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The distribution of seabirds and pinnipeds in Marguerite Bay and their relationship to physical features during austral winter 2001

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Abstract

The distribution of seabirds and pinnipeds and their relationship to physical oceanographic variables were investigated as part of the US Southern Ocean Global Ocean Ecosystem Dynamics field program along a study grid centered around Marguerite Bay on the west Antarctic Peninsula during late fall (April–May) and winter (July–August), 2001. Sea-ice conditions during the cruises provided an opportunity to compare the relationship among physical oceanographic variables and species distributions before and after the development of pack ice. During the fall cruise before pack ice development, both sea-ice-affiliated species and open-water-affiliated were observed in the area. The most common ice-affiliated species observed at this time were snow petrel (*Pagodroma nivea*, 0.7 individuals km^{-2}) and Antarctic petrel (*Thalassoica antarctica*, 0.2 individuals km^{-2}) and the most common open-water-affiliated species were blue petrel (*Halobaena caerulea*, 0.4 individuals km^{-2}), cape petrel (*Daption capense*, 0.2 individuals km^{-2}), and southern fulmar (*Fulmarus glacialoides*, 0.1 individuals km^{-2}). In addition, Antarctic fur seals (*Arctocephalus gazella*, 0.1 individuals km^{-2}) and crabeater seals (*Lobodon carcinophagus*, 0.4 individuals km^{-2}) were observed in low numbers. Akaike's information criterion was used to assess competing models that predicted predator distributions based on physical oceanographic variables proposed to structure predator distribution in previous research. These analyses indicated that predator distributions were primarily associated with water-mass structure and variability in bottom depth during the fall cruise. Crabeater seal, snow petrel, Antarctic petrel, and southern fulmar had higher densities in Inner Shelf Water, particularly near Alexander Island where a coastal current was present. Blue petrel, kelp gull (*Larus dominicanus*), and southern giant petrel (*Macronectes giganteus*) were positively associated with variability in bottom depth in April–May, suggesting that hydrographic processes influenced by bathymetry may have been important in structuring bird distributions. After the development of pack ice, during July and August, only sea-ice-affiliated species, including snow petrel (1.0 individuals km^{-2}), Antarctic petrel (0.1 individuals km^{-2}), Adélie penguin (*Pygoscelis adeliae*, 0.4 individuals km^{-2}), and crabeater seal (0.3 individuals km^{-2}), were observed. Seabirds

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were primarily associated with sea-ice characteristics (e.g. sea-ice concentration, sea-ice type) rather than the water-column environment later in the winter. Results from this study suggest that the timing and extent of sea-ice development in the fall may influence over-winter predation by seabirds and pinnipeds on zooplankton and fish on the western Antarctic Peninsula. Delays in sea-ice development may allow seabirds and pinnipeds access to biologically important areas such as the Inner Shelf Water for a longer period of time thereby increasing predation on zooplankton and fish.

1. Introduction

The close coupling between trophic levels in the Southern Ocean presents a unique opportunity for investigating linkages between physical and biological components of the marine system (Hofmann et al., 2002). The US Southern Ocean Global Ocean Ecosystem Dynamics (US SO GLOBEC) program is a multi-disciplinary effort designed to investigate these linkages by focusing on how krill and other species within the system adapt to austral winter, a critical part of many life cycles. The ultimate goal of the research is to use the understanding of the physical and biological linkages in the marine system to predict the influence of environmental perturbation, such as climate change, through the system to top predators (Hofmann et al., 2002).

Seabirds and marine mammals have been found to be associated with a range of physical variables in the Southern Ocean. In particular, top-predator distributions have been associated with physical properties of the water column (Abrams, 1985; Ainley and Jacobs, 1981; Ainley et al., 1998; Hunt et al., 1992), sea-ice type and concentration (Ainley and Jacobs, 1981; Ainley et al., 1993, 1998; Ribic et al., 1991), and hydrographic structures, such as shelf-slope fronts (Ainley and Jacobs, 1981; Ainley et al., 1998). In near-shore, shallow waters in the Arctic, seabird distributions have been found to be associated with areas where varied bathymetry interacts with currents to form fronts, eddies or upwelling zones (Brown and Gaskin, 1988; Vermeer et al., 1987; Hunt et al., 1998), though associations of this type have not been examined in the Antarctic (Hunt, 1991).

In general, the relationship between predators and physical oceanographic features has been hypothesized to reflect an interaction between species foraging adaptations (Ainley et al., 1993) and prey distribution (Hunt and Schneider, 1987; van Franeker, 1992). The link between seabird distribution and ecosystem characteristics may be particularly strong during late fall and winter in the Antarctic. During this time, seabirds should be continuously associated with foraging habitat as they will not need to be migrating to and from breeding sites. However, little is known about the distribution of seabirds and other top predators and their linkages with oceanographic features in the Southern Ocean during the late fall and winter (Ainley et al., 1994; Fraser and Trivelpiece, 1996; Whitehouse and Veit, 1994). The survey methodology and multi-disciplinary approach of the US SO GLOBEC field program provided an unprecedented opportunity to test competing hypotheses that predict top-predator distributions based on biological and physical variables (Hofmann et al., 2002). The objectives of this paper are to assess the distribution of seabirds and pinnipeds in the US SO GLOBEC study area (see Fig. 1 in Klinck et al., 2004) during two cruises in austral winter 2001 and to describe their associations with environmental structures that have been previously hypothesized to influence predator distributions. Information on relationships with biological factors, linked physical/biological processes, and a discussion of the potential influence of climate change on these linkages will be presented in future papers.

2. Methods

2.1. Cruise tracks

The US SO GLOBEC survey provided multi-disciplinary studies of primary and secondary biological production, Antarctic krill (*Euphausia superba*) ecology and distribution, hydrography, circulation, and top predators in the region around Marguerite Bay, Antarctica. Two survey cruises were conducted in 2001; one during April–May and the second during July–August. The survey cruises were designed to provide broad-scale studies that complement concurrent process-oriented cruises that focused on specific areas of interest in the same study area. On the survey cruise, seabird and marine mammal observations were made in conjunction with hydrographic, bioacoustical, primary production and nutrient surveys on the R.V.I.B. *Nathaniel B. Palmer*. Results from cetacean surveys are reported in Thiele et al. (2004). The April–May 2001 predator survey was a 23-d effort (88 h during daylight) and covered 938.2 km of trackline (Fig. 1). Little sea ice was present in the study area during this cruise. Weather experienced during the cruise was characterized by periodic northerly gale force winds. Air temperature remained at or near 0 °C until the final two weeks of the cruise, after which it dropped to between −6 and −8 °C. Visibility was often limited by fog and snowfall throughout the cruise. The July–August 2001 survey was a 28-d effort (99 h during daylight) and covered 828.6 km of trackline (Fig. 1). Air temperature was typically below −10 °C and southwesterly winds periodically reached gale force. During this cruise, there was less snowfall, fog, and low-lying clouds than during the April–May cruise.

2.2. Visual survey methods

Predator surveys were conducted while the ship traveled at 4–6 kts, the speed at which a multi-frequency acoustical system was being towed (BIOMAPER-II, Woods Hole Oceanographic Institute, Woods Hole, MA, Lawson et al., 2004). A two-person team was used to survey birds and marine mammals during all daylight hours while the ship was underway. Observers surveyed simultaneously, using hand-held binoculars to scan for animals and to confirm species identifications. One observer used 8 × and the other used 10 × magnification binoculars so that each observer's survey capabilities complemented the other, maximizing the team's ability to detect and identify animals in varied conditions. Observations were made from the bridge (15 m above sea surface) from sunrise to sunset, except when

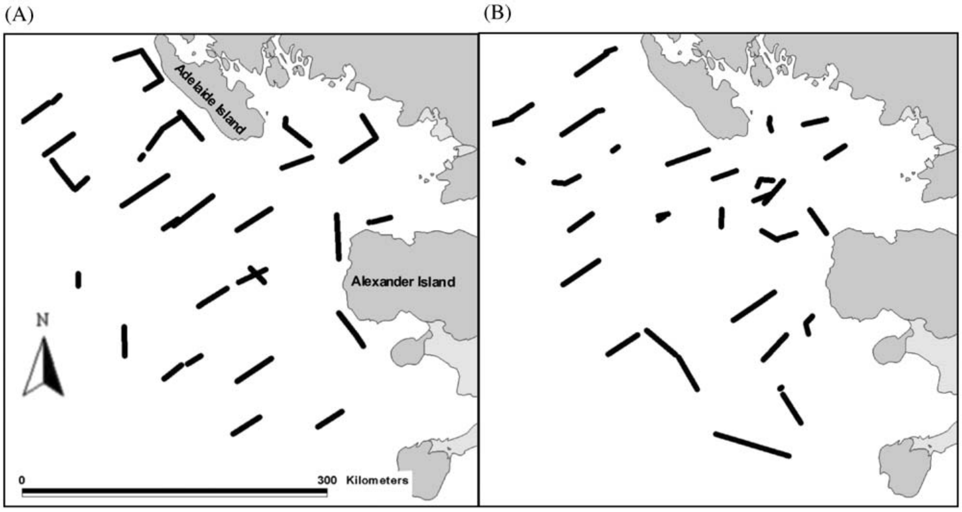

Fig. 1. Predator survey locations in the US SO GLOBEC study area during (A) the April–May and (B) the July–August, 2001 cruise. Survey locations are indicated with black lines. The study area is centered on Marguerite Bay (68°29.5′S, 70°02.3′W) between Alexander and Adelaide Islands which are labeled on map A. Coastline digital data courtesy of the Antarctic Digital Database Version 3.0, Mapping and Geographic Information Centre, British Antarctic Survey.

visibility was <300 m, Beaufort Sea State was >5 (following Ainley et al., 1993), or when the ship was stopped at hydrographic stations. Predator surveys consisted of a continuous 300-m strip transect off the port side of the ship, sweeping from the bow to 90° perpendicular to the ship (Ainley et al., 1993, 1998). Perpendicular distances to animals on the sea ice were determined using a laser range finder (Leica Geovid 7 X 10 BD Binoculars), and distances to flying birds were estimated using a range finder (Heinemann, 1981). A 300-m strip transect width also was used for seal observations (Ribic et al., 1991).

2.3. Data analysis

The continuous strip transects were split into one-half hour segments. For the April–May cruise, 155 one-half hour transects were included in the analysis and the mean length for these transects was 5.2 km (S.D. = 1.5 km). For the July–August cruise, 130 one-half hour transects were analyzed and the mean length for these transects was 4.8 km (S.D. = 0.7 km). The difference in transect lengths between cruises reflected slightly different ship speeds during surveys.

The correlations of bird densities in adjacent transects made during a single day were calculated for days when surveys were conducted for at least three hours, yielding a minimum of five adjacent transects. Using day as a replicate, autocorrelations of bird densities varied from −0.54 to 0.87 for the April–May cruise ($n = 14$ days) and −0.69 to 0.76 for the July–August cruise ($n = 11$ days). Even though there was no significant correlation of bird densities between adjacent transects (using days as replicates: April–May cruise: $r = -0.03$, df = 14, $p > 0.05$; July–August cruise: $r = 0.1$, df = 10, $p > 0.05$), the error variance in the analyses can be too low if autocorrelation is ignored. This causes variables to be declared significant when, in fact, they are not (Cressie, 1993). Thus, a generalized least-squares approach (described below) was used to adjust for autocorrelation between transects when fitting models.

Seabird densities were calculated using corrections for variation in perceived density resulting from the relative movement of ship and birds (flux, as described in Spear et al., 1992) and with ship-following birds down-weighted (Ainley et al., 1998). Many of the pinnipeds were in the water, which made estimation of numbers of animals difficult and density calculations based on line transect methodology (Lakke, 2001) not possible. Therefore, the presence/absence of pinnipeds was analyzed following Ribic et al. (1991).

2.4. Distributions of species

The number of transects along which each bird or mammal species was seen was tabulated. Although the presence/absence of pinnipeds was used in analyses, densities of pinnipeds were mapped and are considered to be a minimum estimate. Species were categorized as being sea-ice- or open-water-affiliated based on criteria given in Ainley et al. (1994), Ribic et al. (1991), and Woehler et al. (2003). These associations are summarized in Table 1. For spatial representation, the mid-point of the transect was used to map the occurrence of the species in the study area using ArcView Geographical Information Systems (Environmental Systems Research Institute Inc., 1996a)

2.5. Relationships with physical features

We investigated the relationships among predator density or the presence/absence with bathymetry characteristics, surface thermohaline properties, water-column environment, sea-ice structure, distance to breeding colony, and distance to the sea-ice edge. These variables have been hypothesized to affect top-predator distributions in the Antarctic (Ainley et al., 1994, 1998; Ribic et al., 1991). The specific variables used were:

(1) bottom depth and variation in depth for bathymetry (variation in bathymetry was used to detect an association with a bathymetrically controlled physical process);
(2) sea-surface salinity and temperature;
(3) temperature maximum below 200 m and salinity at 50 m for water-column environment;

Table 1
Number of 30-minute transects along which predator species were seen during two cruises to the US SO GLOBEC study area during April–May and July–August, 2001

Species	Habitat affiliation	Cruise	
		April–May	July–August
Emperor penguin (*Aptenodytes forsteri*)	Ice	0	7
Adélie penguin (*Pygoscelis adeliae*)	Ice	0	19
Black-browed albatross (*Diomedia melanophris*)	Open water	0	1
Unidentified albatross (*Diomedia* spp.)	Open water	1	0
Southern giant petrel (*Macronectes giganteus*)	Open water	20	6
Southern fulmar (*Fulmarus galcialoides*)	Open water	91	0
Antarctic petrel (*Thalassoica antarctica*)	Ice	56	21
Cape petrel ‘pintado petrel’ (*Daption capense*)	Open water	70	0
Snow petrel (*Pagodroma nivea*)	Ice	54	81
Blue petrel (*Halobaena caerulea*)	Open water	64	0
Sooty shearwater (*Puffinus griseus*)	Open water	1	0
Kelp gull ‘kelp gull’ (*Larus dominicanus*)	Ice	16	0
Antarctic tern (*Sterna vittata*)	Open water	1	0
Imperial cormorant ‘blue-eyed shag’ (*Phalacrocorax atriceps*)	Open water	1	0
Crabeater seal (*Lobodon carcinophagus*)	Ice	8	19
Leopard seal (*Hydrurga leptonyx*)	Ice	2	0
Weddell seal (*Leptonychotes weddellii*)	Ice	1	2
Antarctic fur seal (*Arctocephalus gazella*)	Ice edge	12	0
Unidentified seal		4	0
Total number of transects		155	130

Note: Habitat affiliation is based on Ainley et al. (1994), Ribic et al. (1991), and Woehler et al. (2003).

(4) distance to sea-ice edge, the presence/absence of sea ice, sea-ice type and sea-ice concentration for sea-ice structure; and
(5) distance to land (a proxy for distance to breeding colonies and other potential roosting sites on land).

Bottom depth for each transect was obtained by interpolating depth values for the mid-point of each transect using high-resolution bathymetry data currently being developed for the study region (T. Bolmer and R. Beardsley, Technical Report, Woods Hole Oceanographic Institute, in prep.). The coefficient of variation of bottom depth was calculated for each transect using depth measurements calculated using the one-minute depth values generated from the ship's continuous, underway system. Average sea-surface temperature (°C) and salinity [practical salinity unit (psu)] were calculated for each transect by averaging the one-minute values obtained from the ship's continuous real-time underway system. In July and August, sea ice prevented accurate measurement of the surface water by the ship's underway systems. Therefore, transect surface salinity and temperature values were not calculated for this cruise. Distance to land was calculated using an algorithm within ArcView Spatial Analyst (Environmental Systems Research Institute Inc., 1996b).

The temperature maximum below 200 m and salinity at 50 m along each transect were calculated using the mid-point of the transect and interpolating between the closest conductivity–temperature–depth (CTD) stations using ArcView Spatial Analyst (Environmental Systems Research Institute Inc., 1996b). Water-mass definitions were based on ranges of temperature maximum below 200 m as described in Smith et al. (1999, 1995), Hofmann and Klink (1998), Orsi et al. (1995), and Prézelin et al. (2004) (Table 2). Based on these definitions and interpolated values from CTD data during the study, transects were assigned to a

Table 2
Definitions of sub-surface waters based on temperature maximum below 200 m ($T_{\max\ 200}$) for the US SO GLOBEC study area on the western Antarctic Peninsula during April–May 2001

Sub-surface water mass	Definition	References
ACC	$T_{\max\ 200} \geqslant 1.8\,^{\circ}\mathrm{C}$	Orsi et al. (1995)
ACC-derived newly intruded UCDW	$1.5 \leqslant T_{\max\ 200} < 1.8\,^{\circ}\mathrm{C}$	Smith et al. (1995)
UCDWB	$1.4 < T_{\max\ 200} < 1.5\,^{\circ}\mathrm{C}$	Hofmann and Klink (1998), Table II
MUCDW/shelf water	$1.2 \leqslant T_{\max\ 200} \leqslant 1.4\,^{\circ}\mathrm{C}$	Smith et al. (1999), Fig. 8a
InSWB	$1.1 < T_{\max\ 200} < 1.2\,^{\circ}\mathrm{C}$	Smith et al. (1999), Fig. 8a and b
InSW	$T_{\max\ 200} \leqslant 1.1\,^{\circ}\mathrm{C}$	Prézelin et al. (in press)

InSW: Inner Shelf Water; InSWB: Inner Shelf Water Boundary; MUCDW: modified Upper Circumpolar Deep Water; UCDWB: Upper Circumpolar Deep Water Boundary; UCDW: Upper Circumpolar Deep Water; ACC: Antarctic Circumpolar Current.

particular water mass, which was then included in the models as a categorical variable. Because just two transects were in the Antarctic Circumpolar Current (ACC) during the April–May cruise, these were grouped with the Upper Circumpolar Deep Water (UCDW) in the analysis. In the July–August cruise, two transects were in the Inner Shelf Water and these were combined with transects in the Inner Shelf Water Boundary in the analysis. Densities of all species were calculated separately for each water-mass structure and tabulated.

For the April–May 2001 cruise we looked for a relationship between sub-surface water masses and mean sea-surface temperature and salinity values for the transects using a generalized linear model with a Gaussian error structure. This test was not performed for the July–August 2001 cruise because of missing sea-surface temperature and salinity data.

The sea-ice edge was defined during each cruise through visual analysis of weekly sea-ice concentration analyses of satellite imagery (The National/Naval Ice Center, Washington, DC, 2002) combined with our own field observations. When our field observations disagreed with satellite imagery analyses, field observations took precedence over the sea-ice edge definition based on satellite imagery. The sea-ice edge was defined as the transition region where sea ice covered more than 15% of the ocean surface (Zwally et al., 1983). Distance to the sea-ice edge for each transect was then calculated using ArcView Spatial Analyst (Environmental Systems Research Institute Inc., 1996a, b). During the fall cruise, the sea-ice edge occurred just within the study area as the pack ice developed from the south, and nine of the 155 transects were inside the pack ice. The average distance to the sea-ice edge during this cruise was 139.7 km (S.D. = 81.8 km). During the winter cruise, the pack ice had developed well north and west of the study area and all of the survey transects were within the pack ice. The average distance to the sea-ice edge during this cruise was 421.3 km (S.D. = 82.7 km). Because most transects during the April–May cruise were in open water, the presence of sea-ice was used as the sea-ice structure variable for that cruise. Because all of the transects were within the pack ice during the July–August cruise, we defined sea-ice type using the Antarctic Sea-ice Processes and Climate (ASPeCt) sea-ice observation protocol (University of Tasmania, Antarctic CRC, 1998). For analysis, we grouped the sea-ice types into the following categories; new ice (grease, nilas, frazil, pancake) and brash, cake ice, floes (small, medium, large), and vast floes. Sea-ice concentrations in tenths were averaged across each transect for the July–August cruise.

We used generalized linear models to model density or the presence/absence as a function of the physical variables (McCullagh and Nelder, 1989). Both polynomial and linear relationships with physical variables were considered. Models were fit for any species observed in at least 10% of transects within each cruise. Bird density was log-transformed and modeled with a Gaussian error structure. The presence/absence of pinnipeds was modeled with a binomial error structure.

Models composed of variables corresponding to bathymetry, surface thermohaline properties, water-column environment, and sea-ice structure were developed before analysis commenced (Burnham and Anderson, 1998). Variables with correlations greater than 0.70 were not used in any model to avoid potential problems with multi-colinearity (Weisberg, 1985). Akaike's information criterion (AIC) corrected for sample size was used to select the best model (Burnham and Anderson, 1998). Adjusted-R^2 values (for the Guassian error models) were calculated to assess how much variability was explained by the models. Residual analysis was done to identify influential points using Cook's distance; influential points are points that change the conclusions of the analysis when they are deleted from the data set and the reduced data set is reanalyzed (Cook and Weisberg, 1999). Results from the full data set and the reduced data set are presented when influential points were identified (following Cook and Weisberg, 1999). Significance of the models was assessed at an alpha of 0.05. All models were checked for autocorrelation in the residuals using semivariograms (Cressie, 1993). Spherical semivariograms were used to estimate the error structure, the model was refit using generalized least-squares (Cressie, 1993), and the AIC value recalculated. Analyses were done in S-Plus 2000 (MathSoft, 1999).

3. Results

3.1. Association of sub-surface water masses to surface characteristics

Sea-surface temperature and salinity were associated with distinct sub-surface water masses ($F = 92.2$, df$=3$, 151, $p<0.001$, proportion variance explained$=0.647$). All of the sub-surface water masses, with the exception of the ACC, were associated with a particular combination of temperature and salinity ranges (Table 3).

3.2. Distribution of species

Overall, 11 bird and four pinniped species were recorded during the April–May cruise (Table 1). The majority of the individuals seen was from two sea-ice-affiliated species and three open-water-affiliated species (Table 1). Southern fulmar (*Fulmarus galcialoides*), an open-water-affiliated species, was the most common species observed, followed by snow petrel (*Pagodroma nivea*), cape petrel (*Daption capense*), Antarctic petrel (*Thalassoica antarctica*), and blue petrel (*Halobaena caerulea*). Kelp gull (*Larus dominicanus*) and southern giant petrel (*Macronectes giganteus*) also were observed, though in fewer transects. Adélie penguins (*Pygoscelis adeliae*) were present in the area in unknown numbers as individuals were seen hauled out on islands when the ship was off survey effort. Crabeater seals (*Lobodon carcinophagus*) and Antarctic fur seals (*Arctocephalus gazella*) were the most common pinnipeds seen; however, pinnipeds were relatively rare, being seen on fewer than 10% of the transects. There was a concentration of birds and pinnipeds off the northwest shore of Alexander Island (Figs. 2–5).

During the July–August cruise, six bird and two pinniped species were observed (Table 1) in the survey area. Only sea-ice-affiliated species were seen in July–August, reflecting the presence of sea ice on all transects during this cruise (Table 1).

Table 3
Mean sea-surface temperature (°C) and salinity (psu) associated with predator survey transects grouped by sub-surface water-mass location for data collected within the US SO GLOBEC study area during April–May 2001

Surface property	InSW ($n=29$)	InSWB ($n=7$)	MUCDW ($n=41$)	UCDWB ($n=33$)	UCDW ($n=43$)	ACC ($n=2$)
Sea-surface temperature (°C)	−1.22 (.307)	−.495 (.221)	−.945 (.366)	−.867 (.268)	−.929 (.417)	−.861 (.0005)
Sea-surface salinity (psu)	33.17 (.087)	33.24 (.114)	33.47 (.189)	33.69 (.086)	33.66 (.135)	33.73 (.005)

Note: Standard errors are in parentheses. Each water mass was statistically associated with a particular combination of sea-surface temperature and salinity values during this cruise with. The only exception was ACC due to the low sample size. See Table 2 for sub-surface water-mass definitions.
For explanation of abbreviations see Table 2 footnote.

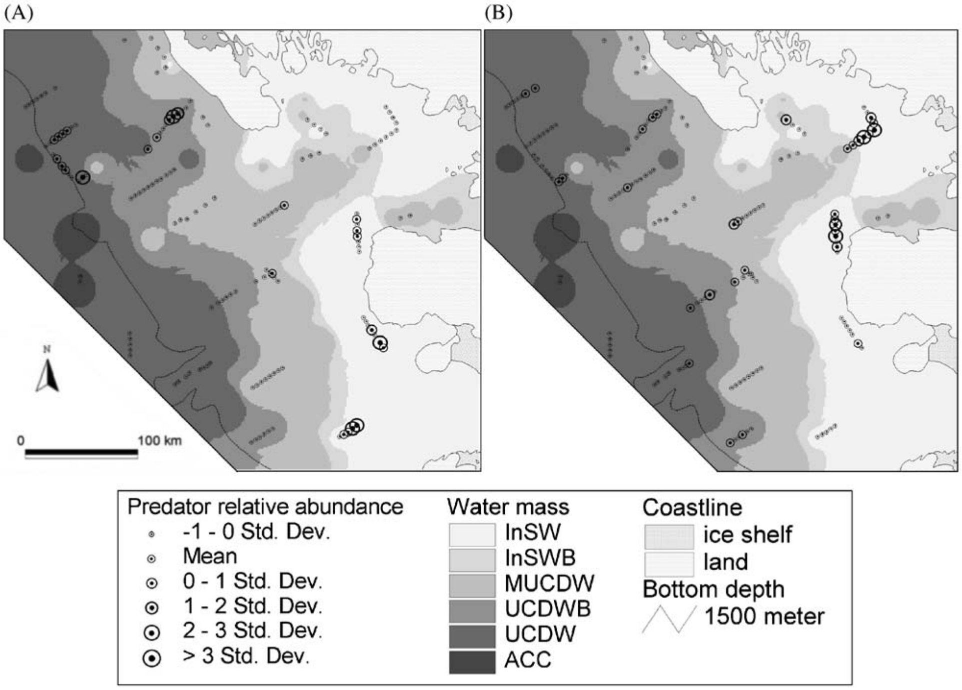

Fig. 2. Relative density for (A) Antarctic petrel (mean density = 0.2 individuals km^{-2}) and (B) southern fulmar (mean density = 0.4 individuals km^{-2}) for 30-minute survey transects during the April–May, 20001 cruise. Water-mass locations also are plotted using interpolated values for temperature maximum below 200-m (see Table 2 for water-mass definitions). See Fig. 1 for data source and map location.

Overall bird densities were lower during the July–August cruise than the April–May cruise (Tables 4 and 5). Snow petrel was the most common bird observed, with Antarctic petrel and Adélie penguin the next most frequently observed species. Crabeater seal was the only commonly seen pinniped in the July–August cruise (Table 5). The concentration of birds and mammals around Alexander Island was markedly reduced from that seen during the April–May cruise (Figs. 6 and 7).

3.3. Relationships with physical variables

During the April–May cruise, water-mass structure was the most common variable included in the best fitting models (present in best models for four species), followed by the presence of sea ice and bottom depth variation (present in best models for three species) (Table 6). At this time, four of the species were found at their greatest densities within the study area in the Inner Shelf Water or the Inner Shelf Water Boundary (Table 4). Antarctic petrel, snow petrel, and southern fulmar densities were highest over the Inner Shelf Water (Figs. 2 and 3), sometimes dramatically so, while kelp gull densities were highest over the Inner Shelf Water Boundary (Table 4, Fig. 5B). Analysis of surface thermohaline characteristics showed a southwesterly flowing coastal current associated with the Inner Shelf Water during the April–May period (Klinck et al., 2004). The Inner Shelf Water also was characterized by relatively fresh, cold surface water (Table 3) and also was the only water mass in which new sea ice and relatively large numbers of icebergs were observed. Specifically, brash and new sea ice in the vicinity of icebergs were found in the region of the Inner Shelf Water immediately north and west of Alexander Island.

The importance of other physical variables in April–May was species dependent (Table 6). Besides being associated with the Inner Shelf Water, snow petrel densities were highest in areas

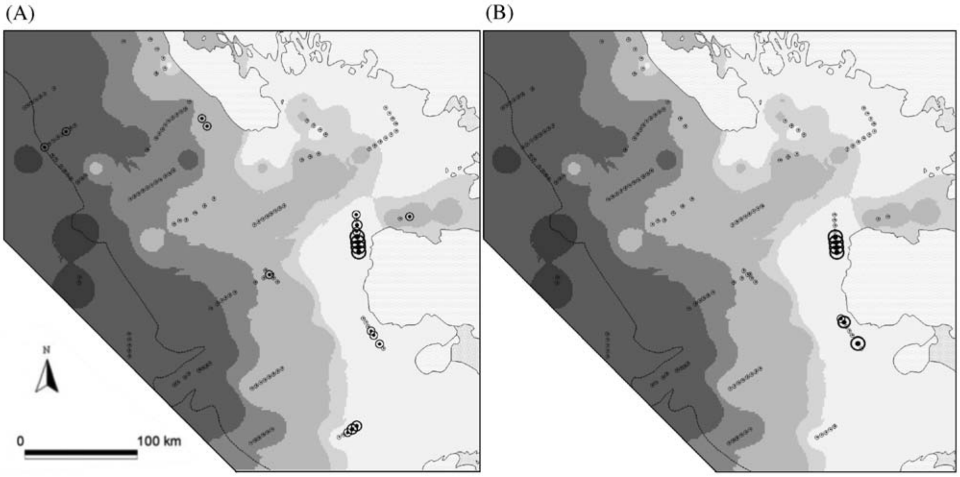

Fig. 3. Relative density for (A) snow petrel (mean density = 0.7 individuals km^{-2}) and (B) crabeater seal (mean density = 0.4 individuals km^{-2}) for 30-minute survey transects during the April–May, 20001 cruise. See Fig. 1 for digital data source and map location. See Fig. 2 for definitions of symbols and water masses.

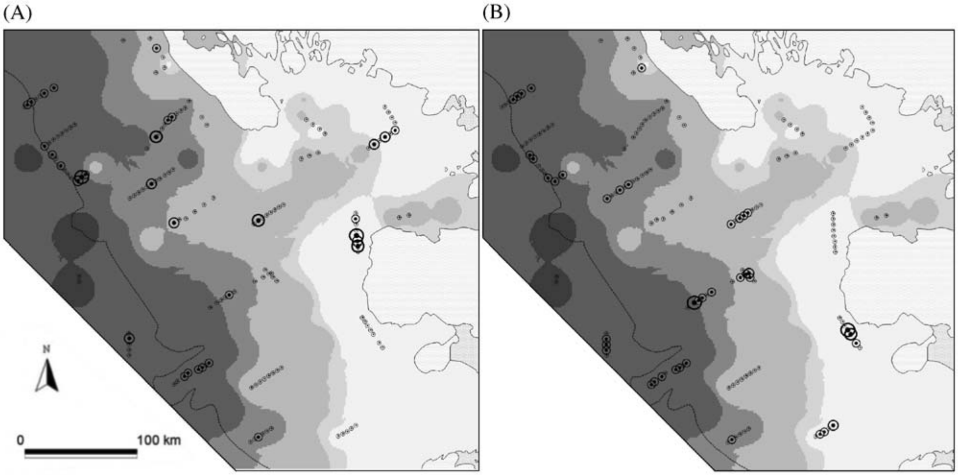

Fig. 4. Relative density for (A) cape petrel (mean density = 0.2 individuals km^{-2}) and (B) blue petrel (mean density = 0.4 individuals km^{-2}) for 30-minute survey transects during the April–May, 20001 cruise. Water-mass locations also are plotted using interpolated values for temperature maximum below 200 m (see Table 2 for water-mass definitions). See Fig. 1 for digital data source and map location. See Fig. 2 for definitions of symbols and water masses.

where sea-surface temperatures were lower and where sea ice was present. The sea-ice concentration where snow petrels were observed was, on average, 0.38. Blue petrel densities were higher where the bottom topography was most variable and in areas farther from land. There was one influential point; when that point was removed, the presence of sea ice was added to the previous model and the adjusted-R^2 increased to 0.175. Transects with higher blue petrel densities and variable bottom topography corresponded to Inner Shelf Water near Alexander Island; otherwise, blue petrel densities were higher in transects farther from land (which occurred in UCDW)

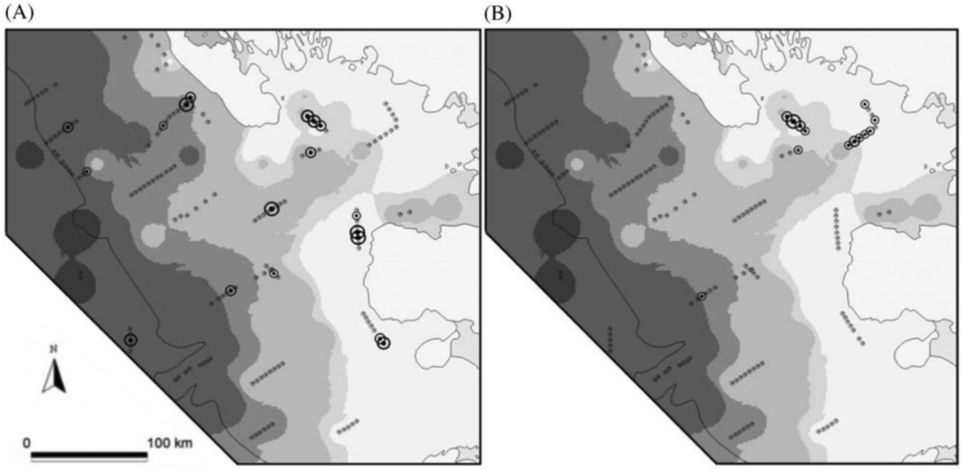

Fig. 5. Relative density for (A) southern giant petrel (mean density = 0.1 individuals km^{-2}) and (B) kelp gull (mean density = 0.1 individuals km^{-2}) for 30-minute survey transects during the April–May, 20001 cruise. See Fig. 1 for digital data source and map location. See Fig. 2 for definitions of symbols and water masses.

Table 4
Average density of top predators (individuals km^{-2}) within each water mass during the April–May 2001 cruise

Species	InSW ($n=29$)	InSWB ($n=7$)	MUCDW ($n=41$)	UCDWB ($n=33$)	UCDW ($n=43$)	ACC ($n=2$)	Overall ($n=155$)
Snow petrel	3.1 (5.7)	0.1 (0.2)	0.2 (0.4)	0.02 (0.1)	0.1 (0.3)	0.0	0.7 (2.7)
Cape petrel	0.3 (0.8)	0.2 (0.4)	0.1 (0.3)	0.1 (0.3)	0.2 (0.4)	0.03	0.2 (0.5)
Southern fulmar	1.2 (2.0)	0.5 (0.5)	0.1 (0.3)	0.3 (0.3)	0.2 (0.3)	0.0	0.4 (1.0)
Antarctic petrel	0.5 (1.1)	0.0 (0.0)	0.04 (0.1)	0.2 (0.6)	0.2 (0.5)	0.0	0.2 (0.6)
Blue petrel	0.4 (1.1)	0.1 (0.3)	0.3 (0.5)	0.3 (0.4)	0.7 (2.1)	0.0	0.4 (1.2)
Southern giant petrel	0.1 (0.2)	0.2 (0.3)	0.1 (0.1)	0.1 (0.2)	0.02 (0.1)	0.0	0.1 (0.2)
Kelp gull	0.4 (0.9)	5.2 (9.5)	0.02 (0.1)	0.02 (0.1)	0.0 (0.0)	0.0	0.3 (2.2)
Total birds	6.0 (6.9)	6.2 (9.4)	0.7 (0.8)	0.9 (0.9)	1.4 (2.2)	0.03	2.2 (4.3)
Antarctic fur seal	0.02 (0.1)	0.2 (0.4)	0.1 (0.1)	0.1 (0.2)	0.1 (0.5)	0.0	0.1 (2.1)
Crabeater seal	2.1 (4.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0	0.4 (0.3)
Total seals	2.1 (4.4)	0.2 (0.4)	0.03 (0.2)	0.1 (0.5)	0.1 (0.5)	0.0	0.5 (2.1)

Note: Standard errors are given in parentheses and are presented for water masses in which at least three transects were conducted. The number of transects in a water mass is given by "*n*".
For explanation of abbreviations see Table 2 footnote.

(Fig. 4B). Higher cape petrel densities were associated with the presence of sea ice. However, this model was influenced by high density in a single transect with brash ice and a sea-ice concentration of 0.57 ice. When this value was removed, water-mass structure was associated with cape petrels; higher densities were found in Inner Shelf Water and UCDW (Table 4, Fig. 4A). Kelp gulls were positively associated with variability in bottom depth as well as with the Inner Shelf Water Boundary. The area where this combination occurred was at the entrance to Marguerite Bay (Fig. 5B) over Marguerite Trough, which is a deep trough extending across the continental shelf (see Klinck et al., 2004). Southern giant petrels were not found to be concentrated in

Table 5
Average density of top predators (individuals km^{-2}) within each water mass during the July–August 2001 cruise

Species	InSW ($n=2$)	InSWB ($n=4$)	MUCDW ($n=49$)	UCDWB ($n=16$)	UCDW ($n=49$)	ACC ($n=10$)	Overall ($n=131$)
Snow petrel	0.0	0.7 (0.7)	0.8 (1.6)	0.8 (1.1)	1.4 (2.7)	1.1 (1.5)	1.0 (2.0)
Antarctic petrel	0.0	0.0 (0.0)	0.03 (0.1)	0.02 (0.1)	0.2 (0.6)	0.1 (0.1)	0.1 (0.4)
Southern giant petrel	0.0	0.0 (0.0)	0.3 (1.3)	0.0 (0.0)	0.01 (0.02)	0.0 (0.0)	0.1 (0.8)
Adélie penguin	0.0	0.0 (0.0)	0.8 (2.4)	0.1 (0.4)	0.1 (0.4)	0.8 (1.8)	0.4 (1.6)
Emperor penguin	0.0	0.4 (0.8)	0.1 (0.4)	0.0 (0.0)	0.04 (0.2)	0.0 (0.0)	0.1 (0.3)
Total birds	0.0	1.1 (1.4)	2.0 (3.3)	0.9 (1.1)	1.7 (3.2)	2.0 (3.3)	1.7 (3.0)
Crabeater seal	0.0	0.8 (1.3)	0.5 (1.2)	0.04 (0.2)	0.1 (0.4)	0.0 (0.0)	0.3 (0.9)
Total seals	0.0	0.8 (1.3)	0.5 (1.2)	0.04 (0.2)	0.1 (0.4)	0.0 (0.0)	0.3 (0.9)

Note: Standard errors are given in parentheses and are presented for water masses in which at least three transects were conducted. The number of transects in a water mass is given by "*n*".
For explanation of abbreviations see Table 2 footnote.

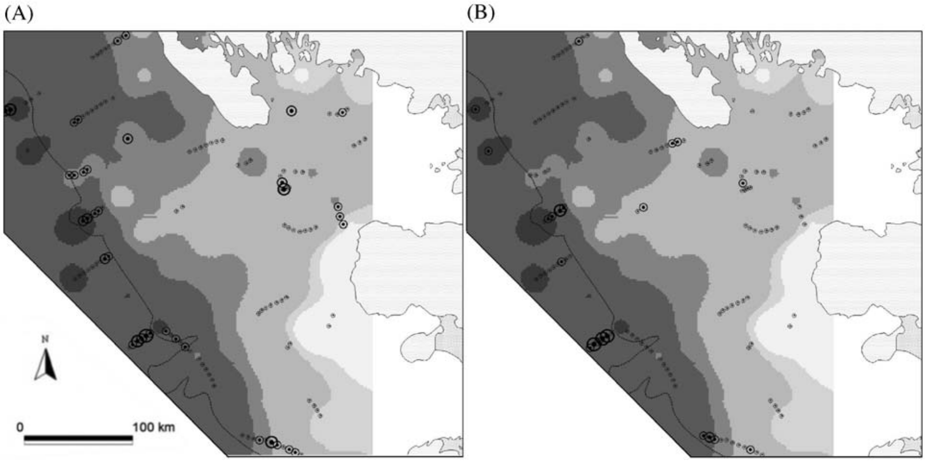

Fig. 6. Relative density for (A) snow petrel (mean density = 1.0 individuals km^{-2}) and (B) Antarctic petrel (mean density = 0.1 individuals km^{-2}) for 30-minute survey transects during the July–August, 2001 cruise. See Fig. 1 for digital data source and map location. See Fig. 2 for definitions of symbols and water masses.

any particular water mass (Fig. 5A). However, this species was found in areas where sea ice was present and where bottom depth variability was higher.

In the July–August cruise, sea-ice structure of some type was the common variable for the best models associated with the bird species (Table 7). Crabeater seals were associated with water-mass structure, specifically modified UCDW/shelf water (Fig. 7B), as well as shallow bottom depths. This combination of modified UCDW/shelf water and shallow bottom depths occurred mainly in the southern portion of the study area and extended from within Marguerite Bay, southwest and offshore to the continental shelf-break (see bathymetry in Fig. 1 of Klinck et al., 2004).

In the July–August cruise, snow petrel abundance showed a nonlinear relationship with ice concentration and salinity at 50 m, peaking at 0.8 coverage and 33.9 psu, respectively, (Table 7). Snow petrel abundance also was highest in new and brash ice and at greater bottom depths

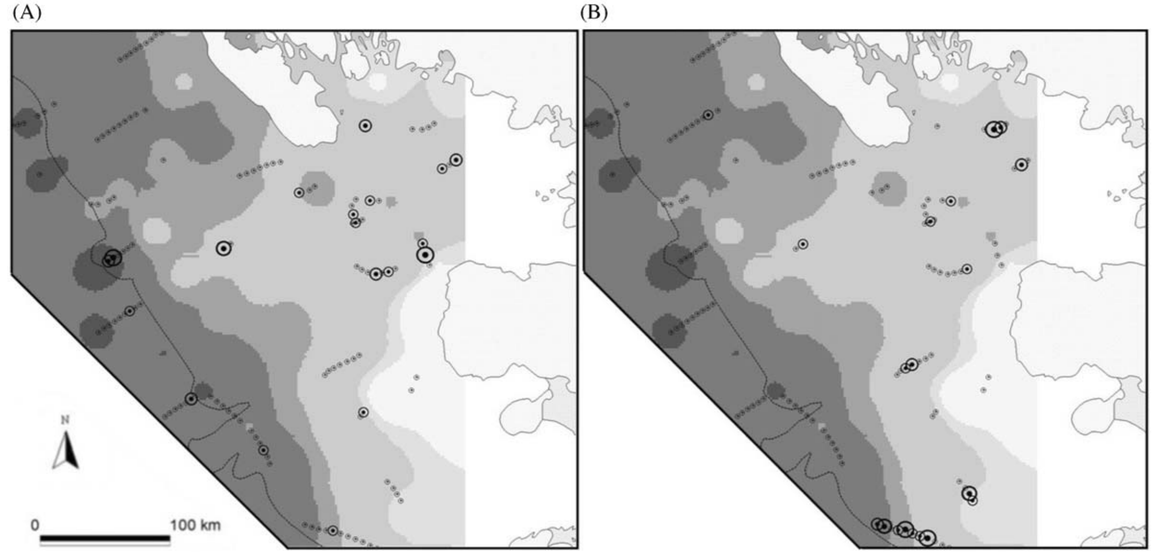

Fig. 7. Relative density for (A) Adélie penguin (mean density = 0.4 individuals km^{-2}) and (B) crabeater seal (mean density = 0.3 individuals km^{-2}) for 30-minute survey transects during the July–August, 2001 cruise. See Fig. 1 for digital data source and map location. See Fig. 2 for definitions of symbols and water masses.

(Table 7). Antarctic petrel density (Fig. 6B) was associated with vast floes, relatively low sea-ice concentration, and deeper waters. Adélie penguin density (Fig. 7A) was associated with newer or light sea-ice types and were found within the pack ice, farther from the sea-ice edge, and in deeper waters within the pack ice.

4. Discussion

4.1. Seabird and pinniped distribution

Overall, the species we encountered in our surveys were typical of the Antarctic seabird and pinniped fall and winter community (Ainley et al., 1993; Whitehouse and Veit, 1994; Woehler et al., 2003). However, during the winter cruise, species abundances were low compared to other studies that took place during the winter (Ainley et al., 1993; Fraser and Ainley, 1986; van Franeker, 1992). The 2001 SO GLOBEC surveys were, on average, over 400 km inside the pack ice while previous winter studies took place within 150 km of the ice edge in both open water and inside the pack ice. Therefore, the differences between the 2001 results and those from previous studies may indicate that seabird densities decrease further inside the pack ice.

Of the seabirds commonly observed in this study, only blue petrel (Watson, 1975) and Antarctic petrel (van Franeker et al., 1999) are known to not breed on the Antarctic Peninsula. Blue petrel is a Sub-Antarctic breeder and is likely only a seasonal migrant into Antarctic waters prior to the development of seasonal pack ice. However, Antarctic petrels are year-round residents of high Antarctic latitudes and were relatively common near Marguerite Bay in the winter (cf. Fig. 6, Table 1). The nearest known Antarctic petrel breeding colony is 1800 km from the SO GLOBEC study area, along the eastern shore of the Weddell Sea (van Franeker et al., 1999). This result could reflect a significant winter migration to the study area, perhaps suggesting that Antarctic petrels are capitalizing on high prey availability near Marguerite Bay during winter. However, it has been speculated that major breeding colonies of Antarctic petrels have yet to be discovered on the Antarctic Peninsula (van Franeker et al., 1999), in which case high densities of this species in winter may represent a lingering association with breeding

Table 6
Variables included in the minimum AIC model for species observed on 10% or more of the transects during April–May 2001

Species	Distance to land (km)	Sea-surface temperature (°C)	Presence of ice	Bottom depth variation (coefficient of variation)	Water-mass structure	Adjusted-R^2	p-Value
Antarctic petrel					InSW 0.53 (1.1)/0.21 (0.5)	0.082	.01
Snow petrel		– −1.22 (0.36)	+ 5.5 (7.5)/ 0.2(0.6)		InSW 3.1 (5.7)/0.2 (0.4)	0.539	<.001
Blue petrel	+ 111.31 (50.94)			+ 0.11 (0.19)		0.091	<.001
Cape petrel			+ 0.5 (1.1)/0.1 (0.3)			0.03	.024
Southern fulmar					InSW 1.2 (2.0)/0.5 (0.5)	0.187	<.001
Kelp gull				+ 0.27 (0.19)	InSWB 5.2 (9.5)/0.4 (0.9)	0.38	<.001
Southern giant petrel			+ 0.16(0.2)/ 0.04(0.2)	+ 0.16 (0.19)		0.05	.006

Note: The sign in the table is the direction of the relationship between the species and the variable (+ = positive, − = negative) in the minimum AIC model. For continuous variables included in the AIC model for each species, the mean and standard error of the variable for transects in the 80th percentile of density values are also given. Where the presence of sea-ice is included in the minimum AIC model, the mean and standard error of species density (individuals km^{-2}) when ice is present and when it is not are given [mean (standard error) with ice/mean (standard error) without ice]. When water-mass structure is present in the minimum AIC model, the water mass where the species was most abundant is listed. The mean and standard error for species density (individuals km^{-2}) over this water mass and the water mass where the species is second most abundant are also given [mean (standard error) where species is most abundant/mean (standard error) where species is second most abundant]. Adjusted-R^2 and p-values for the models are also given.
For explanation of abbreviations see Table 2 footnote.

Table 7
Variables included in the minimum AIC model for species observed on 10% or more of the transects during July–August 2001

Species	Distance to ice edge (km)	Coded ice	Ice conc. (tenths)	Distance to land (km)	Bottom depth (m)	Water mass	Sal. at 50 m.(psu)	Adjusted-R^2	p-Value
Adélie penguin	– −469.39 (92.37)	New and brash ice 1.7 (4.7)/0.3 (1.2)			+ 1228 (1050)			0.136	<0.001
Antarctic petrel		Vast floe 0.12 (0.44)/0.06 (0.17)	– 8.7 (0.6)		+ 1605 (1248)			0.153	<0.001
Snow petrel		New and brash ice 1.9 (2.1)/1.0 (1.3)	Poly (0.8)	+ 118 (62)			Poly (33.9)	0.198	<0.001
Crabeater seal					– 460 (132)/ 1092 (1049)	MUCDW		0.103	0.013

Note: "Poly" indicates where a polynomial relationship was found for a variable. The value where species abundance was highest is given for these variables where the polynomial relationship was found. The sign in the table is the direction of the relationship between the species and the variable (+ = positive, – = negative) in the minimum AIC model. For continuous variables included in the AIC model for each species, the mean and standard error of the variable for transects in the 80th percentile of density values are also given. For crabeater seals, mean and standard errors are given for continuous variable values when this species was present and when it was not present [mean (standard error) when present/mean (standard error) when not present]. Because the presence/absence of crabeater seals was used in the analysis, no abundance values are given for categorical variables in the minimum AIC model for this species. When coded ice is present in the minimum AIC model, the ice code where the species was most abundant is listed. The mean and standard error for species density (individuals km^{-2}) over this ice type and the ice type where the species is second most abundant are also given [mean (standard error) where species is most abundant/mean (standard error) where species is second most abundant]. Distances to the ice edge within the ice are negative. Adjusted-R^2 and p-values for the models are also given.

For explanation of abbreviations see Table 2 footnote.

colonies. Finally, the loss or reduced density of several species that breed on the Antarctic Peninsula, including cape petrels, southern giant petrels, kelp gulls and southern fulmar, on the July–August surveys suggests the movement of these species north to open water and the ice edge as pack ice develops (Ainley et al., 1993).

4.2. *Adélie penguin distribution*

Because Antarctic krill is typically the dominant prey choice of Adélie penguins on the Antarctic Peninsula (Ainley, 2003), understanding Adélie penguin distribution and foraging ecology is of particular importance to the SO GLOBEC objectives. On the southern portion of the Antarctic Peninsula, there are three clusters of Adélie penguin breeding colonies centered on Avian Island (67°46′S, 68°54′W), Renaud Island (65°52′S, 66°15′W), and Anvers Island (64°46′S, 64°04′W) with a combined population of 112,400 breeding pairs (Woehler, 1993). The winter movement of this population is poorly understood (Fraser and Trivelpiece, 1996). Although the 2001 surveys did not indicate a concentration of Adélie penguins offshore within Marguerite Bay during either cruise, it is possible that penguins are using near-shore areas not included within the survey area, particularly in late fall. During the April–May cruise, groups of Adélie penguins were observed hauling out on islands just north of Marguerite Bay and the survey area. In addition, results from a concurrent telemetry study found that Adélie penguins generally restrict their movement to near-shore areas during late fall (Fraser, unpublished data). During the July–August cruise, Adélie penguins were observed in our survey grid and telemetry results began to detect a movement of Adélie penguins further north. These observations suggest that Adélie penguins may be foraging near-shore and hauling out on islands prior to the establishment of sea ice and shifting their distribution offshore in winter, presumably in association with the developing pack ice.

4.3. *Influence of varied bathymetry*

The association of blue petrels, kelp gulls, and southern giant petrels with areas characterized by high bottom depth variability during the fall cruise suggests that bottom topography may be influencing biological processes in the Marguerite Bay region at this time of year. Kelp gulls and southern giant petrels were observed well inshore, which may indicate the presence of bathymetrically controlled fronts, eddies, or upwelling zones; features that seabirds have been associated with in other shallow seas (Russell et al., 1999; Schneider et al., 1987). Blue petrels also were observed further offshore and may be associated with bathymetrically controlled processes near the shelf break as well as features in near-shore areas. During the winter cruise, variation in bathymetry was no longer an important variable in the models, suggesting that sea ice may have prevented access by the top predators to environmental structures (e.g. food) associated with fixed, bathymetric features.

4.4. *Influence of water-column environment and pack ice development*

Previous research has suggested that seabirds in the Southern Ocean have foraging strategies that are adapted to particular sea-ice habitats (Ainley et al., 1992, 1994; Fraser and Ainley, 1986). Furthermore, it has been suggested that this specialization plays an important role in structuring seabird distributions. The only other study during the austral winter on the Antarctic Peninsula found a dramatic shift in species assemblage and abundance presumably due to the development of the winter pack ice (Whitehouse and Veit, 1994). In this study, the development of sea ice appeared to have influenced a shift in seabird and pinniped species assemblage, abundance, and habitat associations. However, the relative contribution of seasonal changes that co-varied with changes in sea-ice habitat between cruises (e.g. reduced day-length, lower ambient temperatures, large-scale shifts in prey distribution and availability) cannot be assessed with our analysis.

Snow petrel, Antarctic petrel, southern giant petrel, Adélie penguin, and crabeater seal all remained within, or moved into, the study area after the pack ice developed between the April–May and July–August cruises. These results are consistent with previous studies that have found these species to be associated with pack ice (Ainley et al., 1993; Ribic et al., 1991; van Franeker, 1992; Woehler et al., 2003). The results from this study also are consistent with previous studies that have found lower species abundance in the Southern Ocean in winter presumably because species typically found in open water, such as cape petrel, blue petrel, southern fulmar (Ainley et al., 1994; van Franeker, 1992; Whitehouse and Veit, 1994) and Antarctic fur seal (Ribic et al., 1991), move north as the pack ice develops.

Additionally, the development of sea ice appeared to reduce predator densities in the study area, a finding that contradicts results from a study in the Scotia–Weddell Confluence during the summer that found higher seabird and seal abundance further inside the pack ice than at the sea-ice edge or in open water (van Franeker, 1992). This may reflect a difference in system characteristics between the southern Antarctic Peninsula and the Scotia–Weddell Confluence, or that the SO GLOBEC surveys were conducted further within the pack and during the winter.

Sea-ice characteristics played an important role in structuring seabird and pinniped distributions within the study area during both the April–May and July–August cruises. However, water-column environment and other physical variables were more strongly associated with species distributions during the April–May cruise, prior to the development of pack ice. At this time, the commonly observed species were associated with physical characteristics of the water column. In particular, most species were associated with Inner Shelf Water just north and west of Alexander Island in the vicinity of brash and new sea ice that covered greater than 0.3 of the ocean surface; all of the crabeater seal sightings also were in this area. These results agree with the findings of Burns et al. (2004) that crabeater seals outfitted with Satellite Relay Data Loggers focused their activity in this region just north and west of Alexander Island. In this study, crabeater seals were observed in shallow water, on-shelf areas during the July–August cruise, a result which also agrees with locations of crabeater seals reported in Burns et al. (2004).

Previous analyses of water-column processes and primary production in western Antarctic Peninsula continental shelf waters suggest the important role of sub-surface processes in determining phytoplankton communities in the surface waters in this region (Prézelin et al., 2000, 2004). The results presented in Tables 3 and 6 show that both physical properties and predator distributions were associated with sub-surface water masses, thereby suggesting that sub-surface processes may be influencing physical and biological processes in surface waters during winter on the western Antarctic Peninsula. Alternatively, the distribution of the temperature maximum below 200 m may have served as a proxy for some other variable that is important for structuring predator distribution, rather than indicating the influence of deep water masses on surface biology.

After the sea ice developed, sea-ice characteristics became more useful in predicting species distributions than the water-column environment and also appeared to modify the relationship between top-predator distributions and physical variables for species observed during both cruises. Snow petrels and Antarctic petrels, previously associated with Inner Shelf Water in the April–May cruise, were no longer associated with a particular water mass after pack ice developed. Instead, in the July–August cruise, these species were associated with a combination of sea-ice characteristics and other water-column variables. Additionally, crabeater seals, previously seen concentrated near Alexander Island in the Inner Shelf Water, became more dispersed throughout the study area and were associated with modified UCDW after the pack ice developed.

5. Conclusions

The results from the 2001 austral fall and winter cruises suggest that some of the more abundant seabird and pinniped species distributions are structured by interactions between sea ice and other environmental variables. As a result, the development of pack ice in winter appears to limit access to environmental or ecosystem structures that arise from water-column processes or bathymetric influences on water flow. Consequently, predation pressure by birds and pinnipeds in the Southern Ocean during the austral winter may be strongly modified by the timing and extent of the development of pack ice during the winter months. Furthermore, these results suggest a link between top-predator distributions and water-column processes on the western Antarctic Peninsula, at least during austral fall, prior to pack-ice development. A better understanding of the physical–biological processes that are responsible for these patterns awaits further synthesis work combining field and modeling research.

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