Title

MARINE ORNITHOLOGY IN THE SOUTHERN DRAKE PASSAGE AND BRANSFIELD STRAIT DURING THE BIOMASS PROGRAM

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Introduction

ONE GOAL of the international Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) Programme was to study the pelagic distributions and abundances of marine birds to understand better their role as consumers in the Antarctic marine ecosystem (BIOMASS, 1977). Subsequently, more specific aims were defined (BIOMASS, 1985) as to:

1. obtain detailed information on the spatial and temporal distribution of avian species, their species diversity, biomass and density;
2. investigate correlations between the distribution of birds at sea and features of the physical and biological environment;
3. determine whether seabirds can be used as indicators of the distribution and abundance of selected prey stocks, especially krill and cephalopods.

Here we review the accomplishments of BIOMASS-related marine ornithological research in the Atlantic sector of the Southern Ocean. The ornithological accomplishments of the BIOMASS Programme include not only the marine bird observations taken during FIBEX (1980–1) and SIBEX (1983–4; 1984–5), but also the development of a set of methods for conducting marine bird observations (BIOMASS, 1982, 1985; BIOMASS Working Party on Bird Ecology, 1992) that facilitate comparison of results, regardless of where or by whom data were gathered. Such standardization of methodology is taken for granted in many mature fields of science; in the relatively new area of marine ornithology, this attempt at standardization meant that many cooperating nations had to change their methods of data collection. In our review of BIOMASS we discuss the ecological and management implications of ornithological observations in southern Drake Passage and Bransfield Strait. We also review what we have learned about the influence of methods on the quality and interpretation of the available data, as well as limitations in how the data may be used.

Pelagic studies of marine birds in southern Drake Passage and Bransfield Strait, Antarctica, prior to the BIOMASS Programme were few. Among the early studies were those of Tickell & Woods (1972) and Kock & Reinsch (1978) in the southern Drake Passage and Bransfield Strait, Brown *et al.* (1975) and Linkowski & Rembiszewski (1978) in the Drake Passage, and Cline *et al.* (1969) in the Weddell Sea. These studies are primarily useful as sources of information on the distributions of species, and to a lesser extent on their relative abundances. Data on the location and abundance of breeding seabirds in the area (Croxall & Kirkwood, 1979; Jablonski, 1984; Croxall *et al.*, 1984*a*; Myrcha *et al.*, 1987; Poncet & Poncet, 1987; Peter *et al.*, 1988; Shuford & Spear, 1988) provide important background

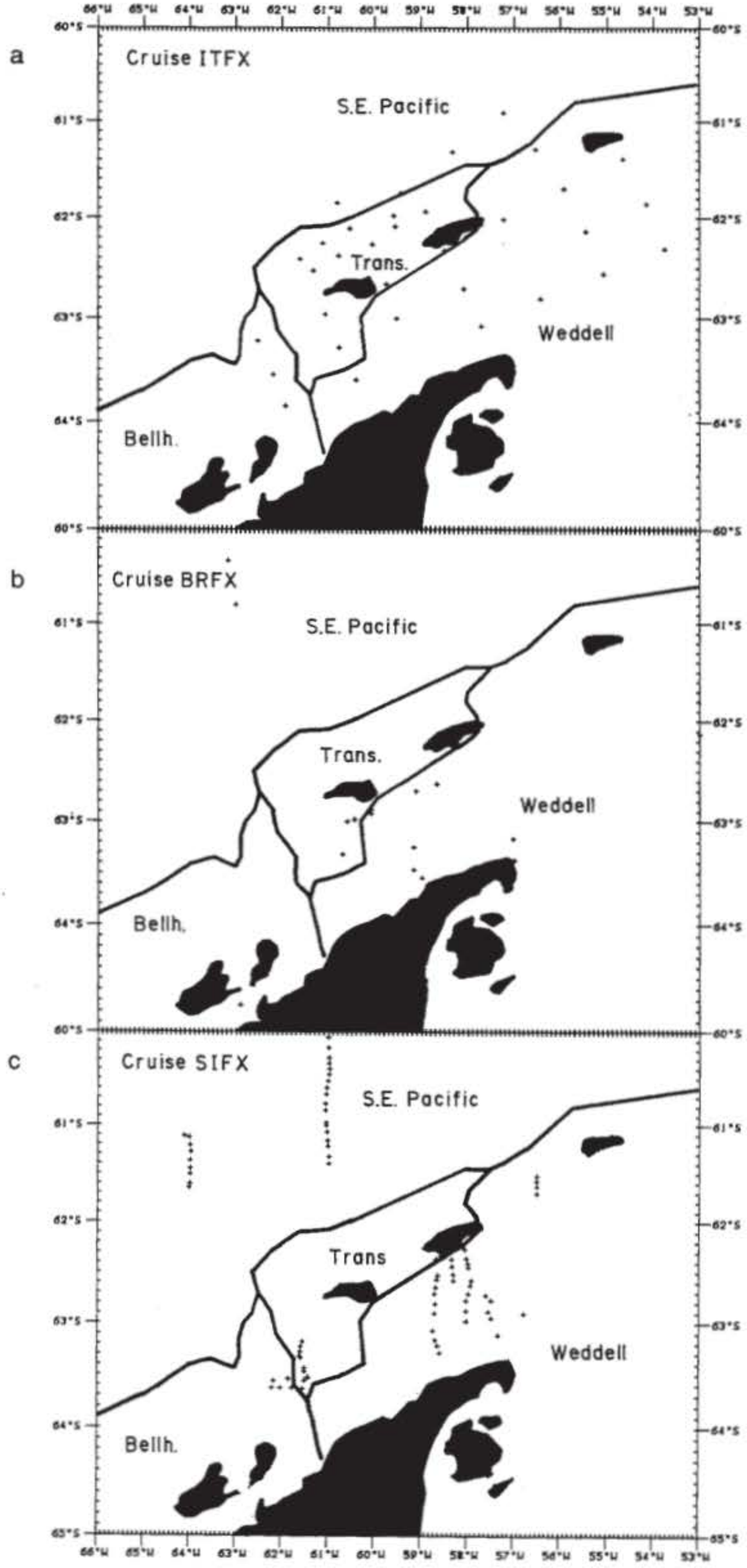
a
Cruise ITFX
S.E. Pacific
Trans.
Weddell
Bellh.
b
Cruise BRFX
S.E. Pacific
Trans.
Weddell
Bellh.
c
Cruise SIFX
S.E. Pacific
Trans
Weddell
Bellh.
66°W 65°W 64°W 63°W 62°W 61°W 60°W 59°W 58°W 57°W 56°W 55°W 54°W 53°W
60°S
61°S
62°S
63°S
64°S
65°S

Table 1. *Seabird data cards submitted to the BIOMASS Data Centre and used in our analysis.*

Cards were judged unsuitable for analysis if the vessel was not underway, if the observations were not made of birds in the foreward quarter, and if the transect was not limited to 300 m width.

Country	Cruise	Duration	Total cards	Cards suitable for analysis
FIBEX				
Chile	ITFF	3–21 Feb 1981	33	29
Poland	SIFX	19 Feb–12 Mar 1981	338	65
U.K.	BRFX	3–29 Mar 1981	296	21
Total FIBEX			667	115
SIBEX				
Poland	SIS1	21 Dec 1983–8 Jan 1984	220	220
Japan	KMS2	10–14 Dec 1984	233	20
U.K.	JBS2	16 Jan–6 Feb 1985	618	583
Total SIBEX			1071	823
Total SIBEX and FIBEX			1783	938

information for the interpretation of the pelagic records. Likewise, colony-based studies of penguin foraging ecology at Admiralty Bay (Trivelpiece *et al.*, 1987, 1990; Volkman *et al.*, 1980) are useful for assessing the impact of these birds on prey populations.

Methods and data

Standardized instructions for recording seabirds at sea were developed for FIBEX (BIOMASS, 1982). However, the participants of a workshop to analyze the FIBEX data concluded that considerably improved and more detailed instructions were needed to provide a uniform methodology for recording quantitatively data on seabirds at sea in the Antarctic (BIOMASS, 1985). These methods (BIOMASS Working Party on Bird Ecology, 1992) are based on recording birds in 10 min time periods (cards). During SIBEX, Hunt *et al.* (1990*b*) and Heinemann *et al.* (1989) recorded birds to the nearest 0.1 min by entering observations as they occurred directly into a hand-held computer. These records were subsequently partitioned into 10 min segments for analysis. Tasker *et al.* (1984) recommended a 'snapshot' technique. JA van Francker (unpublished manuscript) compared the 'snapshot' technique with the continuous count technique employed by Hunt *et al.* (1990*b*) and Heinemann *et al.* (1989) and concluded that the snapshot technique avoided the systematic over-counts of flying birds that result from the continous count technique. These overcounts are on average 1.8 times greater than counts obtained by the 'snapshot' technique. The snapshot method is thus particularly useful if the objective of the research is to obtain estimates of avian biomass which include that of flying birds.

During FIBEX and SIBEX, ornithological observations were made on seven cruises that visited the study area (60–65°S; 53–66°W) (Table 1). Ornithological effort varied considerably on these cruises (Figs 1 and 2), but overall the study area received considerable coverage (Fig. 3). During FIBEX some observers failed to record zero records or transect width, thereby preventing calculation of avian densities or biomass at sea (BIOMASS, 1985). BIOMASS (1985) also documented the substantial

Fig. 1. Location of bird sighting efforts during FIBEX by Chile (a), U.K. (b) and Poland (c), in southern Drake Passage and Bransfield Strait. Names refer to water masses: Trans, Transition Water; Bellh., Bellingshausen Water.

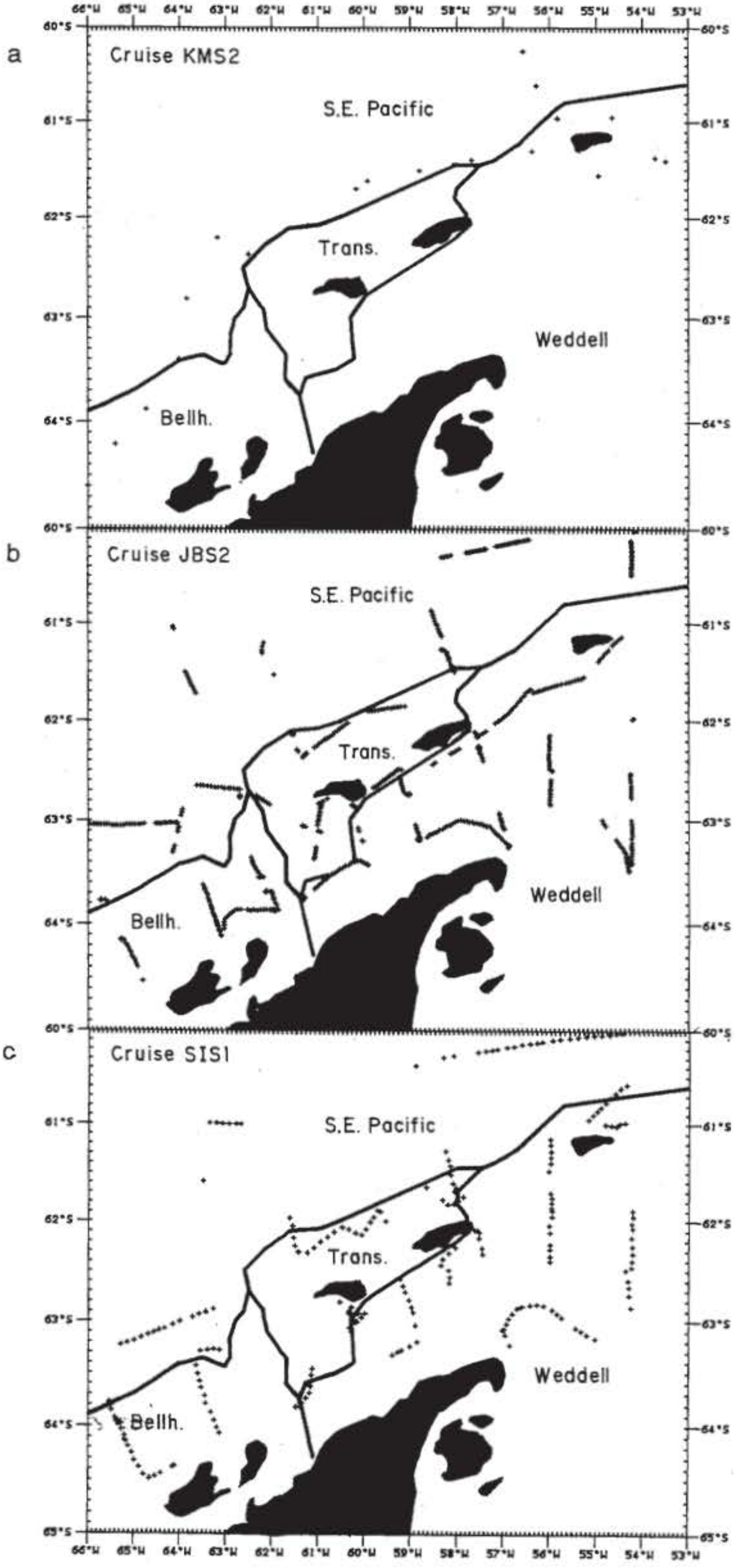
a
Cruise KMS2
S.E. Pacific
Trans.
Weddell
Bellh.
b
Cruise JBS2
S.E. Pacific
Trans.
Weddell
Bellh.
c
Cruise SIS1
S.E. Pacific
Trans.
Weddell
Bellh.
66°W 65°W 64°W 63°W 62°W 61°W 60°W 59°W 58°W 57°W 56°W 55°W 54°W 53°W
60°S
61°S
62°S
63°S
64°S
65°S

Table 2. *Geographical distribution of seabird cards selected for analysis within Bransfield Strait and southern Drake Passage*

Cruise	Total no. of cards	SE Pacific	Weddell Sea	Bellingshausen Sea	Transition Zone
SIFX	63	21	26	4	12
SIS1	220	58	98	28	36
JBS2	583	156	236	92	99
Total	866	235	360	124	147

number of birds associated with, or following, an observer's ship and indicated that, if ship-following birds were not excluded from counts, it would be impossible to provide realistic estimates of seabird density and biomass. The impact of ship-following birds on reported counts remains a difficult feature of the interpretation of multi-investigator data sets when documentation for assessing how ship-following birds were identified and recorded is not available.

In our evaluations of the multiple data sets available in the BIOMASS Data Centre, we have only used records for which observations were made within a transect width of 300 m and a viewing arc of 90° off the bow (three cruises) (Table 2). These restrictions severely limit the number of records for our analyses. Additionally, for the comparison of species abundances within water mass categories, only data from the two SIBEX cruises (SISI, JBS2) were used; data for SIFX were too sparse to permit analysis.

The extent of ornithological effort varies greatly between research cruises, and it is therefore important to understand the influence of sampling effort in obtaining observations of 'uncommon' species, which may be indicative of seasonal or water-mass changes (e.g. Hunt *et al.* 1992*b*), or of rare large flocks. We examined the effect of sample size on the likelihood of observing all bird species actually present, and of observing rare large flocks by using a Monte Carlo analysis. For estimates of species richness, each species was recorded in terms of presence or absence on each of 618 cards generated from 10 min transect segments on the JBS2 cruise. For each species, these presence–absence scores were then randomized independently and assigned back to the cards. A second level of randomization was carried out to reorder the cards. The cumulative number of species was determined by taking the cards in the new order. This process was repeated independently three times. A similar process was used to generate curves depicting the maximum 'flock' size 'seen' as a function of the number of cards. Flock size was defined as the number of birds of a given species recorded on a card. The maximum 'flock' size was determined by taking the cards in the new order and determining the largest 'flock' size, irrespective of species. The process was repeated independently ten times.

Fig. 2. Location of bird sighting efforts during SIBEX by Japan (a), U.K. (b) and Poland (c), in southern Drake Passage and Bransfield Strait. (Abbreviations: as Fig. 1.)

Results and discussion

Because the two cruises with the largest data sets occurred at different seasons and in different years, and the majority of the data came from only three cruises (SIFX, SISI and JBS2), there were insufficient data to separate the effects of year and season. Additionally, inspection of the data suggests that ship-following birds may have been treated differently on each cruise.

Large samples are required if the full suite of species or rare large flocks are to be encountered with certainty by a survey (Fig. 4). Although fewer than 100 of 618 ten-minute counts were required to record 50% of the bird species present in the survey

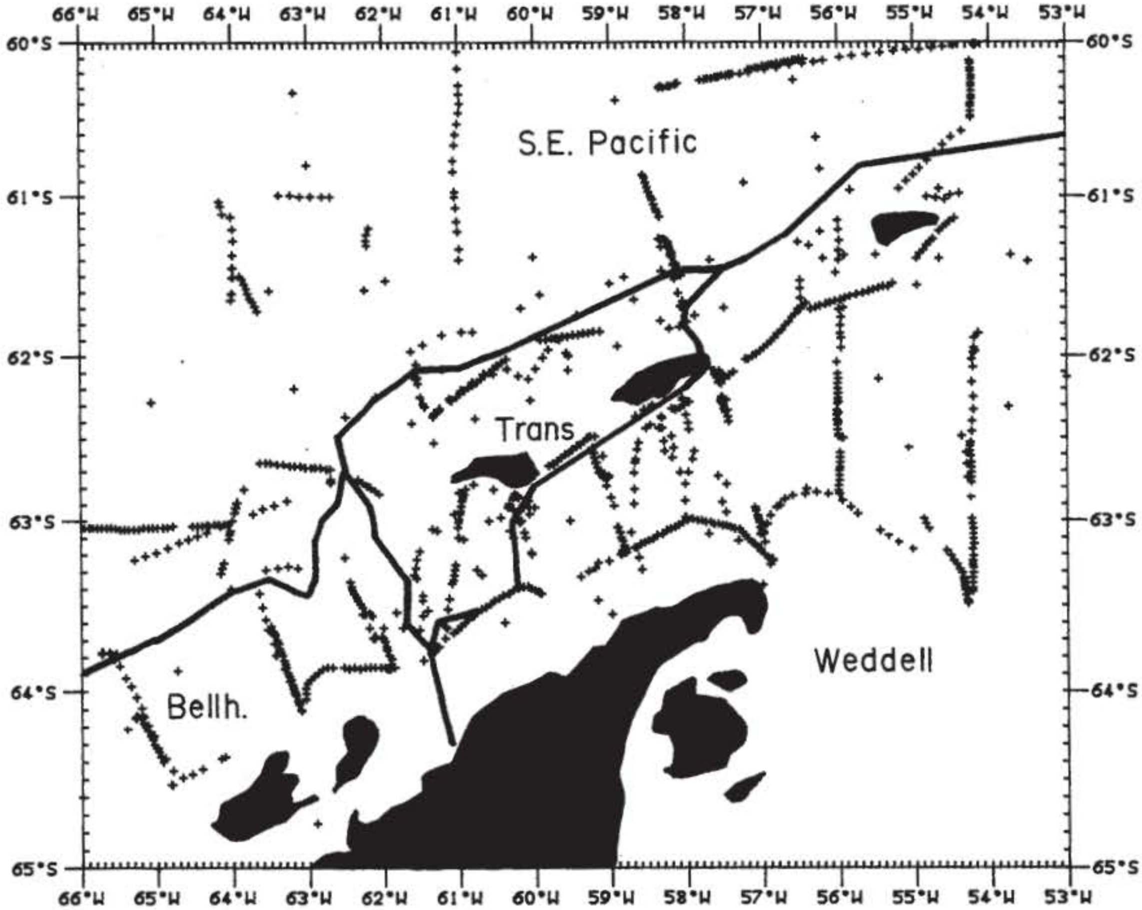

Fig. 3. Bird sighting efforts for FIBEX and SIBEX in southern Drake Passage and Bransfield Strait.

area during JBS2, between 400 and 500 counts were required to find up to 90% of the species present. Seven bird species were recorded on 100 or more cards, but another twelve were seen on five or fewer cards each. Similarly, on average, 300 ten-minute observation periods would be needed to ensure encountering all but the two largest flocks, if flocks were distributed randomly in space. In fact, the largest flock was observed after just over 100 observations. If large foraging flocks assemble owing to prey interacting with geographically fixed physical processes (see Hunt, 1991, for a review), then the inclusion of these flocks on a survey will be extremely sensitive to survey design. In regions where flocks are randomly distributed, extensive surveys are necessary if the largest flocks are to be found.

Distribution patterns

Large-scale maps of seabird distributions based on the FIBEX cruises (Starck & Wyrzykowski, 1982; BIOMASS, 1985) and more detailed mapping of distribution and relative abundance of birds in the study area during SIBEX (Hunt *et al.*, 1990*b*) provide useful descriptions of where species are likely to occur and variation in relative densities of the species present. From these maps it is evident that, even within the confines of the Bransfield Strait,

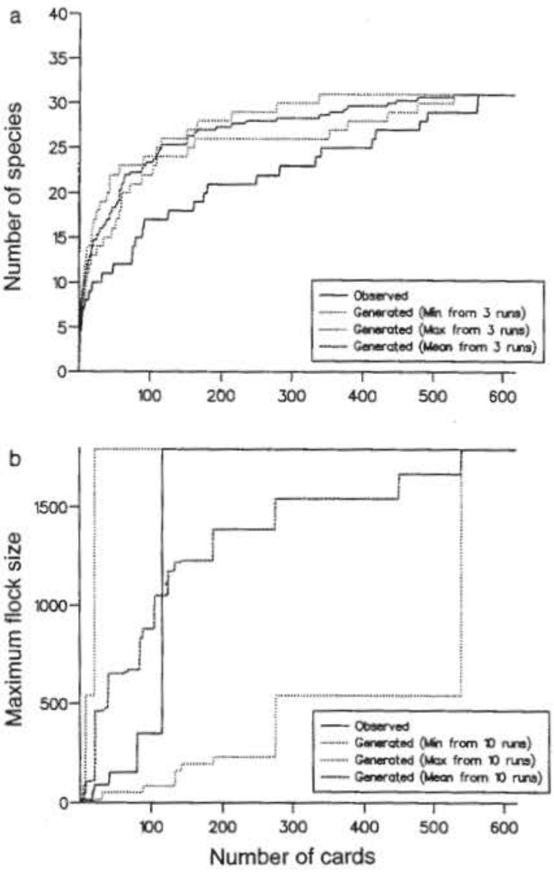

Fig. 4. (a) Number of bird species appearing on cards as a function of observation effort, which provides a comparison of observed values with those generated by randomization of cards and species (see methods). These results suggest that after the most common species are observed, sightings of additional species are roughly proportional to effort, with new species being added even after 500 ten-minute survey periods were completed. (b) Maximum flock size appearing on cards as a function of the observation effort, which provides a comparison of observed values with those generated by a randomization of cards and flock size (see methods). The great variation in the shape of these curves suggests that it will be very difficult to predict the effort needed to ensure adequate sampling of large aggregations. Since the aggregations are almost certainly not randomly distributed, the likelihood of their occurrences in a sample will also be sensitive to the design of the cruise track.

Table 3. *Frequency of occurrence (% cards on which recorded) and abundance when present (mean abundance per card on which recorded) of seabirds on cruises SIFX, SIS1 and JBS2*

The + indicates that penguins were seen in small numbers, but not identified to species.

	Frequency of occurrence			Abundance when present			Rank sum		
Species	SIFX	SIS1	JBS2	SIFX	SIS1	JBS2	SIFX	SIS1	JBS2
Pygoscelis papua	—	—	0.5	—	—	3.0	—	—	15
P. adeliae	+	7.2	6.3	+	21.8	42.9	+	4	1
P. antarctica	+	23.1	27.4	+	13.6	11.3	+	2	2
Diomedea exulans	28.5	1.3	0.3	1.9	1.0	1.0	4	19	21.5
D. melanophris	6.3	59.5	29.1	1.0	2.1	2.0	11.5	5	7
D. chrysostoma	6.3	1.8	6.8	1.0	1.0	3.6	11.5	17.5	9
Phoebetria palpebrata	—	3.1	1.3	—	1.0	1.0	—	16	16.5
Macronectes giganteus	38.0	43.6	17.6	2.0	1.5	1.2	3	7	11
M. halli	26.9	5.0	0.3	1.5	1.0	1.0	6	14	21.5
Fulmarus glacialoides	17.4	59.5	36.7	2.5	3.0	8.4	5	3	3
Thalassoica antarctica	1.5	5.0	1.0	1.0	1.3	1.0	16.5	13	18
Daption capense	65.0	89.5	40.8	9.9	13.6	7.1	1	1	4
Pagodroma nivea	4.7	0.4	0.3	1.0	1.0	1.0	13	20.5	21.5
Pachyptila spp.	4.7	19.5	16.4	1.0	1.4	2.7	14.5	9	8
Halobaena caerulea	—	—	7.0	—	—	1.2	—	—	12
Procellaria aequinoctialis	3	8.1	0.3	—	1.3	1.0	—	11	21.5
Oceanites oceanicus	66.6	53.1	66.3	7.5	1.8	2.9	2	6	5
Fregetta tropica	6.3	19.5	35.1	2.0	1.1	1.9	8	10	6
Pelecanoides spp.	—	—	1.0	—	—	1.3	—	—	16.5
Phalacrocorax atriceps	9.7	0.4	—	5.25	1.0	—	7	20.5	—
Catharacta spp.	3.1	3.1	1.8	1.0	1.1	1.0	14.5	15	14
Sterna spp.	3.1	5.4	2.5	3.0	1.3	21.9	10	12	13
Larus dominicanus	7.9	12.2	0.8	1.4	2.9	1.0	9	8	19
Chionis alba (at sea)	1.5	1.8	—	1.1	1.0	—	16.5	17.5	—

there was considerable spatial pattern both in where species occurred and in their abundances. Temporal shifts in distribution and abundance have not been analyzed statistically (see above), but some temporal shifts are evident based on the analyses of individual cruises. For instance, Hunt *et al.* (1990*b*) recorded blue petrels (*Halobaena caerulea*) on 41 of 583 cards during late January 1985, whereas Starck (1985) working in the same area recorded them on only 6 of 396 cards in late December 1983 and early January 1984. Blue petrels were recorded on 0 of 491 cards obtained from mid-February to mid-March 1981 (Starck & Wyrzykowski, 1982). Starck (1985) reported a greater than two-fold increase between abundances recorded in the autumn (February–March) 1981 cruise and in the early summer (December–January) cruise in SIBEX 1. These latter observations of differences are particularly useful in describing the magnitude of short-term changes because methodology and observers were the same on both cruises.

Bird species varied greatly in the patchiness of their distributions (Table 3). Some species (e.g. black-browed albatross (*Diomedea melanophris*), southern giant petrel (*Macronectes giganteus*), Antarctic fulmar (*Fulmarus glaciloides*), Cape petrel (*Daption capense*) and Wilson's storm-petrel (*Oceanites oceanicus*)) were relatively widespread throughout the study area, as judged by the relatively large percentage of the data cards on each cruise that contained records of their presence. However, one must be cautious in the interpretation of these records because most of these widespread species are also known to follow ships (Griffiths, 1982). In the case of penguins, which do not follow ships, Adélie penguins (*Pygoscelis adeliae*) were

Table 4. *Grouping of seabird species.*

(See Hunt *et al.* (1990*b*), Figs 9 and 10). Data from the two very large foraging flocks were excluded from the cluster analyses because they were statistical outliers.

Dominant bird species in clusters of oceanographic regions based on bird species abundance		Groups with 70% similarity based on a cluster analysis using bird species abundances at the scale of single oceanographic regions	
Water mass clusters	Dominant bird species	Bird species cluster	Dominant bird species
Bellingshausen Water	*D. melanophris* *D. chrysostoma* *F. glacialoides*	Group 1	*D. melanophris* *D. chrysostoma* *F. glacialoides*
South-east Pacific Water	*H. caerulea* *F. tropica* *Pachyptila* spp.	Group 2	*H. caerulea* *F. tropica* *Pachyptila* spp.
Transition Water (group 1)	*P. antarctica* *D. capense* *F. tropica*	Group 3	*P. antarctica* *D. capense* *F. tropica*
Transition Water (group 2)	*O. oceanicus*	Group 4	*O. oceanicus*
Weddell Water	*P. adeliae*	Group 5	*P. adeliae*

abundant, but recorded on a small number of cards compared with chinstrap penguins (*P. antarctica*) which were both abundant and widespread.

Many of the penguin records came from the inshore portions of survey lines where surveys were within the foraging ranges of nearby colonies. Had cruise tracks approached land in areas lacking penguin colonies, or passed closer to larger numbers of colonies, the number of penguins recorded would have varied significantly. Thus, when surveys are conducted near land where and when penguins are breeding, slight variations in cruise tracks can greatly affect the number of penguins seen.

Seabird distribution in relation to physical environment

For the study area, BIOMASS (1985) characterized the physical environment in which each of 24 seabird species or species groups had been recorded. Differences in preferred physical environments primarily reflected the latitudinal distribution of bird species. For instance, species commonly found at low latitudes were typically in areas where water temperature, salinity, and wind speed were relatively high, and ice cover was absent (BIOMASS 1985) (Tables 3–5, Fig. 4). Fraser & Ainley (1986) and DG Ainley *et al.* (unpublished data) working in the Weddell Sea have documented that there are strong differences between seabird species in terms of their affinity for pack ice. These different bird species assemblages shift north and south over a period of days to weeks as the ice edge moves in response to weather. Adélie penguins were usually associated with ice, chinstrap penguins preferred open water to the north of the pack-ice zone. Elsewhere, Ryan & Cooper (1989) showed that the distribution of bird species in the Prydz Bay region of Antarctica reflected the distribution of sea-surface temperatures.

Cluster analyses of bird species groupings within the Atlantic Sector of FIBEX revealed no clusters with similarities greater than 50%, but at the 30% similarity level, 11 of the 24 taxa examined fell into three groupings (BIOMASS, 1985). These three groupings were representative of the birds occupying different latitudinal ranges, with Antarctic petrel (*Thalassoica antarctica*) and snow petrel (*Pagodroma nivea*) forming a high-latitude group; soft-plumaged petrels (*Pterodroma mollis*) and grey-headed albatrosses (*D. chrysostoma*) formed the lowest-latitude (northernmost) group. A third group included species occupying intermediate latitudes.

Table 5. *Abundance ranks of the most abundant seabirds in each of four oceanographic regions*
Giant petrels (*Macronectes* spp.) are excluded because of the frequency of their attraction to ships.

Bellingshausen Water				Southern Pacific Water			
Species	Rank SIS1	Rank JBS2	Combined rank	Species	Rank SIS1	Rank JBS2	Combined rank
D. melanophris	2	2	1.5	*D. capense*	1	4	1.5
F. glacialoides	3	1	1.5	*O. oceanicus*	4	1	1.5
D. capense	1	6	3.5	*P. antarctica*	3	5	3.5
O. oceanicus	4	3	3.5	*Pachyptila* spp.	6	2	3.5
P. antarctica	5	4	5	*D. melanophris*	2	7	5
T. antarctica	6	8.5	6	*F. tropica*	7	3	6
D. chrysostoma	—	5	—	*F. glacialoides*	5	6	7
				H. caerulea	—	8	—

Transition Water				Weddell Water			
Species	Rank SIS1	Rank JBS2	Combined rank	Species	Rank SIS1	Rank JBS2	Combined rank
P. antarctica	2	1	1	*P. adeliae*	2	1	1.5
D. capense	1	3	2	*D. capense*	1	2	1.5
O. oceanicus	5	2	3	*F. glacialoides*	3	3	3
D. melanophris	3	5	4	*P. antarctica*	4	4	4
F. glacialoides	4	6	5	*O. oceanicus*	5	5	5
F. tropica	8	4	6	*D. melanophris*	6	7	6
D. chrysostoma	—	7	—	*F. tropica*	8	6	7
H. caerulea	—	8	—				

Within the southern Drake Passage and Bransfield Strait, Hunt *et al.* (1990*b*) described 11 water masses based on temperature, salinity, and silicate characteristics. They identified five clusters (regions) of these water masses, based on bird species assemblages, using the ten most abundant species. In each of these five regions, different bird species, or groups of species, predominated (Table 4). When bird species were clustered using a correlation matrix, a grouping of species similar to that based on the oceanographic regions was achieved.

Using the SIBEX data for the SISI and JBS2 cruises, we ranked the most abundant bird species recorded in each of the four major oceanographic regions (Table 5). Despite there being a difference in season and observers, the results of the two cruises were remarkably similar. Species abundance rankings between the two cruises were almost identical in Weddell Sea Water, where Adélie penguins were a predominant species. In Transition Water, prions (*Pachyptila* spp.) and storm petrels (*O. oceanicus* and *Fregetta tropica*) had higher abundances than elsewhere. Blue petrels were more abundant in the Transition Water and Southeast Pacific Water during the JBS2 cruise than in other regions. Bellingshausen Water was distinguished by the presence of Antarctic petrels and large numbers of albatrosses, particularly black-browed albatrosses.

Estimates of seabird biomass at sea

Estimates of seabird biomass at sea in southern Drake Passage and Bransfield Strait were calculated by Hunt *et al.* (1990*b*), and were averaged for the study area as a whole (Table 6). Birds present in two large aggregations (see below) made up 32% of the mean density and 44% of the total seabird biomass recorded. Penguins accounted for 84% of the total seabird biomass, and 75% of the biomass when

Table 6. *Estimated mean density and biomass for some seabirds in the southern Drake Passage and Bransfield Strait during JBS2.*

Values in parentheses are means calculated with data from two exceptionally large aggregations excluded.

Species	Mean abundance per nautical mile ± s.d.	Mean density of birds per km^2	Mean biomass (kg per km^2)
Pygoscelis adeliae	3.10±47.37	1.72	7.40
	(0.83±6.30)	(0.46)	(1.98)
P. antarctica	1.72±6.33	0.95	3.61
Diomedea melanophris	0.34±1.04	0.19	0.65
D. chrysostoma	0.16±1.70	0.09	0.33
Fulmarus glacialoides	1.55±9.37	0.86	0.67
	(1.03±4.23)	(0.57)	(0.44)
Daption capense	1.56±8.71	0.87	0.39
	(1.06±3.63)	(0.59)	(0.27)
Pachyptila spp.	0.30±0.94	0.17	0.03
Halobaena caerulea	0.07±0.37	0.04	0.01
Oceanites oceanicus	1.00±1.71	0.55	0.02
Fregetta tropica	0.41±0.84	0.23	0.01
Total	10.21±50.60	5.67	13.21
	(6.95±11.42)	(3.86)	(7.36)

Source: From Hunt *et al.* (1990*b*); values of seabird mass taken from Jouventin & Mougin (1981).

birds in the two large aggregations were excluded. Because penguins are much heavier than flying seabirds, they have a disproportionately large impact on the estimation of avian biomass at sea. Other species such as Antarctic fulmars, Cape petrels and Wilson's storm-petrels together accounted for 40% of the numbers of birds seen, but only 8.2% of the total seabird biomass observed in the study area.

Biomass estimates from at-sea observations have sometimes been used to assess energy or carbon fluxes to seabirds (e.g. Schneider *et al.*, 1986; van Franeker, 1993). In the present case, the spatial heterogeneity in bird distributions caused by water-mass differences and proximity to colonies, and the lack of stratified surveys that would have adequately sampled the study area, precluded a similar analysis. Assessments of prey consumption by Antarctic seabirds have also been derived from estimates of breeding populations (e.g. Croxall *et al.*, 1984*b*, 1985; Croxall & Prince, 1987). However, at the small spatial scale being considered here, knowledge of breeding populations of seabirds other than penguins is grossly inadequate to do this. Critical comparisons of colony- and ship-based estimates of seabird abundance and the resulting estimates of prey consumption are badly needed, but must be based on appropriately designed studies.

Seabird distribution in relation to prey distribution

Heinemann *et al.* (1989) used the results of simultaneous surveys of marine birds and hydroacoustic estimates of krill during SIBEX to examine two statistically independent components of correlation: spatial concordance or association; and numerical concordance, the rank correlation of seabird and krill numbers when both were present. They found a positive spatial association between each of two species of birds (Antarctic fulmar and Cape petrel) and krill. Only two bird species, Adélie penguin ($r=0.60$) and Cape petrel ($r=22$), had statistically significant ($p \leqslant 0.05$) positive numerical correlations with prey abundance, in nautical miles where both predator and prey were present. At spatial scales larger than a nautical mile, positive correlations between predators and their prey appeared stronger for some species, but for others, correlations became negative, possibly because of the inclusion of oceanographic regions with high krill densities in which the birds were not abundant.

Other studies of the spatial and numerical concordance of seabirds and planktonic prey have also had mixed success in demonstrating strong positive correlations, particularly at small spatial scales, when scale dependence has been investigated (e.g. Woodby, 1984; Obst, 1985; Ryan & Cooper, 1989; Hunt *et al.*, 1990*a*; Hunt *et al.*, 1992*a*). There are methodological reasons why the explained variance at small spatial scales is often weak (0.21 to 0.59%) (Hunt *et al.*, 1990*a*), such as the lack of night-time sampling and a lack of acoustical data for the top 10 m of the water column. Additionally, it may be that background levels of prey are sufficiently high that it is not of advantage for birds to seek the densest concentrations of plankton (Woodby, 1984; Hunt *et al.*, 1990*a*). Birds may have considerable difficulty in locating the areas of highest prey abundance, but are able to locate areas where prey is generally at sufficient densities to meet energetic needs. Within these larger areas, the choice of a foraging locale may be a chance event or may be directed by social attraction to previously and/or currently feeding individuals.

The importance of the presence of other species of birds (and marine mammals) is illustrated by the work of Harrison *et al.* (1991) who found black-browed and grey-headed albatrosses foraging on krill in small mixed-species flocks in the daytime near South Georgia. Nineteen species of birds were recorded associated with these flocks; the flocks were usually accompanied by penguins, or Antarctic fur seals (*Arctocephalus gazella*), or both. The pursuit-diving species apparently drove krill to the surface where the non-pursuit-diving species were able to surface seize them or plunge-dive for them. When birds were actively feeding at the surface, other birds quickly joined the flock. Similar observations have been recorded in the Gulf of Alaska (Hoffman *et al.*, 1981) and the northern Bering Sea (Obst & Hunt, 1990).

During the cruises discussed here, a significant proportion of seabird feeding activity involved large aggregations of birds associated with the large patches of krill, which may have important implications for management of krill resources. Hunt *et al.* (1985) described two foraging flocks encountered in the Bransfield Strait during SIBEX. One flock contained 73% of all Adélie penguins recorded during the survey; the other flock contained 32% (not 62% as reported by Hunt *et al.*, 1990*b*) of all Cape petrels and Antarctic fulmars recorded. These flocks were associated, respectively, with the largest and third largest concentrations of krill encountered during the survey (Heinemann *et al.*, 1989). Similarly, on a circumnavigation of Antarctica in 1983, Veit & Hunt (1991) found nearly 45% of all birds recorded during their cruise in two foraging flocks. One flock off Enderby Land (65°41′S, 25°51′E) was estimated to contain as many as one million Antarctic petrels and the second, off Wilkes Land (66°6′S, 110°50′E), was dominated by 100 000 short-tailed shearwaters (*Puffinus tenuirostris*). Although no samples of the prey taken were obtained, there was evidence that one and possibly both flocks were associated with very large aggregations of krill. Others have also commented that the largest aggregations of birds encountered were flocks associated with unusually large aggregations of krill. Thus, Starck (1985) reported that flocks of Cape petrels and Antarctic fulmars were associated with the only large, dense krill aggregations found in the region. Similarly, Starck & Wyrzykowski (1982) reported flocks of Cape petrels and Antarctic fulmars associated with large, dense aggregations of krill. In the Bering Sea, short-tailed shearwaters show similar behaviours in that they form flocks of the tens of thousands of birds when foraging on aggregations of the euphausiid *Thysanoessa raschii* (Guzman & Myers, 1986; G L Hunt *et al.*, unpublished data).

The finescale spatial and temporal distributions of krill aggregations are probably unpredictable because there are so many potential influences operating at a wide variety of temporal and spatial scales. If very large aggregations of krill persist for several days or longer, they may serve as a predictable resource over a short period of time. These large aggregations therefore may be disproportionately important for the foraging success of birds because the aggregation, once located, can be followed and foraged upon repeatedly. These very large aggregations are likely to be the focus for commercial harvesting for the same reason. Thus, the potential for harm to seabird populations would exist if the required large krill aggregations were not available within foraging range of seabird colonies. In penguins, this range is quite restricted. In future studies, it would be profitable to learn more about the importance of these large krill aggregations to foraging birds. In addition, virtually all of our observations of foraging seabirds have occurred in daytime (but see Fraser *et al.*, 1989). Thus, there is also a need to develop means of comparing daytime foraging activities of birds with those that occur at night when krill distributions near the surface are likely to differ greatly from those found during the day (Kalinowski & Witek, 1980; Everson, 1982; Miller & Hampton, 1989).

Regardless of the reasons for the weak correlations between avian predators and planktonic prey, the available data suggest that the pelagic surveys of birds in these BIOMASS studies did not provide a consistent, accurate index of the relative, let alone the absolute, size of krill populations. More generally, although the presence of large flocks of foraging birds is likely to indicate the presence of krill, not all krill swarms are so accompanied, and the number of birds does not correlate well with the amount of krill present (Woodby, 1984; Obst, 1985; Heinemann *et al.*, 1989; but see Ryan & Cooper (1989) for a positive result). For these reasons, even the large flocks are unlikely to be useful indicators of the status of krill stocks, although they are obviously good indicators of the presence of local concentrations of krill. An alternative approach, monitoring of marine birds on colonies, provides data which may more directly reflect variations in their ability to locate prey near the colony (Croxall *et al.*, 1988). However, to interpret these results we need to learn more about the areas over which birds from monitored colonies forage, and how changes in parameters measured at colonies relate to changes in local and regional krill stocks (Hunt *et al.*, 1991).

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