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Modeling the relationship of Antarctic minke whales to major ocean boundaries

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Abstract The population size of Antarctic minke whales *Balaenoptera bonaerensis* has been changing simultaneously with profound changes in the physics, i.e., mesopredator habitat features, of the Southern Ocean. Although the two trends may not be related, distinguishing among the factors responsible requires a better understanding of minke whale habitat preferences. For the first time at a large geographic scale, i.e., between 140° E and 35° W, we use data not constrained by vessels needing to avoid sea ice to model the habitat affinities of this pagophilic mesopredator. Using Maxent, we modeled minke whale proximity to the Antarctic Shelf Break Front (ASBF) and the southern boundary of Antarctic Circumpolar Current (sbACC), as well as association with sea ice, given that global climate change is altering the positions or intensity of these features. We also included water depth and chlorophyll (proxy for productivity) as variables. Minke whale presence data were gathered using strip and line census on 55 cruises on board icebreakers during late spring and summer, 1976–2005. The most important variable was distance to ASBF, followed by water depth and sea-ice concentration. That is, found principally in waters south of the sbACC during summer, minke whales were most abundant near the outer edge of the continental shelf (shallow depth), including areas heavily covered by sea ice. We propose that as the sbACC moves south and sea ice disappears, as projected by global climate models, minke whale habitat will shrink, and likely intra- and inter-specific competition will increase.

Keywords Antarctic circumpolar current · Antarctic minke whale · Antarctic shelf break front · Climate change · Sea ice · Southern Ocean

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Introduction

Profound changes are underway in the physics of the Southern Ocean, including warming of Circumpolar Deep Water (the water upwelled at continental margins), freshening of surface waters in some sectors, increasing flow, with altered boundaries, of the Antarctic Circumpolar Current, and regional changes in sea-ice extent and sea-ice season (Thompson and Solomon 2002; Jacobs 2006; Russell et al. 2006a, Russell et al. 2006b; Stammerjohn et al. 2008; Tynan and Russell 2008; Ainley et al. 2010a; Yin et al. 2011). These are the features and processes that define, at the mesoscale and larger scale, a species' "habitat" in the Southern Ocean. At the same time, the population size of the Antarctic minke whale *Balaenoptera bonaerensis*, clearly a pagophilic ("ice loving") species (or at least one

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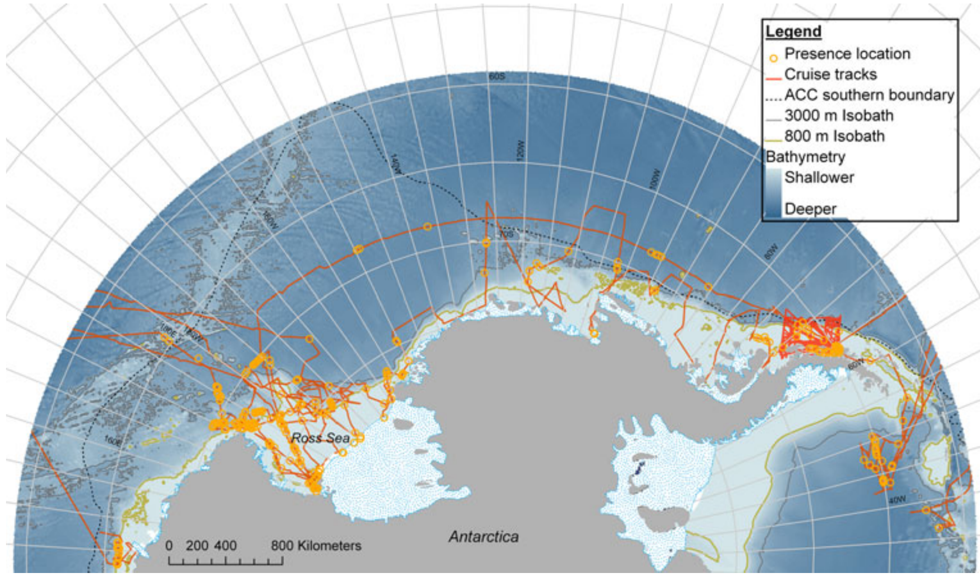

Fig. 1 Cruise tracks on which minke whales were surveyed, with bathymetry as base. Presence locations from which models were created are displayed as *orange circles*

that does not avoid sea ice; Tynan et al. 2010), has been changing although more likely as recovery from decimation by former industrial whaling (Branch 2006), rather than to climate factors. Regardless, in order to understand the degree to which minke whales may be affected by the altering ocean requires, first, a better understanding of their habitat affinities is needed both within and outside of pack ice-covered regions, even if only to better design population surveys.

Baleen whale habitat preferences in the Southern Ocean initially were studied by mapping (e.g., Ainley 1985; Ichii 1990; Murase et al. 2002; Matsuoka et al. 2003) and subsequently by simple correlation analysis (Kasamatsu et al. 1996, 1998, 2000a; Thiele et al. 2000, 2004, 2005; Friedlaender et al. 2006). More recently, with the further development of statistical modeling techniques, analyses have become more sophisticated (e.g., Ainley et al. 2007; Murase 2010; Beekmans et al. 2010; Friedlaender et al. 2011). Specifically with respect to Antarctic minke whales, the fact that large numbers are found within the pack ice, and most analyses to date have been based on data collected by ships that avoid pack ice (exceptions: regional-scale studies by Ribic et al. 1991; Aguayo-Lobo 1994; Thiele and Gill 1999; Ainley et al. 2007), the resulting statistical and spatial models in most cases have had problems describing the true habitat associations of this species (as discussed by Beekmans et al. 2011). According to Ainley et al. (2007), the Antarctic minke whale is perfectly suitable to exploit pack ice habitat, having a slim, compact body and small appendages that allow it to fit into narrow leads between ice floes without catching on ice, and a hard, sharp rostrum for breaking through newly formed sea ice in order to breathe (see also Thiele et al. 2000; Tynan et al. 2010). Indeed, other species (seals, penguins) find those holes sometimes of critical value, making the minke whale to be of major ecological importance in the high-latitude, pack ice-covered seas of the Southern Ocean (Ainley et al. 2006; Smith et al. 2011).

To better understand the habitat affinities of Antarctic minke whales, we modeled their spatial patterns in waters surrounding half of the Antarctic continent, from 140° E to 35° W (Fig. 1) using data collected mainly by icebreakers, which penetrated the pack ice from far offshore to the coast. Included were several of the regions where sea ice is persistent year round, e.g., eastern Ross Sea, Amundsen Sea, southern Bellingshausen Sea, and western Weddell Sea (see Gloersen et al. 1992), which are areas generally not included in surveys by International Whaling Commission census efforts (cf Branch 2006). Data were gathered during periods when minke whale numbers would be stable, i.e., non-migratory, December–February (summer). The principle aim of these cruises was physical oceanography, especially cruises to assess the degree to which Circumpolar Deep Water penetrates the shelf and reaches coastal ice shelves (see Yin et al. 2011), and therefore, cruise tracks comprised a series of lines perpendicular to the coast. The data were largely conducted using strip transects, as line transects are impossible to use on ships constantly changing speed and direction to deal with sea ice and embedded icebergs. Some data, in open waters, were collected using line transects. However, we used only presence data in our Maxent models, not density, and thus, it did not really matter whether the data were gathered by strip or line transect but only that it was done so consistently and continuously. Maxent modeling has been used as well by Friedlaender et al. (2011) to investigate mesoscale and smaller-scale occurrence patterns and habitat affinities of whales in Marguerite Bay, Antarctic Peninsula.

Table 1 Variables used in species distribution models, years of data collection, spatial resolution, and source of original data

Data type	Definition	Years	Original sample resolution (km)	Source
Water depth	Depth in meters		5	ADD Consortium (2000)
Sea-ice cover	Percent daily sea-ice cover	1978–2005	25	NSIDC, Cavalieri et al. (2008)
Chlorophyll	Mg m^{-3} averaged over 10 years (Nov–Jan)	1997–2006	12.5	NASA, J. Comiso, pers. comm.
Distance to shelf break front	Euclidean distance (m) to the 800-m isobath		5	
Distance to southern boundary of Antarctic circumpolar current	Euclidean distance (m) to the average position of the ACC southern boundary		5	From Orsi et al. (1995)
Slope	Angle: maximum change in depth between cells (degrees)		5	

Methods

Species distribution models: explanatory variables

The study area was defined by the extent of the bathymetry layer and minke whale detections and covered areas south of approximately 59° S between 140° E and 35° W (Fig. 1). Environmental covariates were obtained from various sources (Table 1); see also Ainley et al. (2010b) for further discussion of these variables and Appendix Figures A1–A5 for mapped displays of all environmental covariates (see Electronic Supplementary Material).

For model projection purposes, all covariate data were resampled to 5 km resolution using the nearest-neighbor assignment then clipped to the study area using ArcMap 9.3.1 (ESRI 2009). Although higher-resolution bathymetric data are available for parts of the study area (e.g., Davey 2004), we conducted this resampling so that data could be easily matched to the 5 km bathymetry available for the entire study region (ADD Consortium 2000). Daily sea-ice cover grids collected contemporaneously with ship surveys were obtained from the National Snow and Ice Data Center (Cavalieri et al. 2008) and were used to attribute ice cover to minke whale presence locations. If ice data were not available for a specific survey date but were available for adjacent days, the data from the previous day were used. Of the 395 total locations, satellite-derived ice data were not available for 46 locations collected before 1978 (the first year for which satellite data are available). Monthly mean percent sea-ice cover grids were obtained for December–January (summer) for 10 years, 1998–2008 (Cavalieri et al. 2008) and averaged across all years to obtain one mean grid used to geographically project the model results. Although ice cover data were collected by human observers on several of the cruises, these data were not available for 212 of the 395 minke whale presence locations, and preliminary evaluation of models including these data for subsamples of locations where they were available did not improve model performance (see below for description of model evaluation). Slope (rate of change in depth) was derived from the bathymetry layer and was calculated as the maximum change between a given cell and its 8 neighboring cells, expressed as degrees. Distance from the southern boundary of the Antarctic Circumpolar Current (sbACC; Orsi et al. 1995) and distance to the 800-m isobath a proxy for the Antarctic Shelf Break Front (ASBF) were calculated as the Euclidean distance in meters. Finally, chlorophyll concentrations were derived from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite, courtesy of the NASA/Goddard Earth Sciences (GES)/Distributed Active Archive Center (DAAC), and as described further by Smith and Comiso (2008); the data set used, in fact, was the same one used by those authors, averaged over 10 years, Nov–Jan 1997–2006. These months reflect the yearly peak production period. We used this 10-year mean because comparable daily chlorophyll concentration data were not available for the dates most observations were made (pre-SeWiFS).

Species distribution models: dependent variables

Ships, dates, and other characteristics of cruises are listed in Table 2. Using 800-m wide strip transects, counts by (usually) two observers were made from the icebreakers' bridge wings, where eye level was ~16 m above the sea surface, during hours that the ship traveled at speeds exceeding 6 knots during daylight (therefore, surveys were more or less continuous). The ships cruised at a maximum 10–12 knots when in open water. Transects were not made when visibility was <800 m, but rarely was visibility other than excellent. In strip transects, we logged only those whales that passed within 800 m of the side (forequarter) of the ship, on which we positioned ourselves to experience the least glare (AnSlope cruise line transects were to the horizon; AnSlope = acronym for cruises, Antarctic Slope). Transect width was determined using a range finder. Ship's position, updated half-hourly, was determined by satellite navigation. Binoculars (8X) were used to sweep the outer part of the census strip visually about once every 1–2 min. In all but AnSlope cruises, in which line transects were made for whales (involving >2 observers, and more powerful binoc-

Table 2 A summary of cruises on which minke whale occurrence data were gathered, along with number of sightings (not total whales), number of observers, and survey technique

Region	Timing; no. sightings	Data source	Vessel, no. observers, technique	Investigator
Ross Sea	1976–1980, Dec–Feb; 58 sightings	RISP surveys, and others; plus 5 crossings NZ to Ross Sea	*Northwind*, 2 (strip, one side)	Ainley, Jacobs
Drake passage, Ant Peninsula shelf/slope	1977–1994, Summer; 0	7 Crossings drake passage	*Westwind, Glacier, Polar Star*; 2 (strip, one side)	Ainley
Ross Sea to Bellingshausen Sea	1977 Feb; 1	Cruise between McMurdo and Palmer stations	*Burton Island*; 2 (strip, one side)	Ainley
Scotia/Weddell Confluence	1983–1986, Dec and Feb; 25	AMERIEZ; 2 2-ship cruises	*Melville* + *Westwind, Glacier*; 2 (strip, one side)	Ainley, Fraser; 10 other researchers
W Ant Peninsula shelf and slope	1992–2005 Summer; 60	Palmer LTER; several cruises	*LB Gould*; 2 (strip, one side)	Fraser
S. Indian Ocean to the ice edge; 82°–115° E;	1994–1995 Dec–Jan; 5	WOCE I8S, I9S; 2 crossings Aust-Antarctica	*Knorr*; 3 (line, both sides)	Tynan
Amundsen and Bellingshausen seas	Feb–Mar 1994; 35	Jacobs' Antarctic slope project	*NB Palmer*; 2 (strip, one side)	Ainley, Jacobs
Ross Sea shelf and slope	2004 late summer/spring; 212	ANSLOPE, IWC Southern Ocean; 2 cruises	*NB Palmer*; (5, both sides, line)	Thiele, Jacobs; other researchers

Northwind, Westwind, Burton Island, Glacier, NB Palmer are all icebreakers of the same size and speed (in that category, too, ice-strengthened *LB Gould*)

ulars), continuous surveys were broken into half-hour segments equivalent to a "transect." Sightings and their positions were extracted from the line transect effort.

Species distribution: maximum entropy modeling

We modeled the probability of species occurrence using environmental data and species presence (>0 counted) localities from surveys and sources described above (Table 1). Presence data were aggregated for each 5 km cell in the study area, and locations that fell outside of the extent of any of the environmental layers were not used. This resulted in a total of 300 presence locations included in modeling. We used a machine learning, "maximum entropy" modeling method called Maxent (v.3.3.1; Phillips et al. 2006; Phillips and Dudík 2008), and its logistic output format, to estimate probability of minke whale occurrence in each cell given the modeled relationship between the presence locations and the environmental covariates. An ecologically based detailed explanation for Maxent and its limitations are provided by Elith et al. (2011). This is a method that has been used several times recently to achieve goals similar to ours (Kremen et al. 2008; Stralberg et al. 2009; Carroll et al. 2010). Maxent outperforms almost all other existing distribution modeling algorithms and at least equals the best known methods when compared to known distributions, including good performance using a limited number of presence locations (Phillips et al. 2006; Elith et al. 2006; Hernandez et al. 2006; Wisz et al. 2008; Phillips and Dudík 2008). The algorithm estimates the probability distribution that has maximum entropy (most uniform or spread out across prediction space), while meeting the constraints imposed by the (incomplete) information available about the actual distribution and avoiding any other assumptions (Jaynes 1957; Phillips et al. 2006; Phillips and Dudík 2008). These constraints require that the mean of each environmental covariate across the entire prediction space in the model selected by Maxent be approximately equal to the empirical average of this variable across all sample locations. How close to equal these means are is determined by a parameter (called "regularization") that is automatically optimized by Maxent for each model, but which can be manually specified, with higher values resulting in lower likelihood of model over-fitting, but also potentially in lower model specificity. Despite Maxent's capabilities, we acknowledge that the data set was collected in a non-random, long-term fashion, with potential bias introduced by factors associated with annual variability and the surveys themselves that we cannot account for. We experimented with using analytical methods to reduce the bias (e.g., analysis of spatially and temporally more contiguous data), but model performance (see below) was much lower, probably largely due to the associated reductions in effective sample size. To derive standard deviation values

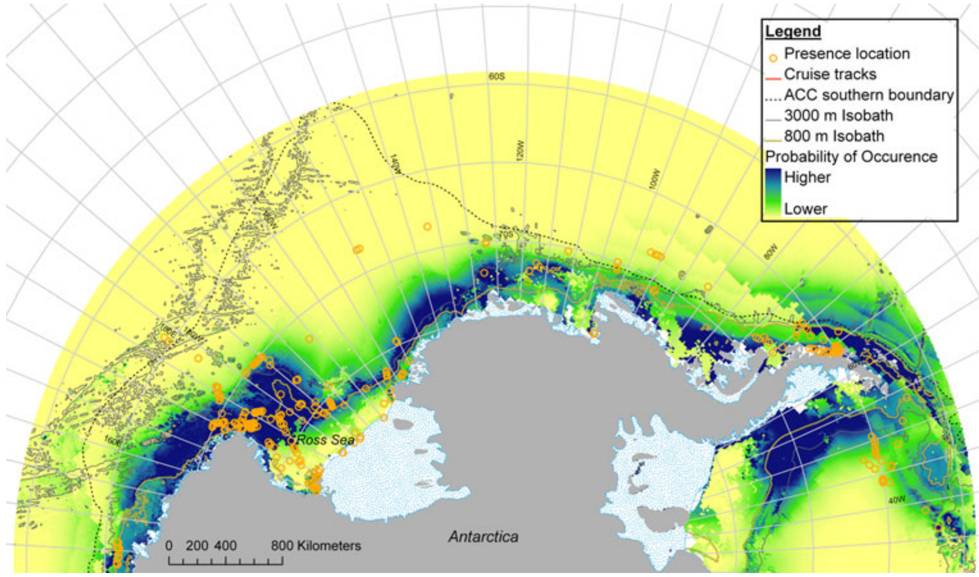

Fig. 2 Results of maximum entropy modeling: mean (from 30 bootstrapped runs) modeled probability of occurrence of minke whales. Presence locations from which models were created are displayed as *orange circles*. 800-m isobath, the shelf break, represents the Antarctic shelf break front

for the model performance and fit, we ran each model 30 times using a bootstrapping approach with the full data set available in a random sort order each time. Thus, the resulting model output is composed of the modeled mean probability of occurrence across the 30 runs, as well as the error associated with this mean.

Covariate data in Maxent were allowed to have six types of relationship to the species occurrence likelihood—linear, quadratic, product (i.e., interaction of two covariates), threshold, hinge, and category indicator. Each type was evaluated with respect to creating a final model that has the highest entropy, with the best version retained. Threshold and hinge covariates allow modeling of an arbitrary response of the species to the covariate from which they are derived.

Model performance

We produced a Receiver Operating Characteristic (ROC) plot (true positives vs. false positives) based on presence and background ("pseudo-absence") data (Elith 2002; Phillips et al. 2006). The ROC area under the curve (AUC) value for a randomly selected 20% test portion of the data in each of 30 model runs evaluated the model performance. Because we did not have true absence data (we did not survey everywhere in the study area), AUC scores represent the probability that a randomly chosen presence location was assessed to be more likely to have the species present than a randomly selected pseudo-absence location chosen from the entire study area (Phillips et al. 2006). Models with AUC above 0.75 are considered potentially useful, 0.80–0.90 good and 0.90–1.0 excellent (Swets 1988; Elith 2002).

While this evaluation method is not perfect, several of the criticisms of AUC do not apply in the context of this paper (e.g., weighting omission and commission errors equally do not impact our findings, as the spatial extent of the models was all the same; Lobo et al. 2007). Visual inspection of model outputs, as well, compared favorably to location data (Fig. 2) and previous expert-based mapping efforts (see Ainley et al. 2010b). We also investigated the contributions of individual covariates for the evidence of model over-fitting and evaluated the effect of raising the Maxent regularization value above the default settings, with and without bootstrapping. The best model performance (in terms of test AUC) was achieved by accepting the default Maxent regularization parameter and bootstrapping. In several cases, however, inspection of the covariate response curves suggested over-fitting and increasing regularization did not penalize AUC substantially. Thus, the bootstrapped results presented are with regularization coefficients set to 2 (i.e., default regularization ×2).

Results

The best Maxent model had an ensemble mean test AUC of 0.947 (SD ± 0.009) and identified two areas where minke whales had particularly high likelihood of occurrence: Ross Sea and northwestern Weddell Sea, in the pack ice bordering the Scotia–Weddell Confluence (Fig. 2). These areas of relatively high probability of minke whale occurrence are consistent with those apparent in results of the IDCR (International Decade of Cetacean Research) and SOWER (Southern Ocean Whale Ecosystem Research) cruises conducted in three sets of circumpolar surveys under the auspices of the International Whaling Commission (IWC; data from Branch 2006, his Table 11). These IDCR–SOWER cruises also identified large numbers of minke whales east of the Weddell Sea, but we did not survey that area.

The factor that was most important to minke whale occurrence, according to our model, was distance to the 800-meter isobath (i.e., ASBF); secondary factors were water depth, sea-ice cover, and distance to the sbACC (Fig. 3). Heuristic estimates for the percent contribution of each of these variables to the model were 48.9, 16.5, 16.3, and 13.2%, respectively. Marginal response curves, which depict how probability of occurrence changes as each environmental variable is varied, while keeping the other variables at their average sample value, are shown in Fig. 3. In contrast to the marginal response curves, individual response curves for models are created using only the corresponding variable (also in Fig. 3). Thus, they reflect the dependence of the model prediction on the given variable and, when compared to the marginal response curves, the dependencies induced by correlations between the given variable and the other variables. The marginal and individual response curves for distance to ASBF show a sharply negative response to increasing distance out to about 600 km from the front, where upon the effect of increasing distance stabilizes, indicating a species' preference to the areas near the shelf break (Fig. 3). The ASBF is where Circumpolar Deep Water meets Antarctic Shelf Water, and to some degree is upwelled (Jacobs 1991). The marginal response curve for water depth showed a positive response with areas shallower than approximately 3500 m. Together with the individual response curve, which showed a positive response with decreasing depth, the model indicates a preference for areas on or near the shelf. Minke whale occurrence was positively associated with sea-ice cover. The marginal response curves showed a gradually increasing association until approximately 90% where the probability increases steeply up to 100% (Fig. 3). The individual response curve for sea-ice cover shows a similar pattern. Distance to sbACC had a positive contribution to minke whale occurrence probability, peaking between about 500 and 1,200 m (Fig. 3). Slope and chlorophyll concentration were relatively unimportant (2.6 and 2.4% contribution, respectively). The fact that chlorophyll was not important fits with the fact that the shelf areas throughout our study area exhibit relatively high chlorophyll (Smith and Comiso 2008), but the relationship could also be due to the fact that we did not have chlorophyll data that coincided temporally with the observation data.

Discussion

Minke whale habitat

Finding minke whales, outside of migratory periods, in waters south of the sbACC is consistent with the findings of Tynan (1998), Nicol et al. (2000), Branch (2006), and Ainley et al. (2007); finding them in shelf or shelf break waters is consistent with Kasamatsu et al. (2000a, b), Thiele et al. (2000, 2004), Friedlaender et al. (2006, 2011), Ainley et al. (2007), and Beekmans et al. (2010); and finding them in association with sea ice well in from the edge is consistent with Ainley et al. (2007). In regard to sea ice, most surveys for minke whales historically have been conducted on vessels incapable of penetrating it, and thus, what has been reported from those is an association of minke whales with the edge of the pack ice (e.g., Kasamatsu et al. 2000b; Murase et al. 2002, Murase 2010; Beekmans et al. 2010; Friedlaender et al. 2011). But, obvious with data from icebreaker surveys, it is clear that this species occurs throughout the ice pack, which often overlies the shelf in the part of the Southern Ocean that we surveyed during summer (especially eastern Ross Sea, Amundsen Sea, and southern Bellingshausen Sea). The statistical modeling reported by Ainley et al. (2007) had difficulty separating the influence of the ASBF vs. the pack ice edge in the Amundsen and Bellingshausen seas, where these two factors mostly coincide during summer; Beekmans et al. (2010) noted a similar problem with their analysis. What our model indicated further was that, independent of the large-scale ice edge, the shelf break and shelf waters inshore of it, with or without sea ice, were the habitats most attractive to minke whales.

Association of the whales with the ASBF, no doubt is one driven by high abundances of prey found there, and especially Antarctic krill (*Euphausia superba*). Murase et al. (2002) and Murase (2010) found a strong correlation between minke whale prevalence and high abundance of krill (see also Ichii 1990; Nicol et al. 2000; Friedlaender et al. 2011). While Antarctic krill are highly associated with the shelf break (Nicol 2006), it appears that a large portion of the krill population also occupies waters overlying deeper depths (south of the sbACC), perhaps to avoid the high predation pressure over the shelf break as proposed by Atkinson et al. (2008). It is possible, however, that the concentrations of krill in those oceanic waters are too dispersed to attract minke whales, which is why they were not found there in our study or that by Beekmans et al. (2010; see Piatt and Methven 1992).

In the Ross Sea, where the continental shelf is the broadest in the Antarctic, the sea ice occurs seaward of the shelf (owing to a large post-polynya over the shelf), unlike the remainder of the Antarctic shelf in summer. A Maxent model geographically constrained to the Ross Sea showed that the shelf break was the most important factor explaining minke whale occurrence there (Ballard et al. 2011; most important AUC scores as follows: distance to shelf break front, 49.5 and chlorophyll, 14.7). In the Ross Sea, it is clear that minke whales occur over the shelf inshore of the shelf break. There the main forage

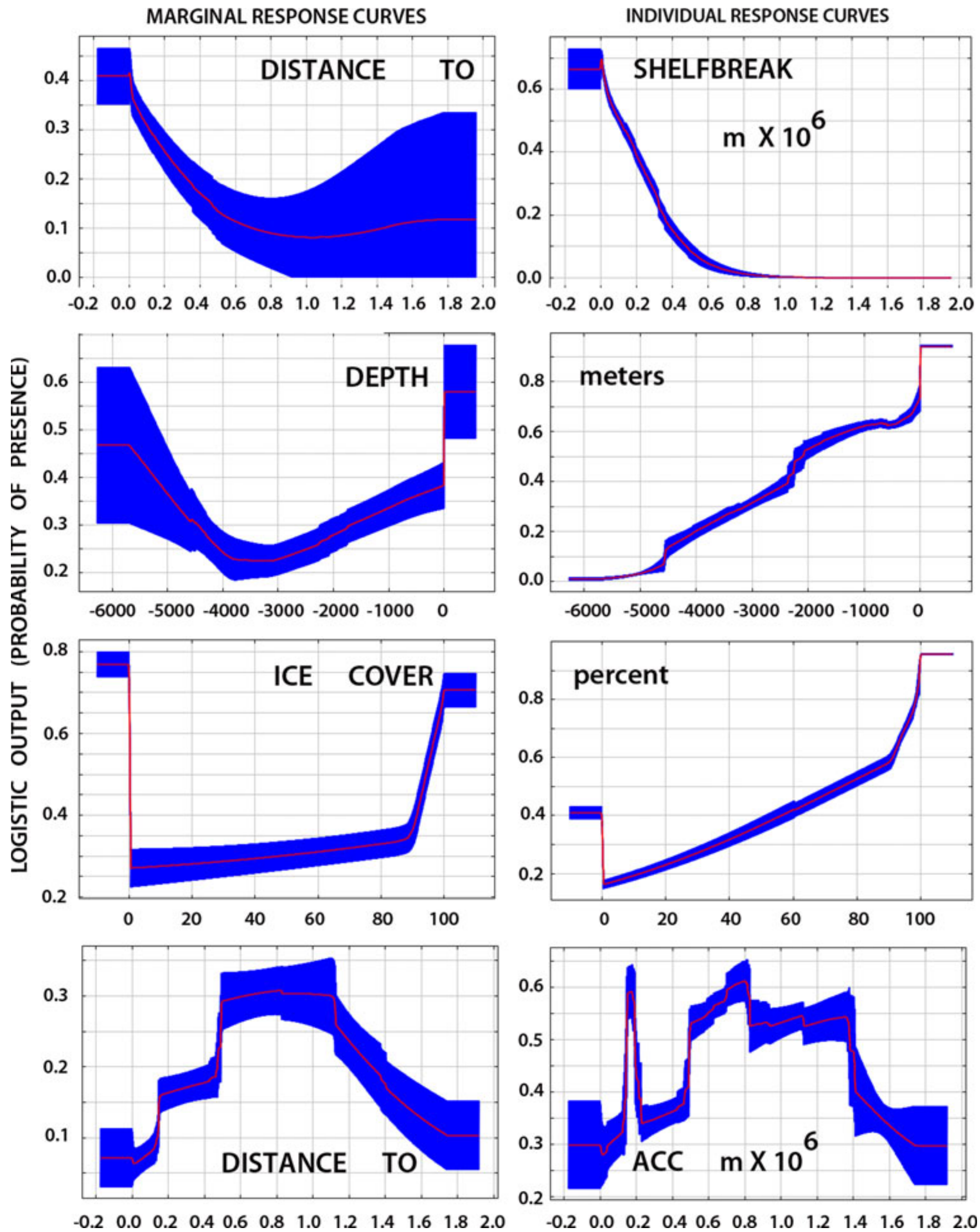

Fig. 3 Mean response (*red line*) and standard deviation (*blue shading*) marginal response *curves* (*left column*) in order of importance of the top for environmental variables for predicting minke whale (WMIN) likelihood of occurrence in Maxent modeling. The *curves* indicate how the model prediction changes (*y*-axis) as each environmental variable is varied (*x*-axis), keeping all other environmental variables at their average sample value. Individual response *curves* (*right column*) reflect the dependence of predicted likelihood of occurrence on the selected variable alone. Dependencies induced by correlations between the selected variable and the other variables are inferred when compared to the marginal response *curves*. Results are from 30 bootstrapped Maxent runs with no data withheld

species are crystal krill (*E. crystallorophias*) and silverfish (*Pleuragramma antarcticum*), as confirmed by Ichii et al. (1998). Further support of that diet is given indirectly by Ainley et al. (2006), who found that while feeding on those two prey species (diet samples obtained), Adélie penguins (*Pygoscelis adeliae*) are forced to alter their foraging behavior when in the presence of minke whales. Accordingly, overlap in small-scale habitat use between these penguins and minke whales has been found to be low (Ballard et al. 2011; Friedlaender et al. 2011). On the basis of the Ainley et al. (2006) results, we would hypothesize this to be a response on the part of the penguins to seek prey patches that have yet to be ravaged by whales.

Implications of environmental change

Climate change models that are appropriate for the Southern Ocean have predicted that the southern boundary of the ACC will continue to shift southward and will do so to a meaningful extent within the next few decades (Russell et al. 2006a; Tynan and Russell 2008). At the same time, sea-ice extent will also begin to decrease elsewhere than just the Antarctic Peninsula, after continuing to increase for awhile in the Ross Sea region (cf. Stammerjohn et al. 2008; Ainley et al. 2010a). The Antarctic ozone hole and middle latitude atmospheric warming have both been implicated as causing Antarctic circumpolar winds to increase, resulting in a southward shift in the sbACC (Thompson and Solomon

2002; Russell et al. 2006a; Tynan and Russell 2008), and a bowing of the polar jet leading to wind patterns that affect the regional sea-ice changes mentioned above (Stammerjohn et al. 2008). Given the association of minke whales with waters south of the sbACC, sea ice, and particularly with the ASBF, it appears that the habitat of Antarctic minke whales will thus be narrowed significantly in the coming decades. Whether or not the loosening of pack ice would facilitate more minke whales in those areas where sea ice currently is dense year round (see Gloersen et al. 1992) remains to be seen.

In this available habitat (which ultimately is projected to decline in availability as described above), increased competition with other whales (as they recover from former decimation) may also make existence more difficult for Antarctic minke whales, particularly as recession of the ice pack would allow access by the larger species to waters where they are now excluded (e.g., Kasamatsu et al. 2000b; Friedlaender et al. 2006). In that regard, the ASBF (with occurrence there of Antarctic krill) appears to be the most important factor explaining the summer distribution also of blue whales *B. musculus* (Branch et al. 2007), a potential competitor, whose numbers are only beginning to recover in the Southern Ocean (Branch et al. 2004). Seemingly, Antarctic minke whales, when forced by competition, would choose habitat inshore of blue whales (i.e., over the shelf), a pattern that was apparent before industrial whaling removed blue whales from the Ross Sea slope in the 1920s (Ainley 2010). In addition, areas of highest abundance of minke whales were areas in which humpback whales (*Megaptera novaeangliae*) are sparse and vice versa, i.e., just west of the Ross Sea and off the west coast of the Antarctic Peninsula (cf. our results and Branch 2006, 2010). The non-overlapping distribution of minke and humpback whales in the Ross Sea region is consistent with historical records (Ainley 2010). In the presence of humpback whales, minke whales forage at depth (Friedlaender et al. 2008), which to us seems an energetically unfavorable compromise, especially for a much smaller species of baleen whale. Therefore, the growth of humpback whale populations may affect minke whale habitat availability as well.

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