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Water masses, ocean fronts, and the structure of Antarctic seabird communities: Putting the eastern Bellingshausen Sea in perspective

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ABSTRACT

Waters off the western Antarctic Peninsula (i.e., the eastern Bellingshausen Sea) are unusually complex owing to the convergence of several major fronts. Determining the relative influence of fronts on occurrence patterns of top-trophic species in that area, therefore, has been challenging. In one of the few ocean-wide seabird data syntheses, in this case for the Southern Ocean, we analyzed ample, previously collected cruise data, Antarctic-wide, to determine seabird species assemblages and quantitative relationships to fronts as a way to provide context to the long-term Palmer LTER and the winter Southern Ocean GLOBEC studies in the eastern Bellingshausen Sea. Fronts investigated during both winter (April–September) and summer (October–March) were the southern boundary of the Antarctic Circumpolar Current (ACC), which separates the High Antarctic from the Low Antarctic water mass, and within which are embedded the marginal ice zone and Antarctic Shelf Break Front; and the Antarctic Polar Front, which separates the Low Antarctic and the Subantarctic water masses. We used clustering to determine species' groupings with water masses, and generalized additive models to relate species' densities, biomass and diversity to distance to respective fronts. Antarctic-wide, in both periods, highest seabird densities and lowest species diversity were found in the High Antarctic water mass. In the eastern Bellingshausen, seabird density in the High Antarctic water mass was lower (as low as half that of winter) than found in other Antarctic regions. During winter, Antarctic-wide, two significant species groups were evident: one dominated by Adélie penguins (*Pygoscelis adeliae*) (High Antarctic water mass) and the other by petrels and prions (no differentiation among water masses); in eastern Bellingshausen waters during winter, the one significant species group was composed of species from both Antarctic-wide groups. In summer, Antarctic-wide, a High Antarctic group dominated by Adélie penguins, a Low Antarctic group dominated by petrels, and a Subantarctic group dominated by albatross were evident. In eastern Bellingshausen waters during summer, groups were inconsistent. With regard to frontal features, Antarctic-wide in winter, distance to the ice edge was an important explanatory factor for nine of 14 species, distance to the Antarctic Polar Front for six species and distance to the Shelf Break Front for six species; however, these Antarctic-wide models could not successfully predict spatial relationships of winter seabird density (individual species or total) and biomass in the eastern Bellingshausen. Antarctic-wide in summer, distance to land/Antarctic continent was important for 10 of 18 species, not a surprising result for these summer-time Antarctic breeders, as colonies are associated with ice-free areas of coastal land. Distance to the Shelf Break Front was important for 8 and distance to the southern boundary of the ACC was important for 7 species. These summer models were more successful in predicting eastern Bellingshausen species density and species diversity but failed to predict total seabird density or biomass. Antarctic seabirds appear to respond to fronts in a way similar to that observed along the well-studied upwelling front of the California Current. To understand fully the seabird patterns found in this synthesis, multi-disciplinary at-sea investigations, including a quantified prey field, are needed.

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1. Introduction

The large-scale oceanographic fronts of the Southern Ocean are known to influence differentially the occurrence patterns of mobile predators, such as seabirds (reviewed qualitatively in Bost et al., 2009), resulting in patterns similar to those detected elsewhere. Seabirds concentrate at fronts, purportedly because food availability is enhanced in various ways (e.g., Decker and Hunt, 1996; Durazo et al., 1998; Hoefer, 2000; Spear et al., 2001; Ainley et al., 2009), and major, well-marked fronts representing water mass boundaries often correspond to boundaries of various species' zoogeographic ranges (e.g., Pocklington, 1979; Ainley and Boekelheide, 1983; Wahl et al., 1989).

The ocean off the western Antarctic Peninsula (i.e., the eastern Bellingshausen Sea) is unusual in its oceanographic complexity owing to the convergence of several major fronts (Hofmann et al., 1996; Hofmann and Klinck, 1998; Klinck, 1998; Dinniman and Klinck, 2004). Unlike elsewhere in the Southern Ocean, the southern boundary of the Antarctic Circumpolar Current (ACC) coincides closely with the western Antarctic Peninsula shelf break and accompanying Shelf Break Front, rather than being separated, for instance by large gyres of Antarctic Surface Water in evidence elsewhere (see Nicol, 2005, Figs. 1, 2). As a consequence of this convergence, understanding the degree to which the different oceanographic factors influence various components of the western Antarctic Peninsula biota is problematic. Both the Shelf Break Front and the southern boundary of the ACC strongly affect abundance patterns of top predators (Ainley and Jacobs, 1981; Ainley et al., 1998; Tynan, 1998; Woehler et al., 2006). Moreover, because the southern boundary of the ACC usually coincides with the approximate outer boundary of sea ice in the Southern Ocean, its presence also dictates the dynamics of the marginal ice zone in the western Antarctic Peninsula (Stammerjohn and Smith, 1996, 1997; Stammerjohn et al., 2003), bringing overlap or close proximity among the southern boundary of the ACC, Shelf Break Front and marginal ice zone. The marginal ice zone strongly affects mesoscale productivity (Smith and Nelson, 1985) as well as the abundance of birds in the Southern Ocean (Fraser and Ainley, 1986) and differences in productivity among water masses have been found to influence seabird occurrence patterns elsewhere (Ballance et al., 1997; Spear et al., 2001; Hyrenbach et al., 2006, 2007).

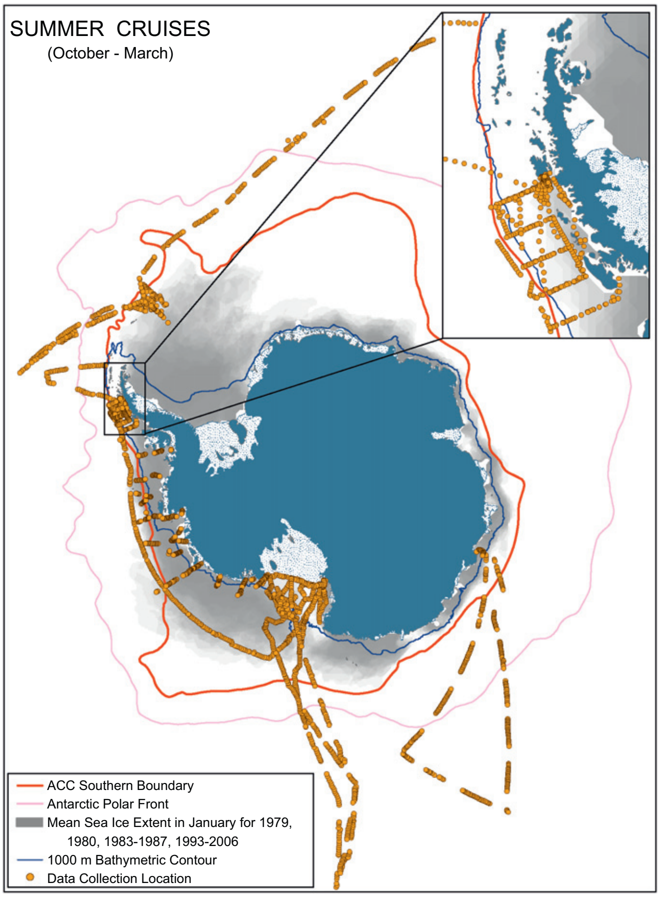

Fig. 1. The survey coverage of the Southern Ocean during summer.

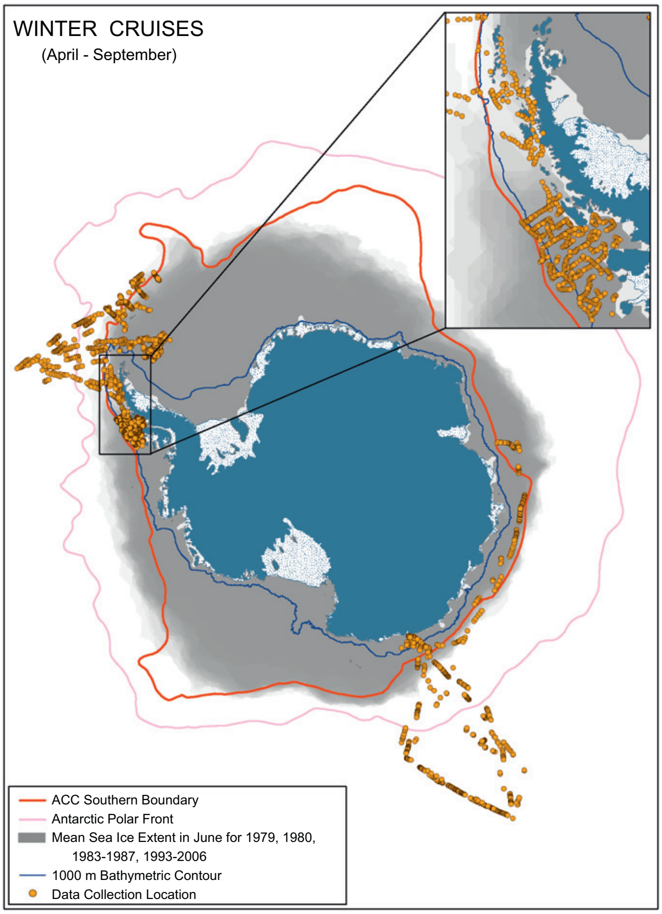

Fig. 2. The survey coverage of the Southern Ocean during winter.

Due to the high mobility of seabirds and the bio-physical complexity of Bellingshausen waters, incorporating a larger-scale context to our knowledge would be a significant contribution towards understanding large and small scale occurrence patterns in this region. Larger-scale analyses of seabird occurrence have been conducted in the Southern Ocean bearing directly on the Bellingshausen patterns (e.g., Ainley and Boekelheide, 1983; Heinemann et al., 1989; Ainley et al., 1998) and indirectly in regard to the fronts and water masses found in adjacent Antarctic regions (e.g., van Franeker et al., 2002; Raymond and Woehler, 2003; Woehler et al., 2003; Bost et al., 2009). With changing climate influencing the strength and position of Southern Ocean frontal boundaries (Russell et al., 2006a, b; Stammerjohn et al., 2008), and certain Bellingshausen predator populations demonstrating recent significant change (Hofmann et al., 2002; Ducklow et al., 2007; Hinke et al., 2007), understanding the importance of frontal boundaries to predators in a larger context will improve our understanding of biotic patterns in a region changing more rapidly due to climate warming than many other oceanic sectors (e.g., Smith et al., 1999).

Herein we attempt to understand better the spatial occurrence patterns of seabirds in the eastern Bellingshausen Sea as influenced by ocean boundaries at the large- to meso-scale. Our strategy is to combine extensive cruise data collected throughout the Southern Ocean to show how the various major ocean boundaries influence seabird occurrence where the boundaries are widely separated. In that way, the relative contribution of the close-lying boundaries within the eastern Bellingshausen might be better elucidated. Unavailable are contemporary measures of productivity (e.g., chlorophyll) and abundance of potential prey, and therefore our analysis is restricted to physical features as proxies for alteration and/or enhancement of prey availability and quality (species composition). The objectives of this paper are to quantify species-frontal relationships at the Antarctic-wide scale where fronts are widely spaced, and consider species' patterns in the eastern Bellingshausen where fronts closely coincide.

2. Methods

2.1. Data collection

Cruises were divided seasonally between winter (April–September) and summer (October–March, Table 1, Figs. 1, 2). The SO GLOBEC cruises (Table 1) will be referred to as the Bellingshausen winter cruises and the PALTER cruises (Table 1) will be referred to as the Bellingshausen summer cruises. The cruises used were those on which seabird surveys were conducted in such a way as to allow correction for seabird flux (movement of birds relative to that of the ship) in the estimation of seabird density, a problem when different data sets are being compared. Specifically ship and wind speed and direction, and direction of flying birds in relation to the ship were recorded (see Spear et al., 1992; Clarke et al., 2003). Strip surveys were made, with the strip typically 300 m wide, and in most cases at least two observers were present on the flying bridge at any given time (see Spear et al., 2004). Survey effort was partitioned into 30-min bins, sequentially, in the continuous counts. The only exceptions were three winter cruises on *Aurora Australis* where data were collected in 10-min bins and could not be combined into 30-min bins. Densities were calculated as number of individuals km^{-2}. All prions except Antarctic prion (*Pachyptila desolata*) were combined into one 'prion spp.' category (*Pachyptila* spp.) as most species of prions are difficult to identify to species at sea.

To standardize environmental variables, we calculated the following distances (km) for each transect: distance to nearest land (nearest mainland or island), distance to the Antarctic coast, distance to the ice edge where the ice edge is defined by 15% ice cover, distance to the ice edge defined by 50% ice cover, distance to the southern boundary of the ACC, distance to the Antarctic Polar Front, and distance to the Shelf Break Front (i.e., the 1000 m isobath). GIS files defining land, the Antarctic coast, and the fronts (southern boundary of the ACC and Antarctic Polar Front) were obtained from the Australian Antarctic Data Centre (Orsi et al., 1995; Orsi and Ryan, 2001 (updated 2006)). The 1000 m isobath was obtained by creating a bathymetric lattice contour GIS file using gridded ETOPO1 data from NOAA's National Geospatial Data Center (NGDC: Amante and Eakins, 2008), then edited to produce one continuous line defining the position of the shelf break.

For each month and year, polygons defining percent sea ice cover were prepared using raster data based on 25 km × 25 km cells, except in 1976 and 1977, which were based on 1° latitude × 1° longitude cells (approximately 110 km × 100 km at 60°S). Each cell contained estimated percent ice cover, with coverage rendered into polygons using a standard contouring algorithm tracing the 15% or 50% isopleth (Cavalieri et al., 1996 (updated 2006), for the years 1978–2006; Chapman and Walsh, 1991 (updated 1996) for the years 1976 and 1977).

Minimum distance from a sampling station to the nearest ice polygon was straightforward in cases where the minimum

Table 1
Number of transects by cruise and water mass for winter and summer cruises. SBACC = southern boundary of the Antarctic Circumpolar Current and APF = Antarctic Polar Front. A dash means no transects were carried out in the specific water mass.

Cruises	General area	Total transects	High Antarctic: South of SBACC	Low Antarctic: APF-SBACC	Subantarctic: North of APF
Winter					
Polar Duke 1985	Bellingshausen	95	69	14	12
Melville and Glacier 1986	Scotia-Weddell Confluence	392	105	165	122
Polar Duke 1987	Bellingshausen	60	36	12	12
Polar Duke 1988	Bellingshausen	261	78	124	59
Aurora Australis 1998 01	East Antarctica	144	0	39	105
Aurora Australis 1998 02	East Antarctica	212	100	65	47
Aurora Australis 1999	East Antarctica	376	145	61	170
N. B. Palmer 2001 (A and B), SO GLOBEC	Bellingshausen	336	336	0	0
N. B. Palmer 2002 (A and B), SO GLOBEC	Bellingshausen	316	316	0	0
Summer					
Northwind 1976	Ross Sea	418	328	16	74
Burton Island 1977	Pacific sector of the Southern Ocean	254	152	102	-
Northwind 1979	Ross Sea	246	55	107	84
Melville and *Westwind* 1983	Scotia-Weddell Confluence	405	64	172	169
Glacier 1979	Ross Sea	172	104	5	63
Polar Star 1987	Bellingshausen	21	-	14	7
Polar Duke 1988	Bellingshausen	28	-	15	13
N. B. Palmer 1994	Amundsen and Bellingshausen Seas	435	393	42	0
Aurora Australis 2000	East Antarctica	341	46	136	159
L.M. Gould, PALTER 1995	Bellingshausen	371	371	0	0
L.M. Gould, PALTER 1996	Bellingshausen	291	278	13	0
L.M. Gould, PALTER 1997	Bellingshausen	232	232	0	0
L.M. Gould, PALTER 1999	Bellingshausen	225	199	26	0
L.M. Gould, PALTER 2003	Bellingshausen	117	117	0	0
L.M. Gould, PALTER 2006	Bellingshausen	135	126	9	0

distance was entirely over water. Where a sampling station lay within the region of 15% or 50% ice cover (i.e., inside the ice), we measured the distance to the edge of the ice polygon and coded that distance as a negative number. Minimum distances that resulted from crossing land (i.e., the nearest ice polygon was separated from the sampling station by the Antarctic Peninsula) were not used.

2.2. Statistical analyses

All analyses were done using R (R Development Core Team, 2004). Unless otherwise noted, significance was assessed at $\alpha = 0.05$. Where means are presented, we also include the standard deviation.

2.2.1. Water masses and assemblages

We were interested in determining if seabird species were concentrated in different water masses. The three water masses considered were: Subantarctic (waters north of the Antarctic Polar Front), Low Antarctic (waters between the Antarctic Polar Front and the southern boundary of the ACC), and High Antarctic (waters south of the southern boundary of the ACC). In this particular analysis, we used only those cruises that sampled all three water masses. Transects were also excluded that were within 15 km of the Antarctic Polar Front and the southern boundary of the ACC to avoid any mixing of species along the water mass boundaries. Six winter cruises were used, with a total of 1396 transects (422 in the Subantarctic water mass, 441 in the Low Antarctic, and 533 in the High Antarctic), and five summer cruises were used, with a total of 1582 transects (549 in the Subantarctic water mass, 436 in the Low Antarctic, and 597 in the High Antarctic).

We used ANOVA to determine if any differences occurred in seabird densities among water masses. Specifically we ran a MANOVA and then individual ANOVAs; within a species, comparisons among water masses were done using Tukey's HSD. Data were log-transformed to meet the assumption of normality. We also standardized the data, subtracting off the individual cruise means and dividing by the overall standard deviation for each species. However, analysis results were equivalent for the log-transformed data and the standardized data so we only report the results for the log-transformed data. We tabulated the species' densities from the Bellingshausen winter and summer cruises and compared the species seen with the water mass results for the Antarctic-wide winter and summer cruises, respectively.

We also were interested in how total seabird biomass, total seabird density, and species diversity varied among the water masses. Densities of the seabird species were multiplied by the average mass (g) of the species [mostly obtained from Williams (1995) and Brooke (2004)] and summed for total biomass per transect (g km^{-2}). Diversity was measured using the Shannon Index (Magurran, 2004). Total seabird biomass and density were log-transformed to meet the assumption of normality; diversity values were symmetric and were not transformed. We used an ANOVA to test each variable and used Tukey's HSD for water mass comparisons.

To determine if species tended to be seen together, we used a clustering approach (Hastie et al., 2001). Clustering was based on species' correlations of the same data used in the water mass analysis; log-transformed densities were used for the correlations. We used hierarchical clustering with average linkage, that being a compromise between single linkage (which produces long chains) and complete linkage (which produces small compact clusters) (Ribic and Ainley, 1988/1989; Hastie et al., 2001). To assess the significance of the clusters we used multiscale bootstrap resampling; 10,000 bootstrap samples were used (module 'pvclus' in R; Shimodaira, 2002, 2004). Significance was assessed at $\alpha = 0.10$ due to the exploratory nature of these analyses. Significant clusters are referred to as species groups. We clustered the species for individual Bellingshausen winter and summer cruises. For the Bellingshausen summer cruises, we used cruises having at least 100 transects to make sample sizes comparable with the other summer cruises; there were nine Bellingshausen summer cruises that met that criterion (Table 1).

2.2.2. Species density-fronts associations

For each season, Antarctic-wide cruises were combined into one data set, bringing the sample to 1591 transects in winter and 2331 in summer. We removed 17 transects from Antarctic-wide cruises that overlapped the Bellingshausen summer cruise grid. Combining the cruises was deemed necessary because each one sampled a different part of the variable space (see Appendix 1 for example); analysis of individual cruises would not allow us to understand how birds respond to fronts at an Antarctic-wide spatial scale. Combining cruises adds additional variability, so we expected proportion variances explained to be low.

To distinguish sampling zeroes (birds not seen but transects done in the species' range) from absolute zeroes (transects done outside species' range), we restricted analyses to those transects that fell within a given species' range. We used Harrison (1985) to determine the nominal species' ranges and compared our data to see if those limits were reasonable for our data. If there were any major discrepancies (i.e., Harrison boundaries did not match our sightings), we used all transects. In addition, for total biomass, total density and seabird diversity, we used data from all transects.

Because of nonlinear relationships between species' densities and the physical variables found by Chapman et al. (2004) and Ribic et al. (2008), we used generalized additive models to model density as a function of the physical variables (Wood, 2006). This approach allows more flexibility in modeling nonlinear relationships, but can also identify linear and polynomial terms where appropriate; we used a gamma of 1.4 to avoid overfitting (Wood, 2006). All variables were modeled with a Gaussian error structure; bird density, total biomass and total density were log-transformed to normalize the data.

Models composed of variables corresponding to the physical variables were developed before analyses (Burnham and Anderson, 2002). We analyzed two sets of models. The first set comprised additive models consisting of one or two terms; the second was the two-term interaction models. We did not use models with >2 variables because many of the variables were highly correlated ($r > 0.80$). Akaike's Information Criterion (AIC) was used to rank the models (Burnham and Anderson, 2002). The model with the minimum AIC value from either set is referred to as the best model. Akaike weights [likelihood of model i/Σ (likelihoods for all models considered)] were used as a measure of the strength of evidence for the best model (Burnham and Anderson, 2002). We used proportion deviance explained to determine if the interaction models were overfitting the data. If the proportion deviance explained for the interaction models was within 5% of the best additive model, we chose the additive model. The best models are tabulated by season for each species. Analyses were done in R using *mgcv* (R Development Core Team, 2004). Summary tables by season were used to determine which physical variables were most common among the seabird species.

To understand if the models developed from the Antarctic-wide analysis were reasonable for the western Antarctic Peninsula, we predicted the species' densities, total biomass, total density, and species diversity using the best Antarctic-wide models and the environmental variables from the Bellingshausen winter and summer cruises. The ranges of environmental variables from the western Antarctic Peninsula cruises fell within the ranges sampled by Antarctic-wide cruises. We calculated spearman's ρ, a non-parametric correlation measure, between the predicted and the observed values (Conover, 1999). For this comparison, we used species that were seen on at least two of the Bellingshausen winter cruises (on at least 10 transects within a cruise) and at least three Bellingshausen summer cruises (on at least 20 transects within a cruise). For any response variable that had consistent negative correlations, we analyzed the individual western Antarctic Peninsula cruises (in the manner outlined above) to determine what environmental variables were important for the observed response.

3. Results

3.1. Winter

3.1.1. Species associations with water masses

Antarctic-wide, seabird density, biomass, and diversity varied significantly among water masses ($p < 0.001$, all tests). Highest densities were found in the High Antarctic water mass (mean density $= 113.1 \pm 1030.5$ birds km^{-2}), then the Low Antarctic water mass (11.8 ± 34.2), with lowest in the Subantarctic water mass (1.2 ± 5.7). Seabird biomass followed the same pattern: highest in High Antarctic water mass (690.3 ± 5886 kg), followed by the Low Antarctic (16.0 ± 85.8) and Subantarctic water mass (5.1 ± 14.6). However, species diversity was lowest in High Antarctic water mass (0.53 ± 0.45), increasing in Subantarctic (0.66 ± 0.59) and highest in Low Antarctic water mass (0.77 ± 0.48). Penguins contributed importantly to High Antarctic water mass biomass and were the primary components of the High Antarctic water mass diversity indices.

Densities of individual species also varied among water masses (MANOVA, Pillai Trace $= 0.51$, df $= 2$, 1393, $p < 0.001$). Those of cape petrel (*Daption capense*), Antarctic prion (*Pachyptila vittata*), and Wilson's storm-petrel (*Oceanites oceanicus*) did not differ ($p > 0.10$, all tests), but densities of remaining species did vary among water masses ($p < 0.001$, all tests; Table 2). Specifically densities were highest for black-browed albatross (*Diomedea melanophris*), diving petrels (*Pelecanoides* spp.), and prion spp. (*Pachyptila* spp.) in the Subantarctic water mass; for blue (*Halobaena caerulea*) and Kerguelen petrel (*Pterodroma brevirostris*), and Arctic tern (*Sterna paradisaea*) in the Low Antarctic water mass; and for southern giant petrel (*Macronectes giganteus*), Adélie penguin (*Pygoscelis adeliae*), and snow petrel (*Pagodroma nivea*) in the High Antarctic water mass. Antarctic fulmar (*Fulmarus glacialoides*) and Antarctic petrel (*Thalassoica antarctica*) were at highest densities in both the Low Antarctic and High Antarctic water masses.

The four Bellingshausen winter cruises took place in the High Antarctic water mass. Average species diversity on these cruises was 0.24 (± 0.12), about half what was seen in the Antarctic-wide analyses. Mean seabird density (1.78 ± 1.78 birds km^{-2}) and biomass (2.92 ± 2.06 kg km^{-2}) were even lower compared to Antarctic-wide results. Six species were consistently seen on the Bellingshausen winter cruises: southern giant petrel, Adélie penguin, snow petrel, Antarctic fulmar, Antarctic petrel, and blue petrel. Species were associated with water masses in a way similar to the Antarctic-wide analysis. The first five species were seen either only in the High Antarctic water mass or in both the Low Antarctic and High Antarctic water masses and the blue petrel was at highest densities in the Low Antarctic water mass during the Bellingshausen winter cruises. Species densities on the Bellingshausen winter cruises were low compared to those seen in the Antarctic-wide analysis (Table 2). Average densities on the Bellingshausen winter cruises varied from a low of 0.05 ± 0.03 birds km^{-2} for southern giant petrel to a high of 0.95 ± 0.22 for snow petrel.

Table 2
Average densities (number km^{-2}) by water mass for species seen on $>5\%$ of transects from Antarctic-wide cruises done during ***winter***; transects within 15 km of a frontal boundary not included. Within a species, numbers with the same superscript are not significantly different at α of 0.05.

Species	Water mass		
	High Antarctic	Low Antarctic	Subantarctic
Cape petrel, *Daption capense*	0.56^{a}	0.81^{a}	0.38^{a}
Antarctic prion, *Pachyptila desolata*	0.13^{a}	0.21^{a}	0.07^{a}
Wilson's storm-petrel, *Oceanites oceanicus*	0.08^{a}	0.14^{a}	0.08^{a}
Black-browed albatross, *Diomedea melanophris*	0^{*a}	0.01^{a}	0.27^{b}
Diving petrel, *Pelecanoides* spp.	0^{a}	0.01^{a}	0.19^{b}
Prion, *Pachyptila* spp.**	0.16^{a}	0.17^{a}	0.68^{b}
Blue petrel, *Halobaena caerulea*	0.23^{a}	0.42^{b}	0.21^{a}
Arctic tern, *Sterna paradisaea*	$<0.01^{a}$	0.28^{b}	0^{a}
Kerguelen petrel, *Pterodroma brevirostris*	0.01^{a}	0.13^{b}	0.06^{c}
Antarctic fulmar, *Fulmarus glacialoides*	1.50^{a}	2.11^{a}	0.08^{b}
Antarctic petrel, *Thalassoica antarctica*	5.65^{a}	4.27^{a}	0.03^{b}
Southern giant petrel, *Macronectes giganteus*	0.15^{a}	0.04^{b}	0.04^{b}
Adélie penguin, *Pygoscelis adeliae*	87.65^{a}	0.82^{b}	0^{b}
Snow petrel, *Pagodroma nivea*	7.05^{a}	1.87^{b}	0^{c}

* Black-browed albatross mean in the High Antarctic water mass is 0.311 due to two large values that skewed the mean; the value in the table is the median.

** Does not include Antarctic prion.

3.1.2. Species assemblages

Antarctic-wide during winter, two species groups were identified although many species were not grouped (Fig. 3): (1) Adélie penguin/snow petrel/Antarctic petrel and (2) southern giant petrel/Antarctic prion/Wilson's storm-petrel/Antarctic fulmar/cape petrel. Not included in a group, likely because of low density in the Antarctic during winter, were diving petrel, black-browed albatross, blue petrel, prion spp., Kerguelen petrel, and Arctic tern. Group 1 was composed of year-round resident species associated with the High Antarctic water mass. Within Group 1, the first pair formed was Antarctic and snow petrel ($r = 0.46$); Adélie penguin was linked due to its correlation with snow petrel (0.18). Group 2 was composed of species primarily found over multiple water masses (only southern giant petrel was associated with the High Antarctic water mass). In this group, the first pair to form was Antarctic fulmar and cape petrel ($r = 0.35$); other species were linked due to their association with that pair.

In the Bellingshausen winter cruises, Adélie penguin and snow and Antarctic petrel were all present [i.e., Antarctic-wide Group 1 (High Antarctic)] but only Antarctic and snow petrels formed a consistent pair; Adélie penguin was not clustered with these (or any) species. Species from Antarctic-wide Group 2 were not consistently seen on the Bellingshausen winter cruises. However, when present, these species did form a group; Antarctic fulmar and cape petrel being the core with southern giant petrel, Antarctic prion, and Wilson's storm-petrel linked due to correlations with that pair. The Bellingshausen winter groups differed from those identified Antarctic-wide mainly in that snow and

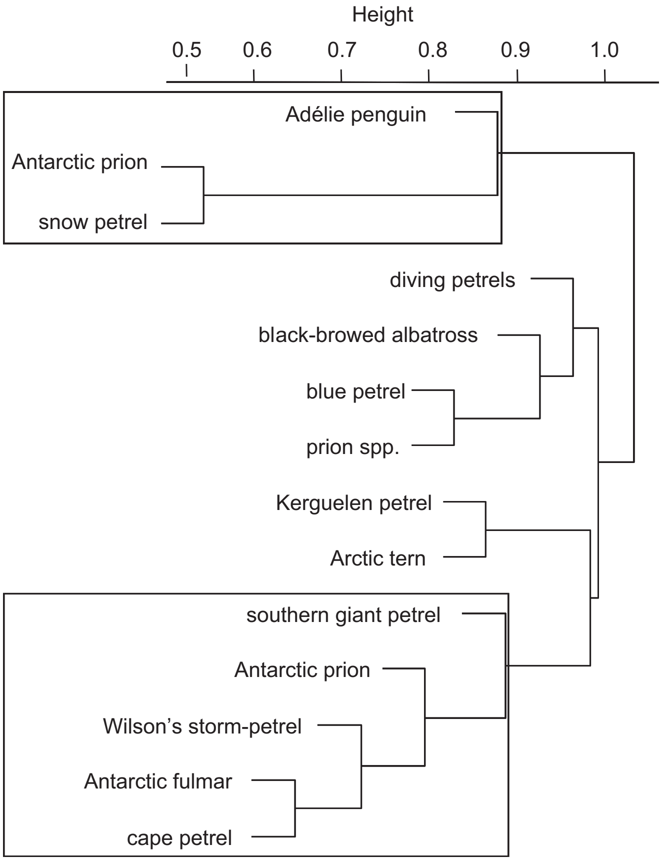

Fig. 3. Dendrogram showing species associations on Antarctic-wide winter cruises. The boxes indicate significant clusters at $p=0.10$.

Antarctic petrel grouped with Antarctic fulmar, cape petrel, and other members of Antarctic-wide Group 2.

3.1.3. *Relationships to major fronts*

Antarctic-wide additive models explained best the observed occurrence patterns relative to fronts for eight of 14 seabird species of sufficient abundance for analysis (Table 3, models explained $<5\%$ of the deviance for southern giant petrel and are not reported). All relationships were unimodal and nonlinear [e.g., gray-headed albatross (*Thalassarche chrysostoma*)], with plateaus [e.g., southern black-backed gull (*Larus dominicanus*)] being common. However, generally increasing or decreasing relationships of density with the different variables could be seen (Tables 3 and 4). Percentage deviance explained ranged from 12% (blue petrel) to 43% (Antarctic fulmar), and the very high (1 or close to 1) AIC weights indicated that these models, of all the models tested, had high support from the existing data. A summary of the best models indicated that distance to ice was important to nine species (Table 4). Distance to the Antarctic Polar Front was important for six species, distance to the Shelf Break Front was important for six species and both of these features were important for two (diving petrels, Antarctic fulmar).

Antarctic-wide, the best model for seabird density was an additive one of distance to the Antarctic Polar Front and distance to the Shelf Break Front (% deviance explained=38.3). Under this model, seabird density was highest on the landward side of the Antarctic Polar Front and was highest at the Shelf Break Front. For seabird biomass, the best model was additive, composed of distance to the southern boundary of the ACC and distance to the Shelf Break Front (% deviance explained=28.5 for seabird biomass). Under this model, seabird biomass increased away from the southern boundary of the ACC and toward the Shelf Break Front. In contrast, the best model for explaining species diversity was additive, composed of distance to the ice edge (50% isopleth) and distance to the Antarctic continent (% deviance explained=34%). Under this model, diversity increased away from the ice edge into open water and was highest closest to the Antarctic continent.

In the Bellingshausen winter cruises, Antarctic fulmar, southern black-backed gull, Antarctic and blue petrels, Adélie penguin, and cape and snow petrels were abundant enough to be modeled. Correlations between the observed and predicted values from the Antarctic-wide models were highest and positive for southern black-backed gull (mean=0.35, $n=2$). Correlations were lower but still positive for cape petrel (0.19, $n=2$), snow petrel (0.19, $n=4$) and blue petrel (0.16, $n=2$). The models were less successful in predicting relative densities of Antarctic petrel (0.03, $n=4$), Adélie penguin (-0.16, $n=3$), and Antarctic fulmar (-0.23, $n=2$). In particular, Adélie penguin and Antarctic fulmar were consistently predicted low when the observed densities were high. The best Antarctic fulmar model from the Antarctic-wide analysis contained the interaction of distance to the Antarctic Polar Front and distance to the Shelf Break Front (Tables 3, 4); on the Bellingshausen winter cruises, the best Antarctic fulmar models also included distance to the Antarctic Polar Front as an interaction, but the other terms varied (distance to the Ice edge (15% isopleth) for cruise 1 and distance to land for cruise 2). During the Bellingshausen winter cruises, Antarctic fulmars were seen at highest densities around 500–550 km (landward) from the Antarctic Polar Front, similar to that found on the Antarctic-wide analysis (Table 3). This was not the case for Adélie penguin. The best Antarctic-wide Adélie penguin model contained the interaction of distance to the Shelf Break Front and distance to the Antarctic continent. However, in the Bellingshausen winter cruises, the best models for Adélie penguin varied among cruises with distance to the ice edge (50% isopleth) included in two of the best models.

Predicting total seabird density and seabird biomass for the Bellingshausen winter cruises using the best models from the Antarctic-wide analysis were not successful (density: average $\rho=-0.26$; biomass: average $\rho=-0.26$, $n=4$ cruises). The best Bellingshausen winter models for total density were interactions containing distance to the ice edge (50% isopleth) in two models and distance to the Antarctic Polar Front in the others. The best Bellingshausen winter models for seabird biomass were also interactions that included distance to the southern boundary of the ACC. Predictions of species diversity were more successful for the Bellingshausen winter cruises in 2002 (average $\rho=0.17$) than for 2001 (average $\rho=-0.17$). The best Bellingshausen winter cruise models for species diversity were primarily additive. In 2002 they were composed of distance to the ice edge (50% isopleth) and distance to the Antarctic Polar Front but in 2001 no consistency existed between the models.

3.2. *Summer*

3.2.1. *Species' associations with water masses*

Similar to winter, Antarctic-wide total summer seabird density and species diversity varied among water masses ($p<0.001$, both tests) but unlike winter, biomass did not ($F=1.5$, df $1=2$, df $2=1579$, $p=0.22$). Highest densities, again, were found in the High Antarctic water mass (mean density 25.6 ± 75.3 birds km^{-2}); lower densities in the Low Antarctic (19.5 ± 188.9) and Subantarctic water masses (29.5 ± 281.6) were not significantly different from each other. In this case, high numbers of Antarctic fulmar, and Antarctic and snow

Table 3
Best models for species seen during Antarctic-wide ***winter*** cruises. All variables are smoothed using splines. DLAND = distance to nearest land (nearest mainland or island), DANT = distance to the Antarctic continent, DICE15 = distance to the ice edge where the ice edge is defined by 15% ice cover, DICE50 = distance to the ice edge defined by 50% ice cover, DSBACC = distance to the southern boundary of the Antarctic Circumpolar Current, DAPF = distance to the Antarctic Polar Front, and DSBF = distance to the Shelf Break Front.

Species	No. transects	Best model	AIC weight	Deviance explained (%)	Interpretation
Black-browed albatross	1416	DICE50 × DSBACC	1	22.1	Two areas of high density: Within 250 km of the southern boundary of the ACC and more than 500 km from the ice edge in open water; More than 1500 km from the southern boundary of the ACC and more than 1000 km from the ice edge in open water
Gray-headed albatross, *Thalassarche chrysostoma*	1591	DICE50 + DSBACC	0.996	12.7	DICE50: unimodal—highest densities 1000–1500 km from the ice edge in open water DSBACC: positive—highest densities more than 1500 km from the southern boundary of the ACC
Diving petrels	1591	DAPF + DSBF	1	24.9	DAPF: positive—highest densities seen 1000 km and farther from the Polar Front DSBF: negative—densities decline 1500 km and farther from the Shelf Break
Antarctic fulmar	1591	DAPF × DSBF	1	43.1	Highest density near the Shelf Break and 500 km landward of the Polar Front
Southern black-backed gull, *Larus dominicanus*	854	DICE15 + DSBF	0.995	22.1	DICE15: positive—highest densities around the ice edge and seaward DSBF: negative: highest densities within 200 km (landward) of the Shelf Break
Antarctic petrel	1430	DICE50 + DAPF	0.992	37.7	DICE50: unimodal—peak density 250 km from the ice edge in open water DAPF: unimodal—peak density 1000 km landward of the Polar Front
Blue petrel	1591	DAPF + DANT	0.99	12	DAPF: unimodal—highest densities around the Polar Front DANT: positive—highest densities farthest from the Antarctic continent
Adélie penguin	897	DSBF × DANT	1	22	Highest densities close to the Antarctic continent and between 200 and 400 km from the Shelf Break
Cape petrel	1591	DICE50 + DSBACC	0.997	17.5	DICE50: unimodal—highest densities between 300 and 400 km from the ice edge in open water DSBACC: positive—highest densities farther from the southern boundary of the ACC
Snow petrel	1251	DICE15 + DAPF	1	41.5	DICE15: unimodal—highest densities within 100 km of the ice edge (within the ice) DAPF: bimodal: highest densities about 1250 km landward of the Polar Front; second smaller peak about 500 km landward of the Polar Front
Antarctic prion	1591	DICE15 × DSBF	1	15.8	Highest value around the Shelf Break and 250 km from the ice edge
Prion spp.	1591	DICE15 + DANT	1	35.4	DICE15: positive—highest densities farthest from the ice edge in open water DANT: unimodal—highest densities about 1500 km from the Antarctic continent
Kerguelen petrel	1591	DAPF × DSBF	1	26.5	Highest densities 250 km from the ice edge and far from the Polar Front (landward)
Wilson's storm-petrel	1591	DICE15 × DSBACC	1	22	Two areas of high density: 200 km from the ice edge in open water and 300 km (landward) from the southern boundary of the ACC; 1000 km from the ice edge in open water and 500 km seaward from the southern boundary of the ACC

petrels in the High Antarctic water mass were the reason for the high densities; these species (average biomass = 548 ± 233 g) are not as heavy as penguins [Adélie penguin: 4.5 kg, Emperor penguin (*Aptenodytes forsteri*): 3.2 kg] and do not contribute as much biomass. In the case of species diversity, similar to winter, lower mean summer diversity was seen in the High Antarctic water mass (0.51 ± 0.47), but unlike winter, species diversity was higher in the Low Antarctic water mass (0.76 ± 0.52) and was highest in the Subantarctic water mass (0.84 ± 0.51).

Individual species' densities varied among water masses (MANOVA, Pillai Trace = 0.48, df = 2, 1579, $p < 0.001$). Specifically summer densities were highest for black-browed albatross, diving petrels, white-chinned petrel (*Procellaria aequinoctialis*), mottled petrel (*Pterodroma inexpectata*), soft-plumaged petrel (*Pterodroma mollis*), sooty shearwater (*Puffinus griseus*), white-headed petrel (*Pterodroma lessoni*), prion spp., and black-bellied storm-petrel (*Fregatta tropica*) in the Subantarctic water mass; for blue petrel, chinstrap penguin (*Pygoscelis antarctica*), cape petrel, Antarctic prion, Kerguelen petrel, and short-tailed shearwater (*Puffinus tenuirostris*) in the Low Antarctic water mass; and for Antarctic petrel, Adélie penguin, snow petrel, south polar skua (*Stercorarius maccormicki*), and Wilson's storm-petrel in the High Antarctic water mass. Antarctic fulmar and southern giant petrel were at their highest densities in both the High Antarctic and Low Antarctic water masses.

The Bellingshausen summer cruises took place primarily in the High Antarctic water mass. Average species diversity was 0.83

Table 4
Summary of best models for species seen during Antarctic-wide winter and summer cruises; I = interaction model, A = additive model. Bolded and italicized characters indicate higher densities within 200 km of the variable. ACC = Antarctic Circumpolar Current. Ice edge 15 = the ice edge is defined by 15% ice cover and Ice edge 50 = the ice edge is defined by 50% ice cover.

Species	Variable (distance in km to)						
	Ice edge 15	Ice edge 50	Southern boundary of the ACC	Antarctic Polar Front	Shelf Break	Land	Antarctic Continent
WINTER							
Black-browed albatross		I	I				
Gray-headed albatross		A	A				
Diving petrels				A	A		
Antarctic fulmar				I	***I***		
Southern black-backed gull	***A***				***A***		
Antarctic petrel		A		A			
Blue petrel				***A***			A
Adélie penguin					***I***		***I***
Cape petrel		A	A				
Snow petrel	***A***			A			
Antarctic prion	I				***I***		
Prion spp.	A						A
Kerguelen petrel				I	I		
Wilson's storm-petrel	I		I				
SUMMER							
Black-browed albatross	A			A			I
Diving petrels	I		***I***				
Antarctic fulmar				I	***I***		
Antarctic petrel			I			I	
Blue petrel			***I***			I	
Adélie penguin		***A***			A		
Chinstrap penguin, *Pygoscelis antarctica*					A		A
Cape petrel					A		A
White-chinned petrel, *Procellaria aequinoctialis*		A		A			
Snow petrel			A		A		
Antarctic prion					A		A
Prion spp.	A		A				
Mottled petrel, *Pterodroma inexpectata*		A					A
White-headed petrel, *Pterodroma lessoni*	I						I
Sooty shearwater, *Puffinus griseus*				***I***			I
Short-tailed shearwater, *Puffinus tenuirostris*			A		***A***		
South polar skua, *Stercorarius maccormicki*			A		A		
Black-bellied storm-petrel, *Fregatta tropica*				I			I

(±0.17) or slightly higher than detected in the Antarctic-wide analysis. Total mean summer density (8.44 ± 3 birds km^{-2}) was lower but biomass (21.3 ± 12.3 kg km^{-2}) was similar to results from the Antarctic-wide analysis. Eleven species were seen on seven or more Bellingshausen summer cruises: southern giant petrel, Antarctic petrel, Adélie penguin, snow petrel, south polar skua, Wilson's storm-petrel, Antarctic fulmar, blue petrel, chinstrap penguin, cape petrel, black-browed albatross, white-chinned petrel, and black-bellied storm-petrel. The first seven were seen either only in the High Antarctic water mass or in both the Low and High Antarctic water masses. Adélie penguin (3.27 ± 3), south polar skua (0.59 ± 0.33), and Wilson's storm-petrel (1.53 ± 1.15) were seen at densities similar to those seen Antarctic-wide. Southern giant petrel (0.38 ± 0.56) and Antarctic fulmar (0.34 ± 0.18) were seen at higher densities on the Bellingshausen summer cruises and Antarctic petrel (0.05 ± 0.05) and snow petrel (0.01 ± 0.02) were seen at lower densities than on Antarctic-wide cruises. Blue and cape petrels and chinstrap penguin were seen at low densities in the High Antarctic water mass Antarctic-wide (Table 5); during the Bellingshausen summer cruises, blue petrel (0.02 ± 0.02) and chinstrap penguin (0.14 ± 0.11) were seen at densities similar to the Antarctic-wide analysis, while cape petrel (0.98 ± 0.86) was seen at higher densities. Antarctic-wide, black-browed albatross, white-chinned petrel, and black-bellied storm-petrel were seen at their highest densities in the Subantarctic water mass and were seen at low densities in the High Antarctic water mass. On the Bellingshausen summer cruises (primarily High Antarctic water mass), black-browed albatross density (0.17 ± 0.13) was more similar to black-browed albatross densities seen in the Subantarctic water mass Antarctic-wide (Table 5). White-chinned petrel density (0.02 ± 0.03) was similar to and black-bellied storm-petrel density (0.03 ± 0.03) was lower than that seen on the Antarctic-wide analysis (Table 5).

3.2.2. *Species assemblages*

At the Antarctic-wide scale, unlike winter, almost all species observed in summer clustered into groups (Fig. 4): (1) Wilson's storm-petrel/Antarctic petrel/snow petrel/Adélie penguin/south polar skua, (2) Antarctic prion/Antarctic fulmar/cape petrel/blue petrel/chinstrap penguin, and (3) short-tailed shearwater/mottled petrel/black-bellied storm-petrel/white-chinned petrel/prion spp./black-browed albatross/sooty shearwater/ diving petrels/white-headed petrel. Summer Group 1 was composed of species found at higher densities in the High Antarctic water mass, and was similar to Winter Group 1 with the addition of two seasonal residents (Wilson's storm-petrel, south polar skua). Summer Group 2 was composed of species found at higher densities in the Low Antarctic water mass (except Antarctic fulmar which was found at similar densities in the Low Antarctic and High Antarctic water masses), and contained species found in Winter Group 2 (occurred in both Low Antarctic and Subantarctic water masses). Summer

Table 5
Average species densities (number km^{-2}) by water mass for species seen on more than 5% of transects from Antarctic-wide cruises done during the ***summer***; transects within 15 km of a frontal boundary not included. Within a species, numbers with the same superscript are not significantly different at α of 0.05.

Species	Water mass		
	High Antarctic	Low Antarctic	Subantarctic
Antarctic fulmar	0.14^{a}	0.08^{a}	0.03^{b}
Black-browed albatross	0.01^{a}	0.09^{a}	0.23^{b}
Diving petrel	0^{a}	0.13^{b}	0.27^{c}
White-chinned petrel	$<0.01^{a}$	0.06^{a}	0.23^{b}
Mottled petrel	0.07^{a}	0.16^{b}	0.31^{c}
Soft-plumaged petrel, *Pterodroma mollis*	$<0.01^{a}$	0.04^{b}	0.09^{c}
Sooty shearwater	0.02^{a}	0.64^{a}	2.86^{b}
Short-tailed shearwater	0.36^{a}	4.93^{b}	7.81^{c}
Black-bellied storm-petrel	0.09^{a}	0.08^{a}	0.27^{b}
White-headed petrel	$<0.01^{a}$	0.11^{b}	0.19^{c}
Blue petrel	0.02^{a}	0.32^{b}	0.04^{a}
Chinstrap penguin	0.13^{a}	0.34^{b}	0.09^{a}
Antarctic prion	0.22^{a}	1.17^{b}	1.07^{c}
Prion spp.	0.03^{a}	0.55^{b}	14.9^{c}
Kerguelen petrel	0.01^{a}	0.11^{b}	0.02^{a}
Cape petrel	0.23^{a}	0.56^{b}	0.40^{a}
Southern giant petrel	0.03^{a}	$0.02^{a,b}$	0.01^{b}
Antarctic petrel	10.66^{a}	0.27^{b}	0^{b}
Adélie penguin	3.58^{a}	0.09^{b}	0^{b}
Snow petrel	6.45^{a}	0.33^{b}	$<0.01^{c}$
Wilson's storm-petrel	2.46^{a}	0.17^{b}	0.06^{b}
South polar skua	0.74^{a}	$<0.01^{b}$	$<0.01^{b}$

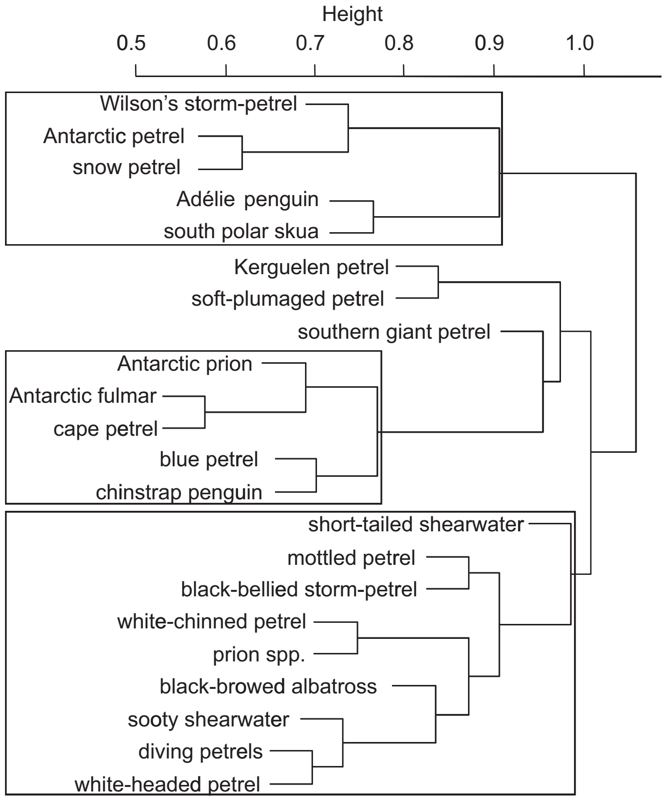

Fig. 4. Dendrogram showing species associations on Antarctic-wide summer cruises. The boxes indicate significant clusters at $p=0.10$.

Group 3 was composed of species that had higher densities in the Subantarctic water mass (except for short-tailed shearwater which was found at higher densities in the Low Antarctic water mass), and all are notably migratory being largely summer residents or visitors in the Antarctic. Therefore, in general, species groupings were driven by species' associations with water masses.

Although species from all three groups were present, no species groups were observed on five of the nine Bellingshausen summer cruises. On the remainder, only species from Summer Group 1 were found in groups. Specifically Adélie penguin and south polar skua formed a group on three of the four cruises with Wilson's storm-petrel included in the group on one cruise; on the fourth cruise, only south polar skua and Wilson's storm-petrel were grouped.

3.2.3. *Relationships to major fronts*

Antarctic-wide, additive models were the best for explaining occurrence patterns for 11 of the 18 species (Table 6, models explained $<10\%$ of the deviance for southern giant petrel and Wilson's storm-petrel and are not reported). The density-variable relationships were nonlinear, with generally increasing or decreasing patterns. Percentage deviance explained ranged from 13.5% (black-bellied storm-petrel) to 62.7% (short-tailed shearwater), with very high (1 or close to 1) AIC weights indicating high support for these models. The lowest AIC weight was found in the best model for white-chinned petrel. In this case, there was an additive model with a ΔAIC of 1.5. This model had distance to the ice edge (15% isopleth) instead of distance to the ice edge (50% isopleth); along with distance to the Antarctic Polar Front, it had a similar deviance explained (26.2%) but had a lower AIC weight (0.32). Summarizing, the best models indicated that distance to land or the Antarctic continent were important for 10 species (Table 4), not a surprising result as, in contrast to winter, these summer nesting species have colonies on land. Distance to the Shelf Break Front was important for eight species and distance to the southern boundary of the ACC was important for seven species; both variables were important for snow petrel, short-tailed shearwater, and south polar skua.

For Antarctic-wide total seabird density, the additive model of distance to the ice edge (50% isopleth) and distance to the southern boundary of the ACC was the best model (% deviance explained = 15.8%). Under this model, total density was higher near the 50% ice edge; total density was also higher farther from the southern boundary of the ACC. For total biomass, the interaction of distance to the ice edge (50% isopleth) and distance to the southern boundary of the ACC was the best model (% deviance explained = 20.6). Under this model, there were two areas of increased biomass: one near the southern boundary of the ACC and near the 50% ice edge and the second was 1000 km south of the southern boundary of the ACC and about 500 km away from the 50% ice edge.

On the Bellingshausen summer cruises, black-browed albatross, Antarctic fulmar, Adélie penguin, cape petrel, and south polar skua were consistently seen and therefore could be modeled. Correlations between the observed and predicted values from the Antarctic-wide models were highest and positive for black-browed albatross (mean 0.40, $n=9$), cape petrel (0.35, $n=9$), and Adélie penguin (0.33, $n=4$). The models were less successful in predicting relative densities of Antarctic fulmar (0.10, $n=9$) and south polar skua (-0.38, $n=9$). In particular, the skua was consistently predicted low despite the high observed densities. The best Antarctic-wide skua model consisted of distance to the southern boundary of the ACC and distance to the Shelf Break Front (Table 6). The best models using the Bellingshausen summer cruises for south polar skua varied by year. Before 1997, the best models contained distance to the Antarctic continent and distance to the Shelf Break Front (1995) or distance to the southern boundary of the ACC (1996); skua densities were highest near the Antarctic continent. From 1997

Table 6
Best models for species seen on Antarctic-wide ***summer*** cruises. All variables are smoothed using splines. DLAND = distance to nearest land (nearest mainland or island), DANT = distance to the Antarctic continent, DICE15 = distance to the ice edge where the ice edge is defined by 15% ice cover, DICE50 = distance to the ice edge defined by 50% ice cover, DSBACC = distance to the southern boundary of the Antarctic Circumpolar Current, DAPF = distance to the Antarctic Polar Front, and DSBF = distance to the Shelf Break Front.

Species	No. transects	Best model	AIC weight	Deviance explained (%)	Interpretation
Black-browed albatross	1489	DICE15 + DAPF	1	13.9	DICE15: negative—highest densities within 1000 km of the ice edge in open water DAPF: positive—highest densities farthest from the Polar Front in open water
Diving petrels	1023	DICE15 × DSBACC	1	50.6	Highest densities occurred around the southern boundary of the ACC, 1000 km seaward from the ice edge
Antarctic fulmar	2034	DAPF × DSBF	1	31.2	Highest densities occurred at the Shelf Break, 500 km south of the Polar Front
Antarctic petrel	1606	DSBACC × DLAND	0.99	30.5	Two areas of high density: 750–1000 km south of the southern boundary of the ACC and between 200 and 400 km from land 500 km south of the southern boundary of the ACC and 1000 km from land
Blue petrel	2205	DSBACC × DLAND	0.817	23.5	Density highest at the southern boundary of the ACC 400–600 km from land
Adélie penguin	1938	DICE50 + DSBF	1	19.9	DICE50: negative—highest densities at the ice edge DSBF: negative—highest densities inshore of the Shelf Break
Chinstrap penguin	1062	DSBF + DANT	1	29.9	DSBF: positive—highest densities occurred farthest from the Shelf Break DANT: negative—highest densities occurred within 1000 km of the Antarctic continent
Cape petrel	2283	DSBF + DANT	1	22.1	DSBF: positive—highest densities occurred farthest from the Shelf Break DANT: negative—highest densities occurred within 500 km of the Antarctic continent
White-chinned petrel	1455	DICE50 + DAPF	0.683	26.5	DICE50: negative—higher densities occurred within 1500 km of the ice edge in open water DAPF: positive—higher densities occurred farther from the Polar Front
Snow petrel	1938	DSBACC + DSBF	1	25.1	DSBACC: negative—higher densities occurred far south of the southern boundary of the ACC DSBF: positive (then plateaus)—densities highest 250 km and farther seaward of the Shelf Break
Antarctic prion	1670	DSBF + DANT	1	18	DSBF: positive—densities highest seaward farther from the Shelf Break DANT: negative—densities highest closer to the Antarctic continent
Prion spp.	1489	DICE15 + DSBACC	0.998	17.8	DICE15: negative—densities highest within 2000 km of the ice edge in open water DSBACC: positive—densities highest farther north of the southern boundary of the ACC
Mottled petrel	1689	DICE50 + DANT	1	25.1	DICE50: positive—higher densities seen farther from the ice edge in open water DANT: negative—higher densities seen within 2000 km of the Antarctic continent
White-headed petrel	589	DICE15 × DANT	1	36.7	Densities highest 1000–1250 km seaward of the ice edge and 1500–1750 km from the Antarctic continent
Sooty shearwater	1109	DAPF × DANT	1	48.2	Two areas of high density: Far from the Polar Front (1000-2000 km) and far from the Antarctic continent (1500-2500 km); Close to the Polar Front (0-500km) and closer to the Antarctic Continent (1000 km)
Short-tailed shearwater	589	DSBACC + DSBF	0.96	62.7	DSBACC: positive—highest densities found farther from the southern boundary of the ACC DSBF: negative—highest densities found at the Shelf Break
South polar skua	1824	DSBACC + DSBF	1	22.7	DSBACC: negative—highest densities found farther south of the southern boundary of the ACC DSBF: negative—highest densities found farther landward of the Shelf Break
Black-bellied storm-petrel	2166	DAPF × DANT	0.987	13.5	Densities highest far north of the Polar Front (1000–1500 km) and far from the Antarctic continent (1000–1500 km)

onward, the best models consistently included distance to the ice edge, with skua densities highest near the edge.

Antarctic-wide models were not successful in predicting total seabird density ($\rho=-0.20$) or biomass ($\rho=-0.28$) for the Bellingshausen summer cruises; they were more successful for species diversity ($\rho=0.18$). Using the Bellingshausen summer cruises, the best models for total seabird density included distance to the ice edge (50% isopleth) in four of the cruises;

distance to the southern boundary of the ACC was included in four of the best models as well. For total biomass, distance to the ice edge (50% isopleth) was included in five of the best models but distance to the southern boundary of the ACC was included in only two.

4. Discussion

4.1. Seabird assemblages

Viewed Antarctic-wide, regardless of season, we identified three seabird groups, each related to one of three water masses: Subantarctic, Low Antarctic and High Antarctic. During winter, the only species found in groups are those that are year-round residents of the High Antarctic water mass. Remaining species, not forming groups, typically occur at low densities in the Antarctic during winter. There are very few winter studies that have defined seabird groups in the Southern Ocean. Ainley et al. (1994) studied seabirds in the marginal ice zone of the Scotia-Weddell Confluence region; in the winter they found two Antarctic species groups similar to those identified in this study. The strong pairing we found of Antarctic and snow petrels in winter is also consistent with that found by Ainley et al. (1994) using recurrent group analysis.

During summer, we found a higher number of species groups, and these were composed primarily of summer-breeding residents. There have been several regional studies undertaken during the spring–summer months in the Southern Ocean with which to compare our findings. In all the studies done in different oceanic sectors of the Southern Ocean (Ainley and Boekelheide, 1983; Working Party on Bird Ecology, 1985; Ribic and Ainley 1988/1989; Hunt et al., 1990; Veit and Hunt, 1991; Ainley et al., 1994; Woehler et al., 2003), the most consistent group across these studies was composed of species from our High Antarctic group, particularly Antarctic and snow petrels. The High Antarctic group appeared to be the least varying assemblage found and its association with the sea ice habitat was noted by other researchers (Working Party on Bird Ecology, 1985; Ribic and Ainley, 1988/89; Veit and Hunt, 1991). While some researchers found species groups similar to our summer Low Antarctic and Subantarctic groups (Ainley and Boekelheide, 1983; Ribic and Ainley, 1988/89; Ainley et al., 1994; Woehler et al. 2003), other researchers found less distinction among them (Working Party on Bird Ecology, 1985; Hunt et al., 1990; Veit and Hunt, 1991; Veit, 1995). For example, Veit (1995) surveying waters just to the north of our study area in summer (South Atlantic/Scotia Sea sector, Argentine Shelf to South Georgia), identified a recurrent species group that was a subset of our summer Subantarctic group; however Antarctic prion, which occurred in the group that Veit (1995) identified for waters south of the Antarctic Polar Front, was a species that was included in our summer Low Antarctic group. Hunt et al. (1990) who also surveyed these more northern waters found a large species assemblage composed of species that occurred in our Low Antarctic and Subantarctic groups. The overlap of mid- and low-latitude species groups has been noted by other researchers (Working Party on Bird Ecology, 1985). The different species composition of groups among studies, besides the factors we identified herein, also likely reflect the distance to Subantarctic breeding sites and the migratory/ foraging routes these species use moving to/from Antarctic waters (Working Party on Bird Ecology, 1985; Woehler et al., 2003).

Our rules for inclusion of species in the analyses did not allow the consideration of all those seen on the cruises. For example, though present on many cruises, Emperor and King penguins (*Aptenodytes patagonicus*) were not observed frequently enough to be included. King penguins were consistently spotted (in low numbers) in the vicinity of the Antarctic Polar Front (see also Charrassin and Bost, 2001; Bost et al., 2004). We propose that our large-scale study and our rules for statistical inclusion detected the ‘core’, or at least the most abundant species in the three water-mass related assemblages of seabirds that occur south of the Subantarctic Front throughout the year around the Antarctic continent.

Ultimately the influence of water masses on species' distributions is a function of overall ocean productivity (as, for instance, indicated by chlorophyll concentration), a pattern shown generally in other ocean systems (see Section 1). Indeed, our results indicated that the highest avian densities and biomasses occurred in waters south of the southern boundary of the ACC [also noted for the Indian Ocean sector of the Southern Ocean (Working Party on Bird Ecology, 1985)], where productivity is known to be the highest among the three water masses that comprise the Southern Ocean, and which we investigated (see mapping of chlorophyll in Tynan, 1998; Smetacek and Nicol, 2005). Lowest productivity was found in waters north of the Antarctic Polar Front and, accordingly, overall avian densities and biomass were found to be lower there. As indicated in our Antarctic-wide clustering, a large number of species move into the Subantarctic and Low Antarctic waters during the summer months, but leave by winter, likely being unable to cope with the cold, stormy conditions, consistent with the findings of Ainley et al. (1994) for the Scotia-Weddell Sea sector.

4.2. Species in relation to fronts (large-scale)

Given the huge literature on seabird occurrence in relation to fronts, including those fronts that we investigated (see Section 1), we expected that the fronts in our study would be areas of increased seabird abundance because of enhanced productivity at fronts (Antarctic Polar Front, Strass et al., 2002; southern boundary of the ACC, Tynan, 1998; Shelf Break Front, Ainley and Jacobs, 1981; marginal ice zone, Fraser and Ainley, 1986). However, we found in our study, in large part, that these fronts appeared to be important mainly as boundaries of water masses and zoogeographic ranges, and not as areas of generally increased seabird abundance (with the exception of a few specific species; see below). The exception was the Shelf Break Front during winter, perhaps due to diverging sea ice which is a consequence of frontal upwelling of warm waters and the nutrient enhancement of the upwelled waters themselves. Areas of open water within the sea ice zone such as polynas and floe leads are well known for attracting vertebrates (e.g., Ainley et al., 2003, Ribic et al., 2008).

As habitats in their own right, the southern boundary of the ACC and the Antarctic Polar Front were important only to three species observed during the summer cruises (blue and diving petrels, sooty shearwater) all of which exhibited increased density in proximity to these fronts. In contrast, within the waters south of the southern boundary of the ACC (i.e., High Antarctic waters), the Shelf Break Front (particularly in the winter, see above) and to a lesser degree the marginal ice zone (see also Fraser and Ainley, 1986; Ainley et al., 1998; Woehler et al., 2006) affected the occurrence of a number of species. Both the southern boundary of the ACC and the Shelf Break Front are prominent in the eastern Bellingshausen Sea, as noted in the Introduction. Accordingly proximity of the southern boundary of the ACC to the western Antarctic Peninsula explains the occurrence, though sparse, of blue petrels in the eastern Bellingshausen; however, it does not explain the absence of sooty shearwaters.

Unlike sooty shearwaters, the Antarctic Shelf Break Front is important to foraging short-tailed shearwaters (Woehler et al., 2006), a sister-species whose at-sea range minimally overlaps sooty shearwater, one being primarily Indian Ocean and the other primarily South Pacific, respectively [see Shaffer et al. (2006) for occurrence to the north]. Both species are very abundant, with breeding populations in the millions (Brooke, 2004). The absence of sooty shearwater in the eastern Bellingshausen and to the north (also noted by Working Party of Bird Ecology, 1985 for the Atlantic sector of the Southern Ocean), an apparent anomaly on the basis of oceanography, is perhaps best explained by a biological factor: the high abundance in those waters of Antarctic petrel, a subsurface-forging species of the same size as the sooty shearwater, and the subsurface foraging Adélie and chinstrap penguins. Neither Antarctic petrel nor these penguins are very abundant off East Antarctica (other than in the vicinity of Prydz Bay, 70–80°E) compared to the Ross Sea (Victoria Land)-Bellingshausen seas (Antarctic Peninsula) sector (Antarctic petrel: van Franeker et al., 1999; Adélie and chinstrap penguins: Woehler 1993; see also Ainley et al., 1998). Therefore we hypothesize that competitive exclusion may be operating, with Antarctic petrel and the penguins excluding sooty shearwater from High Antarctic and Shelf Break Front waters of the Peninsula region (and eastern Bellingshausen waters in general). We know that competitive relationships between sooty shearwaters and other subsurface foragers are important in the California Current (Northeast Pacific GLOBEC; Ainley et al., 2009).

4.3. Smaller-scale perspectives

Seabirds search for food in a hierarchical multi-sensory manner at sea (e.g., Hunt and Schneider, 1987; Fauchald and Tveraa, 2006; Pinaud and Weimerskirch, 2007; Nevitt, 2008). Initially they head to areas that have spatially and/or temporally predictable prey present and then search more intensively once there (Nevitt, 2008). This more intensive search keys on smaller-scale fronts and opportunities, such as subsurface features that influence or determine circulation and prey availability (summarized in Bost et al., 2009). Such a pattern has been shown specifically for the eastern Bellingshausen by Ribic et al. (2008), who in addition to physical features (cf. Chapman et al., 2004), also related top-predator mesoscale distribution during winter directly to prey patches and particularly to those of Antarctic krill (*Euphausia superba*). However, results varied among species of top predators, with the distribution of some species more closely related to physical features (e.g., bathymetry) than to actual prey patches, no doubt because most species of top predators have a diverse diet in the Southern Ocean, and the Bellingshausen specifically (e.g., Karnovsky, 1997). In addition, as shown by Ainley et al. (2009) in the California Current, the distributions of top predators coincide with their more widely-distributed prey in small-scale frontal regions, such as coastal upwelling fronts, not showing an association with equally abundant prey of the same species outside of the front. The question of why prey availability might be greater in proximity to fronts must be answered empirically (see also, e.g., Schneider et al., 1987; Hunt and Schneider, 1987; Hunt et al., 1998), specifically actual behavioral observations of the prey taxa are required. In that regard, the importance of fronts in affecting predator distribution relative to prey availability in the better-studied California Current has additional bearing on the interpretation of our results. For example, it has been proposed that in addition to an increase in prey abundance or predictability of occurrence (e.g., Decker and Hunt, 1996; Skov et al., 2000; Weimerskirch, 2007) at fronts, the alteration of prey behavior at fronts may affect predator distribution (Ainley et al., 2009). When prey are seeking to renew their own condition or to increase growth rate and foraging success at a front, they may be more susceptible to predation themselves, a result apparent in the modeling exercises of Alonzo (2002) and Alonzo et al. (2003) (see also Fiksen et al., 2005). Alternatively certain aspects of fronts, such as changes in water stratification, could also make prey more vulnerable (Hunt and Harrison, 1990; Skov and Durinck, 2000).

In addition to how the physics of fronts contribute to attracting seabirds, biological factors are also important, such as local enhancement (visual recruitment: predators attracted to other predators; Hoffman et al., 1981; Haney et al., 1992; Grunbaum and Veit, 2003; Silverman et al., 2004), particularly in regard to certain subsurface predators enhancing the foraging success of others, particularly surface foragers (e.g., Harrison et al., 1991; Ainley et al., 2009). Also involved could be previous success and therefore accumulated knowledge of front prevalence (Irons, 1998; Ford et al., 2007; Weimirskirch, 2007). In eastern Bellingshausen waters, seabirds seem to respond to the Shelf Break Front and the marginal ice zone (Ribic et al., 2008) in a way similar to that observed for the upwelling front investigated in the California Current (Northeast Pacific GLOBEC; Ainley et al., 2009).

5. Conclusions

This synthesis of seabird assemblages and relationships of species to fronts by combining Southern Ocean at-sea regional data bases to put regional studies in context is the first time this has ever been done for any stretch of the World Ocean. We have established core assemblages for the Southern Ocean in two seasons, noting the paucity of information for the winter season. The winter assemblages reflect the core Antarctic year-round residents; the summer assemblages reflect the influx of summer breeders in addition to the Antarctic residents. We found that understanding the spatial relationships among fronts was important for understanding seabird species assemblages. During the summer, a period of more abundant resources, fronts appear to act more like faunal boundaries while during the winter, when resources are more limited, the fronts, in particular the Antarctic Polar Front, appear to be areas of increased resources as reflected in increased densities for many Antarctic resident seabirds. Winter seabird assemblages of the eastern Bellingshausen reflected the Antarctic-wide High Antarctic winter species assemblage but summer assemblages were not consistently found. However, the ability of the Antarctic-wide frontal models to predict individual seabird species density was better for the summer Bellingshausen cruises than the winter cruises. Seabirds in the winter in the eastern Bellingshausen Sea may be taking advantage of other smaller-scale features that result from the interaction between the Antarctic Circumpolar Current and the complex bathymetry of the eastern Bellingshausen that result in prey concentrations, important during the Antarctic winter (Chapman et al., 2004; Ribic et al., 2008).

With this study as well as the work of others (e.g., Hunt and Schneider, 1987; Hunt, 1991; Ainley et al., 2009; Bost et al., 2009), we need to move the subject of seabirds associating with fronts in the Southern Ocean or other oceanic regions, either investigated in real time or by way of telemetry/satellite imagery, away from pattern detection to hypothesis generation. The hope is that synthesis studies such as ours can be used to help focus the development of additional multi-disciplinary investigations, similar to GLOBEC, but where the full suite of predators (fish, mammals, birds) and predator behavior is investigated in the context of a quantified prey field. In this way both top-down and bottom-up forcing factors can be assessed for their roles in influencing prey availability and predator presence. This is especially critical in the Southern Ocean, and particularly the eastern Bellingshausen Sea, where the increasing abundance of cetaceans, if allowed to recover from former decimation, may well be affecting the relationships among predators and prey, and their response to physical forcing (i.e., climate change), particularly for the high-energy, diving species (Ballance et al., 2006; Ainley and Blight, 2008; Friedlaender et al., 2008; Ainley et al., 2010).

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Appendix 1

Coverage of distance to the ice edge (km) where the ice edge is defined by 15% ice cover and distance to the Antarctic Polar Front (km) for the Antarctic-wide summer analysis. Transects within the ice have negative distances in relation to the ice edge. Transects landward of the front have negative distances. X=*Northwind* 1976, upside-down triangle=*Polar Star* 1987, diamond=*Northwind* 1979, += *Polar Duke* 1988, small triangle= *N. B. Palmer* 1994, square with x=*Glacier* 1979, open circle= *Melville* and *Westwind* 1983, small solid circle=*Aurora Australis* 2000, and triangle=*Burton Island* 1977. (Fig. A1)

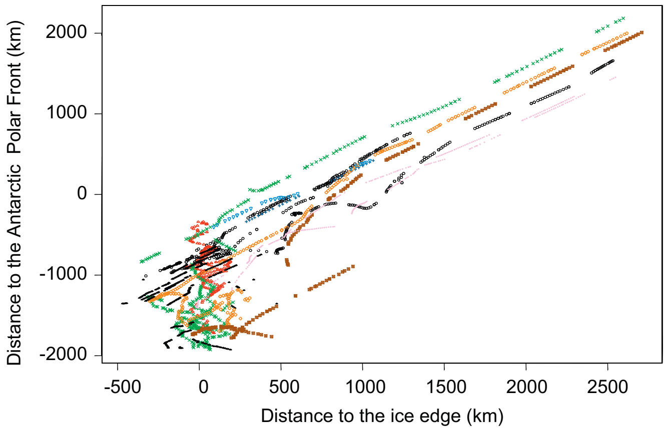

Fig. A1

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