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Using passive acoustics to model blue whale habitat off the Western Antarctic Peninsula

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ABSTRACT

Habitat preferences of calling blue whales were investigated using data from two multidisciplinary oceanographic cruises conducted off the Western Antarctic Peninsula (WAP) during the austral falls of 2001 and 2002. Data were collected on depth, temperature, salinity, chlorophyll *a* (Chl-*a*) concentration, krill biomass, zooplankton abundance, and blue whale call presence. In 2001, the study area was sea ice free, high Chl-*a* concentrations occurred over a small area, krill biomass and zooplankton abundance were high, and few blue whale calls were detected. In 2002 the sea ice covered the southern part of the survey area, Chl-*a* was high over a large area, krill and zooplankton were low, and there were more blue whale calls. Logistic regression analysis revealed blue whale calls were positively correlated with depth and SST, and negatively correlated with the mean zooplankton abundance from 101 to 300 m and the mean krill biomass in the top 100 m. The negative correlation between blue whale calls and zooplankton could occur if feeding animals do not produce calls. Our survey area did not cover the full range of blue whale habitat off the WAP, as blue whales probably follow the melting and freezing ice edge through this region. Passive acoustics can provide insight to mesoscale habitat use by blue whales in the Southern Ocean where visual sightings are rare, but the ability to localize on the calling animals would greatly improve the ability to model at a finer scale.

1. Introduction

The earliest scientific understanding of baleen whale habitat associations came from the *Discovery* investigations of the 1930s, the goal of which was a systematic exploration of the Southern Ocean resources, particularly ones linked to the whaling industry. Well-known whaling grounds were associated with prominent atmospheric and physical features (Kellogg, 1929; Beklemishev, 1960), as well as high abundance of krill (Marr, 1962) that are the primary food source for baleen whales in the Southern Ocean (Mackintosh and Wheeler, 1929; Mackintosh, 1965; Kawamura, 1994a).

Southern Ocean productivity is affected by circulation patterns and sea ice dynamics (Nicol et al., 2000; Constable et al., 2003). Off the Antarctic Peninsula, the Antarctic Circumpolar Current (ACC) brings intrusions of oceanic, relatively warm (1.5–2 °C), and salty (34.6–34.7) water, Upper Circumpolar Deep Water (UCDW), on the shelf (Klinck et al., 2004). The larger Marguerite Bay shelf area (Fig. 1) gets entirely covered by the sea ice in the winter (Stammerjohn and Smith, 1996). These shelf regions generally have higher rates of primary productivity than open waters off the shelf (Holm-Hansen et al., 1997; Constable et al., 2003) and feature relatively high krill biomass (Marr, 1962; Lascara et al., 1999; Atkinson et al., 2004) important for feeding whales (Kawamura, 1994b).

Blue whales (*Balaenoptera musculus*) are generally found in the Southern Ocean in the spring and the summer and are thought to migrate to lower latitudes in the fall (Mackintosh, 1965; Kasamatsu et al., 1988, 1996; Branch et al., 2007). While in the Antarctic, they may undertake extensive circumpolar movement (Brown, 1954, 1962; Branch et al., 2007). Based on acoustic recordings, blue whales can be heard in the Antarctic year-round (Širović et al., 2004, 2009).

Blue whales are relatively rarely sighted in the Southern Ocean (Branch and Butterworth, 2001; Thiele et al., 2004), but they can be reliably detected from their calls (Širović et al., 2004, 2006). Blue whales in the Southern Ocean produce several call types (Ljungblad et al., 1998; Rankin et al., 2005). One type, the "28 Hz tonal", is up to 18 s long, consists of a tone generally followed by down swept segments, and is often repeated at regular intervals (Širović et al., 2004; Rankin et al., 2005). Similar low frequency, repetitive calls (termed songs) produced by blue whales off California are attributed to males and are presumed to function as mating displays (McDonald et al., 2001; Oleson et al., 2007a). Blue whales also produce variable, frequency modulated "D calls" that last up to 4 s and sweep downward in frequency from approximately 100 to 40 Hz (Thompson et al., 1996; Rankin et al., 2005; Širović et al., 2006). D calls off California and in the Southern Ocean have been associated

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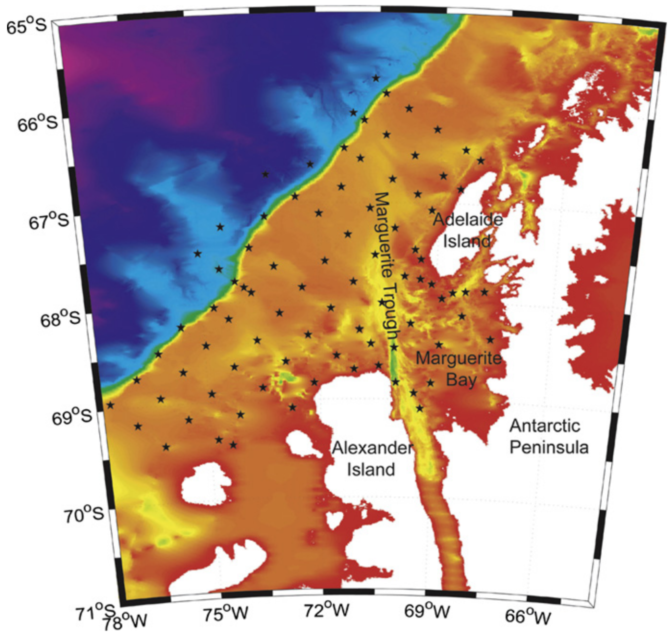

Fig. 1. Survey area of the US Southern Ocean GLOBEC cruises, with color from red to violet indicating increasing depths, land is white. Approximate depths: orange 200 m, dark blue 3000 m. Stars represent locations of CTD survey stations (for interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

with feeding blue whales and are produced by both sexes (Rankin et al., 2005; Oleson et al., 2007a).

Recent integrative ecology work in the Southern Ocean has focused on humpback (*Megaptera novaeangliae*) and Antarctic minke whales (*Balaenoptera bonaerensis*), which are more abundant there than blue whales (Moore et al., 1999; Branch and Butterworth, 2001; Murase et al., 2002; Thiele et al., 2004; Friedlaender et al., 2006, 2009). The continental slope that coincides with the ice edge is an important feeding ground for minke whales, while humpback whales are associated with the areas of high krill and chlorophyll *a* density (Nicol et al., 2000; Murase et al., 2002). In the WAP region, both humpback and minke whale distributions are influenced by zooplankton presence as measured by volume backscatter, distance to the ice edge, and bathymetry (Friedlaender et al., 2006). Spatially explicit analytical techniques quantify relationships between cetacean species and their environment and generate predictive habitat models of cetacean use (see Redfern et al. (2006) for a review of this topic).

The Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) program was designed to test hypotheses about the interactions between the Antarctic krill (*Euphausia superba*) and their environment and predators, and provide a benchmark for future multidisciplinary research in the Antarctic (Hofmann et al., 2002). The field program consisted of multiple, multidisciplinary oceanographic cruises along the WAP. The goal of this study was to investigate the possibility for using passive acoustics to study the mesoscale (10–100 km) habitat of blue whales. This scale corresponds with the typical range of several tens of km expected for acoustic survey of baleen whales using sonobuoys (McDonald, 2004). We describe the relationship between the distributions of calling blue whales and the physical and biological variables in the US Southern Ocean GLOBEC study area on the WAP shelf in the austral falls of 2001 and 2002. In particular, the relationships with bathymetry, sea ice and sea surface temperature (SST), UCDW intrusions, surface chlorophyll *a* concentrations, krill biomass and abundance of other zooplankton (e.g. copepods and siphonophores) and fish were investigated. Advantages and limitations of using passive acoustics for whale habitat modeling are discussed.

2. Methods

Data were collected during two SO GLOBEC survey cruises aboard the RVIB *Nathaniel B. Palmer* in the Western Antarctic Peninsula region near Marguerite Bay: from 23 April to 6 June 2001 and from 9 April to 21 May 2002. The surveys were designed to provide a broad-scale, synoptic look at an area approximately 240 km × 480 km (Fig. 1) by collecting data on the hydrography, nutrients, primary production, zooplankton, and top-predator distribution characteristics. In these analyses, only the data from the southward pass through the survey grid were used to ensure contemporaneous oceanographic and acoustic data during each year. In this paper, when referring to the survey year, it is implicit that the periods discussed are the survey months of April and May, not the entire year.

2.1. Environmental data collection

Hydrographic data collected during the two surveys covered much of the same area on the WAP shelf, north and south of Marguerite Bay, as well as within the Bay. The survey started at the north end of the region and moved southward in both years. Thirteen cross-shelf transects were conducted perpendicular to the coastline and the shelf break. Stations were mostly spaced at 40 km intervals, with some stations at 10 km intervals to provide finer resolution of rapidly changing areas, such as the shelf break region (Klinck et al., 2004). The southbound survey consisted of 81 hydrographic stations in 2001, and 92 stations in 2002. Temperature and salinity measurements were made using a SeaBird 911+Niskin/Rosette conductivity–temperature–density (CTD) sensor system. The Rosette system consisted of 24 10-liter Niskin bottles and water samples were taken at standardized depths. Chlorophyll *a* concentrations were measured from the water samples using a Turner Designs Digital 10-AU-05 Fluorometer. In this study, sea surface temperature (SST) and surface chlorophyll *a* (Chl-*a*) concentration were reported. Also, the temperature maximum below 200 m depth (T_{max200}), and the salinity at 50 m (Sal_{50}) were determined. $T_{max200} > 1.8$ °C is representative of the ACC waters, and the waters with T_{max200} between 1.5 and 1.8 °C are indicative of the UCDW (Klinck et al., 2004). Bathymetry data were collected using a SeaBeam multibeam system mounted on the hull of the ship (Bolmer et al., 2004).

Acoustic backscatter and target strength data were collected using BIOMAPER-II, which was equipped with five pairs of transducers with center frequencies at 43, 120, 200, 420 kHz, and 1 MHz (Lawson et al., 2004). BIOMAPER-II was "tow-yoed" up and down through the water column between 20 and 400 m depths, while the ship was steaming between the hydrographic stations at speeds of 4–6 kts. Acoustic methods were developed from measurements of volume backscatter and target strength at 43 and 120 kHz, yielding estimates of krill biomass (Lawson, 2006; Lawson et al., 2007a). Krill were separated from the rest of the zooplankton because they are the primary prey species for blue whales in the Southern Ocean (Kawamura, 1980; Kawamura, 1994a). The remainder of the volume backscatter signal was used as a proxy for other zooplankton species with different target strengths, such as copepods and siphonophores, and also included fish (Ashjian et al., 2004; Lawson et al., 2004). Details on acoustic methods for estimation of krill biomass and the limitations and uncertainties in the available data are detailed in Lawson et al. (2004, 2007a) and Lawson (2006). Mean volume backscatter (dB) and krill biomass (g m^{-2}) were integrated over 0–100 and 101–300 m and averaged over the 20 km along-track intervals centered at the passive acoustic receiver (sonobuoy) deployment locations for which BIOMAPER-II data were available. This yielded 36 and 41 points with concurrent active and passive acoustic data in 2001 and 2002 survey years, respectively, which were used for model development. Hydrographic data from CTD stations were used for estimation of temperature, salinity, and chlorophyll *a* concentration at sonobuoy deployment locations as well, using the IDW interpolation method discussed in Section 2.3.

2.2. Passive acoustic data collection and analysis

Blue whale calls were analyzed from sonobuoy recordings made during two survey cruises. Sonobuoys are expendable, radio-linked underwater listening devices that were deployed when whales were visually detected, before CTD stations, and sporadically throughout the cruises, to provide coverage of the entire surveyed area. Both omnidirectional (AN/SSQ-57B) and directional sonobuoys (DIFAR, AN/SSQ-53D) were used. Omnidirectional sonobuoys have a broader frequency response than the directional sonobuoys (10–20,000 and 10–2400 Hz, respectively), but the latter type provide data on the sound source direction. A total of 59 sonobuoys were deployed on the southbound pass of the 2001 cruise: 2 omnidirectional and 57 DIFAR. During the southbound portion of the 2002 cruise, a total of 47 sonobuoys were deployed: 44 omnidirectional and 3 DIFAR. A total of 4 omnidirectional and 3 DIFAR sonobuoys failed upon deployment during these cruises, giving a failure rate of 9% and 5%, respectively.

Custom electronics and software were used to record and analyze sonobuoy data during and after the cruises. Two antennae were available for the reception of the sonobuoy radio signal aboard the RVIB *Nathaniel B. Palmer*: a 162–173.5 MHz eight-element directional Yagi and a 138–174 MHz two dipole omnidirectional SRL-210-A2 Sinclair antenna. The maximum range for the radio transmission during these cruises was 16 nmi for the Yagi, and 10 nmi for the Sinclair, but the range was dependent on the weather conditions. We used software controlled ICOM IC-PCR1000 scanner radio receiver, modified to provide improved low frequency response, for the reception of the sonobuoy signal. Data were recorded continuously to digital audiotapes at 48 kHz sample rate using Sony PCM-300 and PCM-M1 digital audio recorders during 2001 and 2002 cruises, respectively. Upon each deployment the following information was recorded: time, latitude, longitude, and bottom depth at deployment, sonobuoy type and channel, reason for deployment (whale sighting, CTD station, etc.). Also, ship speed and course, and general weather and sea ice conditions were noted. After deployment, the sonobuoys transmitted their radio signal to the underway ship for a maximum of 8 h before scuttling and sinking. Duration of recording per sonobuoy varied depending on other activities occurring on the ship and ranged between 1 and 8 h.

After the cruise, data were digitized and converted into 35 min wav files by playing the audiotapes on a Sony PCM-M1 and re-digitizing the analog signal using the real-time signal recording feature in software program *Ishmael* (Mellinger, 2001). Since the calls of interest occurred at frequencies <100 Hz, data were first filtered with an eighth order Chebyshev type I low-pass filter, and then decimated by a factor of 80 to obtain recordings at a new sample rate of 600 Hz. The decimated data were analyzed on a 1.7 MHz Pentium 4 personal computer with Creative Sound Blaster Live! sound card with an automatic cross-correlation detector (Mellinger and Clark, 2000) available in *Ishmael*. Parameters of call characteristics used for the blue whale tonal call detection kernels were the same as those described in Širović et al. (2004). The detection threshold was set low to detect a high percentage of the calls, and therefore yielded numerous false detections. All detections were saved as individual wav files, and true detections were selected by visual inspection of spectrograms. The files that did not contain blue whale tonal calls were not used in further analyses. This automatic detection method was used for the tonal calls only. The irregular frequency and temporal characteristics of blue whale D calls make them difficult to detect automatically, therefore their presence was determined by visually scanning all the data. Downswept calls lasting 1–4 s, ranging in frequency between 100 and 40 Hz were identified as D calls, and periods when these calls were recorded were noted. The presence or absence of blue whale calls at the sonobuoy deployment locations was used as the response variable in our model (see Section 2.3 for more details).

One limitation of the acoustic data is that they provide information only on the presence of whales. If no calls are detected, the whales could either be absent or not calling. When calls were detected, on the other hand, we could not distinguish if they came from a single or multiple whales. In this paper we used the number of detection locations as a proxy for whale abundance in the survey area during the fall of that year, assuming that the calls produced at different locations were not produced by the same whale. More information, however, is needed on the blue whale calling behavior and rates of call production for a better interpretation of the calling data in future studies (e.g. Oleson et al., 2007a).

2.3. Spatial analysis

All the physical and biological data used in this study (Table 1) were imported into ESRI ArcView 9.1. Values of all the environmental data were used to create interpolated raster surfaces using the Inverse Distance Weighted (IDW) function in the Spatial Analyst toolbox (Chapman et al., 2004). In this way, we achieved spatial coincidence between the sonobuoy deployment locations and hydrographic and Chl-*a* data used for modeling. IDW was used because in ecological data, the similarity between points decreases with an increasing distance. For plotting, we used a cell size (resolution) of 20 km for krill and zooplankton, and 40km for the thermohaline properties and Chl-*a*. Individual locations of sonobuoys with blue whale call detections were compared qualitatively with environmental conditions measured or interpolated at those locations during the two surveys. Only sonobuoy

Table 1
Physical and the biological variables available for the study, with units and resolution at which data were collected, and notation whether the variable was used for model fitting.

Variable	Abbr.	Unit	Resolution	Model
Depth		m	Continuous, along-track sample	Y
Sea surface temperature	SST	°C	40 km sampling, IDW interpolation	Y
T_{max} below 200 m	T_{max200}	°C	40 km sampling, IDW interpolation	Y
Salinity at 50 m	Sal_{50}	N/A	40 km sampling, IDW interpolation	N
Surface chlorophyll *a*	Chl-*a*	$\mu g\ l^{-1}$	40 km sampling, IDW interpolation	Y
Mean krill biomass 0–100 m	mk1	$g\ m^{-2}$	Continuous sample, 20 km average	Y
Mean krill biomass 101–300 m	mk3	$g\ m^{-2}$	Continuous sample, 20 km average	Y
Mean backscatter 0–100 m	mz1	dB	Continuous sample, 20 km average	Y
Mean backscatter 101–300 m	mz3	dB	Continuous sample, 20 km average	Y

deployment locations that had concurrent active acoustic data and hydrographic data were used for modeling.

We used logistic regression to explore the quantitative nature of the relationship between whale call presence and the environmental variables. Due to the small number of blue whale detections in 2001 and small number of locations with D calls in both years, data for the two years and different call types were pooled. Additionally, pooling of data across years allows for a development of a more robust model that is not limited to conditions from one year. A null model was built based only on the presence of calling blue whales at each sonobuoy, with an assumed binomial error structure. Correlations between environmental variables were calculated to check for colinearity and only variables with correlation <0.7 were used in model fitting (Weisberg, 2005). A forward–backward stepwise selection process was used to find the model with the best fit to the data from the available variables. The best model fit was determined using Akaike's Information Criterion (AIC) at each step. The added contribution of each variable to the model fit was evaluated from the change in the deviance by the addition of that variable. Since AIC has a tendency to over-fit the data, all the variables were sequentially tested for significance ($\alpha=0.05$) using a χ^2-test for reduction of overall deviance (McCullagh and Nelder, 1989). We calculated the squared multiple correlation coefficient, R^2, to estimate the proportion of the variation in the presence or calling blue whales explained by the final model. The final model was checked for autocorrelation in the residuals and the regression coefficients were standardized to the same units for easier inter-comparison (Selvin, 1998). All the analyses were done using *S-PLUS* 6 *for Windows*.

3. Results

3.1. Qualitative comparison

The overall hydrographic and biological conditions were very different between the two survey years. In 2001, the sea ice formed relatively late (Perovich et al., 2004). Even though the 2001 cruise started two weeks later in the season than in 2002, no sea ice had formed during the former, but by the time of the latter cruise, the sea ice had already covered the southern portion of the survey area. In the fall of 2002, the krill biomass was 0 mg m^{-2} across a large part of the survey area that had at least 6 mg m^{-2} in 2001 (Lawson et al., 2004, 2007b). High zooplankton abundance occurred over a larger area in 2001. The maximum observed values of Chl-*a* were similar between years, but in 2002, high levels of Chl-*a* extended further south and closer inshore. More blue whale calls were detected in 2002, but no blue whales were sighted by experienced marine mammal visual observers during either cruise (Thiele et al., 2004). During both years the ACC was flowing just off the shelf break and there was evidence of the UCDW intrusions onto the shelf.

There were distinct differences in the distribution of calling blue whales between the years. In 2001, blue whale calls were detected on just three sonobuoys (Fig. 2). On one sonobuoy, deployed off the shelf break in the middle of the survey area, the calls were "28 Hz tonals" (for simplicity referred to as "tonals" through the rest of the paper). D calls were detected on two different sonobuoys, deployed in the vicinity of Alexander Island. In 2002, blue whale tonal calls were detected on 21 sonobuoys, mostly in the northern and middle shelf areas. Also, D calls were detected on four of those sonobuoys. The sonobuoys on which calls were detected were deployed along Marguerite Trough, the trough west of Alexander Island, and off the shelf break (Fig. 2).

In 2001, the survey area had SST >-1.7 °C and was largely free of the sea ice (Fig. 3; Thiele et al., 2004; Friedlaender et al., 2006). SST was lower than -1.7 °C and the sea ice covered the southern part of Marguerite Bay and much of the southwestern portion of the survey grid in the fall of 2002 (Thiele et al., 2004). All the whale call detections occurred in ice-free waters, but there were more detections in the year when the sea ice was already forming. Fig. 4 shows the ACC ($T_{max200}>1.8$ °C) flowing just off the shelf break during both surveys, with a somewhat stronger signal in 2002. During both surveys, the UCDW intrusions onto the shelf occurred along Marguerite Trough, starting at the shelf break in the northwest end of the survey area, and extending into the Bay along the western side of Adelaide Island. Most blue whale calls were associated with the regions of the ACC and the UCDW intrusions (Fig. 4).

The maximum surface Chl-*a* values were similar between the two years (2.01 and 2.16 μg l^{-1} in 2001 and 2002, respectively), but during 2002, high Chl-*a* concentrations extended over a larger area (Fig. 5). In 2001, the blue whale call detections occurred outside the areas of high Chl-*a*. In 2002, blue whale call detections occurred both in areas of high and low Chl-*a* concentrations.

Krill had higher biomass and zooplankton had higher abundance in 2001 than 2002 (Figs. 6–9). Generally, in both years, the highest concentrations occurred on the northwest side of Alexander Island, along the west and north shores of Adelaide Island, and in south Marguerite Bay. Both the mean krill biomass and the mean zooplankton abundance were higher in the 100–300 m depth range than in the top 100 m. The highest krill biomass occurred off the western Alexander and the northern Adelaide Islands in both years (Figs. 6 and 7). In 2002, the zooplankton abundance in the top 100m was high in the southwestern parts of the survey area, with

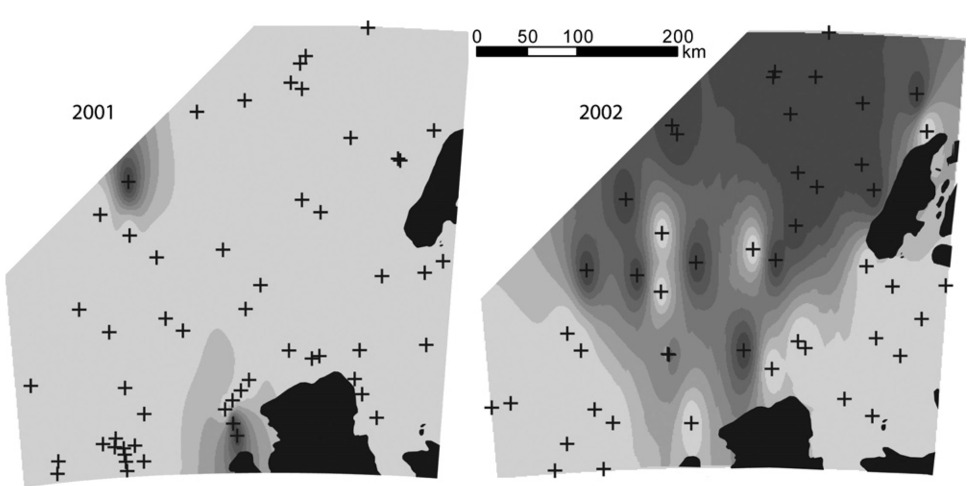

Fig. 2. Areas with high calling blue whale presence during the two survey years are shown with darker shading based on IDW. Pluses are locations of all sonobuoy deployments during that survey. Black areas represent land.

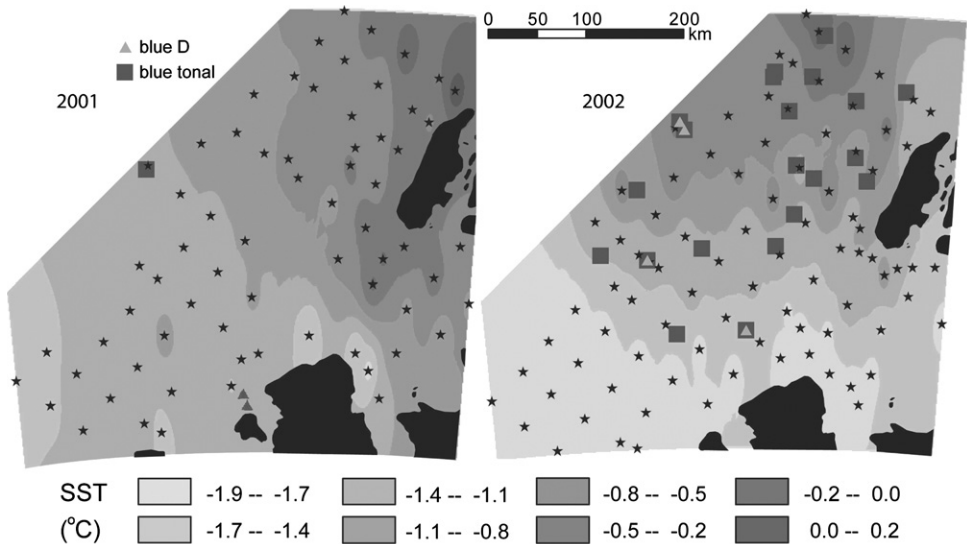

Fig. 3. Sea surface temperature (sea ice cover proxy) during the two survey years, smoothed with IDW. Stars represent locations of CTD survey stations. Blue squares are sonobuoy deployment locations on which blue whale tonals were detected and blue triangles are blue whale D call locations. Black areas represent land.

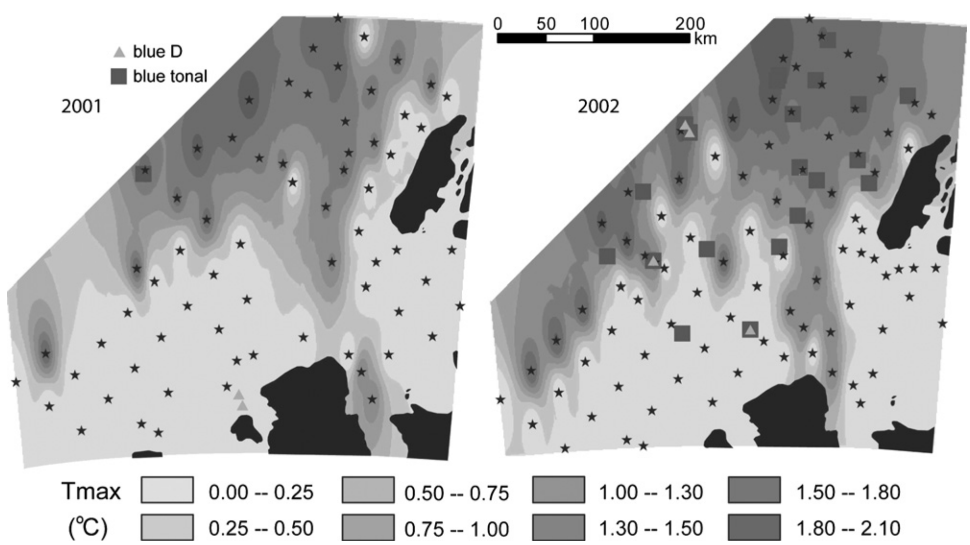

Fig. 4. Temperature maximum below 200 m (UCDW proxy) during the two survey years, smoothed with IDW. Symbols are the same as in Fig. 3.

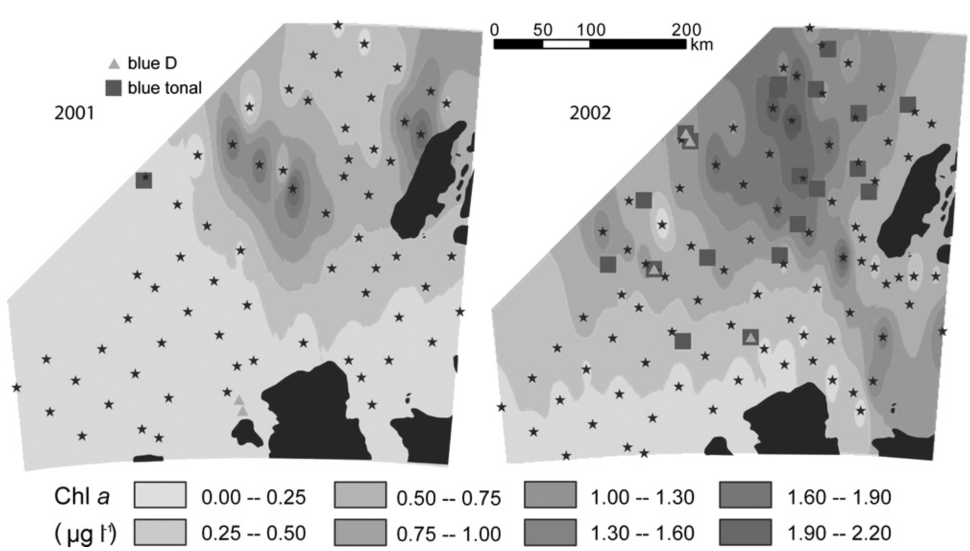

Fig. 5. Surface chlorophyll *a* concentrations during the two survey years, smoothed with IDW. Symbols are the same as in Fig. 3.

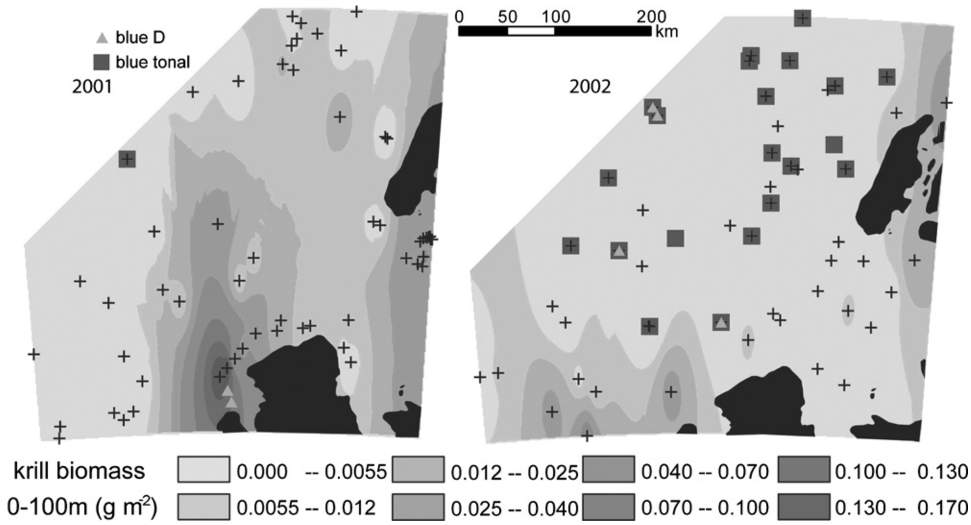

Fig. 6. Mean krill biomass in the top 100 m during the two survey years, smoothed with IDW. Pluses represent center locations of the 20 km along-track intervals over which the mean krill biomass was calculated. Blue squares are sonobuoy deployment locations where blue whale tonals were detected and blue triangles are blue whale D call locations. Black areas represent land.

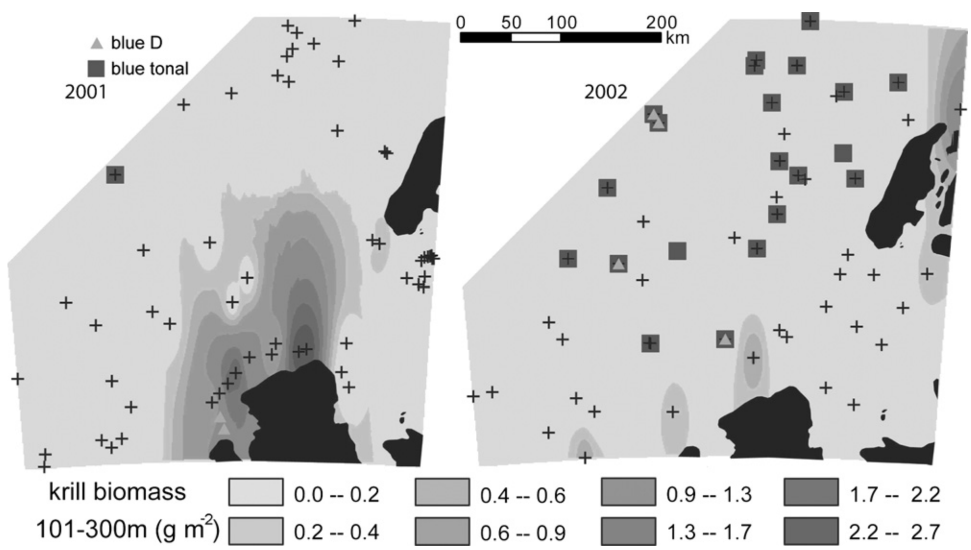

Fig. 7. Mean krill biomass at depth (101–300 m) during the two survey years, smoothed with IDW. Symbols are same as in Fig. 6.

the highest values at the southeastern end of Marguerite Bay (Fig. 8). In 2001, the zooplankton abundance at depth (101–300 m) was high in most of the survey region, peaking at the southern end (Fig. 9). In both years, small krill aggregations dominated numerically, but the small numbers of very large aggregations contributed the majority of the biomass (Lawson, 2006).

In 2001, blue whale D calls were detected twice in the area with the highest krill biomass and zooplankton abundances, but the next year, D calls were detected in the areas of low krill biomass and zooplankton abundances. In 2002, the northwest shelf, where most blue whale tonal calls were detected, had 0 g m^{-2} krill biomass. All other regions where blue whale tonals and D calls were detected that year had low krill biomass, as well, both in the surface 100 m and in the 100–300 m depth range (Figs. 6 and 7).

3.2. Modeling results

Eight of the available nine environmental variables were used for the model fitting (Table 1). T_{max200} and Sal_{50} had a correlation of 0.740, indicating they are both related to the UCDW intrusions, so only T_{max200} was used in the model selection process. The variables that were found to be significantly explanatory of the calling blue whale presence were: depth, the mean krill biomass in the 0–100 m range, the mean zooplankton abundance in the 101–300 m range, and the sea surface temperature ($\chi^2=49.179$, df$=4$, $p<0.0001$; Table 2). Depth and the sea surface temperature were positively correlated with the presence of the calling blue whales, and krill and zooplankton were negatively correlated (Fig. 10; Table 2). This model explained almost 59% of the blue whale call presence data ($R^2=0.587$).

4. Discussion

These results come from the first fall surveys in larger Marguerite Bay area that combined blue whale presence data with the environmental data since the *Discovery* expedition. They offered an uncommon opportunity to investigate distribution patterns by calling blue whales in the Southern Ocean. While some mesoscale

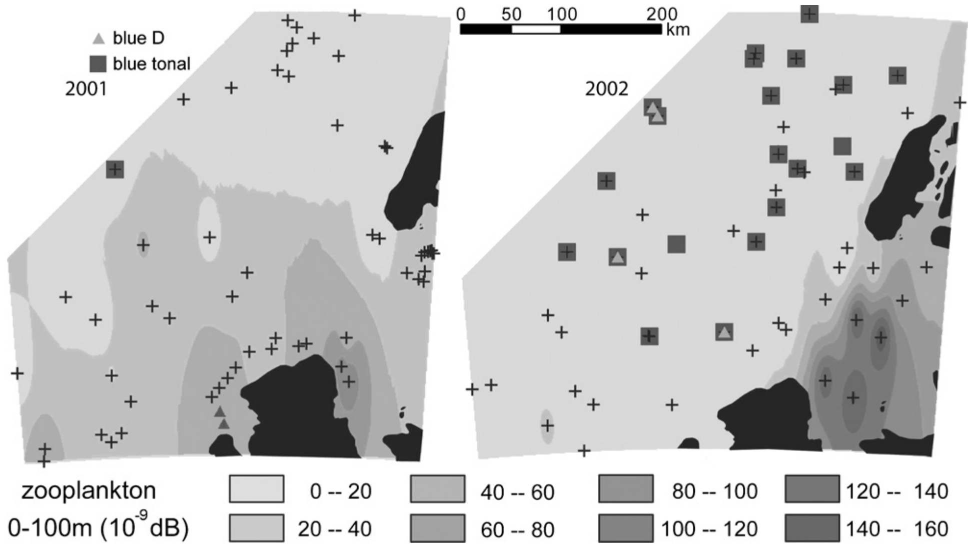

Fig. 8. Mean zooplankton abundance in the top 100 m during the two survey years, smoothed with IDW. Symbols are the same as in Fig. 6.

use patterns can be gleaned from passive acoustic data for this type of modeling, the interpretation of the data was limited by the constraints imposed by the differences in scales at which different data were collected, which are fully addressed in Section 4.2.

These fall surveys showed a high degree of interannual variability in this region of the Southern Ocean. One notable difference in the conditions between the two years was the timing of the sea ice formation (Perovich et al., 2004). The sea ice cycle is an important feature that affects physical and biological processes (Nicol et al., 2000; Nicol, 2006) and the sea ice cover differences between the surveys were broadly paralleled by the differences in the distribution and abundance of Chl-*a*, krill, zooplankton and calling whales. Consistent between the years, however, high krill and zooplankton abundances coincided with the areas of steep bathymetry, such as Marguerite Trough (Ashjian et al., 2004; Lawson et al., 2004).

The negative relationship we found between the calling blue whales and the krill and zooplankton could indicate that the calling blue whales are not feeding. In addition to this negative relationship between the calling blue whales and the zooplankton, there was also an apparent negative relationship between the zooplankton and Chl-*a* (Lawson, 2006). This may indicate a degree of top-down control in the area, with zooplankton depleting the Chl-*a* and blue whales depleting the zooplankton (Beklemishev, 1960; Carpenter et al., 1985). The linkage between Chl-*a* and the calling blue whales, however, was not significant.

Humpback and Antarctic minke whale habitat preferences were analyzed previously from the sighting data collected during the same two surveys (Friedlaender et al., 2006). As for the blue whales, the distribution of humpback and minke whales was related to the ice edge and bathymetry, but humpback and minke whales had a positive relationship with zooplankton. These analyses, however, were based on sighting data, not acoustic detections. Different baleen whale survey methods (visual versus acoustic) may sample animals in different behavioral states (Oleson et al., 2007b, 2007c), which could account for the differences in their zooplankton linkages.

4.1. Blue whale distribution

Correlations between the calling blue whale distribution and the bathymetry and the SST were also found in the North Pacific (Croll et al., 1998; Fiedler et al., 1998). The difference was that in temperate and tropical regions, the SST was negatively correlated with the blue whale distribution. All the whale detections in this study occurred in the warmer, ice-free waters. This difference in the direction of the correlation is likely due to the fact that in the polar region in the fall, a low surface temperature is not an expression of the upwelled, nutrient rich waters, but rather indicates sea ice formation. So even though the SST appears to be an important predictor of blue whale habitat in a variety of environments, the underlying ecology differs.

A number of studies found that rorquals in different geographic regions are associated with their prey at various scales, ranging from a few km to thousands of km (Croll et al., 1998; Tynan, 1998; Nicol et al., 2000; Reid et al., 2000; Friedlaender et al., 2006). Positive correlations at fine scales are harder to demonstrate (Reid et al., 2000; Baumgartner et al., 2003), but the scale used in this study (10 s of km) should be large enough to test the general relationships between the whales and the krill. The negative correlation between the calling blue whales and krill biomass and zooplankton abundance could be the result of several factors. In 2002, the krill biomass in much of the northern part of the survey area, where most blue whale calls were detected, was 0 g m^{-2}. Although it is possible that existing krill patches were missed by the very narrow BIOMAPER-II tracks, the consistent absence of krill over several track lines strengthens the idea there were no krill in this region.

Blue whales come to the Southern Ocean primarily to feed (Kawamura, 1994b), but they most likely do not spend all their time foraging. Therefore, it is necessary to consider other behavioral contexts of whale presence in the WAP region. Evidence from California suggests that blue whales producing tonal, song-like calls may not be feeding, but are moving through the area (McDonald et al., 1995; Oleson et al., 2007a). Thus, we should not always expect to find calling blue whales in areas with high krill biomass. Blue whales making D calls are more likely to be feeding (Oleson et al., 2007a, 2007c). Rankin et al. (2005) recorded both tonal and D calls in the vicinity of apparently feeding animals during the austral summer. During our surveys, two out of six times blue whale D calls were detected, they were associated with high krill biomass and zooplankton abundance. It has been found previously that blue whales are tightly linked to krill in the Antarctic during the spring and the summer (Hardy and Gunther, 1935), but it is possible that by the fall, the whales are well fed and, as the krill move into the coastal regions (Lascara et al., 1999; Lawson, 2006), the whales start engaging more in other behaviors, such as tonal calling, which may also be linked to swimming or migration out of the area or pairing in preparation for mating (McDonald et al., 1995; Oleson et al., 2007a). This shift in behavior could explain some of the seasonal differences noted in the long-term abundance of blue whale calls off the WAP

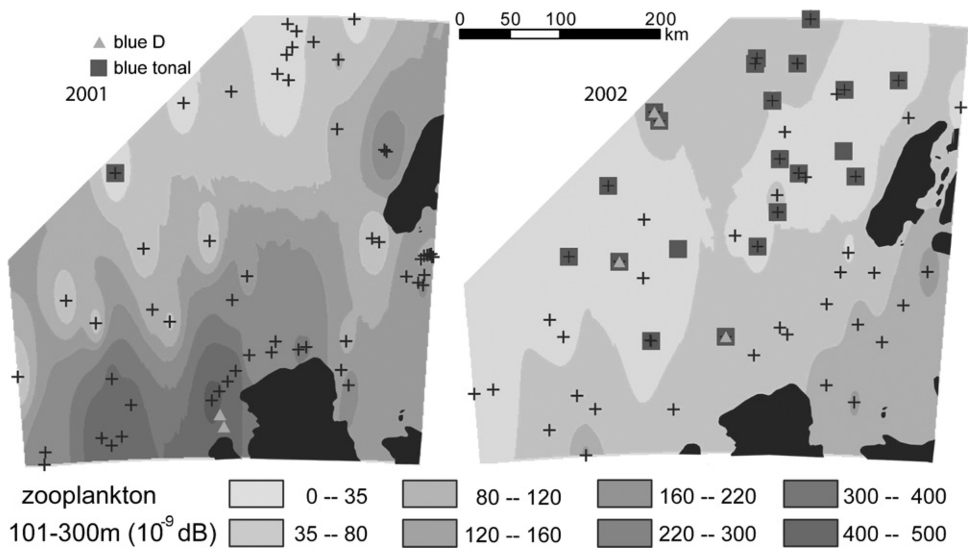

Fig. 9. Mean zooplankton abundance at depth (101–300 m) during the two survey years, smoothed with IDW. Symbols are the same as in Fig. 6.

Table 2
Results of the stepwise linear regression modeling, showing all the significant variables: mz3 is the mean backscatter in the 101–300 m depth range, mk1 is the mean krill biomass from 0 to 100 m depth, and SST is sea surface temperature.

Model	Coefficient	df	Deviance	*p*-Value
Normal		76	83.743	
+Depth	0.582	75	71.536	0.0005
+mz3	−2.481	74	58.051	0.0002
+mk1	−32.560	73	45.248	0.0003
+SST	1.458	72	34.564	0.0011

(Širović et al., 2004) and the lack of blue whale calls in December, when whales may be mostly feeding.

If we assume feeding and tonal calling are mutually exclusive, low whale call detections in 2001 could indicate the whales were still feeding at the time of the survey cruise. Alternatively, they could have been closer to the ice edge which they might be using as a reliable location of aggregated prey (Brierley et al., 2002; Nicol, 2006). Our survey certainly covered smaller area than the total area used by the foraging blue whales in the WAP region. The temporally bimodal distribution of blue whale calls recorded on bottom-moored instruments in the larger WAP area (Širović et al., 2004) indicates that the whales could be moving through our survey area with the retreating and advancing ice edge. If the whales are simply swimming when they produce tonal calls, we would not expect to find any association with prey aggregations. The presence of a negative correlation, however, may imply that the production of blue whale tonal calls in the WAP in the fall indicates the end of foraging.

4.2. Data limitations

There were several problems associated with the interpretation of acoustic volume backscatter data collected during these surveys. The 43 kHz transducer did not function properly in 2001 and, therefore, krill biomass data were not as reliable as in 2002 (Lawson, 2006). Also, while it is clear that *E. superba* is the primary prey species of blue whales in the Southern Ocean (Kawamura, 1994a), it is unclear which krill species were observed with active acoustics. Size estimates from the acoustic data, as well as net tows and Video Plankton Recorder data, indicate that deep, dense, costal patches, that dominate biomass estimates, are likely *E. superba* (Ashjian et al., 2004; G. Lawson, pers. comm.), but some aggregations off Alexander Island could have been *E. crystallorophias* (Ashjian et al., 2004). Information on zooplankton species composition would be useful for a more accurate interpretation of the negative relationships between the calling whales and krill and other zooplankton.

There was a mismatch between the scales over which BIOMAPER-II and hydrographic data were collected, and the ranges over which blue whales could be detected. Temperature, salinity and Chl-*a* data were collected mostly at 40 km intervals. BIOMAPER-II data were collected continuously along transects, but they were subsequently averaged over 20 km, centered at the sonobuoy deployment locations. Blue whale calls in the Southern Ocean propagate over long distances (up to 100 km, Širović et al., 2007) and the sonobuoy monitoring range in this study extended over tens of km (McDonald, 2004). The relationship between the sonobuoy locations and the environmental parameters, therefore, does not necessarily reflect the exact relationship between the whales and the environment, which makes it more challenging to use acoustic data for habitat modeling. No blue whales were sighted during these surveys (Thiele et al., 2004), so passive acoustics were the only method available to investigate these relationships. Passive acoustics without localizations, however, should be used only for mesoscale comparisons between whales and their environment, and small-scale linkages should be attempted only if localization of calling whales is possible.

Physical and biological variables are autocorrelated over different spatial scales. Thermohaline properties tend to autocorrelate over large spatial scales and krill abundance, for example, can vary over very small scales (Haury et al., 1978; Dickey, 1990). To use relevant scales when modeling whale habitat, it is important to know the operational scale of the response variable (Baumgartner et al., 2003). If acoustic signals are the response variable, this is further complicated by the fact that the exact location of the calling animal may be unknown and could, in fact, be tens of km away (Širović et al., 2007; Stafford et al., 2007). The primary goals of the SO GLOBEC program were not focused on the ecology of baleen whales, so the sampling strategy was not optimized for these purposes. In future studies of blue whale habitat associations, it would be important to know the scales over which whale distributions change, so that adequate sampling protocols can be adopted, with the minimum sampling resolution corresponding to the whale's integration scales.

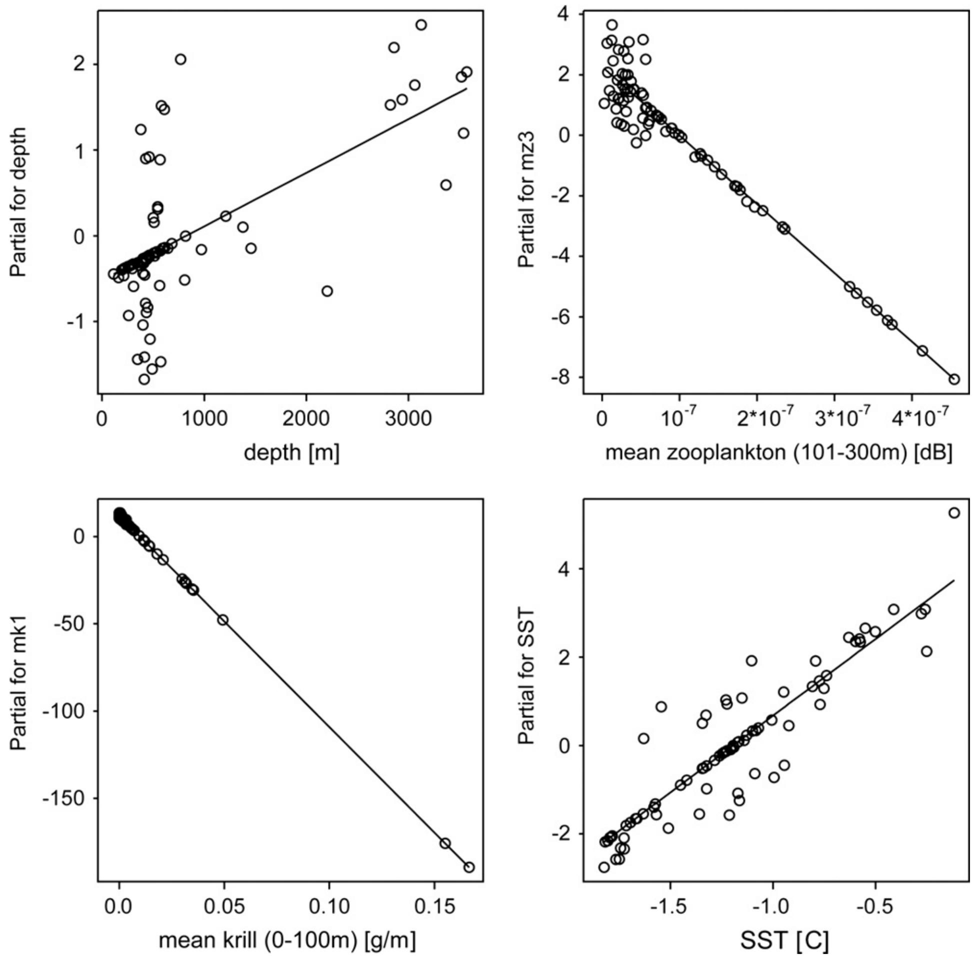

Fig. 10. The mean-adjusted partial fits (straight line) for all the significant predictor variables of the linear regression model of blue whale call presence. Circles are partial residues mz3 is the mean backscatter in the 101–300 m depth range, mk1 is the mean krill biomass from 0 to 100 m depth, and SST is sea surface temperature.

These surveys provided a static look at fall conditions during two years. Ecological processes in the Southern Ocean are dynamic and therefore these results should be considered only in the context of these individual cases. The differing ice conditions between the years provided some insight into the system variability and show its importance in the system. Habitat relationships, however, would have to be followed over many years to conclude what parameters are important in describing and predicting blue whale distributions (Hardy and Gunther, 1935). Passive acoustics can provide insight to distribution and mesoscale habitat use by blue whales in the Southern Ocean where visual sightings are rare, but the ability to localize on the calling animals would greatly improve the ability to model at a finer scale. However, while habitat modeling may provide some insights into the possible behavioral context of calling in these animals, more direct studies of calling behaviors are needed.

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