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Journal

Continental Shelf Research, 10(3)

ISSN

0278-4343

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Publication Date

1990-03-01

DOI

10.1016/0278-4343(90)90021-d

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The distribution, abundance and community structure of marine birds in southern Drake Passage and Bransfield Strait, Antarctica

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(Received 9 February 1989; accepted 25 May 1989)

Abstract—We studied the distribution and abundance of marine birds in Bransfield Strait and southern Drake Passage during January and February 1985. We identified clusters of bird species, “communities” with similar distributions, and examined the extent to which the distributions of these seabird communities reflected the underlying physical oceanography of the region. Based on temperature, salinity and silicon data, we identified 11 water masses which resulted from varying degrees of mixing of water from the Pacific Basin, the Bellingshausen Sea, the Weddell Sea and terrestrial runoff. Seabird species assemblages were associated with contiguous clusters of water masses, suggesting a response by the birds to apparently subtle differences in their marine habitat.

INTRODUCTION

THE distribution of marine birds in relation to physical features of the ocean's surface has received considerable attention in the past (BROWN, 1980; HUNT and SCHNEIDER, 1987). Although most of the early work focused on one or a few species, recently there has been increased interest in the composition of marine bird communities and their relation to physically characterized marine habitats (ABRAMS, 1983, 1985; AINLEY and BOEKELHEIDE, 1983; POCKLINGTON, 1979; SCAR, 1985). Many of these studies have dealt with large areas of open ocean and hence bird community distribution on broad oceanic scales. A visit to the Bransfield Strait from 17 January to 5 February 1985, provided the opportunity to examine the concordance of pelagic bird communities with physically defined ocean regions over much smaller scales. Our effort was integrated with the British Antarctic Survey's participation in the Second International BIOMASS Experiment (SIBEX).

Drake Passage and Bransfield Strait are frequently traversed by research ships, and there is considerable information on the distribution of seabirds in the region. CROXALL and KIRKWOOD (1979) provide a detailed atlas of penguin colonies, and CROXALL *et al.* (1984) give an overview of the breeding sites and colony size for all marine birds. Reports of the pelagic distribution or abundance of birds in the area include surveys by CLINE *et al.*

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(1969) in the Weddell Sea, BROWN *et al.* (1975) in Drake Passage, and TICKELL and WOODS (1972) in the South Atlantic. Two studies, those of KOCK and REINSCH (1978) and STARCK and WYRZYKOWSKI (1982) provide data for the southern Drake Passage and Bransfield Strait.

In this paper, we focus on the patterns of bird distribution, their community organization and the relationship of the communities to different water masses. Elsewhere (HEINEMANN *et al.*, 1989), we examine the relationship between the abundance of birds and that of their principal prey species, Antarctic krill (*Euphausia superba*).

STUDY AREA

The Bransfield Strait, between the Antarctic Peninsula and the South Shetland Islands, is an area of complex bottom topography (Fig. 1) and hydrography, receiving surface waters from the Weddell Sea, the Bellingshausen Sea and the southeast Pacific Basin. The general pattern of water mass distribution and circulation within the Bransfield Strait is well documented (CLOWES, 1934; GORDON and NOWLIN, 1978; HEYWOOD, 1985). Weddell Sea surface water enters the Strait from the east, through the Antarctic Sound and round Joinville and d'Urville Islands, and flows along the northern shelf of the Antarctic Peninsula. In the vicinity of Deception and Trinity Islands, it meets warmer and less saline

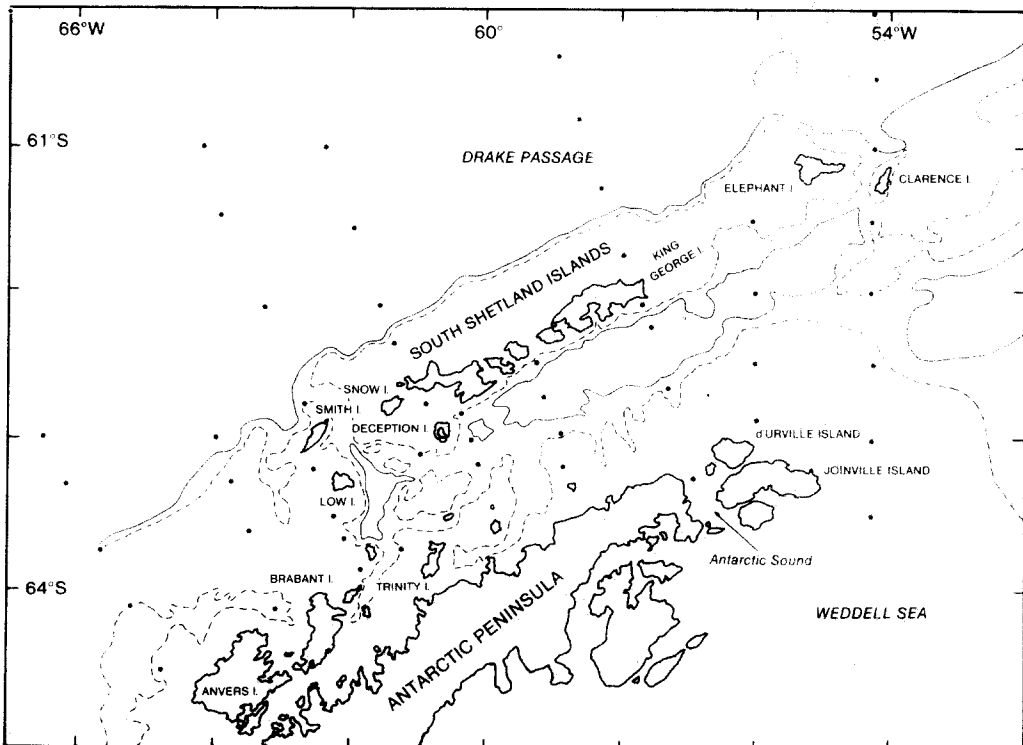


Fig. 1. Bathymetry of the southern Drake Passage and the Bransfield Strait, as depicted by the 500 m (dashed) and 1000 m (solid) depth contours. The positions of the SIBEX oceanographic stations are also shown (dots).

surface water of southeast Pacific Basin origin, flowing in the Antarctic Circumpolar Current, which enters the Strait from the southern Drake Passage. The Weddell Sea surface water sinks below this lighter water, and is forced by the bottom topography to turn north, and then northeast to flow back up the center of the Strait. The Drake Passage water also flows northeastward up the Strait, and is largely confined to the southern shelf of the South Shetland Islands by the Weddell Sea surface water. Water of Bellingshausen Sea origin, flowing northwards along the Antarctic Peninsula as a coastal current, also enters from the west, in the vicinity of Trinity and Low Islands, to flow in the northeast current through the Strait.

METHODS

All data were collected from the British Antarctic Survey's R. R. S. *John Biscoe*. During our studies, physical oceanographic observations were made to near-bottom with a Neil Brown conductivity-temperature-depth profiler (CTD) at 53 stations set along 13 transects within the research area, between 60 and 69°S. CTD temperature values were checked against reversing thermometer readings. Calibration data for the conductivity cell were obtained with each CTD profile by analysing water samples on a Guildline high-precision laboratory induction salinometer. Data from all 53 profiles were combined in the calculation of calibration constants to minimize possible operator and contamination-of-sample errors. The accuracy and precision of both CTD temperature and calculated salinity data used in this paper are $\pm 0.005\%$. Expendable bathythermograph (XBT) profiles between CTD stations increased the resolution of the thermal field (to a depth of 750 m), and surface (3 m depth) samples taken at the launch of each XBT were analysed to increase the resolution of the surface salinity distribution. Filtered water samples were analysed for dissolved molybdate-reactive silicon using an autoanalyser, with an accuracy of $\pm 0.14\%$ (TECHNICON, 1976).

Waters from different areas of the world ocean can be distinguished by characteristic potential temperature-salinity relationships, and these relationships provide a means of studying water-mass interactions and transformations (NAMAYER, 1975). HEYWOOD (1985) used this form of analysis to describe in detail how the three original water bodies gradually changed in character as they mixed on passage through Bransfield Strait during the late summer of 1982, and again in the present study.

We counted birds during daylight hours from the bridge wing of the ship (10 m above sea level). Counts were made in an arc of radius 300 m from directly ahead to 90° off the side of the ship with the best visibility when traveling at 8–11 kn. Ship-following birds were noted when they joined the ship, but were not recorded again. Observations were recorded to the nearest tenth of a minute on a hand-held microcomputer. Data files were subsequently added to the British Antarctic Survey Offshore Biological Program database. All bird counts were standardized to a survey distance interval of 1 nmi. Estimates of density were calculated by dividing the number of birds counted by the area of transect surveyed. Biomass estimates were calculated by multiplying bird density by the mass of the species.

We obtained bird data in 16 blocks, separated by at least one night period and usually by more than 10 nmi (Fig. 2). These temporally and, on all but one, spatially segregated areas provided statistically independent samples of bird distribution. Blocks frequently crossed the boundaries of physically defined ocean regions (see below) and were distributed independently of these regions.

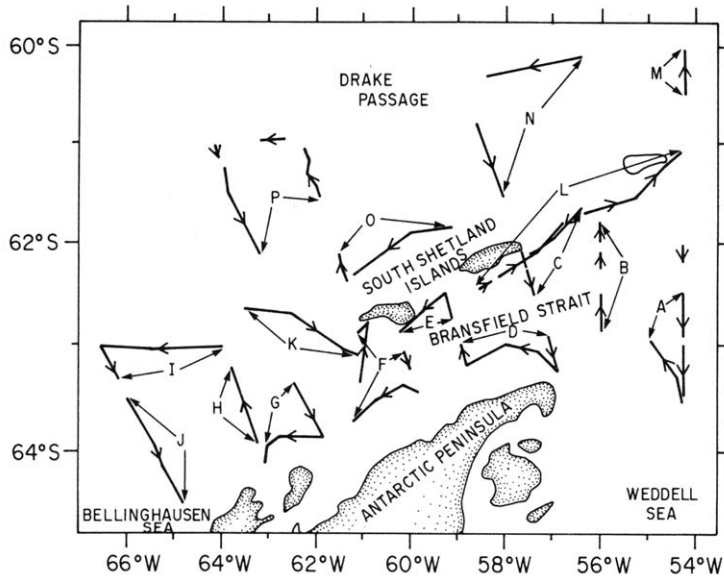


Fig. 2. Locations of SIBEX transect lines and sampling blocks.

We also grouped our bird data by observations occurring in 11 oceanographic regions determined on the basis of temperature, salinity and silicon characteristics over the entire water column (Fig. 3). Data in a region frequently included data from more than one block. We chose 10 species of birds for which we had observations in at least 50 nmi. Two species, the giant petrels (*Macronectes giganteus* and *M. halli*), for which we had adequate sample sizes, were excluded from the analysis. These species followed the ship, frequently departing and subsequently returning. It was thus particularly difficult to assess whether individuals were newly joining the ship or were long-distance ship followers that had been temporarily out of sight.

To examine the extent to which bird communities reflected the underlying oceanic habitats, we performed cluster analyses using the SYSTAT statistical package (WILKINSON, 1986). Clusters of regions and species were obtained from a matrix of log-transformed mean densities of the 10 species in the 11 regions using the Pearson correlation metric, a measure of similarity, and the average linkage method (ALDENDERFER and BLASHFIELD, 1984). We chose the Pearson correlation metric over the Euclidian distance metric because the latter simply gave clusters of species with similar abundances. The average linkage method was chosen because it gave the most interpretable clusters. Differences between these analyses and those using region means were interpreted as due to the influence of oceanographic features associated with different water masses on seabird distributions.

RESULTS

We identified 11 distinctive water masses within the research area (Fig. 3). Weddell Sea surface water was clearly the dominating influence within the Bransfield Strait. The analysis of water-mass origins required data from throughout the whole water column. In contrast, the bird species studied are confined to either the top few meters (volant species)

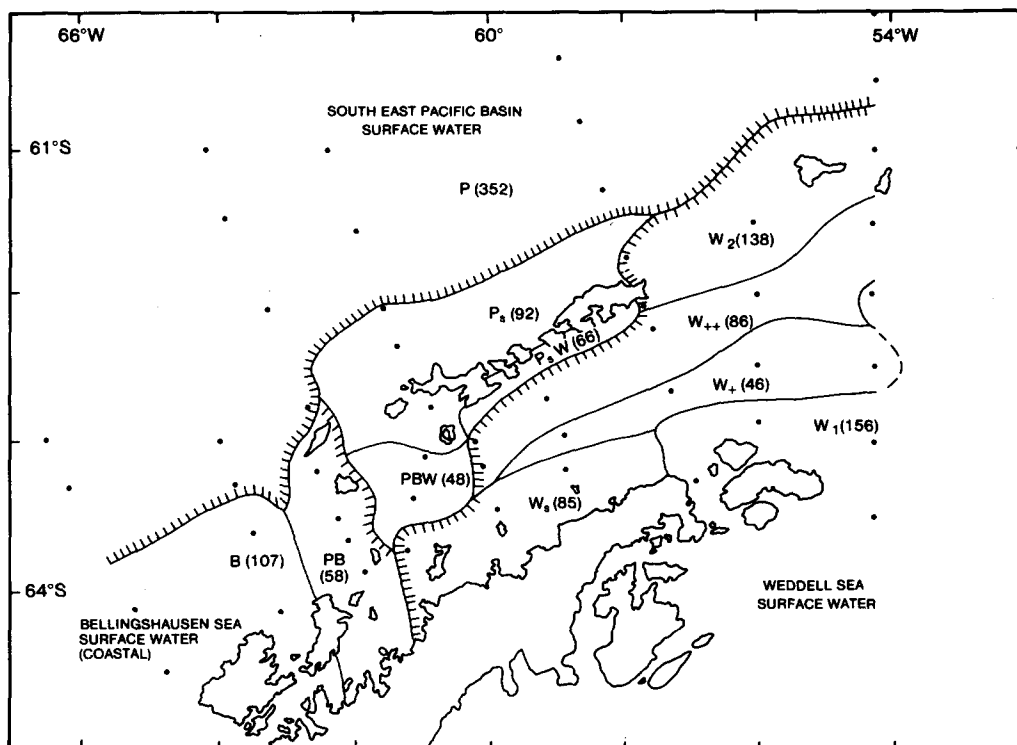


Fig. 3. Location of various water masses which can be identified from the potential temperature–salinity relationships. The boundaries within which the original water masses are thought to be dominant are indicated by the hatched lines. Numbers in parentheses indicate the number of nautical miles surveyed for bird distribution in each water mass.

or 100 m (penguins), and their prey mainly live within the upper 250 m. The surface waters of the Weddell Sea have characteristically high salinity and silicon levels, and we used the horizontal distribution of these variables to determine the extent of Weddell Sea influence within the depth strata of importance to the predators (Fig. 4). There is a strong congruence between the boundary positions obtained from the two sets of analyses (Figs 3 and 4), and therefore, we assumed that the 11 water masses identified from whole water column potential temperature–salinity relationships represent a degree of water-mass mixing which could reasonably be expected to be reflected in prey community structure.

There was considerable variation within the study area between bird species in density and contribution to avian biomass (Table 1). Adelie (*Pygoscelis adeliae*) and chinstrap (*P. antarctica*) penguins were by far the largest contributors to avian biomass, with the albatrosses (black-browed *Diomedea melanophris*, and grey-headed *D. chrysostoma*) and the fulmarine petrels (Antarctic fulmar *Fulmarus glacialisoides*, and Cape petrel *Daption capensis*) the most important contributors among flying species. The two penguins and the fulmarine petrels were numerically dominant.

During the study, 12 species in addition to those listed in Table 1 were seen. These included: northern and southern giant petrels (seen in 118 nmi intervals); Antarctic tern (*Sterna vittata*; seen in 24 miles, mostly in Bransfield Strait close to the South Shetland

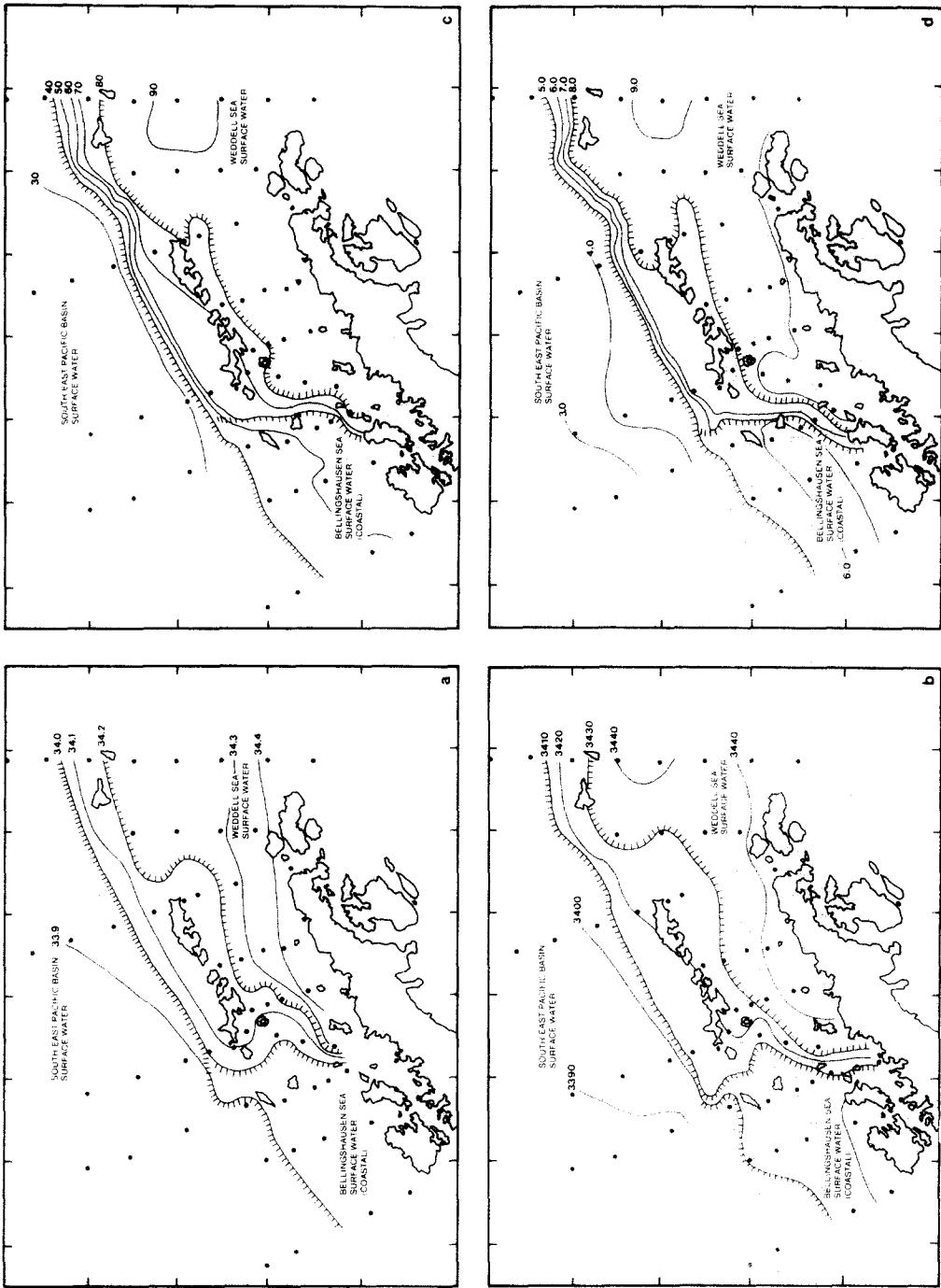


Fig. 4. The boundaries (hatched line) within which the original water masses are thought to be dominant, as indicated by: (a) salinity at 10 m depth; (b) salinity integrated for the surface 100 m layer; (c) silicon (mmol m^{-3}) at 10 m depth; and (d) silicon (mmol m^{-3}) integrated for the surface 100 m layer.

Table 1. Abundance, density, individual body mass and biomass of the seabirds counted during our survey of the southern Drake Passage and Bransfield Strait. Values in parentheses are means calculated with the data from the two very large aggregations excluded

Species	Mean abundance of birds per nautical mile \pm S.D.	Mean density of Birds per km ²	Mean biomass (kg km ⁻²)	Body* mass (kg)
Adelie penguin	3.10 \pm 47.37 (0.83 \pm 6.30)	1.72 (0.46)	7.40 (1.98)	4.3
Chinstrap penguin	1.72 \pm 6.33	0.95	3.61	3.8
Black-browed albatross	0.34 \pm 1.04	0.19	0.65	3.4
Grey-headed albatross	0.16 \pm 1.70	0.09	0.33	3.6
Antarctic fulmar	1.55 \pm 9.37 (1.03 \pm 4.23)	0.86 (0.57)	0.67 (0.44)	0.78
Cape petrel	1.56 \pm 8.71 (1.06 \pm 3.63)	0.87 (0.59)	0.39 (0.27)	0.45
Unidentified prions	0.30 \pm 0.94	0.17	0.03	0.18
Blue petrel	0.07 \pm 0.37	0.04	0.01	0.19
Wilson's storm-petrel	1.00 \pm 1.71	0.55	0.02	0.034
Black-bellied storm-petrel	0.41 \pm 0.84	0.23	0.01	0.57
Total	10.21 \pm 50.60 (6.95 \pm 11.42)	5.67 (3.86)	13.12 (7.36)	

* Body masses from JOUVENTIN and MOUGIN (1981).

Table 2. Mean abundances (number/nautical mile) of the principal bird species by oceanographic regions. Data listed opposite region headings are means for the regions under that heading

Region*	Species									
	Adelie penguin	Chinstrap penguin	Black-browed albatross	Grey-headed albatross	Antarctic fulmar	Cape petrel	Blue petrel	Uniden-tified prion	Wilson's storm-petrel	Black-bellied storm-petrel
Weddell	7.5	2.6	0.08	0.00	2.5	2.8	0.01	0.03	1.3	0.33
W ₁	24.1	0.02	0.01	0.00	0.26	0.76	0.00	0.00	1.2	0.03
W ₂	0.00	8.5	0.20	0.00	7.6	7.8	0.02	0.12	0.93	0.83
W _s	0.25	0.29	0.00	0.00	0.24	0.72	0.00	0.00	2.3	0.09
W ₊	0.67	0.13	0.09	0.00	0.83	1.6	0.00	0.02	1.6	0.13
W ₊₊	0.09	1.6	0.08	0.00	1.9	1.2	0.00	0.00	0.87	0.40
Pacific	0.01	0.55	0.32	0.07	0.60	0.74	0.18	0.97	0.86	0.61
Transition	0.00	2.1	0.24	0.05	0.11	0.76	0.11	0.08	0.68	0.47
P _s	0.00	2.3	0.37	0.09	0.15	0.89	0.10	0.15	0.93	0.68
P _s W	0.00	2.9	0.02	0.00	0.00	0.47	0.00	0.00	0.18	0.02
PBW	0.00	0.77	0.29	0.06	0.19	0.90	0.27	0.04	0.90	0.69
Bellingshausen	0.00	0.81	1.3	1.0	2.3	0.49	0.02	0.00	0.75	0.13
B	0.00	0.58	1.6	1.5	3.2	0.42	0.03	0.00	0.54	0.12
PB	0.00	1.2	0.71	0.02	0.48	0.60	0.00	0.00	1.1	0.14

* Regions displayed in Fig. 3.

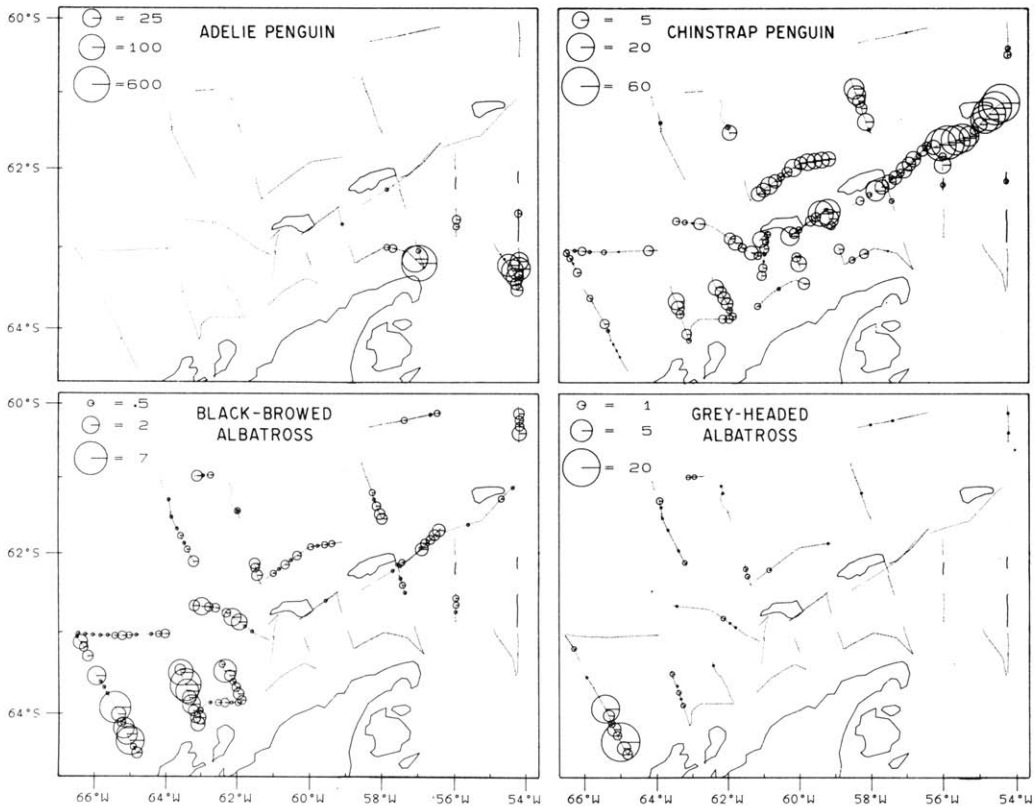


Fig. 5. Distribution of Adelie and chinstrap penguins and black-browed and grey-headed albatross. Symbols in this figure and Figs 6 and 7 reflect birds observed per nautical mile averaged over 5 nmi intervals.

Islands); diving petrels (*Pelecanoides* sp., in 13 miles); skuas (*Catharacta* sp., in 21 miles); kelp gull (*Larus dominicanus*, in 6 miles); gentoo penguins (*P. papua*, in 6 miles); snow petrel (*Pagodroma nivea*, in 4 miles); and wandering albatross (*Diomedea exulans*, in 2 miles). Light-mantled sooty albatross (*Phoebetria palpebrata*) and Antarctic petrel (*Thalassoica antarctica*) were each seen in 7 mile segments, and both were most commonly encountered to the southwest of Bransfield Strait. Blue-eyed shags (*Phalacrocorax atriceps*) were seen only close to the coast.

We encountered two very large aggregations of foraging birds: Adelie penguins foraging near Antarctic Sound, and Cape pigeons and Antarctic fulmars foraging between King George and Elephant Islands (HUNT *et al.*, 1985). These aggregations contained 76% of the Adelie penguins, 62% of the Cape pigeons and 62% of the Antarctic fulmars seen during our survey and were closely associated with large aggregations of krill. Because they were extreme numerical outliers, data from these aggregations were excluded from the cluster analyses.

The geographic distribution of birds differed by species over the study region (Figs 5–7, Table 2). For example, Adelie penguins were found exclusively in Weddell Sea water and closely related water types in contrast to chinstrap penguins, which generally were absent

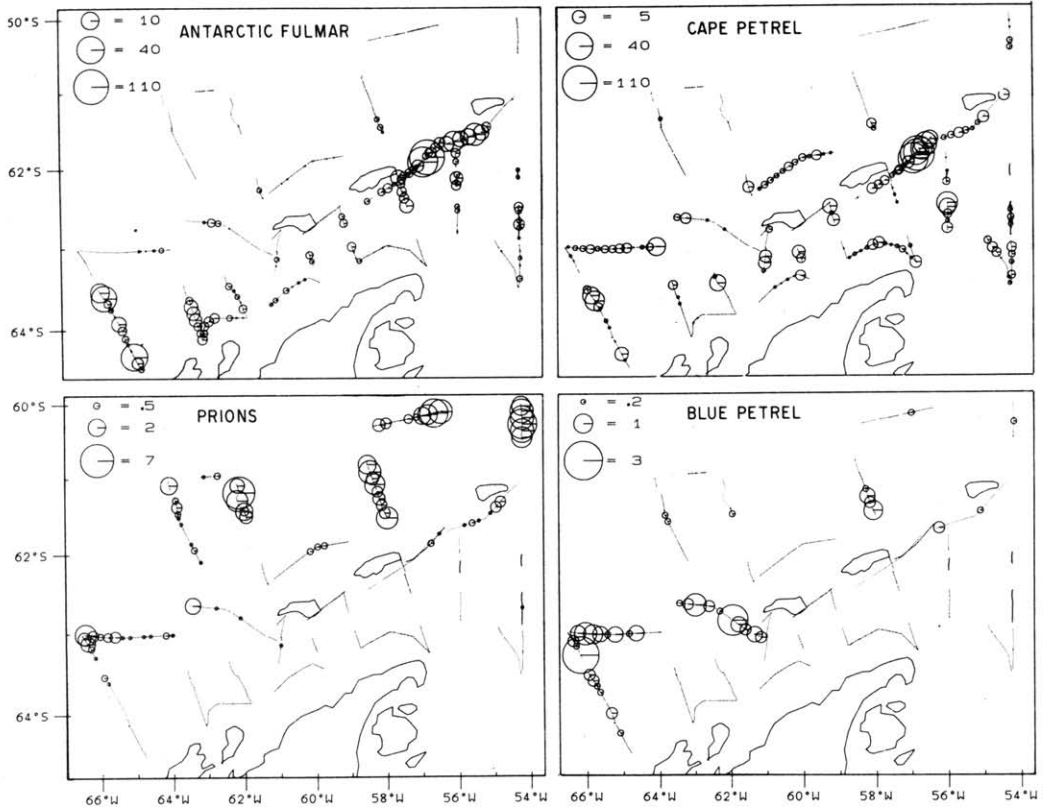


Fig. 6. Distributions of Antarctic fulmar, Cape petrel, prions and blue petrel.

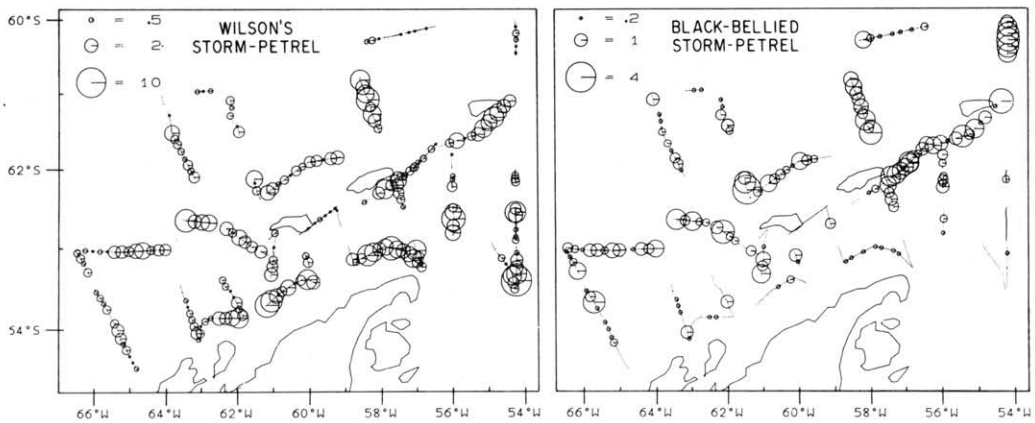


Fig. 7. Distributions of Wilson's and black-bellied storm-petrels.

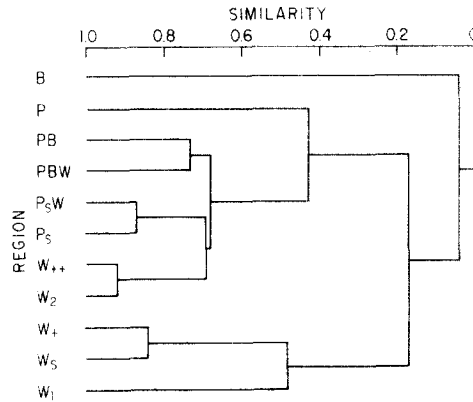


Fig. 8. Dendrograms from clustering regions.

from waters adjacent to the Antarctic Peninsula but were common near the South Shetland Islands. Black-browed albatrosses were relatively scarce in Weddell Sea waters, but were found in moderate numbers in Pacific Basin water and were most common in Bellingshausen water. More so than any other species, Wilson's storm-petrels were found evenly dispersed throughout the study area, with the exception of areas of Weddell Sea-derived water, where they were unusually abundant.

The cluster analyses of regions (Fig. 8) revealed four pairs of regions where bird faunas were similar and five major groupings (similarity index 0.5–0.6) of regions. Each of the four pairs (W_+ and W_s ; BP and PBW; P_sW and P_s ; W_{++} and W_2) were spatially contiguous regions and consisted of "related" water masses. All subsequent higher order linkages also grouped spatially contiguous regions. The five major groupings consisted of the three parental water masses, W_1 , P and B, the southern side of Bransfield Strait (W_+ and W_s), and the northern side of Bransfield Strait plus the South Shetland and Elephant Islands (BP, PBW, P_sW , P_s , W_{++} and W_2). There was, however, considerable distance in the linkage of bird communities present in W_1 and W_2 , both Weddell Sea water.

The bird communities characterizing each of the five major groupings from the cluster analysis were dominated by one to three species that stood out in abundance (Fig. 9). The groupings correspond well with a clustering of species using the correlation matrix (Fig. 10). The triplet of the two albatrosses and Antarctic fulmar were characteristic of Bellingshausen Sea water. The albatrosses cluster close together because they were rare in Bransfield Strait waters, while Antarctic fulmars were common there (Figs 5 and 6). Cape petrels and chinstrap penguins both achieved their highest abundances in the vicinity of the South Shetland and Elephant Islands (Figs 5 and 6), an area of strong mixing between all three parent water masses. The triplet of black-bellied storm-petrel, blue petrel and prions is clearly a species assemblage characteristic of the Pacific Basin water mass (Figs 6 and 7). Blue petrels and black-bellied storm-petrels clustered more closely together because they were not restricted to offshore waters as were the prions. Finally, Adelle penguin and Wilson's storm-petrel cluster together because they were characteristic of Weddell Sea water near the Antarctic Peninsula. Their low similarity, relative to other pairings, resulted from a difference in the center of abundance between Adelle penguins (W_1) and Wilson's storm-petrels (W_s and W_+). The reason for the linkage of the pair, W_2 and W_{++} to the large cluster rather than to a Weddell Sea-derived cluster is unclear, but the linkage

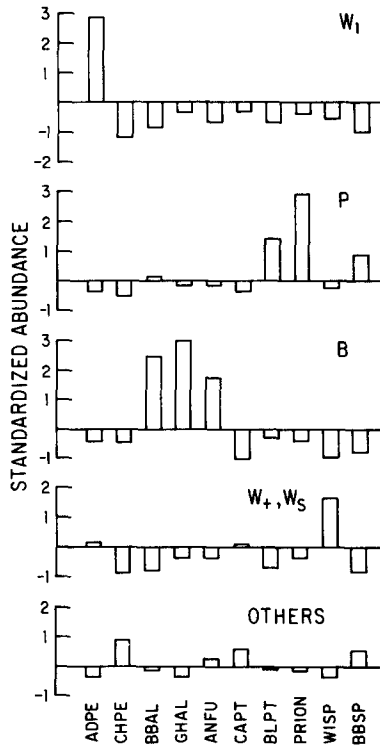


Fig. 9. Standardized species' abundances for each of the unique regions or clusters of similar regions identified in Fig. 9. Abundances were standardized by removing the grand mean, and dividing by the standard deviation among the 11 region means. ADPE, Adelie penguin; CHPE, chinstrap penguin; BBAL, black-browed albatross; GHAL, grey-headed albatross; ANFU, Antarctic fulmar; CAPT, Cape petrel; BLPT, blue petrel; PRION, all prions; WISP, Wilson's storm-petrel; BBSP, black-bellied storm-petrel.

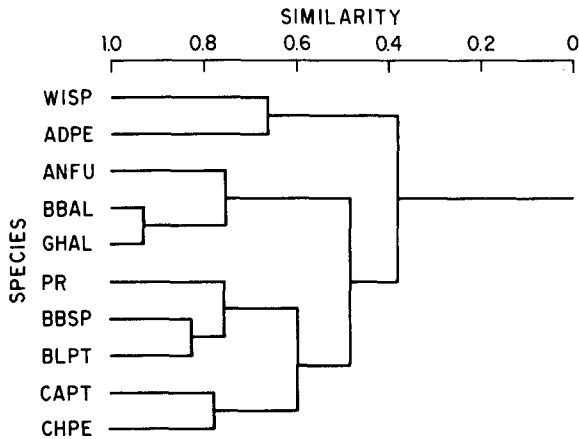


Fig. 10. Dendrograms from clustering species, at the region scale. Species abbreviations as in Fig. 9.

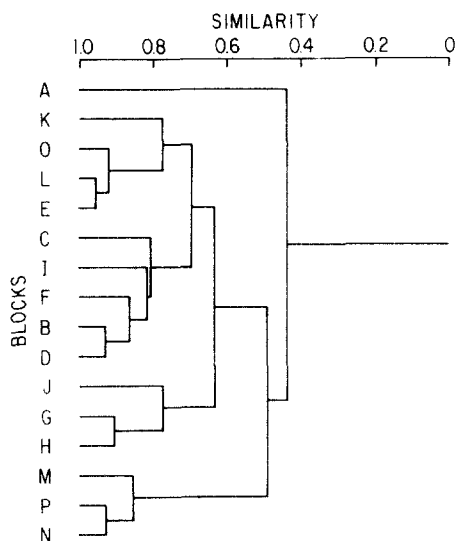


Fig. 11. Dendrograms from clustering blocks.

may have been driven by high numbers of chinstrap penguins and black-bellied storm-petrels in both regions.

The cluster analysis of blocks resulted in numerous pairs of adjacent blocks, most of which were contained in the same or similar oceanic regions (Fig. 11, e.g. blocks N, P and M, or H and G). The cluster analysis had one higher order cluster in which blocks that were neither contiguous nor from the same water mass were joined (D, B and F with I).

DISCUSSION

The distribution patterns of most bird species found in our study were similar to those reported by STARCK and WYRZYKOWSKI (1982) who surveyed the same region, but later in the season, from mid-February to late March, 1981. In both studies, black-browed albatrosses, grey-headed albatrosses and prions were found most commonly in Pacific and Bellingshausen waters, and were generally absent from Bransfield Strait and Weddell Sea water. Similarly, in both studies, Antarctic fulmars were found mostly within Bransfield Strait and Bellingshausen water, and were generally absent from the Drake Passage. Wilson's storm-petrels were ubiquitous and common in both studies. Observations of wandering albatross, Antarctic terns, skuas, Dominican gulls, snow petrels and blue-eyed shags (*Phalacrocorax atriceps*) were generally similar for the areas where the two studies overlapped in area covered.

For other species, distribution patterns differed between the two studies. We encountered large numbers of both chinstrap and Adelie penguins, mostly in Bransfield Strait or Weddell Sea water, and mostly close to shore. In contrast, STARCK and WYRZYKOWSKI (1982) reported few penguins, and these mostly far from shore in the Drake Passage, a difference most likely reflecting the penguins' presence on colonies or ice for molting at the time of the 1981 survey. Although most Cape petrels were found in close proximity to the South Shetland Islands in both studies, more were seen in the Drake Passage in 1981 than

in 1985. We found more black-bellied storm-petrels in Bransfield Strait than did Starck and Wyrzykowski, although in both studies these storm-petrels were most common in Pacific Basin water. Blue petrels, absent from the study region in 1981, were relatively common in Pacific Basin water in 1985.

In 20 days of dawn-to-dusk observations of pelagic birds, we saw only two large aggregations of foraging birds, but these aggregations contained the vast majority of all feeding birds seen (HUNT *et al.*, 1985). Although such large patches are rare, they almost certainly are important to some seabirds. We know little about the dynamics of these patches. The relative importance of physical oceanographic processes or behavioral responses of krill in determining the location and persistence of these prey patches is not understood. Although the krill patch attended by Cape petrels and Antarctic fulmars occurred in a region where physical processes might have been expected to concentrate krill (HEYWOOD and PRIDDLE, 1987); evidence in EVERSON and MURPHY (1987) suggests that krill were carried passively through the region in the prevailing currents without being concentrated or retained. STARCK and WYRZYKOWSKI (1982) also found Cape pigeons and Antarctic fulmars together in large feeding flocks associated with krill patches.

The clustering of water-mass regions based on the similarity of seabird communities suggests that birds were using as similar habitats, water masses with similar origins. Regions within these clusters, while sharing similar physical properties, did not share similar abundances of krill. HEINEMANN *et al.* (1989) found that the proportion of the variance in seabird distribution explained by the distribution of krill was greatest when observations were clustered by seabird species composition or krill depth profiles, rather than by water-mass characteristics. Thus, we cannot explain the particular clustering of regions as derived in any simple way from the distribution of krill that we observed. To the extent that birds use both prey distribution patterns and physical characteristics in their choice of habitat, the lack of linkage between prey and areas delimited by physical properties will diminish the correlation between birds and physically characterized water masses.

The fact that the region clusters were in all cases spatially contiguous may reflect a common response by the birds to the similar characteristics of adjacent water masses, or it may reflect spatial autocorrelation generated by the proximity of breeding colonies. For instance, over 90% of the Adelie penguins breeding in the study area occupy colonies at the tip of the Antarctic Peninsula, and the large aggregation of these penguins was within 25 km of Hope Bay, the site of the largest colony in the Antarctic Peninsula-Scotia Sea sector of the Southern Ocean (CROXAL *et al.*, 1984).

In contrast, the distributions of other species did not reflect the distribution of their colonies. In some cases breeding species were in waters distant from colonies (e.g. Wilson's storm-petrel, prions, and grey-headed albatross). In the case of black-browed albatrosses, the study area was beyond the predicted foraging ranges of individuals nesting at the nearest colonies in the Diego Ramirez Islands, Chile (SCHLATTER, 1984; CROXALL *et al.*, 1984); we infer that the individuals of this species recorded on our surveys were non-breeders. Additionally, blue petrels had completed breeding and were not constrained by colony location. Thus, for these species, characteristics of the water masses or prey distributions are likely to have been of paramount importance in habitat selection.

Even in those cases where there is a correspondence of colony distribution and foraging distribution, the former is only a proximate explanation of the latter. In the long run, the availability and predictability of prey must have an important influence on the location and

persistence of breeding colonies, especially for species with constrained foraging ranges such as penguins (CROXALL *et al.*, 1984). The concentration of Adelic penguin and chinstrap penguin colonies near headlands and island passes may reflect the dependence of these, and other, krill specialists on foraging areas with hydrographic features that may concentrate prey (e.g. gyres; PRIDDLE *et al.*, 1988). At present we are unable to evaluate the relative importance of dynamic processes and water-mass characteristics for the selection of foraging habitat by birds in the Bransfield Strait region, but it seems likely that at least in some cases, birds are responding to the different water masses as if they were different habitats.

Acknowledgements—We thank the Captain, officers and crew of the R.R.S. *John Biscoe* for support in the field. A. G. Wood and C. Mitchell provided invaluable assistance in data management and analysis. John Croxall provided helpful comments on an early draft of this manuscript. Financial support was provided by the Natural Environment Research Council to the British Antarctic Survey, and by the National Science Foundation, Grant no. DPP-8318464, to G. L. Hunt.

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