sightings have been collected under IO mode) had g(0) values assigned to them which were averages of the g(0) values for the other vessels that had collected IO sightings data in the same Area over the years.

Remote sensing data

The IWC/IDCR-SOWER cruises were specifically designed for the detection of cetaceans. Relatively few abiotic data were collected during those cruises, compared to cruises under multi-disciplinary programmes such as GLOBEC. Furthermore, no observations were made on krill during the IWC/IDCR-SOWER cruises. As a result, only remote sensing datasets were used for the derivation of potential covariate values. Bathymetric data were derived from the General Bathymetric Chart of the Oceans (GEBCO) one-minute dataset (IOC *et al.*, 2003). For sea ice concentrations, we used passive microwave remote sensing data on a weekly basis, generated from the Scanning Multichannel Microwave Radiometer (SMMR) onboard the Nimbus-7 satellite and from the Special Sensor Microwave/Imagers (SSM/I) onboard Defense Meteorological Satellite Program (DMSP) satellites F8, F11 and F13. The version 2 sea ice concentration data had a 25 x 25 km resolution (Cavalieri *et al.*, 1996, updated 2006). Weekly 9 x 9 km 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, we used the Optimum Interpolation version 2 Sea Surface Temperature (hereafter OISST) data (Reynolds and Smith, 1994; Reynolds *et al.*, 2002), that were provided on weekly one-degree of latitude-longitude grids (ftp://ftp.emc.ncep.noaa.gov/cmb/sst/oisst_v2/). Information on frontal zone positions was obtained from two sources. Firstly, we used positions 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) were used based on absolute geostrophic velocities provided by AVISO on weekly 1/3° x 1/3° Mercator grids based on altimetry instruments onboard the Topex/Poseidon, Jason-1, ERS and ENVISAT satellites.

Spatial models and potential covariates

We used the minke whale sightings in spatial models based on line transect data using generalised additive models (GAMs). Spatial modelling was based on the count method developed by Hedley *et al*. (1999), for which we divided the transect line into equal segments of ten nautical miles. We derived an estimate of whale density corrected for the detection probability of Antarctic minke whales using a Horvitz-Thompson-like estimator of the expected minke whale density per segment. We used these estimates as the response variable of GAMs that considered the environmental variables as nonlinear predictors. The GAMs assumed an overdispersed Poisson error structure and log-link.

The GAMs were fitted independently by survey year using the mgcv-package (V1.3-28) of program R, V2.6.0 (R Development Core Team, 2007). To avoid overfitting, we constrained the degree of covariate smoothing by using the argument gamma=1.4 within the gam-function of the mgcv-package (Wood, 2006, p. 256).

We also examined the autocorrelation between segment data by comparing the output of models with and without an exponential spatial correlation structure. GAMs without a spatial correlation structure were only developed if the estimated autocorrelation ranges were negligible and if the AIC scores suggested a lack of improvement by fitting a spatial correlation structure. Spatial autocorrelation structures based on euclidean distances between sighting locations and an exponential structure (Pinheiro and Bates 2000) were fitted using the generalised additive mixed modeling (GAMM) framework developed by Wood (2006).

Variables considered as potential covariates for the spatial models were: distance from the sea ice edge, defined at 15% sea ice concentration (Tynan and Thiele, 2003), bathymetric depth and distance from the shelf edge, defined as the 1000m depth contour, Sea Surface Velocity (SSV) and distances from the SACCF and SBACC, OISST, chlorophyll-a concentration and latitude. GAM selection was based on maximisation of explained deviance and minimisation of the Generalised Cross Validation (GCV) score, while excluding GAMs that generated extreme density values.

The selected GAMs were used to create predicted minke whale density surfaces for each Area and year. To investigate changes in minke whale density over time due to covariate main effects , such as OISST and distance from the sea ice edge, we used new GAMs that combined data classified by survey that pertained to the same management Area. The new GAMs included year-specific environmental variables and year, defined as a factor. To investigate the relationships between whale densities and covariates for a given survey year and examine if changes in those relationships over the years coincided with trends in Antarctic minke whale densities, we derived density surfaces for areas with similar survey coverage that were surveyed at least three times. .

PRELIMINARY ANALYSIS

Whale sightings and g(0) estimation

Table 1 gives an overview of total numbers of Antarctic minke whale sightings under primary effort mode for the various surveys. Mean school size of the surveys per unit primary effort per Area ranged from 0.025 (Area III) to 0.0522 (Area V) per km^2 primary effort. Mean number of Antarctic minke whale sightings per unit primary effort per Area ranged from 0.057 (Area III) to 0.134 (Area II) per km^2 primary effort. G(0) value estimates used for this study are shown in table 2. The g(0) values ranged from 0.514 (SE= 0.052) to 0.891 (SE=0.036), dependent on vessel.

Spatial models and selected covariates

Autocorrelations coefficients for the various surveys did not exceed 0.01, indicating that spatial correlation structures were not necessary for the predictive models. Therefore, we developed simple GAMs, which output is given in table 3. Explained deviances were high, ranging between 24.5% (1982/83 survey, Area I) and 66.8% (2000/2001 survey, Area VI). This allowed us to develop good spatial models based on the physical environment for all surveys, except for the 2001/2002 survey in Area V.

Seven of nine potential covariates were included in the selected GAMs. Only SSV and chlorophyll-a concentration were not included in the models. Of the other covariates, distance from the sea ice edge (icedist), OISST and latitude were most often included in the models (respectively 20, 19 and 19 times out of 24 models), whereas only two GAMs included distance from the shelf edge (1000m-dist) as an explanatory variable. Table 3 shows the relationships between the covariates and their effect on Antarctic minke whale density. In most models that included icedist there was a negative relationship between icedist and its effect on Antarctic minke whale density. This suggested that Antarctic minke whale densities tended to be higher close to the sea ice edge for those surveys. Similarly, most spatial models indicated a negative relationship between density and OISST, meaning that Antarctic minke whales tended to occur in colder waters. Both icedist and OISST showed variability in the relationship with their effects on Antarctic minke whale densities.

Either distance from the SACCF (SACCFdist) or distance from the SBACC (SBACCdist) was included in 21 out of 24 spatial models, but neither covariate showed a dominant relationship with its effect on Antarctic minke whale density. The latter can also be said for the two bathymetric explanatory variables (i.e. depth and distance from the shelf edge). Some of the models showed an unexpected positive relationship between distance from the sea ice edge and its effect on Antarctic minke whale densities (e.g. for the 1987/88 (Area III) and 1998/99 surveys (Area IV)).

Relatively high Antarctic minke whale densities were predominantly found close to the sea ice edge (Figure 1). The reason for these results, seemingly contradicting with the GAM covariate selection, is that the predicted Antarctic minke whale densities are the combination of the different additive effects of the various covariates. Thus, the positive icedist-density effect relationship was probably mitigated by the strong negative OISST-density effect for the 1998/99 spatial model, thereby resulting in higher predicted whale densities close to the sea ice edge. However, OISST is highly negatively correlated to sea-ice extent (Forcada *et al.* 2006), and can be interpreted as a positive association between minke whale and sea-ice extent.

The spatial models showed changes in the distribution of predicted Antarctic minke whale densities throughout the years. Figure 2 shows prediction grids for Antarctic minke whale densities within the Ross Sea sector (165ºE-170ºW) for three surveys (1985/86, 1991/92 and 2003/04). Most of the high Antarctic minke whale densities for the 2003/04 survey were predicted within the 70-73ºS latitudinal band. However, the prediction plots for the earlier surveys showed wider latitudinal bands enclosing the regions characterised by relatively high predicted Antarctic minke whale densities.

Mean Antarctic minke whale densities are shown in table 4 together with a characterisation of the relationship between a year-specific covariate (icedist or OISST) and its effect on Antarctic minke whale density. Apart from the 145-120ºW, 60-72ºS region in Area VI, predicted mean densities were lowest for the most recent surveys in the same region. This is in line with preliminary abundance estimates for the SOWER surveys (Branch, 2005). In four out of ten regions, the lowest mean density was predicted for the most recent survey, which coincided with a non-significant relationship between at least one year-specific covariate and its effect on Antarctic minke whale density. However, these relationships could be affected by several aspects of survey design which have changed over the years:

- for surveys since the 1992/93 season, the full latitudinal range has been surveyed between 60ºS and the sea ice edge. The upper boundaries of the areas covered by earlier surveys did vary: see Branch and Butterworth (2001b) for maps of those survey areas;
- surveys from 1994/95 onwards started about 2-3 weeks later than earlier surveys in the same Area with the exception of the 2001/02-2003/04 surveys in IWC Area V (Branch and Butterworth, 2001a);
- during the 1981/82 and 1982/83 surveys, one of the vessels generally collected data near the sea ice edge, while the other vessel was surveying the area in a grid pattern, with alternating legs of fixed longitude and latitude. From 1983/84 onwards, all vessels followed a consistent zigzag pattern (Branch and Butterworth, 2001a).

Branch (2006) considered the variation in latitudinal range and changed timing of the surveys as having a small effect on the trend in Antarctic minke whale densities. Furthermore, the decline in Antarctic minke whale densities also occurred in regions that were only surveyed by a zigzag pattern. The change in survey design may thus not be the primary cause of the decline in predicted mean Antarctic minke whale densities for most areas within the Southern Ocean.

Non-significant relationships between year-specific covariates and their effects on Antarctic minke whale density only happened in spatial models for the most recent surveys conducted in four regions. It may well be that these relationships reflect changes in the sea ice environment, which are not captured by the covariates we considered for the spatial models. Examples are changes in total polynya area (Murase *et al.*, 2005) and sea ice quality (Thiele *et al.*, 2005). Therefore, we plan to more fully investigate the variability in relationships between covariates and their effects on Antarctic minke whale densities. We will focus our study on the possible relationships between this variability and changes in overall environmental features that characterised the surveyed regions, such as changes in sea ice extent, both within and between surveys.

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Table 1 Survey and Antarctic minke whale sighting information for the various surveys, grouped per IWC Area. Sighting information refers to sightings made during primary effort and Independent Observer (IO) mode. Schools and sightings are standardised per unit primary effort.

IWC Area	Survey season	Survey period	Area size (10^6 km^2)	Primary effort (km)	IO effort (km)	# schools	# schools/ effort	# sightings	# sightings/ effort
Area I (120-60°W)	1982/83	1 Jan – 18 Feb 1983	1.099	16,953	n/a	974	0.057	2599	0.153
	1989/90	28 Dec 1989 – 15 Feb 1990	1.473	12,766	6,389	538	0.042	1147	0.090
	1993/94	29 Dec 1993 – 13 Feb 1994	2.290	10,425	5,291	236	0.023	503	0.048
	1999/2000	12 Jan 1999 – 14 Feb 2000	0.776	4,934	2,197	42	0.009	84	0.017
Area II (60°W-0)	1981/82	26 Dec 1981 – 8 Feb 1982	1.078	24,091	n/a	1053	0.044	2941	0.122
	1986/87	25 Dec 1986 – 9 Feb 1987	1.699	29,315	8,190	1053	0.036	3875	0.132
	1996/97	13 Jan – 17 Feb 1997	1.479	7,324	3,776	168	0.023	354	0.048
	1997/98	16 Jan – 15 Feb 1998	1.053	5,873	2,982	116	0.020	253	0.043
Area III (0-70°E)	1987/88	20 Dec 1987 – 27 Jan 1988	1.645	10,705	2,753	332	0.031	775	0.072
	1992/93	25 Dec 1992 – 2 Feb 1993	1.527	12,380	6,065	349	0.028	834	0.067
	1994/95	12 Jan – 27 Feb 1995	1.470	6,817	3,421	145	0.021	318	0.047
	2004/05	10 Jan – 27 Feb 2005	0.720	6,128	2,559	114	0.019	256	0.042
Area IV (70-130°E)	1984/85	28 Dec 1984 – 21 Feb 1985	1.105	16,990	n/a	536	0.032	1204	0.071
	1988/89	28 Dec 1988 – 12 Feb 1989	1.622	15,283	5,195	570	0.037	1541	0.101
	1998/99	20 Jan – 23 Feb 1999	1.329	8,388	4,526	98	0.012	190	0.023
Area V (130°E-170°W)	1985/86	22 Dec 1985 – 20 Feb 1986	3.305	32,678	8,817	1717	0.053	4644	0.142
	1991/92	27 Dec 1991 – 12 Feb 1992	1.522	9,293	4,221	606	0.065	1522	0.164

Area V (cont.)	2001/02	25 Dec 2001 – 13 Feb 2002	0.690	4,991	3,695	81	0.071	188	0.165
	2002/03	22 Dec 2002 – 26 Feb 2003	1.653	10,740	4,439	200	0.019	465	0.043
	2003/04	21 Dec 2002– 1 March 2003	1.446	10,236	3,952	541	0.053	1598	0.156
Area VI **(170-120°W)**	1983/84	3 Jan – 18 Feb 1984	2.516	24,871	n/a	772	0.031	1791	0.072
	1990/91	2 Jan – 13 Feb 1991	1.912	8,628	4,626	186	0.022	401	0.046
	1995/96	10 Jan – 24 Feb 1996	1.531	8,041	3,700	190	0.024	340	0.042
	2000/2001	8 Jan – 22 Feb 2001	1.553	5,376	1,911	137	0.025	378	0.070

Table 2 Overview of estimated g(0) values, detection probabilities for sighting an Antarctic minke whale group on the survey line. Estimation was based on Independent Observer (IO) data. All models assumed point independence. As the estimated g(0) for vessel K27 (1985/86 season) was very low, we decided to use the mean value of g(0)s for vessels SM1 and SM2 instead. The g(0) estimates for both vessels that surveyed during the 2004/2005 season were almost 1, so we decided to use IO sightings collected during the 1992/93 and 1994/95 seasons instead.

IWC Area	Survey Season	Vessel	Number of IO sightings per vessel	Model / method	Datasets used	Truncation distance (km)	Number of IO sightings in model	G(0) ± SE
Area I	1982/83	SM1	n/a	Hazard-rate	1989/90 + 1993/94 + 1999/2000	1.3	139	0.832 ± 0.040
		SM2	n/a	Hazard-rate	1989/90 + 1993/94 + 1999/2000	1.5	226	0.737 ± 0.039
		V34	n/a	Mean of SM1 and SM2				0.785 ± 0.028
	1989/90	SM1	87	Half-normal	1989/90	n/a	87	0.613 ± 0.077
		SM2	166	Hazard-rate	1989/90	n/a	166	0.744 ± 0.043
	1993/94	SM1	49	Hazard-rate	1989/90 + 1993/94	1.3	134	0.808 ± 0.044
		SM2	65	Hazard-rate	1993/94	1.5	62	0.664 ± 0.080
	2000/2001	SM1	6	Hazard-rate	1989/90 + 1993/94 + 1999/2000	1.3	139	0.832 ± 0.040
		SM2	9	Hazard-rate	1989/90 + 1993/94 + 1999/2000	1.5	226	0.737 ± 0.039
Area II	1981/82	SM1	n/a	Hazard-rate	1986/87 + 1996/97 + 1997/98	2.5	209	0.639 ± 0.044
		SM2	n/a	Hazard-rate	1986/87 + 1996/97 + 1997/98	n/a	49	0.832 ± 0.070
		V34	n/a	Mean of SM1, SM2 and K27				0.739 ± 0.033

Area II (cont.)	1986/87	SM1	155	Hazard-rate	1986/87	2.5	154	0.514 ± 0.052
		SM2	3	Hazard-rate	1986/87 + 1996/97 + 1997/98	n/a	49	0.832 ± 0.070
		K27	108	Hazard-rate	1986/87	1.2	105	0.746 ± 0.055
		V34	n/a	Mean of SM1, SM2 and K27				0.746 ± 0.055
	1996/97	SM1	40	Hazard-rate	1996/97 + 1997/98	2.0	55	0.775 ± 0.076
		SM2	37	Hazard-rate	1996/97 + 1997/98	0.8	43	0.782 ± 0.088
	1997/98	SM1	17	Hazard-rate	1996/97 + 1997/98	2.0	55	0.775 ± 0.076
		SM2	9	Hazard-rate	1996/97 + 1997/98	0.8	43	0.782 ± 0.088
Area III	1987/88	SM1	n/a	Hazard-rate	1992/93 + 1994/95	1.2	93	0.800 ± 0.058
		SM2	110	Hazard-rate	1987/88	1.4	103	0.590 ± 0.063
	1992/93	SM1	53	Hazard-rate	1992/93 + 1994/95	1.2	93	0.800 ± 0.058
		SM2	140	Hazard-rate	1992/93	n/a	140	0.825 ± 0.040
	1994/95	SM1	48	Hazard-rate	1994/95	n/a	48	0.702 ± 0.085
		SM2	84	Hazard-rate	1994/95	1.3	81	0.723 ± 0.072
	2004/05	SM1	26	Hazard-rate	1992/93 + 1994/95	1.2	93	0.800 ± 0.058
		SM2	9	Hazard-rate	1992/93 + 1994/95	1.3	214	0.801 ± 0.037
Area IV	1984/85	SM1	n/a	Hazard-rate	1988/89 + 1998/99	n/a	74	0.517 ± 0.072
		SM2	n/a	Hazard-rate	1988/89 + 1998/99	n/a	105	0.593 ± 0.064
		K27	n/a	Mean of SM1 and SM2				0.555 ± 0.048

Area IV (cont.)		V34	n/a	Mean of SM1 and SM2				0.555 ± 0.048
	1988/89	SM1	60	Hazard-rate	1988/89 + 1998/99	n/a	74	0.517 ± 0.072
		SM2	66	Hazard-rate	1988/89 + 1998/99	n/a	105	0.593 ± 0.064
	1998/99	SM1	14	Hazard-rate	1988/89 + 1998/99	n/a	74	0.517 ± 0.072
		SM2	39	Hazard-rate	1988/89 + 1998/99	n/a	105	0.593 ± 0.064
Area V	1985/86	SM1	171	Hazard-rate	1985/86	n/a	171	0.517 ± 0.046
		SM2	188	Hazard-rate	1985/86	1.5	183	0.599 ± 0.046
		K27	119	Mean of SM1 and SM2				0.558 ± 0.033
		V36	n/a	Mean of SM and SM2				0.558 ± 0.033
	1991/92	SM1	206	Hazard-rate	1991/92	1.5	194	0.678 ± 0.052
		SM2	73	Hazard-rate	1991/92	n/a	73	0.618 ± 0.069
	2001/02	SM1	10	Half-normal	1991/92 + 2001/02 + 2002/03	1.5	232	0.772 ± 0.040
		SM2	8	Hazard-rate	1991/92 + 2001/02 + 2002/03	1.7	100	0.683 ± 0.060
	2002/03	SM1	28	Half-normal	1991/92 + 2001/02 + 2002/03	1.5	232	0.772 ± 0.040
		SM2	22	Hazard-rate	1991/92 + 2001/02 + 2002/03	1.7	100	0.683 ± 0.060
	2003/04	SM1	114	Hazard-rate	2003/04	n/a	114	0.891 ± 0.036
		SM2	122	Hazard-rate	2003/04	n/a	122	0.844 ± 0.042

Area VI	1983/84	SM1	n/a	Hazard-rate	1990/91 + 1995/96 + 2000/2001	n/a	81	0.736 ± 0.059
		SM2	n/a	Hazard-rate	1990/91 + 1995/96 + 2000/2001	1.2	77	0.738 ± 0.069
		K27	n/a	Mean of SM1 and SM2				0.737 ± 0.045
		V34	n/a	Mean of SM1 and SM2				0.737 ± 0.045
	1990/91	SM1	48	Hazard-rate	1990/91 + 1995/96 + 2000/2001	n/a	81	0.736 ± 0.059
		SM2	19	Hazard-rate	1990/91 + 1995/96 + 2000/2001	1.2	77	0.738 ± 0.069
	1995/96	SM1	24	Hazard-rate	1990/91 + 1995/96 + 2000/2001	n/a	81	0.736 ± 0.059
		SM2	42	Hazard-rate	1990/91 + 1995/96 + 2000/2001	1.2	77	0.738 ± 0.069
	2000/2001	SM1	9	Hazard-rate	1990/91 + 1995/96 + 2000/2001	n/a	81	0.736 ± 0.059
		SM2	19	Hazard-rate	1990/91 + 1995/96 + 2000/2001	1.2	77	0.738 ± 0.069

Table 3 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 = distance from the sea ice edge (defined at 15% sea ice concentration), OISST = Optimally Interpolated Sea Surface Temperature, 1000m-dist = distance from the shelf edge (defined at 1000m depth), SACCFdist = distance from the Southern Antarctic Circumpolar Current Front (SACCF), SBACCdist = distance from the Southern Boundary of the Antarctic Circumpolar Current (SBACC). Legend for the relationship characterisations: — = negative, + = positive, 0 = no clear signal, U = minimum effect on density in middle of covariate range, n = maximum effect on density in middle of covariate range, NL = complex non-linear relationship, NS = covariate non-significant, thus not included in model.

IWC Area	**Survey season**	**Explained Deviance (%)**	**Covariates**					
			Icedist	**OISST**	**depth**	**1000m-dist**	**SACCF-dist**	**SBACC-dist**
Area I (120-60°W)	1982/83	24.5	—	—	+	NS	NS	NS
	1989/90	27.1	NS	—	NS	NS	NS	N
	1993/94	47.1	U	NL	NS	NS	NS	U
	1999/2000	55.8	NS	—	0	NS	NS	NS
Area II (60°W-0)	1981/82	40.2	—	—	NS	NS	NS	+
	1986/87	43.8	0	0	+	NS	NS	0/—
	1996/97	44.0	—	0	NS	NS	NS	0
	1997/98	61.2	+/n	NL	N	NS	NS	+
Area III (0-70°E)	1987/88	49.6	+	0	NS	NS	—	NS
	1992/93	41.6	NL	NS	NS	NS	+	NS
	1994/95	55.2	NL	—	NS	0	NL	NS
	2004/05	44.6	—	—	0	NS	+	NS
Area IV (70-130°E)	1984/85	41.4	—	—	—	NS	NS	—
	1988/89	44.3	—	0/+	—	NS	0	NS
	1998/99	55.1	+	—	NS	NS	N	NS

Area V	1985/86	31.7	—	NL	0	NS	NL	NS
(130°E-170°W)	1991/92	38.3	NS	NS	NS	NS	NS	0/—
	2001/02	NS	NS	NS	NS	NS	NS	NS
	2002/03	32.5	—	0	NS	NS	NS	0
	2003/04	47.7	—	NS	NS	NS	+/n	NS
Area VI	1983/84	29.3	0/+	NS	n	0/+	+	NS
(170-120°W)	1990/91	25.6	NL	—	NS	NS	—/n	NS
	1995/96	34.4	+/n	0	—	NS	NS	NL
	2000/2001	66.8	—/0	u	NS	NS	NS	—

Table 4 Densities and year-specific effects of distance from the sea ice edge (icedist) and Optimally Interpolated Sea Surface Temperature (OISST) on Antarctic minke whale density. Legend for the relationship characterisations: **—** = negative, 0 = no clear relationship, U = minimum effect on density in middle of covariate range. NS = non significant year-specific effect on density. Bold cells highlight the coincidences between lowest Antarctic minke whale densities in a comparable area and non-significance of the icedist and/or OISST.

IWC Area	Survey season	Region	Density	Icedist		OISST		Region	Density	Icedist		OISST	
				p-value	Signal	p-value	Signal			p-value	Signal	p-value	Signal
Area I (120-60°W)	1982/83	120-60°W 60-72°S	1.26	< 0.001	—	< 0.001	0	80-60°W 60-72°S	1.14	< 0.001	0	< 0.001	—
	1989/90		0.99	< 0.001	—	< 0.001	—		0.94	< 0.001	0	< 0.001	0
	1993/94		0.71	< 0.001	—	< 0.001	—		0.78	< 0.001	0	< 0.001	0
	1999/2000								**0.39**	< 0.05	0	**NS**	
Area II (60°W-0)	1981/82	30°W – 0 60-71°S	1.27	< 0.001	—	< 0.001	0	60-25°W 60-71°S	1.01	< 0.01	0	< 0.001	—
	1986/87		2.68	< 0.001	0	< 0.001	—		4.71	< 0.001	0	< 0.001	—
	1996/97		0.89	< 0.001	—	< 0.001	—						
	1997/98								**0.96**	**NS**		< 0.01	0
Area III (0-70°E)	1987/1988	0-40°E 60-70°S	2.66	< 0.001	U	< 0.001	0	40-60°E 60-70°S	0.72	< 0.05	—	< 0.001	—
	1992/93		1.04	< 0.001	—	< 0.001	0						
	1994/95								0.81	< 0.001	—	< 0.001	—
	2004/05		0.65	< 0.001	—	< 0.001	—		**0.12**	**NS**		**NS**	
Area IV (70-130°E)	1984/85	80-130°E 60-68°S	1.07	< 0.001	0	< 0.001	—						
	1988/89		1.45	< 0.001	—	< 0.001	—						
	1998/99		0.62	< 0.01	0	< 0.001	0						
Area V	1985/86	165°E-170°W	3	< 0.001	0	< 0.001	—	165°E-170°W	5.5	< 0.001	—	< 0.001	—

(130°E-170°W)	1991/92	60-70°S	2.98	< 0.01	—	< 0.001	—	60-78°S	3.55	< 0.05	0	< 0.001	—
	2001/02												
	2002/03		0.89	< 0.001	—	< 0.001	—						
	2003/04		0.68	< 0.01	—	< 0.05	—		1.35	< 0.01	—	< 0.05	—
Area VI	1983/84		1.78	< 0.001	0	< 0.001	0		0.85	< 0.001	—	< 0.01	—
(170-120°W)	1990/91	170-140°W	1.11	< 0.01	—	< 0.001	—	145-120°W	0.98	< 0.001	0	< 0.001	0
	1995/96	60-72°S	**0.74**	< 0.01	0	**NS**		60-72°S					
	2000/2001								1.15	< 0.001	U	< 0.001	0

FIGURES

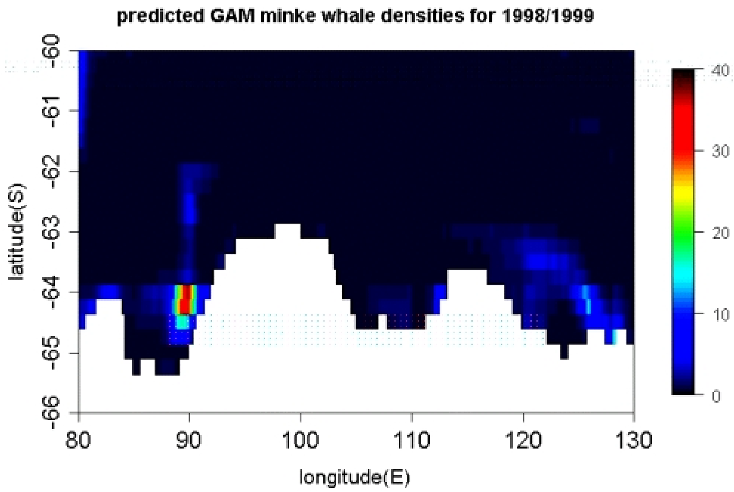
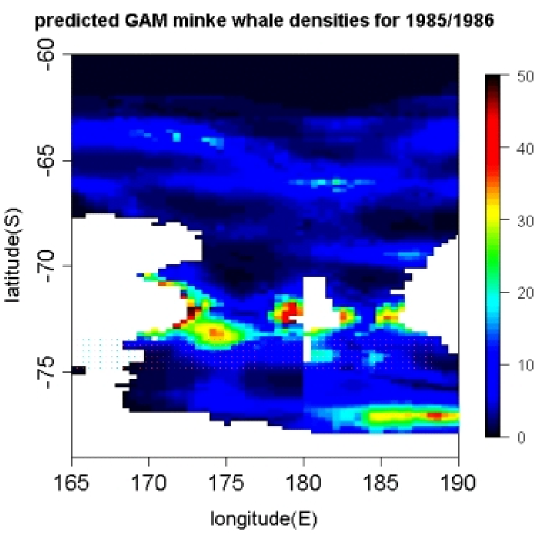
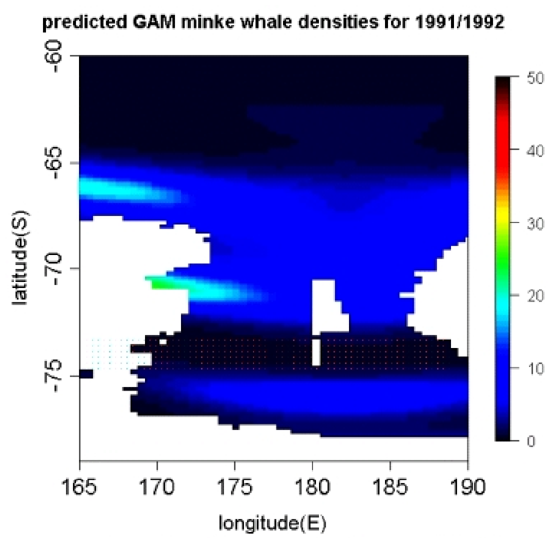


Figure 1 Prediction grid of Antarctic minke whale densities within the Indian sector (80-130ºE, below 60ºS). Coloured areas show open water regions (i.e. regions with less than 15% sea ice concentration). Both the pack ice region and land mass are represented by the white region.





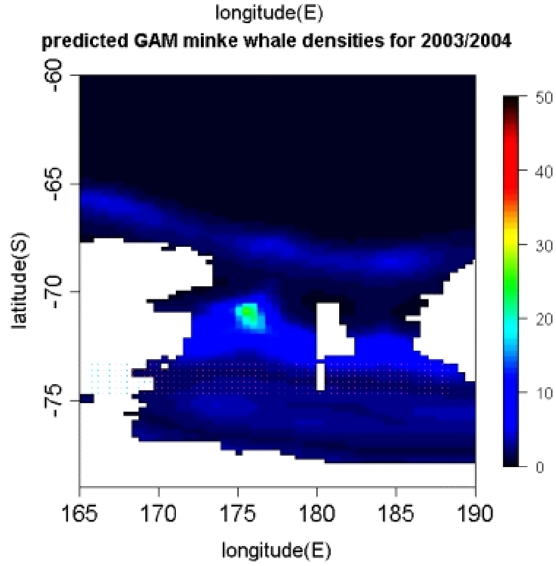


Figure 2 Prediction grids of Antarctic minke whale densities within the Ross Sea sector (165ºE-170ºW) for three surveys (1985/86, 1991/92 and 2003/04). Coloured areas show open water regions. White regions represent either the pack ice region or land mass.