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The Distribution and Abundance of Aerial Seabirds in Relation to Antarctic Krill in the Prydz Bay Region, Antarctica, During Late Summer

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Summary. The distribution patterns of aerial seabirds are analysed from counts made in the Prydz Bay region, Antarctica, during the African legs of SIBEX I and II in late summer (end of February to April), and compared with those made farther west at the same time of year during FIBEX. Species composition and abundances were similar in all three surveys, with sooty shearwaters *Puffinus griseus* contributing approximately half of the total aerial bird energy demand. Differences between surveys are explained in terms of longitudinal or seasonal differences in sampling areas and periods. Correlations between bird distribution patterns and environmental parameters are used to infer the scale-dependent factors affecting bird dispersion at sea. Two macro-scale bird assemblages, identified by physical parameters, were separated along latitudinal gradients (temperature and salinity) associated with the Antarctic Divergence. These assemblages are consistent with the Intermediate and Southern High Latitude Groups identified during FIBEX. At smaller spatial scales, almost all species were correlated with the abundance of Antarctic krill *Euphausia superba*, both across the entire SIBEX I grid, and within the areas north and south of the Antarctic Divergence. Similarly, during SIBEX II, seabird densities were six times greater when krill was abundant than when krill was scarce. Sooty shearwaters, which appeared to be moving through the area, were the only abundant bird species not correlated with krill abundance. Possible reasons why previous studies have not detected correlations between seabird and krill abundances are discussed.

Introduction

The international BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) programme aims to assess the stocks of living resources in the Southern Ocean and to gain an understanding of the structure and functioning of Antarctic marine ecosystems. The First International BIOMASS Experiment (FIBEX) determined the distribution and abundance of Antarctic krill *Euphausia superba* and its predators, and was conducted during the austral summer of 1980–1981. FIBEX was followed by the Second International BIOMASS Experiments (SIBEX) during the summers of 1983–1984 (SIBEX I) and 1984–1985 (SIBEX II). SIBEX investigated specific areas of interest identified during FIBEX. The African legs of SIBEX were chosen to study the large concentration of Antarctic krill reported during FIBEX from the Prydz Bay region (Hampton 1983; Miller 1986a).

The distribution patterns of aerial seabirds in Antarctic waters have been characterized both in terms of environmental parameters and the distribution of prey species such as Antarctic krill (e.g. Ainley and Jacobs 1981; Ohyama and Naito 1982; Starck and Wyrzykowski 1982; Abrams 1983; Griffiths 1983; Ainley et al. 1984; Obst 1985; BIOMASS Working Party on Bird Ecology 1985; Fraser and Ainley 1986; Montague 1988; Heinemann et al., in press). However, most studies in the Indian Ocean sector have been based on single surveys and there has been little consideration of temporal variability in seabird distribution patterns. This study examines the distribution patterns of aerial seabirds observed during the African legs of SIBEX I and II, and contrasts these with the distribution patterns reported from the African leg of FIBEX (Abrams 1983; BIOMASS Working Party on Bird Ecology 1985). Possible factors affecting the distribution patterns of birds at sea are discussed, with particular reference to Antarctic krill.

Study Area

Observations of birds at sea off Enderby, Kemp and MacRobertson Lands, to the west of Prydz Bay, were made from the *MVSA Agulhas* during SIBEX I and from the *RS Africana* during SIBEX II. SIBEX I covered a grid from 62 to 66°S and from 52 to 64°E between 27 March and 19 April 1984 (Fig. 1, Allanson and Parker 1985). SIBEX II was divided into two sections: Phase 1, which

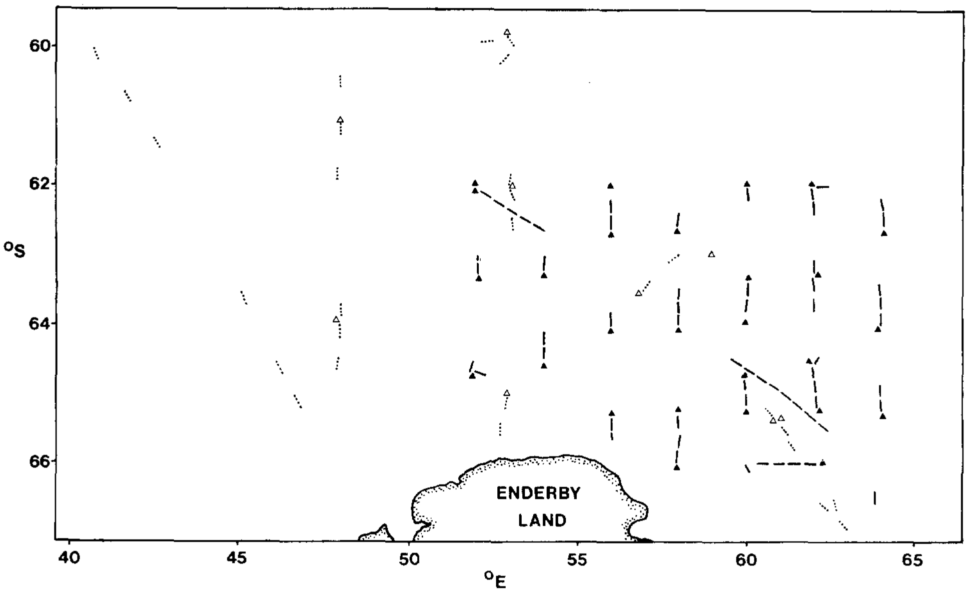

Fig. 1. The location of one-hour transect counts of aerial seabirds during the African legs of SIBEX I (*solid lines*) and II (*dotted lines*). *Triangles* depict stations where bird counts were made during SIBEX I (*closed*) and SIBEX II (*open*)

repeated the Australian leg conducted earlier the same season and sampled from 60 to 66°S and from 48 to 53°E; and Phase 2, a less structured survey of meso- to fine-scale krill swarm dynamics (Miller 1986b). Phase 2 was not completed due to a mechanical failure, and observations were made only between 27 February and 8 March 1985 (Cooper 1986). The African sector of FIBEX sampled farther west, from 59 to 69°S and from 15° to 30°E, between 16 February and 10 March 1981 (Abrams 1983).

The physical conditions prevailing during the SIBEX I and II surveys have been described (Allanson and Boden 1985; Miller 1986b). During SIBEX I, there was a distinct change in physical conditions at approximately 64° S, the Antarctic Divergence, which followed the 0° C sea-surface isotherm. Salinity and chlorophyll levels were greater to the south of the Divergence than to the north (Brundrit 1985; Allanson 1985). Sea-surface temperatures generally were higher during SIBEX II than during SIBEX I, when little work was conducted near the edge of the pack-ice due to the early curtailment of the cruise. The SIBEX and FIBEX surveys avoided dense pack-ice, with only the southernmost stations abutting loose pack-ice.

There was no evidence of a gyre purported to result in Antarctic krill aggregations in the Prydz Bay region (Hampton 1983; Smith et al. 1984), and krill abundance was relatively low during both SIBEX I and II (Miller 1985, 1986b). These findings suggest that krill concentrations in the Prydz Bay region are more ephemeral and localised than previously thought (Miller 1985).

Methods

Counts of birds were made both while cruising (transect counts) and while at oceanographic/trawl stations (stationary counts) during daylight hours. All counts were recorded on standard 10-min cards (BIOMASS Working Party on Bird Ecology 1984). Transect counts were made from the bridge (*SA Agulhas*) or monkey-island (*Africana*, both 17 m above sea level), scanning a 90° quadrant approximately 300 m wide between the bow and beam on the side of the ship with the best viewing conditions (BIOMASS Working Party on Bird Ecology 1984; Tasker et al. 1984). The ships travelled at between 18 and 24 $\mathrm{km\,h^{-1}}$. Transect counts ignored birds which followed the ship, and generally were made in hour-long blocks. After each hour a stern count of birds following the vessel was made. Environmental parameters recorded during transects included wind strength (knots), sea state (ranked 0–4), sea-surface temperature (° C) and the presence of sea-ice (oktas). Hydroacoustic estimates of krill abundance were made to a depth of 100 m while steaming during SIBEX II (see Miller 1986b for details).

Stationary counts of birds were made every half-hour during daylight while the ship was at oceanographic/trawl stations. Each count lasted 10 min and recorded the maximum numbers of each species seen to the horizon through an arc of at least 270° (see Cooper 1985). Up to 10 counts were made at each station. Environmental parameters recorded at stations where bird counts were made (24 stations with both stationary counts and adjacent transect counts, see below) during SIBEX I included salinity (23 stations, Brundrit 1985), primary production (22 stations, Allanson 1985), numbers of krill larvae (20 stations, Miller 1985), and estimates of the biomass of adult krill from Bongo and neuston trawls (16 and six stations respectively, see Miller 1985, 1986a for sampling and analysis procedures).

The densities of aerial seabirds (excludes penguins) were estimated from steaming observations by dividing the number of birds seen by the area surveyed (transect width X length). Birds following the ship were ignored in these calculations. Estimates of avian energy demands were used as a common currency to enable multi-species comparisons. Energy demand was calculated using an allometric equation for estimating daily energy expenditure (DEE) for free-ranging seabirds (Nagy 1987), and an assumed assimilation efficiency of 75% (Adams 1984; Jackson 1986). These consumption figures should not be interpreted as accurate estimates of actual consumption by seabirds, but rather as a more useful basis for comparing relative differences between regions than either bird numbers or biomass. Mass data for the allometric equation were derived from Cramp and Simmons (1982) and Croxall (1984). Three parameters were considered: the total (aerial) bird energy demand, the total less the contribution of sooty shearwaters (which were thought to be moving rapidly through the area and thus not closely linked to environmental conditions - see results), and the major crustacean feeders (here defined as Antarctic fulmars, Antarctic, pintado, snow and blue petrels, prions, and Wilson's storm-petrels, after Harper et al. 1985). Scientific names of all species are listed in Table 1. Less than 50 individuals of three penguin species (*Pygoscelis antarctica*, *P. adeliae* and *Aptenodytes forsteri*) were observed (see Enticott 1986), but are not considered further due to the difficulty of detecting penguins in the open sea away from pack-ice.

The distribution patterns of aerial seabird species were analysed in relation to those of other seabirds and environmental parameters. Mean flock sizes during transect counts were calculated. Spatial co-occurrence between species pairs (presence-absence) was calculated at 10-min intervals for the whole sample grid (SIBEX I and II) and for the areas north and south of the Antarctic Divergence (SIBEX I). Chi-squared tests were used to estimate the significance of spatial co-occurrence or avoidance, assuming independent (random) assortment to calculate expected co-occurrence values. For species pairs that co-occurred significantly, linear correlations between numbers of birds were calculated at both 10-min and 60-min sampling scales (ignoring zero-zero points).

Simple linear and Spearman rank correlations were used to relate bird distribution patterns to environmental parameters. During SIBEX I, estimates of Antarctic krill abundance and other biological and physical parameters were available only from fixed stations. To test the value of seabird counts made during oceanographic stations, station counts were compared with both the numbers of birds recorded during transects in the hour preceding a station, and the numbers of birds following the ship (stern counts) before the station. Transect counts gave a better estimate of natural bird distribution patterns, because bird counts made while at stations generally were better correlated with stern counts than with transect counts; six of nine species had better correlations between station and stern counts, and only one of the remaining three species, the sooty shearwater, had a significant correlation between station and transect counts. Consequently, attempts were made to explain the transect counts made in the hour preceding or following a station in terms of the environmental parameters recorded at a station. One-hour transects were preferred over shorter periods, because the sample area is larger, giving a better estimate of bird distribution patterns (Ryan and Cooper, unpublished data). Also, we believe that aerial seabirds in the Southern Ocean have effective short-term foraging ranges of at least twenty kilometers, the distance covered during a 1-h transect. Where transects were performed both before and after a station, the mean count from both hours was used.

Too few stations were completed during SIBEX II for a comparison of biological parameters and bird numbers attending oceanographic stations. Bird densities recorded during transects were related to hydroacoustic estimates of krill abundance made during certain sections of the cruise (Miller 1986b). Due to the small sample size, Miller's (1986b) four-ranked scale of krill abundance was condensed into two; krill scarce (ranks 1–2) or abundant (ranks 3–4).

Results

Totals of 58.5 and 27.5 h of transect counts were made during SIBEX I and II respectively. Counts of birds at stations were made at 26 stations during SIBEX I and 10 stations during SIBEX II. No consistent trends in bird numbers attending stations as a function of time at a station were detected.

Seabird Distribution Patterns

The species composition and abundance of seabirds was similar during SIBEX I and II, although counts generally were higher during SIBEX II (Table 1). Mean biomass of aerial birds was estimated as 9.2 and 15.3 $\mathrm{kg\,km^{-2}}$ for SIBEX I and II, respectively, accounting for daily energy demands of 13.4 and 23.1 $\mathrm{MJ\,km^{-2}\,d^{-1}}$ (Table 1). Of the abundant species, prions, white-chinned petrels, and Wilson's storm-petrels were at least twice as numerous during SIBEX II, whereas Antarctic fulmars and pintado petrels were more numerous during SIBEX I.

The seabird assemblages recorded during SIBEX I and II were similar to those recorded during the African leg of FIBEX, with average seabird densities and energy demands during FIBEX intermediate between those recorded for SIBEX I and II (Table 1). The main difference in species abundances between FIBEX and the two SIBEX surveys was the small numbers of terns (chiefly Arctic terns *Sterna paradisaea*) during SIBEX. Prions were much less abundant during SIBEX I than during either SIBEX II or FIBEX, but this trend was less marked for blue petrels (Table 1).

Sooty shearwaters were the most abundant birds, contributing 55% and 54% to the total aerial bird energy demand during SIBEX I and II, respectively. Almost all sooty shearwaters were in flocks that were not observed to feed and that moved rapidly through the study area, predominantly from west to east, suggesting that some regular movement occurs in the area in late summer (cf. Falla 1937; Naito et al. 1979). Sooty shearwaters were confined to the northern half of the SIBEX I grid (north of 64° S), but occurred slightly farther south (to 65° S) earlier in summer during SIBEX II (Fig. 2), when surface waters were warmer farther south. Excluding sooty shearwaters, mean energy demand estimates for aerial seabirds were 6.0 and 10.6 $\mathrm{MJ\,km^{-2}\,d^{-1}}$ for SIBEX I and II respectively, and the distribution of energy demand was scattered throughout the two sample grids (Fig. 3).

Mean flock size was larger for sooty shearwaters than for other species, with the exception of blue petrels during SIBEX II (Table 2). Flock size of blue petrels during SIBEX II was greatly influenced by two feeding groups of approximately 100 and 500 individuals. Excluding these groups, mean flock size was 1.64 birds (sd = 1.24, $n = 28$). All other species had mean flock sizes of less than 2.0, and there was little variation in mean flock size between SIBEX I and II (Table 2).

Two species assemblages, identified by greater than expected co-occurrence indices, were detected within the study area. Prions, blue petrels, sooty shearwaters, white-chinned petrels and Kerguelen petrels occurred together in warmer waters to the north of the study area, whereas snow petrels, Antarctic petrels, Antarctic fulmars, and, to a lesser extent, pintado petrels and Wilson's storm-petrels, occurred together in colder waters to the south (Table 3, Fig. 4). White-headed petrels and grey-headed albatrosses also were found only in warmer waters (Fig. 4). Only light-mantled sooty albatrosses and the scarce southern giant petrels were seen at uniform densities throughout the study area. These patterns of co-occurrence were detected irrespective of sample scale (10- or 60-min intervals).

To test whether the co-occurrence patterns were a function of meso-scale (100–1 000 km, Hunt and Schneider 1987) latitudinal gradients, the SIBEX I grid was divided into two regions, north and south of the Antarctic Divergence at 64° S, thus excluding gross latitudinal changes in sea-surface temperature and salinity. In the south, only Antarctic petrels-snow petrels and light-mantled sooty albatrosses-pintado petrels co-occurred significantly (Table 4), whereas in the north, sooty shearwaters no longer co-occurred with other members of the warm water assemblage (Table 5).

Table 1. The approximate densities of aerial seabirds (number. km^{-2}) during transects in the African legs of SIBEX I and II, with the values from FIBEX for comparison. Mean biomass and energy demand estimates are given. Species are listed in order of combined ranked abundances

Species (number of 10-min cards)	SIBEX I (351)		SIBEX II (165)		FIBEX (549)	
	No. km^{-2}	*n*	No. km^{-2}	*n*	No. km^{-2}	*n*
Sooty shearwater *Puffinus griseus*	6.12	2170	10.39	1829	6.46	3605
Prions *Pachytila* spp.	1.61	572	8.53	1433	9.18	5118
Blue petrel *Halobaena caerulea*	2.01	711	3.87	646	4.51	2541
Snow petrel *Pagodroma nivea*	0.39	128	0.43	69	0.36	178
Antarctic petrel *Thalassoica antarctica*	0.78	266	0.42	62	0.23	101
White-chinned petrel *Procellaria aequinoctialis*	0.30	112	1.74	314	0.22	130
Antarctic fulmar *Fulmarus glacialoides*	0.98	329	0.30	45	0.06	35
Kerguelen petrel *Pterodroma brevirostris*	0.17	64	0.24	39	0.58	327
Wilson's storm petrel *Oceanites oceanicus*	0.07	26	0.44	71	0.11	59
Light-mantled sooty albatross *Phoebetria palpebrata*	0.41	143	0.10	17	0.11	58
Terns *Sterna* spp.	0.03	10	0.10	16	1.24	663
White-headed petrel *Pterodroma lessoni*	0.04	14	0.13	23	0.06	31
Pintado petrel *Daption capense*	0.36	123	0.04	6	0.03	14
Grey-headed albatross *Diomedea chrysostoma*	0.01	5	0.13	21	<0.01	2
Southern giant petrel *Macronectes giganteus*	0.03	9	0.02	4	0.02	11
Wandering albatross *Diomedea exulans*	0.01	3	0.07	11	0.01	5
Diving petrels *Pelecanoides* spp.			0.04	7		
South polar skua *Catharacta maccormicki*	<0.01	1	0.01	2		
Total number of birds	13.32	4686	27.00	4615	23.18	12878
Total biomass (kg. km^{-2})	9.15		15.29		9.20	
Total energy demand (MJ. km^{-2}. d^{-1})	13.4		23.1		15.5	
Total less sooty shearwaters	7.20	2516	16.61	2786	16.72	9273
Biomass less soooty shearwaters	4.11		6.74		3.88	
Energy demand less sooty shearwaters	6.0		10.6		7.7	

Correlations between numbers of seabirds were significant more often when analysed at 60-min (nine species pairs: Antarctic petrel–Antarctic fulmar, $r = 0.33$, $n = 42$, Antarctic petrel–pintado petrel, $r = 0.46$, $n = 43$; Antarctic petrel–snow petrel, $r = 0.65$, $n = 38$; Antarctic fulmar–snow petrel, $r = 0.51$, $n = 42$, Antarctic fulmar–pintado petrel, $r = 0.34$, $n = 45$; pintado petrel–light-mantled sooty albatross, $r = 0.79$, $n = 43$; prion–blue petrel, $r = 0.61$, $n = 33$; prion–white-chinned petrel, $r = 0.54$, $n = 33$; blue petrel–Kerguelen petrel, $r = 0.57$, $n = 33$) than at 10-min sample intervals (five species pairs: Antarctic petrel–Antarctic fulmar, $r = 0.21$, $n = 174$; Antarctic petrel–snow petrel, $r = 0.19$, $n = 125$; pintado petrel–light-mantled sooty albatross, $r = 0.31$, $n = 116$; prion–blue petrel, $r = 0.39$, $n = 161$; blue petrel–Kerguelen petrel, $r = 0.40$, $n = 126$). This may result from species pairs tracking the same coarse-scale (1–100 km, Hunt and Schneider 1987) features, but different fine-scale (< 1 km) features. Equally, however, it may reflect the inadequacy of a 10-min interval to sample

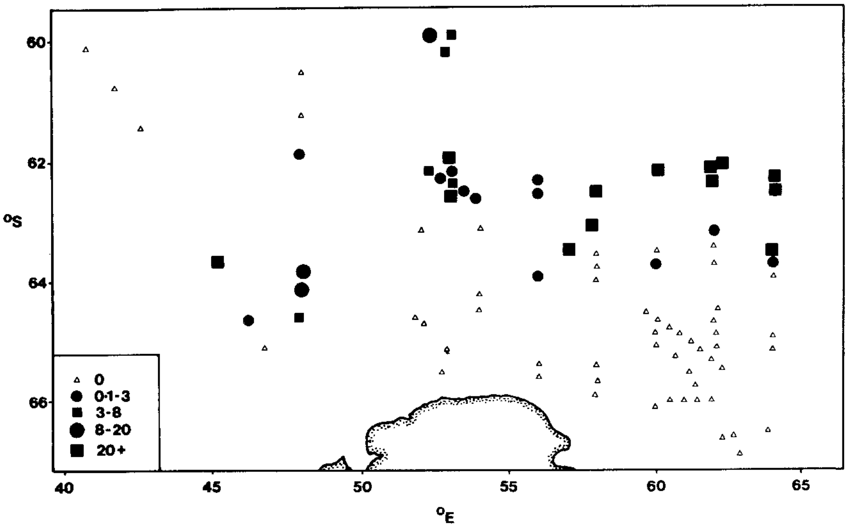

Fig. 2. The spatial distribution of energy demand of sooty shearwaters during the African legs of SIBEX I and II, estimated from transect counts (legend in MJ km^{-2}d^{-1})

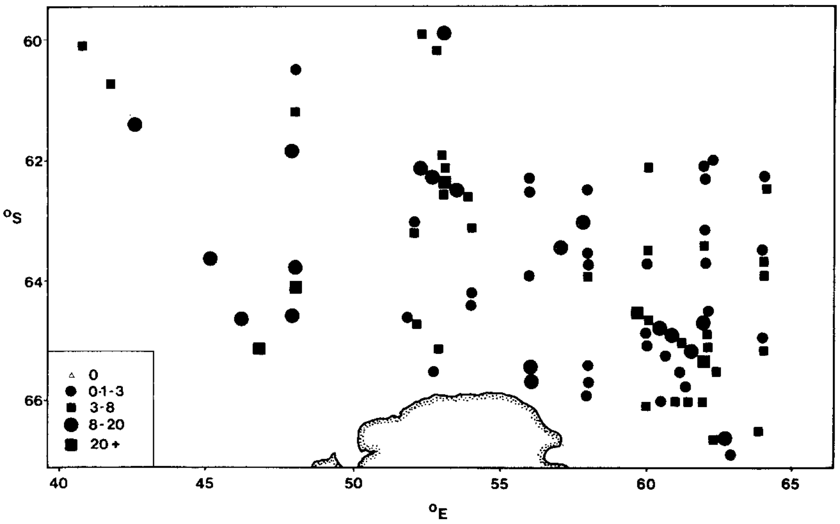

Fig. 3. The spatial distribution of energy demand of all aerial birds excluding sooty shearwaters during the African legs of SIBEX I and II, estimated from transect counts (legend in MJ km^{-2}d^{-1})

Table 2. Flock size of abundant seabird species recorded during transects in the African legs of SIBEX I and II

Species	SIBEX I				SIBEX II			
	Mean	SD	*n*	Max	Mean	SD	*n*	Max
Sooty shearwater	9.18	22.01	237	185	9.40	16.73	184	100
Blue petrel	1.38	2.07	510	40	21.53	92.14	30	500
Prions	1.41	1.12	403	11	1.35	2.50	1 084	50
Antarctic petrel	1.39	1.04	188	8	1.34	1.07	47	6
Antarctic fulmar	1.26	0.83	255	7	1.29	0.71	35	4
Snow petrel	1.30	0.95	96	8	1.01	0.12	68	2
Pintado petrel	1.42	1.05	85	7	1.00	0.00	6	1
White-chinned petrel	1.05	0.26	102	3	1.22	1.32	258	20
Light-mantled sooty albatross	1.24	0.90	116	6	1.00	0.00	17	1
Kerguelen petrel	1.17	0.87	53	3	1.00	0.00	39	1

effective distribution patterns, given the high mobility of aerial seabirds (Ryan and Cooper, unpublished data).

Factors Affecting Bird Distribution Patterns

Not all of the environmental and biological parameters used to describe seabird distribution patterns during SIBEX I varied independently (Table 6). The negative correlations between sea-surface temperature and salinity resulted from latitudinal gradients (due to different water masses north and south of the Antarctic Divergence, see Brundrit 1985). Other correlated parameters such as wind strength, sea state and the biological parameters were less influenced by latitude, although primary production and

Table 3. Chi-squared values for spatial co-occurrence (presence/absence) between seabird species in transect counts during the African legs of SIBEX I and II. Observed co-occurrence at the 10-min sampling scale was compared with expected values assuming independent assortment ($n = 464$). Superscripts show significance level: $+P < 0.05$, $++P < 0.01$, $+++ P < 0.001$. + spatial co-occurrence, − spatial avoidance

Species	Species									
	Antarctic fulmar	Pintado petrel	Snow petrel	Wilson's storm-petrel	L-m sooty albatross	Prions	Blue petrel	White-chinned petrel	Kerguelen petrel	Sooty shearwater
Antarctic petrel	43.56^{+++}	15.60^{+++}	54.87^{+++}	15.99^{+++}	0.03	29.73^{---}	14.92^{---}	20.61^{---}	8.24^{--}	23.30^{+++}
Antarctic fulmar		22.05^{+++}	31.25^{+++}	12.98^{+++}	0.80	22.49^{---}	9.63^{--}	23.84^{---}	10.32^{--}	20.64^{---}
Pintado petrel			5.02^{+}	0.16	34.00^{+++}	2.58	0.00	2.68	2.76	5.53^{-}
Snow petrel				22.41^{+++}	0.35	16.54^{---}	13.98^{---}	14.60^{---}	8.95^{--}	11.38^{---}
Wilson's storm-petrel					0.44	3.09	6.77^{--}	3.21	2.05	2.95
L-m sooty albatross						0.09	1.01	0.05	0.12	1.03
Prions							26.33^{+++}	57.91^{+++}	20.82^{+++}	27.99^{+++}
Blue petrel								5.70^{+}	12.11^{+++}	17.35^{+++}
White-chinned petrel									11.62^{+++}	20.28^{+++}
Kerguelen petrel										4.62^{+}

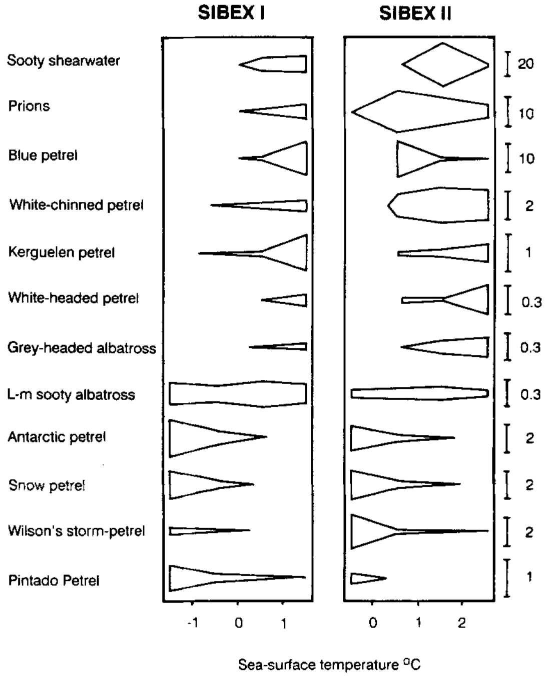

Fig. 4. The mean number of birds per 10-min observation period (transect counts) as a function of sea-surface temperature during the African legs of SIBEX I and II. Transects are lumped into categories of 1°C increments. Note that there are consistent warm- and cold-water assemblages, with only light-mantled sooty albatross occurring at equal densities throughout

the abundance of Antarctic krill tended to be greater in the south of the grid (Allanson 1985; Miller 1985, 1986a). Dividing the SIBEX I grid into the area north and south of the Antarctic Divergence left wind strength and sea state being significantly correlated (both in the southern and northern regions, $r = 0.95$, 0.79, $n = 13$, 11, respectively) and gave a positive correlation between adult krill (Bongo) and sea-surface temperature ($r = 0.86$, $n = 10$). The neuston net estimate of adult krill abundance remained correlated with both primary production and the Bongo net estimate of krill abundance because neuston trawls were made only in the southern region.

Five seabird species, all belonging to the southern, cold-water assemblage, had distributions positively correlated with the distributions of either adult or larval Antarctic krill abundance (Table 7). This result was not determined by a few outlying points, because rank correlations also were significant for all species except Antarctic petrel ($r_S = 0.50$): r_S for Antarctic fulmar = 0.62, for snow petrel = 0.54, for pintado petrel = 0.53 and for Wilson's storm-petrel = 0.49. The proportion of variation in species' distribution patterns that could be explained in terms of adult krill distribution (estimated from Bongo trawls) ranged between 0.55 and 0.86 for the four larger petrels, whereas the distribution of larval krill explained 0.34 of variation in Wilson's storm-petrel distribution. By comparison, none of the species typical of the northern, warmwater assemblage was positively correlated with a measured biological parameter. Correlations between species' distributions and sea-surface temperature and salinity presumably are related to the latitudinal gradients in these parameters, and reflect the two discrete bird assemblages described above.

Total bird energy demand was correlated only with the abundance of adult Antarctic krill estimated from neuston trawls (Table 7), based on only six trawls, all lacking sooty shearwaters. Excluding sooty shearwaters, the distribution pattern of the remaining bird energy demand was strongly correlated with the distribution of adult krill, as was the distribution of crustacean feeders (Table 7, Fig. 5). These results also held for rank correlations ($r_S = 0.66$, 0.84, respectively). The proportion of variation in bird distribution explained by adult krill distribution was greater for the subset of crustacean feeders (0.83) than for all species excluding sooty shearwaters (0.69).

To isolate the effects of latitudinal gradients, correlations between bird distributions and biological and environmental parameters were calculated separately for the areas north and south of the Antarctic Divergence (64° S).

Table 4. Chi-squared values for spatial co-occurrence (presence-absence) between seabird species in transect counts south of the Antarctic Divergence during the African leg of SIBEX I ($n = 129$). Only the distributions of the more abundant species are compared. Conventions as in Table 3

Species	Species				
	Antarctic fulmar	Pintado petrel	Snow petrel	Wilson's storm-petrel	L-m sooty albatross
Antarctic petrel	1.33	0.93	4.09^{+}	0.01	0.12
Antarctic fulmar		2.50	0.70	1.58	1.62
Pintado petrel			1.34	0.00	10.95^{+++}
Snow petrel				0.14	0.20
Wilson's storm-petrel					0.26

Table 5. Chi-squared values for spatial co-occurrence (presence-absence) between seabird species in transect counts north of the Antarctic Divergence during the African leg of SIBEX I ($n = 167$). Only the distributions of the more abundant species are compared. Conventions as in Table 3

Species	Species						
	Prions	Blue petrel	White-chinned petrel	Kerguelen petrel	L-m sooty albatross	Pintado petrel	Antarctic fulmar
Sooty shearwater	0.01	1.00	1.00	0.21	2.21	0.88	1.55
Prions		8.18^{++}	5.05^{+}	4.55^{+}	1.23	1.62	0.01
Blue petrel			4.27^{+}	5.66^{+}	0.01	0.08	0.31
White-chinned petrel				0.03	1.82	2.00	0.02
Kerguelen petrel					0.01	0.04	1.54
L-m sooty albatross						7.62^{++}	0.30
Pintado petrel							0.98

Table 6. Simple linear correlations between environmental parameters recorded at stations with adjacent transect counts of birds during the African leg of SIBEX I, Significance symbols as in Table 3

Parameter (n)	Parameter						
	Sea state (24)	Sea-surface temperature (24)	Salinity (23)	Primary production (22)	Adult krill (Bongo) (16)	Adult krill (neuston) (6)	Larval krill (20)
Wind strength (24)	0.894^{+++}	0.087	−0.157	0.004	−0.318	0.270	−0.217
Sea state (24)		0.106	−0.032	−0.003	−0.252	−0.086	−0.058
Sea-surface temperature (24)			-0.681^{---}	-0.407^{-}	−0.206	0.208	−0.291
Salinity (23)				0.605^{+++}	0.638^{+}	0.549	0.054
Primary Production (22)					0.555^{+}	0.924^{+}	0.273
Adult krill (Bongo) (16)						0.997^{++}	0.079
Adult krill (neuston) (6)							0.253

The distributions of species in the southern, cold-water assemblage were again positively correlated with the distribution of adult krill, whereas the blue petrel was the only species in the northern, warm-water assemblage whose distribution was correlated with adult krill distribution (Table 8). The estimated energy demand of all birds except sooty shearwaters and the energy demand of crustacean feeders was correlated with both adult krill abundance (Bongo) and sea-surface temperature in the northern region (Table 8). However, rank correlations were significant only between bird and krill abundances ($r_S = 0.69$, 0.82, $n = 10$ for birds and krill, compared with 0.36, 0.16, $n = 11$ for birds and sea-surface temperature).

Indications of a strong relationship between the distributions of various crustacean-feeding seabirds and that of krill also were found during SIBEX II. Overall bird densities were six times greater when krill was abundant than when krill was scarce (Table 9). Densities of Antarctic fulmars, snow and Antarctic petrels, prions and Wilson's storm-petrels were all significantly greater when krill was abundant, whereas the density of light-mantled sooty albatrosses apparently was not related to krill abundance (Table 9).

Table 7. Simple linear correlations between transect counts of birds adjacent to stations and the environmental parameters recorded at stations during the African leg of SIBEX I. Significance symbols as in Table 3

Species	Parameter							
	Wind strength (24)	Sea state (24)	Sea-surface temperature (24)	Salinity (23)	Primary production (22)	Adult krill (Bongo) (16)	Adult krill (neuston) (6)	Larval krill (20)
Antarctic petrel	−0.257	−0.173	-0.412^{-}	0.680^{+++}	0.677^{+++}	0.923^{+++}	0.954^{++}	0.308
Antarctic fulmar	−0.384	−0.323	−0.354	0.506^{+}	0.398	0.701^{+++}	0.565	0.566^{++}
Pintado petrel	−0.268	−0.186	−0.182	0.359	0.569^{+}	0.928^{+++}	0.981^{+++}	0.252
Snow petrel	−0.337	−0.248	-0.411^{-}	0.507^{+}	0.571^{++}	0.833^{+++}	0.847^{+}	0.435
Wilson's storm-petrel	−0.293	−0.249	-0.442^{-}	−0.165	0.035	−0.103	−0.273	0.585^{++}
L-m sooty albatross	−0.050	−0.127	0.225	−0.373	−0.009	−0.082	0.579	−0.163
Blue petrel	0.190	−0.067	0.567^{++}	−0.330	−0.302	0.017	−0.202	−0.139
Prions	0.067	0.033	0.655^{+++}	-0.530^{--}	−0.267	−0.253	0.000	−0.305
White-chinned petrel	0.307	0.454^{+}	0.433^{+}	−0.353	−0.174	−0.255	0.000	−0.029
Sooty Shearwater	0.377	0.341	0.291	−0.294	−0.278	−0.153	−0.202	−0.187
Total bird energy demand	0.350	0.299	0.330	−0.274	−0.224	−0.018	0.884^{+}	−0.147
Total sooty shearwaters	−0.172	−0.248	0.177	0.131	0.313	0.829^{+++}	0.881^{+}	0.231
Total crustacean feeders*	−0.270	−0.295	−0.059	0.412	0.424^{+}	0.913^{+++}	0.876^{+}	0.361

*See text for species included

Discussion

Macro- and Meso-Scale Distribution Patterns

The seabird assemblages recorded during the African legs of SIBEX and FIBEX encompass both macro-scale (longitudinally) and meso-scale (latitudinally) distribution patterns (see Hunt and Schneider 1987). The warm and cold water assemblages identified during SIBEX I and II correspond to the Intermediate Latitude Group and Southern High Latitude Group identified during FIBEX (BIOMASS Working Party on Bird Ecology 1985), and have been recognized for some time (e.g. Falla 1937). Differences between the FIBEX and SIBEX bird assemblages can be explained a posteriori in terms of the seasonal and longitudinal differences between the sampling grids. For example, the relatively low numbers of prions recorded during SIBEX I may be attributable to a later sampling period, and the greater number of terns counted during FIBEX may be related to the FIBEX area lying farther west, closer to the Atlantic migration route of Arctic terns.

Despite these specific differences between the three sample grids, the overall composition and abundance of seabird assemblages recorded during both SIBEX I and II and during FIBEX are similar. Specific flock sizes and behaviour patterns (e.g. sooty shearwater movements) also are consistent between the different sampling grids. These findings suggest that the low diversity seabird assemblages found at high latitudes in Antarctica are predictable over fairly large spatial scales, as has been suggested elsewhere (e.g. Ainley and Boekelheide 1983). The low densities of species typical of the Southern High Latitude Group, such as Antarctic and snow petrels, relative to those recorded during late summer in the Ross Sea area (Zink 1981; Ainley et al. 1984) and earlier in the summer in the Prydz Bay region (Montague 1988) may be related to the virtual absence of sea-ice during the FIBEX and SIBEX cruises.

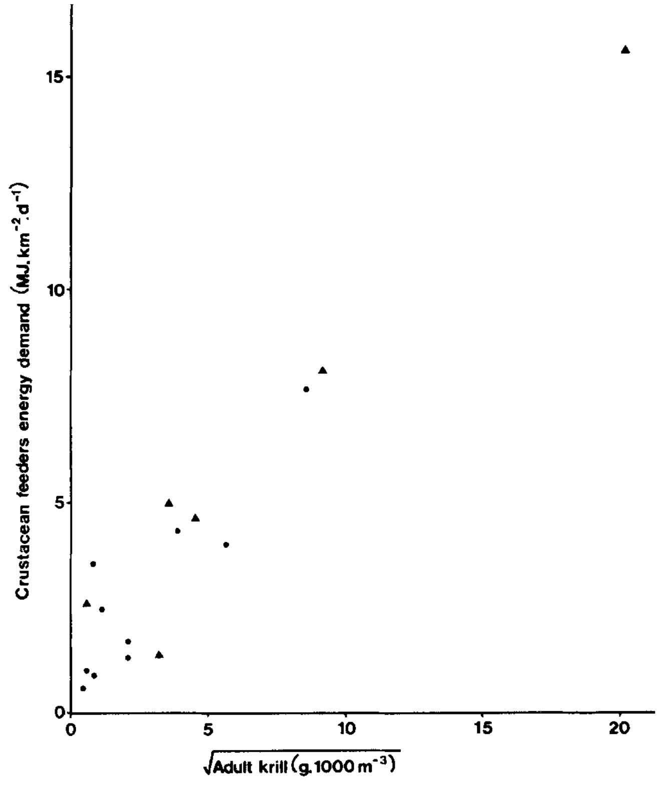

Fig. 5. The total energy demand of crustacean feeders (estimated from 1-h transects) as a function of adult Antarctic krill biomass (estimated from Bongo net-trawls). Triangles are stations south of the Antarctic Divergence, circles those to the north of it

Table 8. Simple linear correlations between transect counts of birds adjacent to stations and environmental parameters recorded at stations to the south and north of the Antarctic Divergence during the African leg of SIBEX I. Species with less than 10 individuals are omitted. Significance symbols as in Table 3

Species	Parameter							
	Wind strength	Sea state	Sea-surface temperature	Salinity	Primary production	Adult krill (Bongo)	Adult krill (neuston)	Larval krill
Southern area (*n*)	(13)	(13)	(13)	(13)	(11)	(6)	(6)	(11)
Antarctic petrel	−0.158	−0.085	−0.092^{-}	0.636^{+}	0.643^{+}	0.976^{+++}	0.954^{++}	0.186
Antarctic fulmar	−0.307	−0.305	−0.042	0.369	0.231	0.716	0.565	0.457
Pintado petrel	−0.240	−0.200	0.071	0.327	0.497	0.980^{+++}	0.981^{+++}	0.096
Snow petrel	−0.273	−0.196	−0.155	0.384	0.529	0.856^{+}	0.847^{+}	0.392
Wilson's storm-petrel	−0.249	−0.230	−0.403	−0.070	−0.117	−0.390	−0.273	0.590^{+}
L-m sooty albatross	0.005	−0.060	0.057	−0.404	−0.068	0.459	0.579	−0.159
Total bird energy demand	−0.256	−0.226	−0.046	0.392	0.481	0.951^{++}	0.884^{+}	0.274
Total crustacean feeders*	−0.266	−0.218	−0.072	0.496	0.485	0.953^{++}	0.876^{+}	0.338
Northern Area (*n*)	(11)	(11)	(10)	(11)	(11)	(10)	(0)	(9)
Antarctic fulmar	−0.207	0.075	−0.091	0.227	0.520	0.227		0.742^{+}
Pintado petrel	−0.053	0.116	−0.015	−0.018	0.707^{+}	0.119		0.744^{+}
L-m sooty albatross	−0.363	−0.381	−0.070	−0.173	0.235	−0.147		−0.008
Blue petrel	0.105	−0.303	0.758^{+}	−0.290	−0.446	0.869^{++}		−0.067
Prions	−0.549	−0.429	0.198	0.288	0.148	0.048		−0.229
White-chinned petrel	0.159	0.538	−0.473	0.553	0.370	−0.217		0.585
Sooty Shearwater	0.470	0.411	−0.039	−0.114	−0.390	−0.241		−0.159
Total bird energy demand	0.474	0.383	0.026	−0.146	−0.408	0.260		−0.146
Total-sooty shearwaters	−0.166	−0.436	0.625^{+}	−0.236	−0.005	0.741^{++}		0.185
Total crustacean feeders*	−0.124	−0.402	0.764^{++}	−0.117	−0.101	0.894^{+++}		0.222

*See text for species included

Table 9. Numbers of seabirds (mean ± SD) per 10-min observation period as a function of Antarctic krill abundance (see text for source), determined hydro-acoustically on a six-hour transect during SIBEX II ($n = 18$ for both categories)

Species	Krill abundant		Krill scarce	
	Mean	SD	Mean	SD
Wilson's storm-petrel	2.61	3.43	0.06	0.24
Snow petrel	2.22	2.34	0.89	1.08
Antarctic petrel	1.56	3.11	0.22	0.73
Antarctic fulmar	1.83	2.28	0.06	0.24
Prions	0.61	1.24	0.00	0.00
Light-mantled sooty albatross	0.11	0.32	0.22	0.73
Total numbers of birds	8.94	7.76	1.50	1.95

Coarse-Scale Distribution Patterns

It has been hypothesized that within their macro-scale ranges, the coarse-scale patchiness in specific seabird distribution patterns is related to prey distribution patterns (e.g. Hunt and Schneider 1987). In Antarctic coastal waters, various studies have searched for correlations between the distributions of seabirds and that of their principal prey, Antarctic krill (e.g. Ohyama and Naito 1982; Torres 1982; Obst 1985; Heinemann et al., in press). Obst (1985) showed that in the Antarctic Peninsula area, the densities of small and medium sized procellariiform seabirds were good predictors of the presence of krill, but found no correlations between seabird and krill abundances. Heinemann et al. (in press) found correlations between the abundances of some seabird species and that of krill, but these relationships were very weak. The results presented here are the first demonstration of strong correlations between the abundances of a suite of Antarctic seabirds and their prey.

The lack of correlations between the distribution of sooty shearwaters and environmental parameters is consistent with the hypothesis that sooty shearwaters were moving through the study area; the distribution pattern of birds involved in rapid, long-range movements is unlikely to closely parallel the distribution patterns of available prey. Sooty shearwaters may not feed in the area, or may do so at night when no observations were made. The movement of sooty shearwaters may also account for the absence of correlations between their dispersion and that of other seabird species.

The coarse-scale distribution patterns of large procellariiform species, such as light-mantled sooty albatrosses and white-chinned petrels, also could not be explained in terms of environmental parameters. This probably is related to their high mobility and consumption of larger prey items (i.e. the relationship to krill may be obscured by intermediate trophic steps). Obst (1985) found large procellariiforms to be poor predictors of the presence of krill.

With the exception of prions, the distribution patterns of all the medium and small procellariiform species were correlated to the distribution and abundance of Antarctic krill. Also, the proportions of variation in bird distributions explained by krill abundance are much greater than those typically attained for pelagic seabirds (e.g. Abrams 1985; Heinemann et al., in press). These results are somewhat surprising given the many factors which can adversely effect the relationship between the distributions of seabirds and their prey; e.g. exogenous factors (response lags, weather conditions, diel cycles in prey availability) and endogenous factors (satiation, reproduction, migration) which compromise foraging efficiency and hence prey tracking (cf. Heinemann et al., in press). Added to these problems are the differences between human and bird sampling of prey availability. Any of these factors could be responsible for the poor correlations frequently reported between bird distribution patterns and those of their prey (e.g. Woodby 1984; Obst 1985; Schneider and Piatt 1986; Heinemann et al., in press).

Several factors favoured good correlations between the distributions of seabirds and their prey in this study. Sampling for SIBEX I occurred after the breeding season of the majority of birds, thus excluding problems associated with commuting, when birds are constrained to feed in the vicinity of breeding colonies. Also, sampling occurred in a relatively homogenous environment, lacking the complex topography and oceanography of the Antarctic Peninsula region (cf. Obst 1985; Heinemann et al., in press). The absence of sea-ice from much of the study area probably removed much habitat heterogeneity (Fraser and Ainley 1986) and may account for the correlation between the distributions of Antarctic and snow petrels, which in pack-ice situations do not feed in association with each other (Ainley and Boekelheide 1983). Finally, the low krill abundances during both the SIBEX surveys may have contributed to the close tracking between birds and krill. If krill abundance in the Prydz Bay region is highly variable, with periodic superabundances (Miller 1985), it is reasonable to expect that the distributions of krill-eating birds will most closely correspond with the distribution of krill when krill is scarce.

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References

Abrams RW (1983) Distribution of seabirds in the African sector of FIBEX. S Afr J Antarct Res 13:24–28

Abrams RW (1985) Environmental determinants of pelagic seabird distribution in the African sector of the Southern Ocean. J Biogeogr 12:473–492

Adams NJ (1984) Utilization efficiency of a squid diet by adult King Penguins (*Aptenodytes patagonicus*). Auk 101:884–886

Ainley DG, Boekelheide RJ (1983) An ecological comparison of oceanic seabird communities of the South Pacific Ocean. Stud Avian Biol 8:2–23

Ainley DG, Jacobs SS (1981) Sea-bird affinities for ocean and ice boundaries in the Antarctic. Deep-Sea Res 28A:1173–1185

Ainley DG, O'Connor EF, Boekelheide RJ (1984) The marine ecology of birds in the Ross Sea, Antarctica. Orn Monogr 32, American Ornithologists' Union, Washington DC

Allanson BR (1985) The South African SIBEX I cruise to the Prydz Bay region, 1984. VII. Light, chlorophyll *a* and primary production. S Afr J Antarct Res 15:24–27

Allanson BR, Boden BP (1985) Preliminary results of the South African SIBEX I cruise to the Prydz Bay region, Antarctica, 15 March–3 May 1984: overall résumé. S Afr J Antarct Res 15:3–5

Allanson BR, Parker L (1985) The South African SIBEX I cruise to the Prydz Bay region, 1984. Introduction, track charts and cruise description. S Afr J Antarct Res 15:6–7

BIOMASS Working Party on Bird Ecology (1984) Recording observations of birds at sea (rev edn). BIOMASS Handbk 18:1–20

BIOMASS Working Party on Bird Ecology (1985) FIBEX seabird data interpretation workshop. BIOMASS Rep Ser 44:1–40

Brundrit GB (1985) The South African SIBEX I cruise to the Prydz Bay region, 1984. II. Temperature, salinity, and density overview. S Afr J Antarct Res 15:8–11

Cooper J (1985) The South African SIBEX I cruise to the Prydz Bay region, 1984. XI. Distribution and abundance of birds at sea. S Afr J Antarct Res 15:53–55

Cooper J (1986) Ornithology. In: Miller DGM (ed) SIBEX-II: Report of the South African study in the sector (48–64° E) of the Southern Ocean. S Afr Natn Sci Prog Rep 132:12–13,37

Cramp S, Simmons KEL (eds) (1982) Birds of the Western Palearctic, vol III. Oxford University Press, Oxford

Croxall JP (1984) Seabirds. In: Laws RM (ed) Antarctic ecology, vol 2. Academic Press, London, pp 533–618

Enticott JW (1986) Distribution of penguins at sea in the southeastern Atlantic and southwestern Indian Oceans. Cormorant 13:118–142

Falla RA (1937) Birds. B A N Z Antarct Res Exped 1929–1931, Rep Ser B, No 2

Fraser WR, Ainley DG (1986) Ice edges and seabird occurrence in Antarctica. BioScience 36:258–263

Griffiths AM (1983) Factors affecting the distribution of the snow petrel (*Pagodroma nivea*) and the Antarctic petrel (*Thalassoica antarctica*). Ardea 71:145–150

Hampton I (1983) Preliminary report on the FIBEX acoustic work to estimate the abundance of *Euphausia superba.* Mem Natl Inst Polar Res Spec Iss 27:165–175

Harper PC, Croxall JP, Cooper J (1985) A guide to foraging methods used by marine birds in Antarctic and Subantarctic seas. BIOMASS Handbk 24:1–22

Heinemann D, Hunt GL Jr, Everson I (in press) The distribution of marine avian predators and their prey, *Euphausia superba,* in Bransfield Strait and southern Drake Passage, Antarctica. Mar Ecol Prog Ser

Hunt GL Jr, Schneider DC (1987) Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall JP (ed) Seabird feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge, pp 7–41

Jackson S (1986) Assimilation efficiencies of Whitechinned Petrels (*Procellaria aequinoctialis*) fed different prey. Comp Biochem Physiol 35A:301–303

Miller DGM (1985) The South African SIBEX I cruise to the Prydz Bay region, 1984: IX. Krill (*Euphausia superba* Dana). S Afr J Antarct Res 15:33–41

Miller DGM (1986a) Results from biological investigations of krill (*Euphausia superba*) in the southern Indian Ocean during SIBEX I. Mem Natl Inst Polar Res Spec Iss 40:117–139

Miller DGM (ed) (1986b) SIBEX-II: Report of the South African study in the sector (48–64° E) of the Southern Ocean. S Afr Natn Sci Prog Rep 132:1–47

Montague TL (1988) Birds of Prydz Bay, Antarctica: distribution and abundance. Hydrobiologia 165:227–237

Nagy KA (1987) Field metabolic rate and food requirements scaling in mammals and birds. Ecol Monogr 57:111–128

Naito Y, Nasu K, Suzuki H (1979) Distribution of the Antarctic sea-birds in the outer margin of the summer pack ice area. Antarct Rec 66:50–63

Obst BS (1985) Densities of Antarctic seabirds at sea and the presence of the krill *Euphausia superba.* Auk 102:540–549

Ohyama Y, Naito Y (1982) Visual observations of the Antarctic sea birds during the FIBEX cruise of the Kaiyo Maru. Mem Natl Inst Polar Res Spec Iss 23:87–93

Schneider DC, Piatt JF (1986) Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Mar Ecol Prog Ser 32:237–246

Smith NR, Dong Z, Kerry KR, Wright S (1984) Water masses and circulation in the region of Prydz Bay, Antarctica. Deep-Sea Res 31:1121–1147

Starck W, Wyrzykowski R (1982) Seabird observations in the southern Drake Passage and the Bransfield Strait (BIOMASS-FIBEX programme) in February-March 1981. Pol Polar Res 3:313–332

Tasker ML, Jones PH, Dixon T, Blake BF (1984) Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. Auk 101:567–577

Torres D (1982) Antarctic birds registered during the FIBEX-Chile Expedition, February 1981. INACH Sci Ser 28:195–199

Woodby DA (1984) The April distribution of murres and prey patches in the southeastern Bering Sea. Limnol Oceanogr 29:181–188

Zink RM (1981) Observations of seabirds during a cruise from Ross Island to Anvers Island, Antarctica. Wilson Bull 93:1–20