Dispersion of seabirds at sea
in the Southern Ocean

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DISPERSION OF SEABIRDS AT SEA IN THE SOUTHERN OCEAN

TABLE OF CONTENTS

ABSTRACT

The feasibility of obtaining information on the dispersion of seabirds at sea precise enough to reflect changes in their prey was investigated. A standardized technique for counting birds from a moving ship, designed to limit biases due to birds circling, following and/or deviating towards/from the ship, is suggested. An interspecific comparison of 31 seabird species was made to determine which species yielded the most accurate censuses. Although many species are attracted towards the ship, only the Wandering Albatross Diomedea exulans follows for long periods. Counts from a stationary ship are shown to be unsuitable for abundance and biomass estimates, because of the accumulation of birds around the ship. The avifauna at sea is described in terms of species richness, diversity, abundance, biomass and trophic groups of 42 pelagic species (penguins excluded). Birds eating plankton and cephalopods are the most abundant; few birds eat fish. Plankton- and cephalopod-eaters occur most abundantly in the south and north of the study area, respectively. An association between their distribution and the availability of their principal prey is proposed. The effect of five abiotic features on seabird distribution was investigated. Although significant preference for specific ranges of features is demonstrated, linear correlations are weak (maximum correlation coefficient (r) = 0.325). Abiotic features associated with the distribution of the Snow Petrel Pagodroma nivea and the Antarctic Petrel Thalassoica antarctica were investigated in greater detail. Statistical relationships between the species' occurrence and measured oceanographic and meteorological features are inconclusive. Associations with prey are discounted, because of the birds' apparently unspecialized diet and opportunistic feeding. The two species occur in or near sea-ice. Their restriction to this area and the concomitant absence of other procellariiform species appears to be consequent on the species' flight characteristics. The merits of using seabirds at sea as biological indicators of prey resources are discussed.

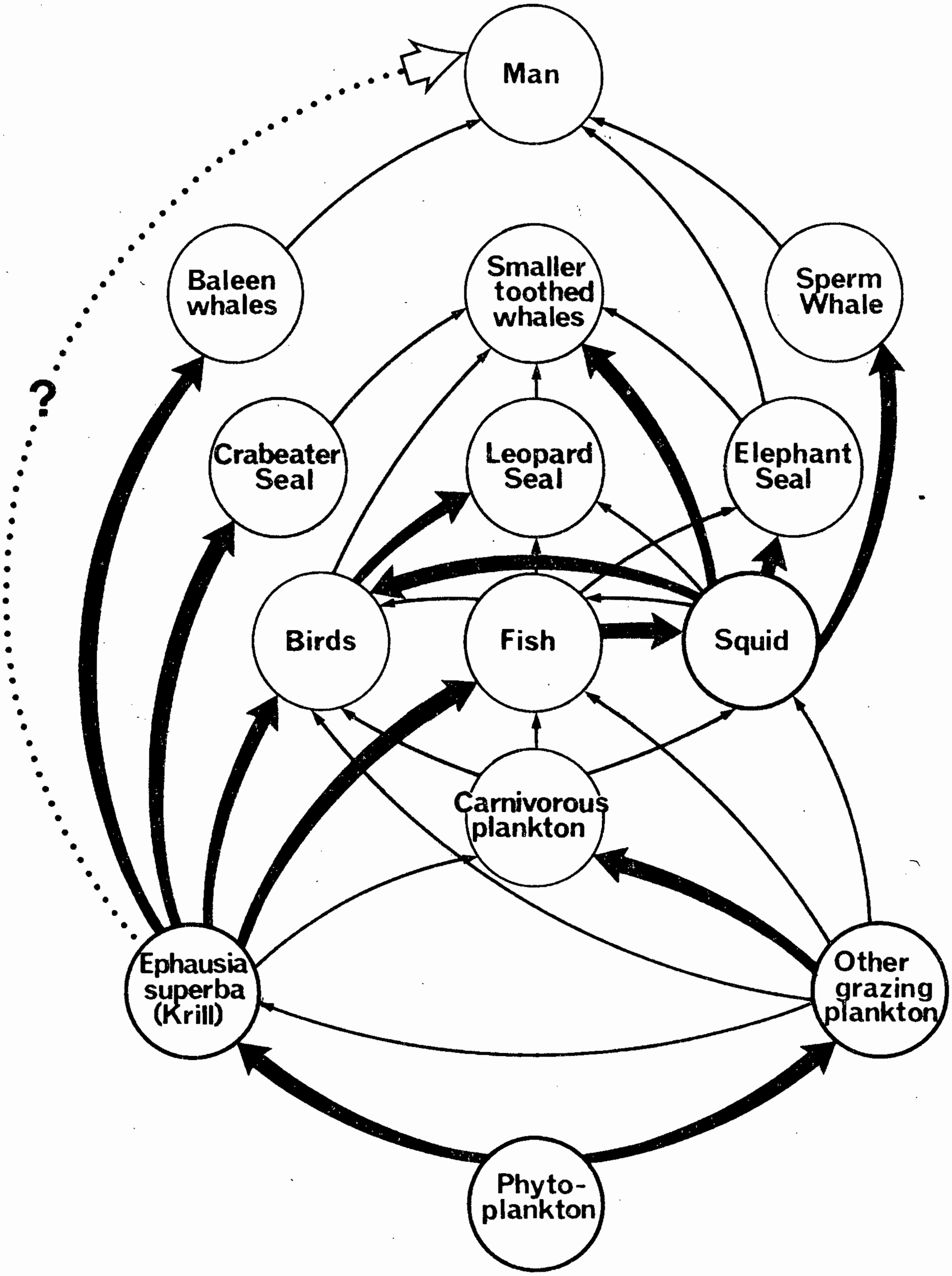

FIGURE 1. Major trophic relations in the Southern Ocean. Heavy arrows indicate the probable diet of the groups to which they point

INTRODUCTION

The BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) research programme seeks a deeper understanding of the structure and functioning of the Southern Ocean ecosystem (Anon 1977). The position of seabirds as top predators in the food chain (Fig. 1) suggests that they may be useful indicators of ecological conditions in the Southern Ocean (Anon 1977). The future use of seabirds at sea as biological indicators depends *inter alia* on the realization of three objectives which form the basis of this thesis.

1). REFINEMENT OF EXISTING METHODS OF CENSUSING SEABIRDS AT SEA FROM A SHIP.

The variety of methods used to count birds has made comparisons of results difficult. Standardization of precise methods is required for the efficient collation by BIOMASS of seabird data collected by many nations.

2). DESCRIPTION OF THE SEABIRD COMMUNITY AT SEA.

Information on the spatial and temporal distribution of species richness, diversity, abundance and biomass, and groups of birds, classified according to their principal prey, in the Southern Ocean is required.

3). DETERMINATION OF THE ASSOCIATIONS BETWEEN SEABIRDS AND BIOTIC AND ABIOTIC FEATURES OF THEIR ENVIRONMENT.

This thesis treats each of the above objectives with respect to volant species (mainly albatrosses and petrels) only. Penguins are difficult to observe at sea, and usually dive to avoid ships. Thus, the feasibility of using them as biological indicators is not investigated here. Data on seabirds' reactions to a ship, seabird distribution, and oceanographic and meteorological data were collected in that area of the Southern Ocean of most interest to South Africa, the African sector. It is defined here as extending from 30°S to 70°S, and from 20°W to 40°E. Field work in the area was undertaken on seven cruises from April 1979 to April 1980.

The objectives stated above are considered separately: Parts 1 and 2 of the thesis consider objective 1. Part 1 concentrates on standardization of counting methods, based on an investigation of four species showing a range of reactions to a ship. A detailed comparative study of the reactions of common volant species to a moving, and a stationary, ship is given in Part 2. Thus, Parts 1 and 2 explain how best to count seabirds, and suggest which species are likely to give the most reliable census results. Objective 2 is discussed in Part 3 which describes the overall composition and distribution of the avifauna. Part 4 considers the association of the avifaunal components (described in Part 3) with selected abiotic environmental features (surface-water and air temperatures, depth, wind strength and weather condition). Part 5 discusses these associations at the individual species level.

The scientific names of all seabird species have been omitted from the main text, but are listed in Appendix 1. The categorization of seabirds according to their diet and feeding method (Appendix 1), is based primarily on Ashmole's (1971) review of the subject and my records of seabird feeding (Appendix 2).

STUDY AREA

The circumpolar Southern Ocean may be divided latitudinally into three regions: the Subtropical, Subantarctic and Antarctic zones (Fig. 2) (see Deacon 1933, Sverdrup et al. 1942, Knox 1970, Jacobs & Georgi 1977, and Baker 1979 for general reviews). Generally, the oceanographic features which characterize these water masses (eg. water temperature, salinity, nutrient concentrations) have latitudinal gradients, whereas longitudinal variation is much less pronounced (Deacon 1937, Clowes 1938, Mackintosh 1946). The seasonal changes are greatest latitudinally, such as the northward encroachment of ice in the austral winter (Fig. 2).

The Subtropical and Antarctic convergences and the Antarctic Divergence (Fig. 2) are particularly rich in nutrients (nitrate, phosphate and silicate). Nutrients increase in concentration from Subtropical to Antarctic zones (Deacon 1933, Clowes 1938, Holm-Hansen et al. 1977). Solar radiation varies seasonally and with the extent of ice coverage. Both nutrient concentration distribution and the degree of insolation affect phytoplankton distribution (Ryther 1963, Cushing 1971). Phytoplankton standing crop and productivity show both spatial and temporal variation (Holdgate 1967, Zernova 1970, Plancke 1977). Many species of phytoplankton (Hart 1942) and zooplankton (Baker 1954, 1965, Foxton 1956, Mackintosh 1960) reflect oceanographic regimes by having circumpolar distributions with minimal longitudinal and marked latitudinal variation. Zooplankton are most abundant in the Antarctic, and least abundant in the Subtropical zone, with areas of upwelling and subsidence creating localized zones of high

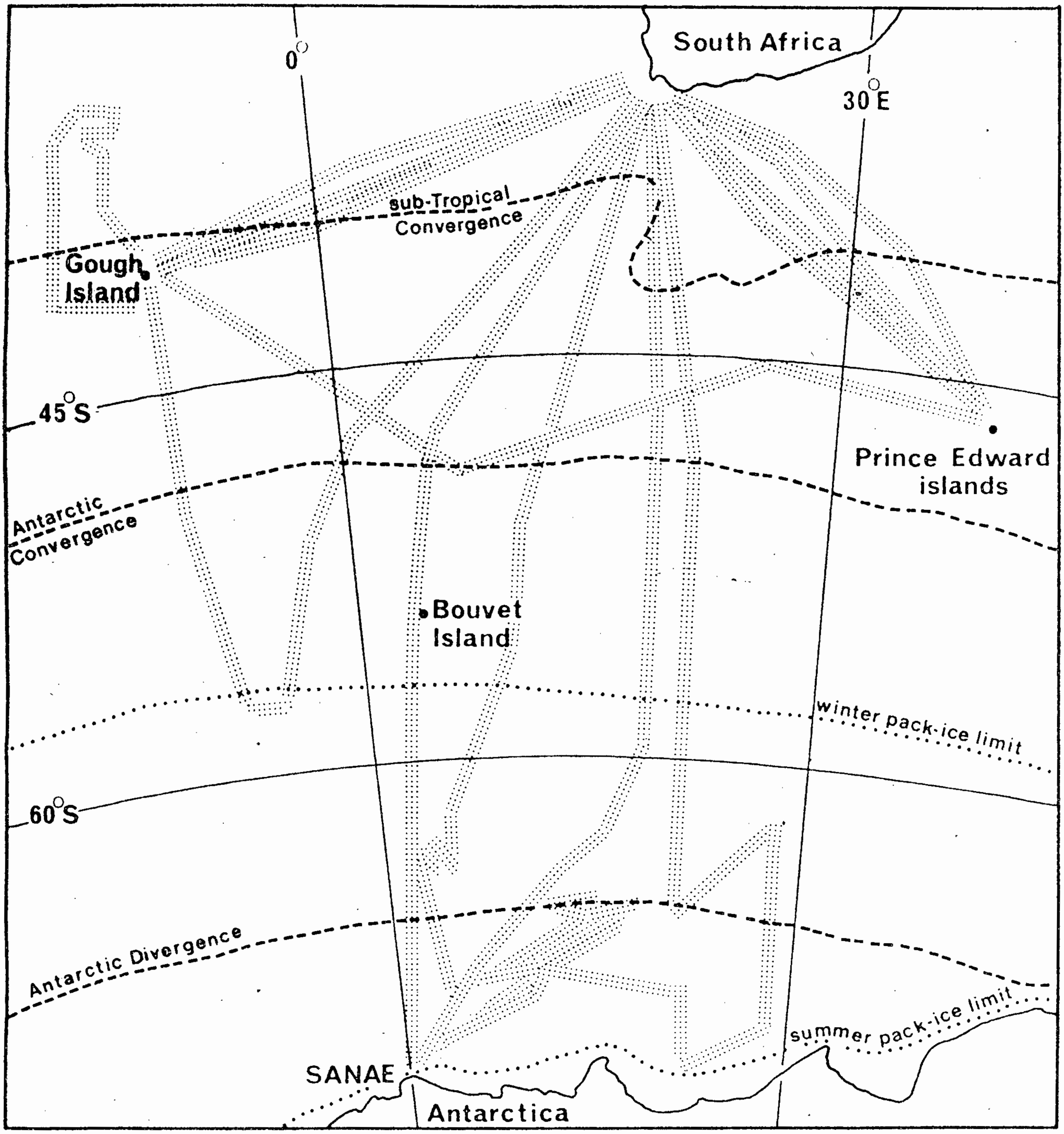

FIGURE 2. Tracks of the M.V. S.A. Agulhas during seven separate cruises made during April 1979 to April 1980

biomass (Voronina 1966). The highest biomass of mesoplankton (excluding euphausiids) is found in the region of the Antarctic Convergence between 48°S and 53°S (Foxton 1956). The biomass of Antarctic krill (mainly Euphausia superba) may equal the total biomass of all other zooplankton (Holdgate 1967). The distribution of krill is associated closely with phytoplankton (Makarov et al. 1970). Although krill have a circumpolar distribution, they are concentrated off Enderby Land in the southwest Indian Ocean (southern limits of the study area) and in the Scotia Arc (Marr 1962, Mackintosh 1973). In the former area, krill which habitually form dense surface swarms occur between the Antarctic Divergence (about 63°S) and the Antarctic Convergence (about 51°S) in the west, and south of the Divergence in the east (Marr 1962, Makarov et al. 1970). Zooplankton in the surface waters (ie. readily available to birds) also increases from the Subtropical to the Antarctic zone (Fig. 3). This surface zooplankton shows large seasonal variation of occurrence (Foxton 1964, Holdgate 1967, Mackintosh 1973).

Though little is known about the distribution of cephalopods in the Southern Ocean (Clarke 1966), the stocks are apparently large (Everson 1977). Many species undergo seasonal and diel vertical migration (Roper & Young 1975) to the surface where they would become available to seabirds.

The study area includes three island groups. A total of 29 pelagic species (excluding penguins) breed there: 19 at Tristan-Gough (Elliot 1957, A.J. Williams in litt.), 22 at Prince Edward-Marion (Williams et al. 1979) and six at Bouvet Island (Watkins in press). Of the 42+ species (prions and divingpetrels were not identified to species) included in this study (Appendix 1), three

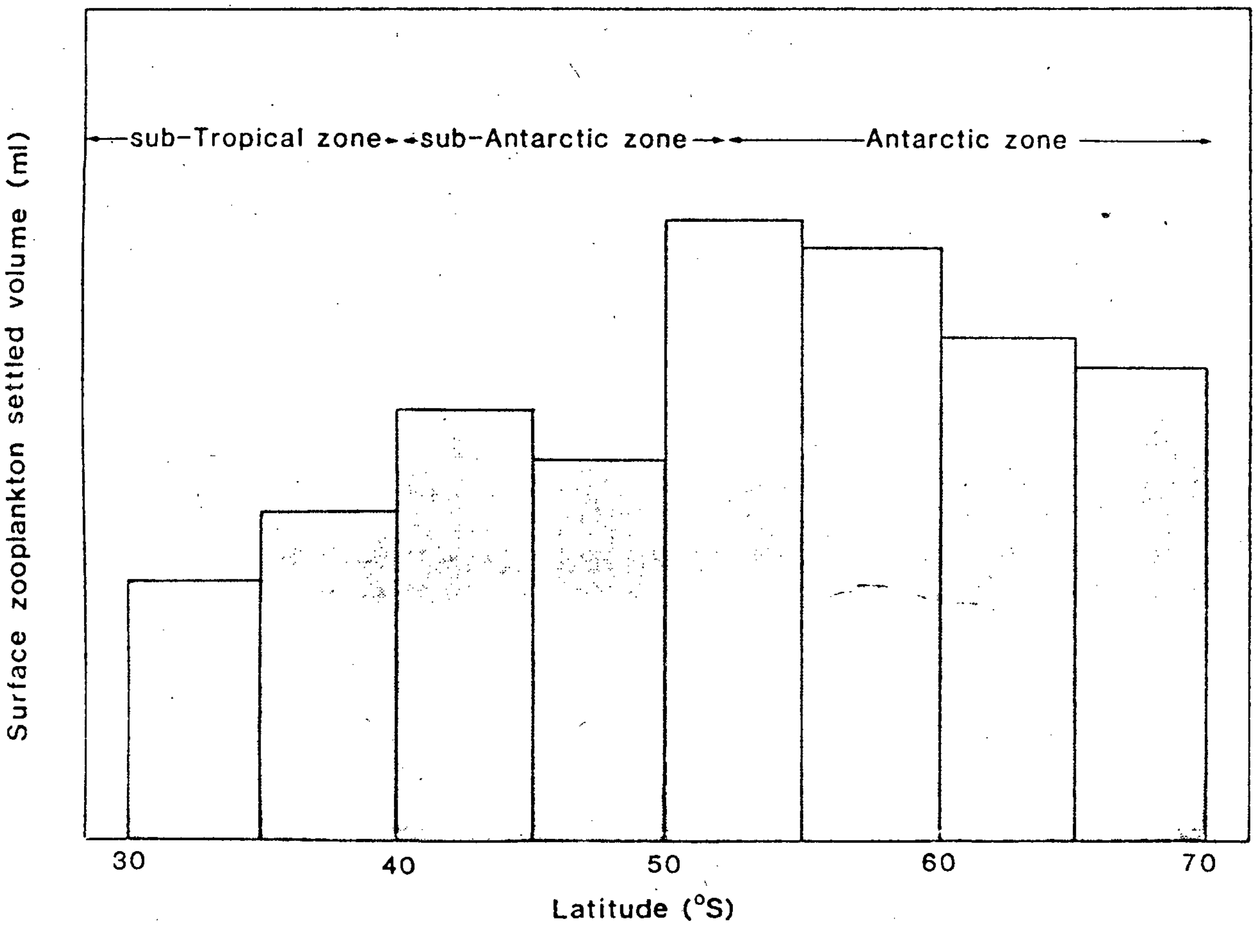

FIGURE 3. Latitudinal distribution of settled volume (ml) of zooplankton from the surface (5m) of the Southern Ocean (after Foxton 1964)

species breed on Antarctica south of the study area, four (termed Southern Ocean migrants) breed on islands elsewhere in the Southern Ocean, and nine are Holarctic migrants.

PART 1

BIASES IN CENSUSES OF PELAGIC SEABIRDS AT SEA IN THE SOUTHERN OCEAN

ABSTRACT

An analysis was made of two potentially major sources of bias in the censuses of seabirds in the pelagic environment of the Southern Ocean. The varying distances from the ship at which four procellariiform seabird species were detected by a ship-borne census-maker are discussed in relation to the birds' reactions to the ship. Their reactions are also considered in relation to the need to distinguish between birds following the ship, and those largely or completely ignoring the ship. A standardized technique for censusing seabirds in the Southern Ocean is suggested.

INTRODUCTION

Ideally, a census should comprise an instantaneous count of a population. In practice, however, this is difficult to achieve for seabirds in the pelagic environment (Bailey & Bourne 1972, Wiens _et_ _al_. 1978). Here I analyse two potentially major sources of bias in counts of selected species of pelagic seabirds in the Southern Ocean with particular reference to the birds' reactions to a ship, and consider the preliminary results in relation to the need for standardization of techniques for counting birds at sea.

METHODS

Data on the distribution and abundance of pelagic seabirds were obtained during three separate cruises of the M.V. _S_._A_. _Agulhas_ in the austral winter of 1979, when the ship operated in an area bounded by 33°S and 56°S, and 10°W and 40°E. The ship progressed at an average speed of 26km/h (14 knots). Seabirds were counted during one-hour sessions split into 10-minute periods, since I found it difficult to maintain constant concentration for longer watches. A truncated arc of 130° (Fig. 4) was scanned at least five times with 10 X 40 binoculars every 10-minute period. Birds were classed as either "following" or "flying past". "Following" included birds accompanying the ship for more than 10 minutes and which were present at the end of a one-hour session (stern count), whereas "flying past" included birds flying past without changing their flight path, birds which changed direction to fly away from the ship (avoidance), and birds which flew towards the ship and accompanied it for less than 10 minutes (normal count). The temporal distinction is made to prevent birds being counted more than once. Only birds that apparently crossed a line perpendicular

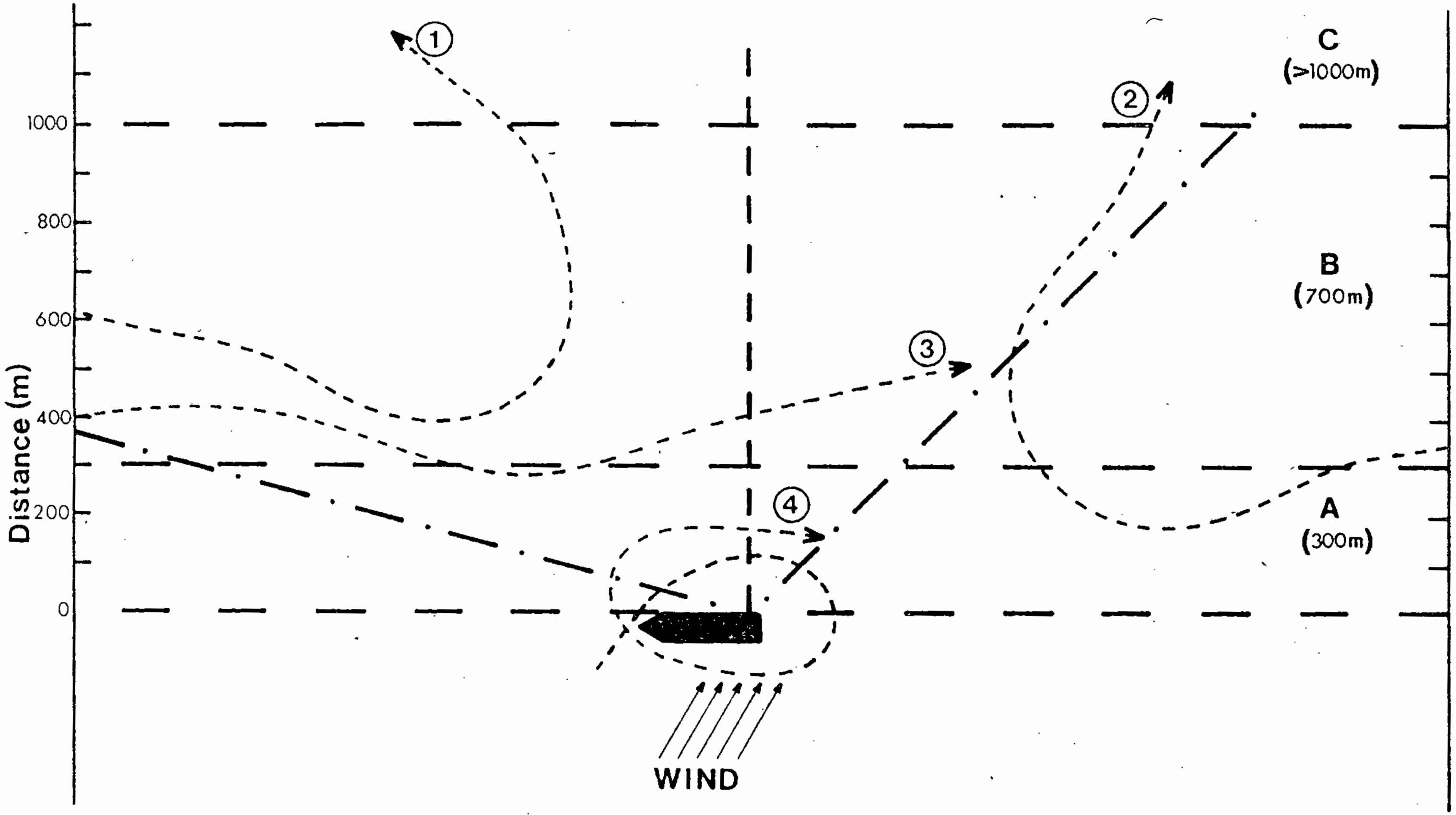

FIGURE 4. Hypothetical flightpaths of four birds in relation to 130 arc scanned by shipboard observer, distance categories A (0 - 300m), B (300 - 700m) and C (> 1 000m), and imaginary line used in counting birds

to the transect direction were included in the census. The elevated viewing deck (9m above sea level) near the stern allowed observation of birds following as well as flying past. Observation from a point farther forward, as suggested by Bailey & Bourne (1972), was not practicable because of inadequate protection from the inclement weather. A "stern count" of birds following the ship was made at the end of each one-hour session.

Birds were placed into one of three categories, depending on the estimated distance at which they passed the ship: A (0 - 300m), B (300 - 1 000m), and C (> 1 000m) (Frost 1976). The C-category width extended to 10km during periods of infinite visibility, the horizon being 11km from the observer's position on the ship. Counts were not made when visibility was less than 1km.

Using a combination of range finders and visual estimation, Wiens _et al_. (1978) split their observations into six distance categories. Increasing the number of distance categories increases the likelihood of inaccurately categorising the distance of any one bird from the ship. I did not find a range finder practicable because of adverse sea conditions and the occasional super-abundance of birds. Therefore, accuracy in six distance categories was not normally possible in the Southern Ocean.

It is difficult to estimate distances at sea. However, since I made 95% of the observations reported here, any errors in distance estimation are approximately constant.

RESULTS AND DISCUSSION

The relative occurrences of Wandering Albatrosses, Whiteheaded, Softplumaged and Blue petrels according to their distance from the ship are summarized in Figure 5. The proportions of birds reported in each of the three distance categories were computed as in Table 1 for the Softplumaged Petrel. Significantly fewer birds farther than 1km from the ship were detected by observers (Fig. 5). The paucity of birds recorded in category C stresses the need for a maximum limit to the observation area used for assessing abundance. Total counts for a few large species may be almost doubled if birds beyond 1km are included in the sample.

The difference between the numbers of birds in categories A and B (Fig. 5) are due to the birds' reactions to the ship, rather than to their detectability. Considering categories A and B only, Blue Petrels (X^2 = 246.29; $p < 0.0001$) approached the ship and Softplumaged Petrels (X^2 = 9.03; $p < 0.01$) avoided it, whereas Whiteheaded Petrels (X^2 = 0.02; $p > 0.05$) and Wandering Albatrosses (X^2 = 0.21; $p > 0.5$) apparently were unaffected (Fig. 5). However, this is clearly spurious for the Wandering Albatross at least, since the species is known to follow ships regularly.

Only 4% of Wandering Albatrosses observed were recorded as "flying past" (Table 2). Thus, birds joining the ship, but first seen close to the ship, probably would be counted erroneousely as "following" instead of "flying past". Two factors tend to bias the proportion of birds following the ship: (i) "stern counts" comprise birds drawn from 360° and thus a larger area is surveyed than in "normal counts" which scan 130°, and (ii) birds following the ship may be included in two or more stern counts whilst birds flying past are unlikely to be recorded in more than one normal count. Many census-makers have included in their counts all birds seen in observation arcs ranging from 90° to 360° (Gill 1967, Wiens et al. 1978). Thus, for example, by including bird 1 and 2

Table 1: Proportionate occurrence of Softplumaged Petrels in relation to distance from the ship in the Southern Ocean during April - July 1979. A = 300m. B = 700m. C = 540m (obtained by averaging values for each separate count).

	Distance categories		
	A	B	C
No. birds recorded	130	410	158
No. birds per metre	0,43	0,59	0,03
Weighted proportion*	41	56	3

$$* \text{ Weighted proportion } = \frac{n_i m^{-1}}{\Sigma n_i m^{-1}} \times 100$$

where n_i = No. of birds recorded in a particular distance category.

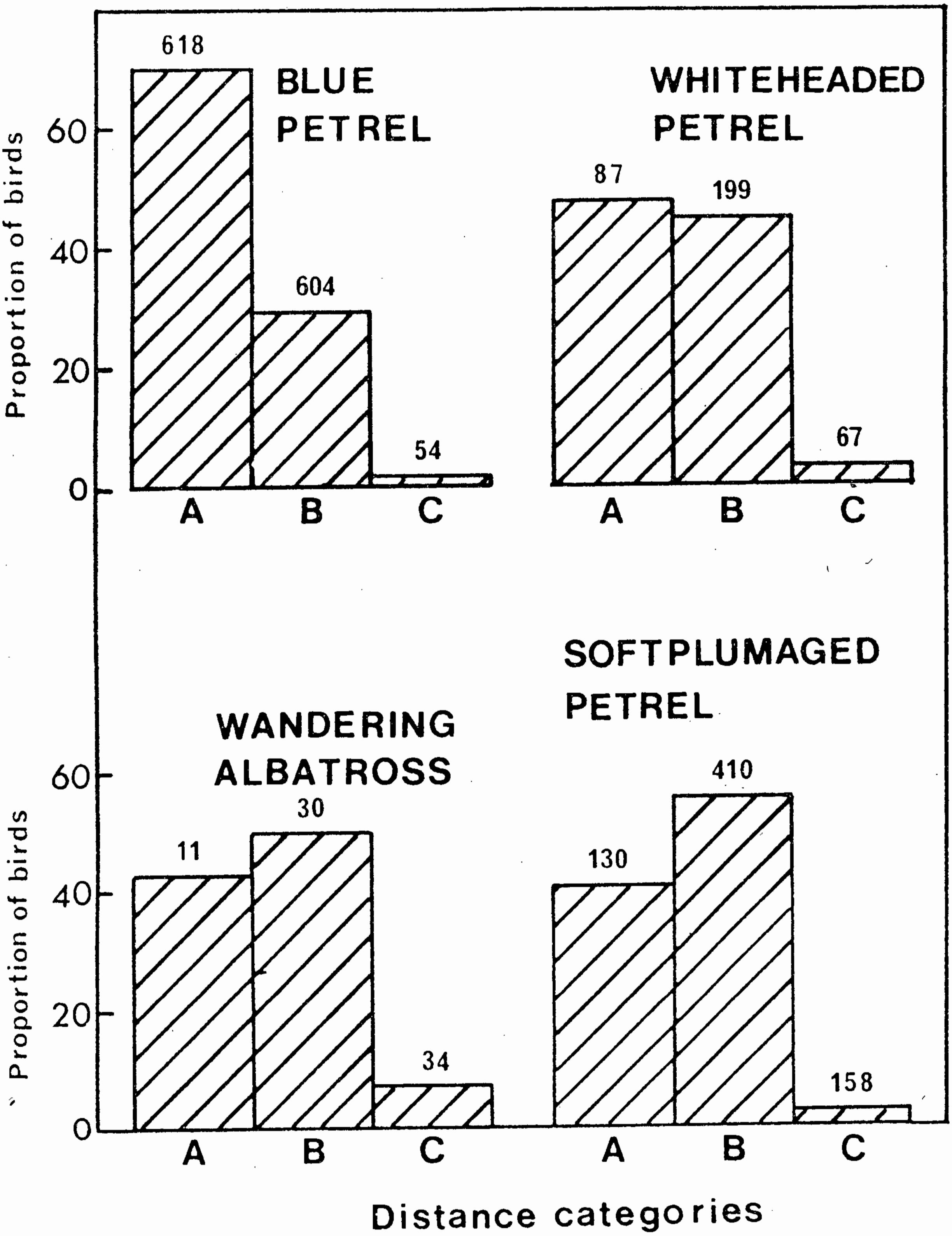

FIGURE 5. Proportionate occurrence of four species of seabirds in relation to distance from the ship in the African sector of the Southern Ocean during April - July 1979. The figures at the heads of the histograms are numbers of birds recorded. See text and Table 1 for further particulars

Table 2: Incidence of seabirds either "flying past" or "following" the ship in the Southern Ocean during April - July 1979.

	Per cent "flying past"	Per cent "following"	No. birds counted
Softplumaged Petrel	96	4	727
Whiteheaded Petrel	88	12	401
Blue Petrel	66	34	1 938
Wandering Albatross	4	96	1 875

(Fig. 4) in the census, the same area is surveyed more than once, and the transect length effectively increased. In all cases, the magnitude of error resulting from counting birds within the arc more than once is difficult to determine.

According to Brown et al. (1975), conversion of relative abundance to actual abundance of seabirds is possible if the birds' reactions to ships, inter alia, are quantified. However, since the magnitude of the ship's effect on each species is different, these reactions are applicable to relative abundance as well. At this stage I am reluctant to apply "detection co-efficients" (Emlen 1971) to my data; I suggest that detection co-efficients are affected by temporally and spatially variable features such as weather, light conditions and seabird densities and activities.

CONCLUSIONS AND RECOMMENDATIONS

Since instantaneous counts of all birds in particular areas can seldom be achieved at sea, it is recommended that only those birds which are observed to cross an imaginary line should be included in any particular count. This line should extend for 1km on one side of, and perpendicular to, the long axis of the ship (Fig. 4). Records of birds observed beyond this limit should be used in presence:absence analyses only. Birds should be counted when first sighted only, so that accumulative counts are not obtained. It is not feasible to adjust tallies mathematically, because the decision to record a bird as "flying past", as opposed to "following", is highly subjective. This is so particularly when birds circle temporarily out of view, on the side of the ship not occupied by the observer. (Bird 4, Fig. 4). In addition to counting the birds crossing the imaginary line (Bird 3, Fig. 4), the observer should note all birds seen within an observation arc, so that relatively inconspicuous birds, such as stormpetrels (Hydrobatidae) and divingpetrels (Pelecanoididae) are included in the survey.

Finally, all observers of birds at sea should be aware of the fact that the ship acts as an extrinsic factor in influencing the proximate distribution of birds, and that this factor is relevant to relative and absolute abundances and any interspecific comparisons of birds at sea. I recommend against the use of mathematical corrections of raw data to obtain densities of seabirds in the pelagic environment. Meaningful data on the abundance of birds at sea can be obtained by means of first scanning an arc to detect and identify birds and then counting only those which cross an imaginary line, perpendicular to the ship.

PART 2

REACTIONS OF SOME SEABIRDS TO A SHIP IN THE SOUTHERN OCEAN

ABSTRACT

The reactions of 31 species of seabirds (mainly Procellariiformes) to a moving and a stationary ship were investigated in the Southern Ocean. Birds were categorized according to the distance at which they flew past the moving ship. The proportions of individuals of each species following the ship, as opposed to flying past it, were calculated. Few species allow accurate censuses of their abundance. The time spent following by individual birds is discussed with respect to "turn-over rates" of ship-following species. Species strongly attracted to the ship were scavengers. Food is believed to be the ultimate factor influencing the attraction of seabirds to ships, although albatrosses may have followed to use air currents generated by the ship. Within an hour of the ship stopping most species had increased in abundance. The implications of assessing avian abundance and biomass from a stationary ship are discussed.

INTRODUCTION

One of the simplest ways to assess the numbers of seabirds in an area of ocean is to count them from a ship. However, some species will be seen more readily than others. Species attracted to, or following, a ship are likely to be overestimated, whilst counts of species which avoid ships may be artificially low. The reactions of a particular species depend on the type of ship, and its activity. If one does not allow for species' reactions, abundance and biomass estimates will be inaccurate. This paper compares the reactions of 31 seabird species to a research vessel, both moving and stationary, in the African sector of the Southern Ocean.

METHODS

Seabirds were counted during seven cruises of the M.V. S.A. Agulhas in the Southern Ocean during the period April 1979 to April 1980 (see Part 1).

Observations from the moving vessel

Altogether 2 250 10-minute bird observations were analysed; 1 864 being normal counts (birds flying past the ship or sitting on the water) and 386 being stern counts (birds following the ship). The ship progressed at an average speed of 24km/h (13 knots). During normal counts, individual birds were categorized according to the distance at which they passed an imaginary line perpendicular to the ship's course: A = 0 - 300m; B = 300 - 1 000m; and C = 1 000m - horizon, which varied with visibility between 1 000 and 11 000m (see Part 1). Excepting the small stormpetrels (Hydrobatidae) and divingpetrels (Pelecanoididae), I am confident that most birds within 1 000m of the ship were recorded. A chi square analysis

(Sokal & Rohlf 1969) was performed on the occurrence of birds in categories A and B (expected frequency = 300:700) to determine the significance of avoidance or attraction. The weighted proportions of birds in categories A, B, and C were calculated as in Table 1.

Birds following the ship were recorded once an hour by counting in one continuous scan. A chi square test was performed on the numbers of birds following the ship as opposed to the numbers flying past the ship, to determine whether species were followers or non-followers of the ship. To determine the overall reactions shown by the 31 species, a correspondence analysis in one dimension (Greenacre 1978) was performed on both the distance category and the following/flying past data.

The times that seven species (35 individuals) spent following the ship were recorded. Only individuals observed continously from their time of arrival to time of departure were analysed. Two of these species, the Wandering Albatross and the Lightmantled Sooty Albatross were timed following directly in the wake of, and alongside, the ship.

Observations from the stationary vessel

The numbers of species and individuals within 500m of the ship were recorded at 12 oceanographic stations (no fishing activity) in the area bounded by 62°35'S - 69°29'S, 1° 47'E - 28° 37'E in February 1980. All birds were counted in one continuous scan at five-minute intervals from the moment the ship stopped. Seven of these stations were occupied for one hour, and the remaining five for up to two hours. For comparison, all analyses are restricted to the first hour after the ship stopped.

RESULTS AND DISCUSSION

Reactions to the moving vessel

Most, if not all, seabirds are able to fly faster than the ship. Thus, they can react to it as they choose. With the exception of the Greater Shearwater, very few birds were recorded sitting on the water. Birds seen flying past within 1 000m of the ship either ignored (five species), flew towards (19 species), or deviated from (seven species), the ship (Fig. 6). The low detectability of the divingpetrels strongly influenced their apparent attraction. Very few birds were seen in category C. This was due largely to the difficulty of detecting them at this range (see also Wiens et al. 1978). The ship's effect on birds beyond 1 000m could not be ascertained. Ship-following was practised by 12 species (Fig. 7). Eighteen species were classed as non-followers, and one species showed no preference. All but three species followed the ship at least once. Overall, attraction was commoner than avoidance (Fig. 8). Giant petrels were attracted more than any other species. Only a few species (eg. Blue Petrel, Cory's and Little shearwaters, and divingpetrels) were attracted towards the ship but did not follow it (Fig. 8). Ship-following species which apparently avoided flying past close to the ship (eg. the Whitechinned Petrel) may have been omitted erroneously from the category A records. Seabirds following the ship tended to circle it, usually within distance category A. Since individuals rarely could be distinguished, many birds, assumed to have been circling, might actually have been flying past. This may have reduced the numbers recorded close to the ship, resulting in an underestimate of the

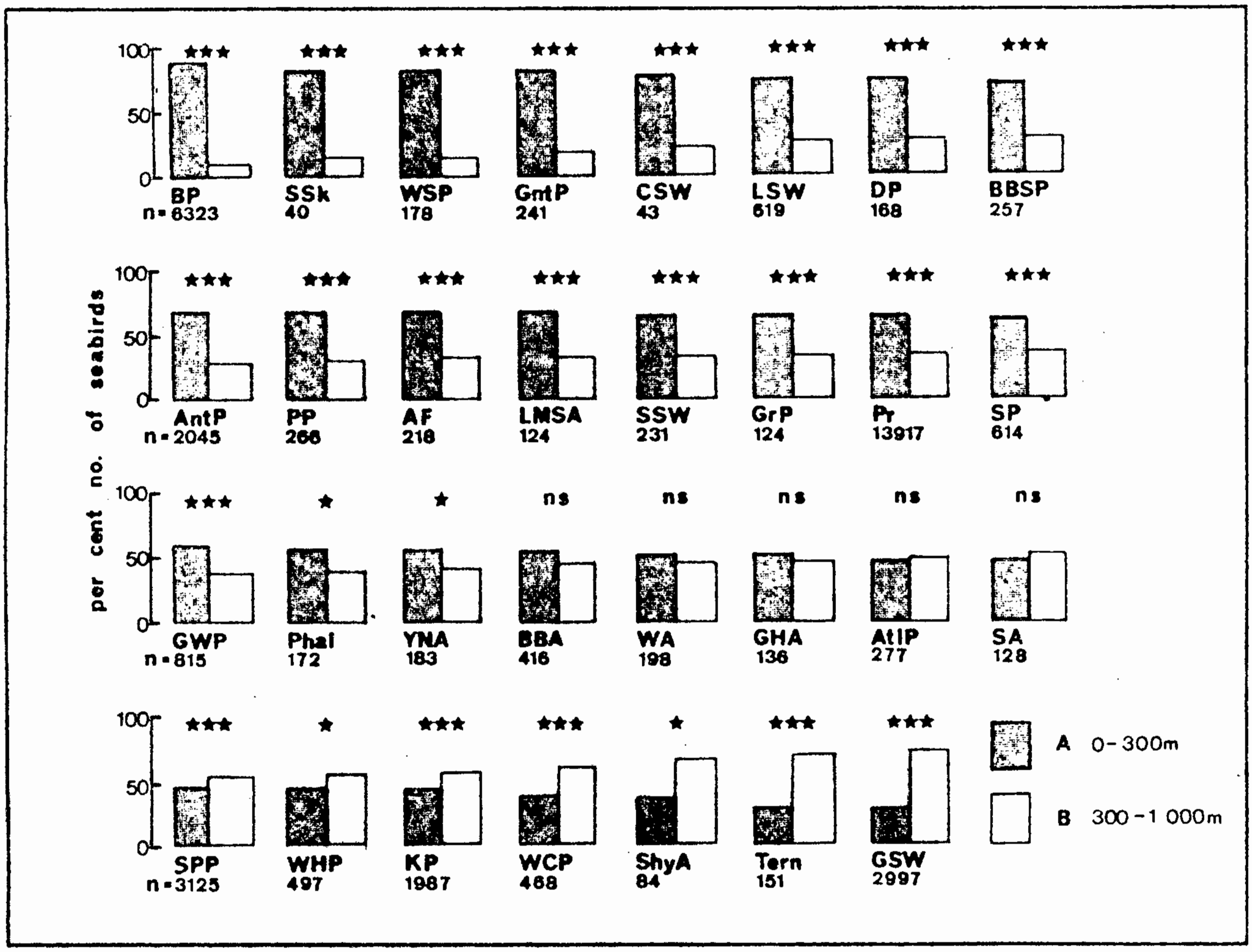

FIGURE 6. Relative frequency (%) of individuals of 31 pelagic seabird species according to the distances at which they were observed flying past the moving ship. A = 0 - 300m; B = 300 - 1 000m. Chi square (Sokal & Rohlf 1969) significance denoted by NS = p > 0.1; * = 0.01 < p < 0.1; ** = 0.0001 < p < 1.01; *** = p < 0.0001. The total number of individuals (n) recorded within 1 000m of the ship is given for each species. Species' name abbreviations in all figures are listed in Appendix 1

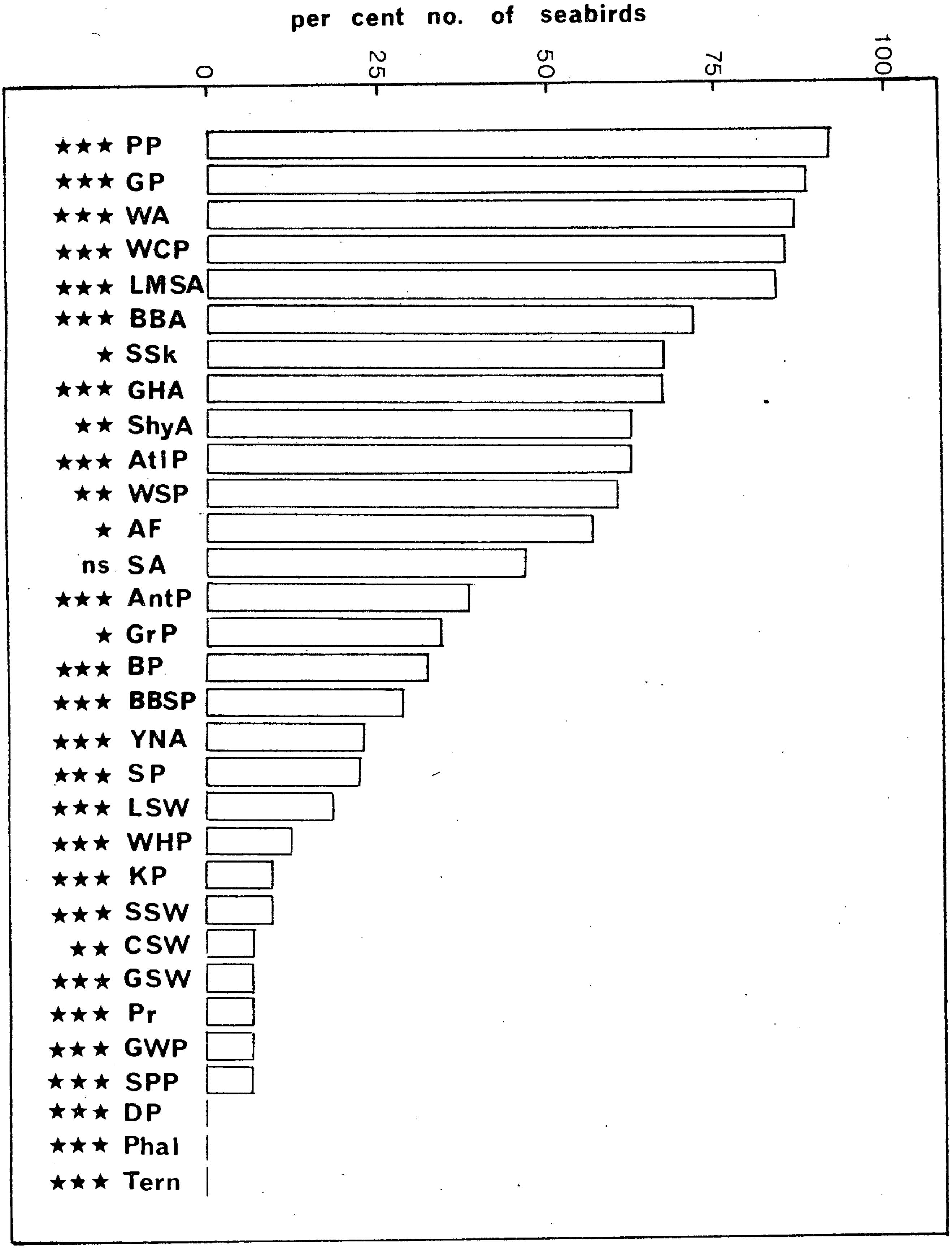

FIGURE 7. Relative frequency (%) of individuals of 31 pelagic seabird species following the moving ship. Chi square significance as in Figure 6

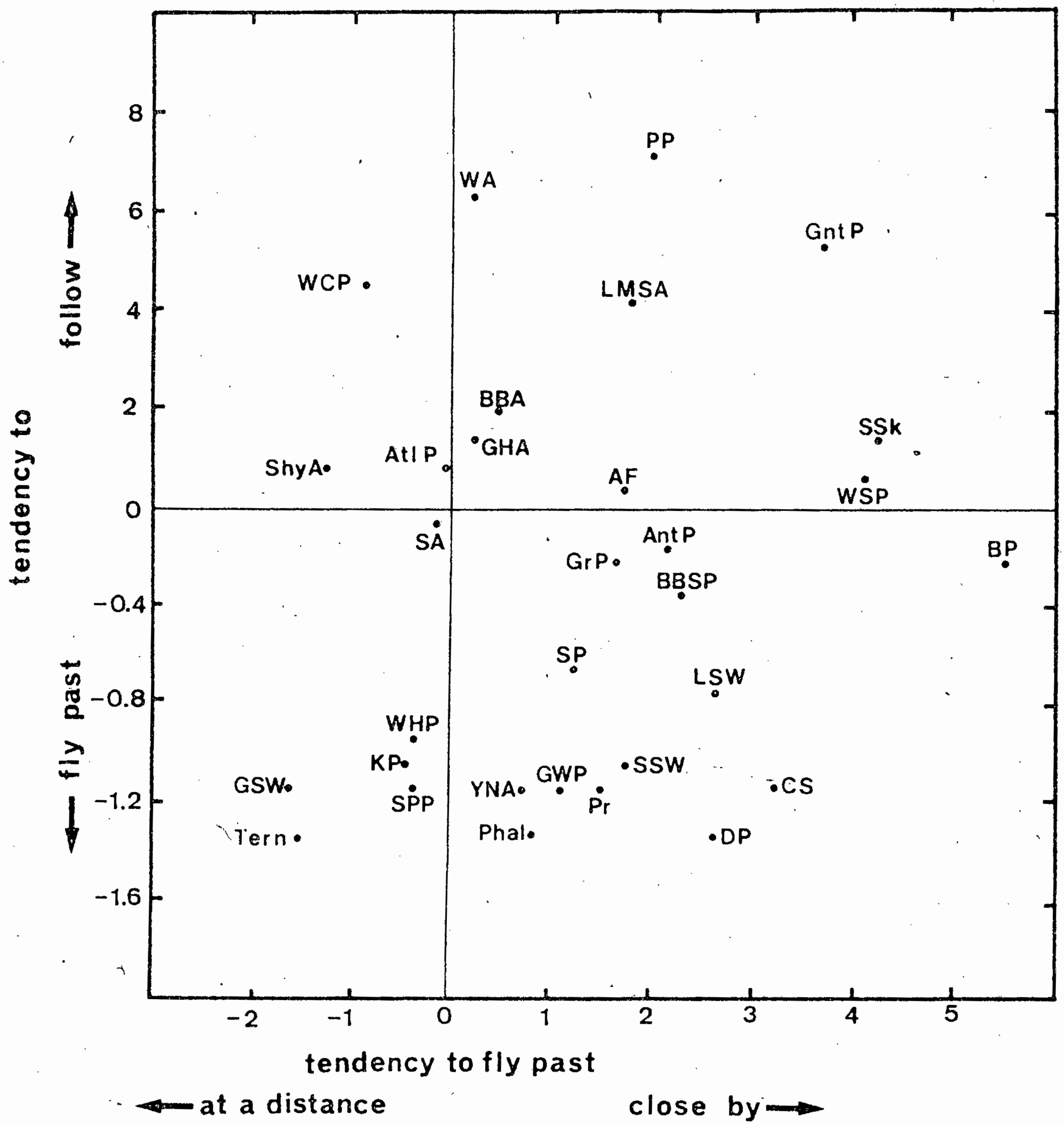

FIGURE 8. Overall responses (attraction versus avoidance) of 31 pelagic seabird species to the moving ship as calculated by correspondence analyses (Greenacre 1978). Projections onto the horizontal and vertical axes show the correspondence analyses on the distance category, and following/flying past data, respectively. The species plotted farthest from the origin showed the greatest reaction to the ship

effect of attraction. Species apparently least affected by the ship were Softplumaged, Whiteheaded, and Kerguelen petrels. The statistical significance of their avoidance is due largely to the high numbers of individuals recorded (Fig. 6).

The tendencies for the 12 species to follow the ship (Fig. 7) may have been exaggerated by a few individuals being recorded in more than one stern count (ie. individuals following for more than one hour). However, the mean times individual birds spent following the ship (Table 3) were shorter than are generally accepted (Murphy 1914, Dixon 1933). These times, which match Peakall's (1960) observations on following Wandering Albatrosses, may be underestimates, since many longer records were not completed when separation of individual birds became uncertain. The results (Table 3) indicate high "turn-over rates" of birds following the ship. The strong following tendencies of the seven species timed (Fig. 7) were therefore due to many individuals, rather than a few individuals being counted again and again, and are representative of the species.

Different feeding methods are used by species attracted to, and those avoiding, the ship. The ship-followers are mainly scavengers, whilst non-followers use a variety of feeding methods. Species most attracted to refuse discarded from the ship were Wandering Albatross, Blackbrowed Albatross and giant petrels. Procellariiformes feed mainly at night when their prey migrate to the surface (Imber & Berruti 1981). Few birds appeared to follow at night. During the day, instead of sitting on the water, which may use more energy than non-flapping flight (Kanwisher et al. 1978), the birds may fly randomly near where they last fed. Birds may be attracted towards, and follow, ships for the additional

Table 3: Time (min.) individual seabirds spent following the ship.

	Number counted	Maximum time	Average time
Wandering Albatross	13	582	80,5
Greyheaded Albatross	2	5	4
Shy Albatross	2	50	34
Blackbrowed Albatross	4	35	17,8
Lightmantled Sooty Albatross	5	10	6,2
Southern Giant Petrel	6	42	21,5
Antarctic Fulmar	3	26	11,3

bonus of food, in the form of garbage, during the day. The species attracted most strongly are also common around fishing trawlers off southwestern Africa (Sinclair 1978), where they get an abundance of fish offal.

Another feature attracting birds to a moving vessel may be ship-generated air-streams in which birds can glide, and thus save energy. Whilst following, Wandering Albatrosses spent more time directly above the ship's wake than Lightmantled Sooty Albatrossess (Table 4), which tended to fly alongside, apparently using the upward-directed air-streams generated by the ship. Wandering Albatrosses, while also benefiting from these winds, apparently were positioned better to obtain discarded refuse. Lightmantled Sooty Albtrosses rarely alighted next to garbage, so food is unlikely to be the attractant of this species. Generally, albatrosses tended to use upward-directed air-streams on the windward side of the ship. When circling the ship, these birds flew slowly past close to the windward side, and returned by flying much faster and farther from the ship. Birds kept close to the water on the leeward side, but flew much higher on the windward side. The large albatrosses' characteristic non-flapping flight is suited for taking advantage of these winds. Non-following species attracted to the ship (Fig. 8) also could have benefited from its air-streams, but these benefits would have been brief and probably not the ultimate cause of attraction.

Reactions to the stationary vessel

Reactions to a stationary vessel should be more accentuated than those to a moving vessel because of the longer time available for the reactions to be effected. This is particularly true of

Table 4: Time (min.) spent following in, and out of, the wake of the ship by Wandering and Lightmantled Sooty albatrosses.

	Total time observed	% time in wake	% time out of wake
Wandering Albatross	174	25,3	74,7
Lightmantled Sooty Albatross	44	13,9	86,1

attraction: once attracted, birds need only stay in the area for the effect to be cumulative. Ten species were recorded at 12 oceanographic stations (Table 5). When the ship stopped, the mean number of species increased from 3.1 (vessel stopping) to a plateau of 4.5 within the first hour, whilst the numbers of individuals increased four-fold (Fig. 9). Most of the birds that accumulated during the stations stayed behind when the ship began moving again.

Four trends in the changes in numbers of individuals were evident: those generally increasing, those generally decreasing, those increasing and then decreasing, and those fluctuating randomly or maintaining their initial numbers. The smaller fluctuations within these trends result from birds sitting on the water, drifting out of view, and returning later <u>en</u> <u>masse</u>. This was particularly relevant for the Wandering Albatross and the Whitechinned Petrel. No trends were evident when the ship remained stationary for longer than one hour (five stations).

Most (four out of 10) species increased in abundance. The Antarctic and Blue petrels (Table 5) had the largest increases in absolute numbers. These two species were not habitual ship-followers (Fig. 7) and, therefore, the increases probably were not due to their catching up with the ship after it had stopped. Wandering Albatrosses and, to a lesser extent, Antarctic Fulmars did follow the ship (Fig. 7). Their initial peaks of abundance (Table 5) at five and 10 minutes, respectively, were due to birds catching up with the ship from its wake.

The only species to decrease steadily in abundance was the Lightmantled Sooty Albatross (Table 5). These birds did not sit on the water, so their decrease was real, and not an artefact caused

Table 5: Changes in relative abundance (%) and mean maximum numbers of 10 pelagic seabirds (absence excluded) around ship during the first hour after stopping.

	Relative abundance per five-minute scan													Mean maximum numbers	No. stations observed
	0	5	10	15	20	25	30	35	40	45	50	55	60		
Antarctic Petrel	2	4	36	37	42	42	48	55	58	57	62	73	100	65,0	4
Blue Petrel	19	49	60	39	53	48	45	76	72	67	89	100	93	21,3	9
Wandering Albatross	44	67	33	56	56	67	89	67	89	100	100	100	93	1,5	7
Antarctic Fulmar	29	29	53	41	41	47	82	82	59	71	100	94	100	1,4	12
Lightmantled Sooty Albatross	92	89	100	87	95	56	67	51	46	59	49	56	56	4,9	8
Prions	7	27	20	40	53	40	33	100	47	33	33	20	0	5,0	4
Snow Petrel	29	43	57	29	29	57	71	71	100	14	29	14	43	1,8	4
Pintado Petrel	42	50	75	58	75	67	100	100	33	75	67	25	67	1,3	9
Kerguelen Petrel	8	33	67	42	42	92	100	100	42	67	83	92	75	1,3	9
Whitechinned Petrel	78	58	33	63	65	65	80	23	90	90	100	70	90	5,0	10

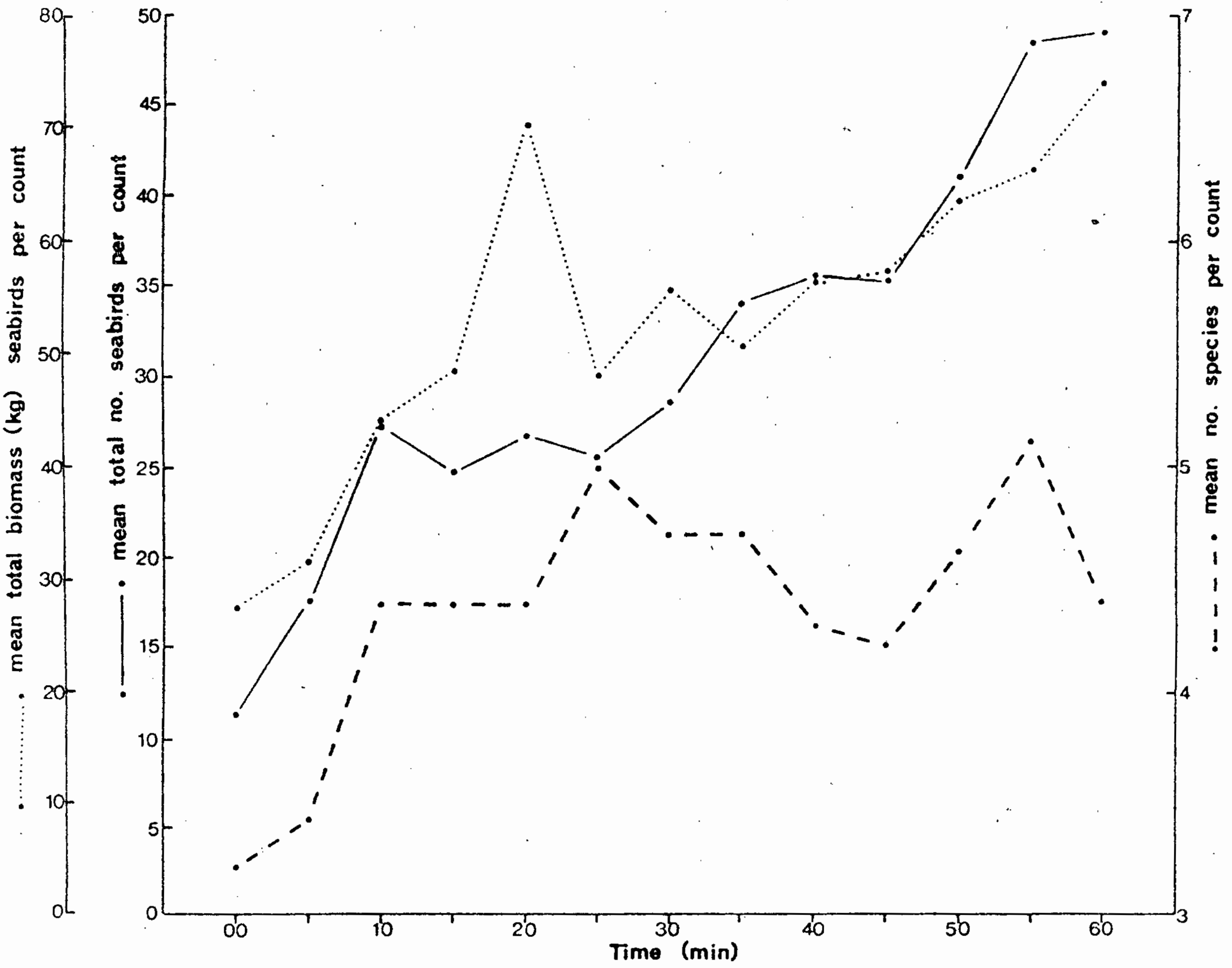

FIGURE 9. Mean total number of individuals (continuous line), species (dashed line) and total biomass (dotted line) for pelagic seabirds during the first hour after the ship had stopped at 12 oceanographic stations

by their drifting out of sight. This lends support to their apparent lack of interest in the ship as a potential food source.

Prions increased to peak numbers at 35 minutes (Table 5), and decreased steadily thereafter. The moving ship apparently had no effect on them (Fig. 8), and their abundance-trend on station is puzzling. Snow Petrels and Pintado Petrels (Table 5) reached maximum numbers at 30 - 40 minutes, and varied considerably thereafter. Pintado Petrels followed the ship more than any other species (Fig. 7), and it is possible that they took a while catching up with the ship after following at a distance. I cannot explain the erratic changes in the numbers of Snow and Pintado petrels.

Numbers of Kerguelen and Whitechinned petrels fluctuated without apparent pattern (Table 5). Kerguelen Petrels avoided the ship so their irregular presence at the stations was probably coincidental.

Two possible causes of attraction are increased food availability and shelter in the lee of the ship. Birds may be attracted either to the ship itself, or to aggregations of birds already there, or both. To ascertain which is the attractant, six species present simultaneously at six of the stations were investigated (Fig. 10). (The Kerguelen Petrel has been omitted from Figure 10 because of the incidental nature of the species' presence.) Antarctic Fulmars, Blue Petrels and Wandering Albatrosses all more than doubled their numbers during the one-hour period. Lightmantled Sooty Albatrosses and Whitechinned Petrels were present in relatively high numbers at the beginning of the stations, and increased only slightly throughout the hour. When the ship stopped, the latter species began circling and/or sitting within

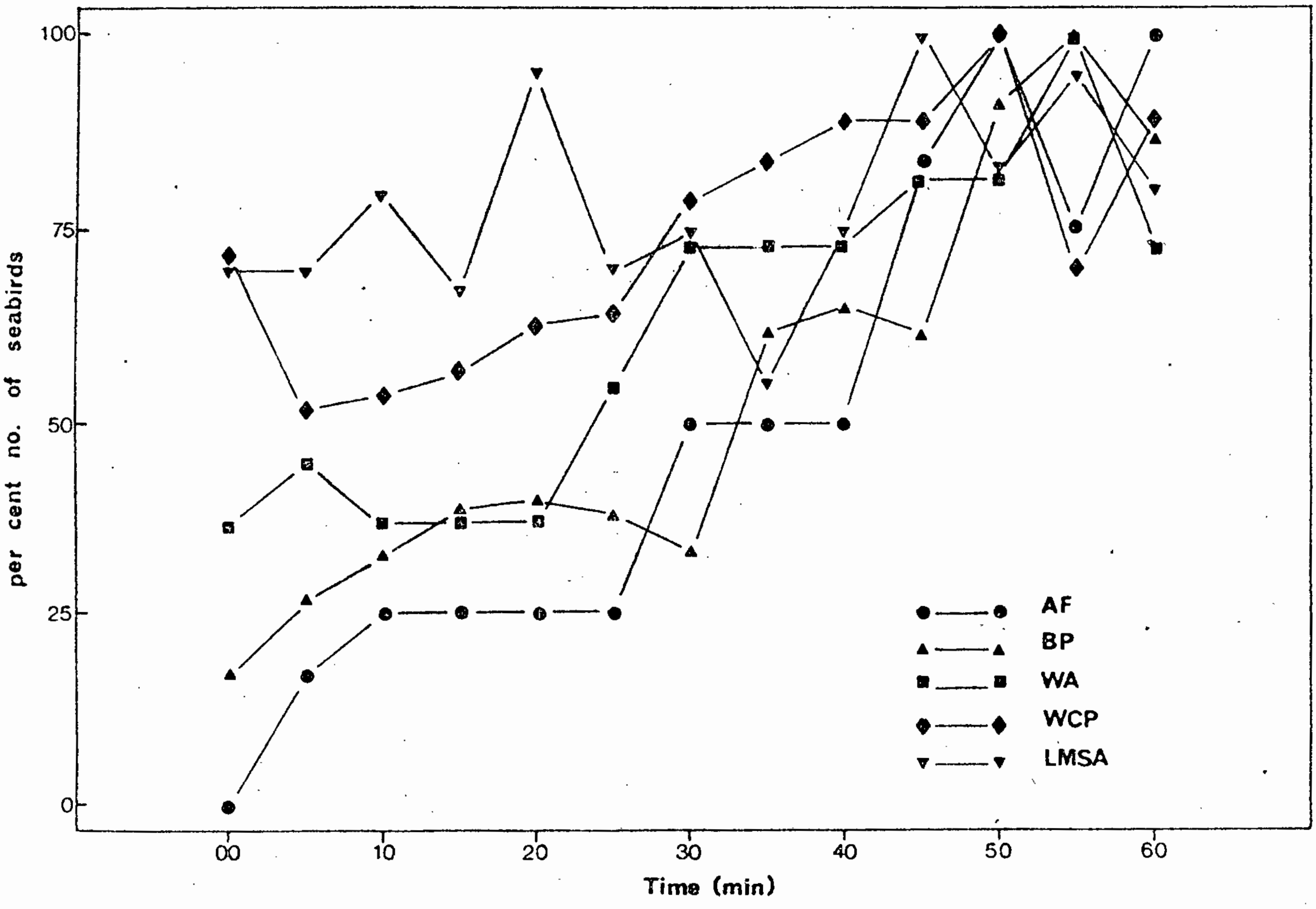

FIGURE 10. Changes in the relative abundance of five pelagic seabird species occurring simultaneously around the ship during the first hour at six oceanographic stations

500m of it, perhaps signalling the presence of potential food to birds more distant from the ship. Birds settling on the water showed no preference for a particular side of the ship in relation to wind direction. They apparently were not seeking shelter from the ship. I suggest that the Lightmantled Sooty Albatross and, particularly, the Whitechinned Petrel may have been acting as "nuclear", or "catalyst" species (see Sealy 1973, Wiens et al. 1978), attracting Antarctic Fulmars, Blue Petrels and Wandering Albatrosses towards the ship during the first 50 minutes at six stations. Similar analyses of birds at fishing trawlers, where food is available and the numbers of birds are much higher, should elucidate the patterns of feeding-flock formation.

Assessments of relative abundance from a stationary ship are less accurate than from a moving ship. The differences in the results of these two census methods became more pronounced the longer the ship was stationary. It is reasonable to assume that the total number (or biomass) of birds counted at the beginning of a station was not an underestimate, since the tendency to avoid the ship was minimal (Fig. 6). Indeed, these birds are primarily ship-following species (Fig. 7), and since they are mostly large (Appendix 1), a biomass assessment at the start of a station is likely to be an overestimate. Again, this becomes more exaggerated the longer the ship remains stationary. After only 20 minutes, the abundance had increased by 142% and biomass by 174% (Fig. 9). A count of Antarctic Petrels 10 minutes after the ship had stopped would have resulted in an overestimate of 1 760% (Table 5).

CONCLUSIONS

1. Many species are attracted strongly towards, and follow, the ship whilst few avoid it. Counts of Softplumaged, Whiteheaded, and Kerguelen petrels flying past the ship provide the most accurate estimates of species' abundances available.

2. Species most strongly attracted to the ship are scavengers. Food is regarded as the ultimate attractant of seabirds to ships.

3. The larger species, and the Lightmantled Sooty Albatross in particular, make use of wind currents generated by the ship. Ship-generated wind currents are regarded as a proximate attractant.

4. The accumulation of species around the stationary ship results in inaccurate censuses. Counts from the moving ship more accurately reflect species' abundances.

PART 3

ECOLOGICAL STRUCTURE OF A PELAGIC SEABIRD COMMUNITY IN THE SOUTHERN OCEAN

ABSTRACT

The pelagic avifauna (excluding penguins) of the African sector of the Southern Ocean is described quantitatively, based on 3 005 10-minute observations of seabirds during seven oceanic cruises in April 1979 - April 1980. The avifauna is characterized according to species richness, diversity, abundance and biomass. These indices are correlated with groups of birds ordered into principal diet and feeding-method classes. Birds eating either plankton, cephalopods or a mixed diet accounted for 51, 23 and 22% of the total avifaunal abundance and 22, 49 and 25% of the total biomass, respectively. Piscivores were represented poorly. Planktivores were especially abundant south of the Antarctic Convergence and, to a lesser extent, at the Subtropical Convergence. Cephalopod-eaters were most abundant north of the Subtropical Convergence. The greatest abundance of omnivores occurred where planktivores and cephalopod-eaters were least abundant. The distribution of the planktivores and cephalopod-eaters is related tentatively to the availability of the birds' principal prey.

INTRODUCTION

Included in the objectives of the international BIOMASS research programme is scientific knowledge of the roles of seabirds as consumers in food-webs of the Southern Ocean. More particularly, detailed, quantitative assessments of the interactions between seabirds and their principal prey are required in developing strategies for the conservation-management of the Southern Ocean's living resources, chiefly krill and cephalopods which also are the seabirds' main food (Fig. 1, Anon 1977).

Almost all modern ecological studies of seabirds in the Southern Ocean have been carried out on land at the birds' breeding stations (Croxall in press). Consequently, very little is known, in quantitative terms, about the distribution and abundance of non-breeding seabirds in the pelagic environment. Such information is of fundamental importance in assessing the impact of the birds on prey populations in the Southern Ocean. Here I report a first quantitative description of the distribution, abundance and ecological structure of the pelagic avifauna (volant species only) of the African sector of the Southern Ocean.

I characterize the avifauna according to species richness (BSR), diversity (BSD), abundance and biomass and correlate these indices with groups of birds ordered into principal diet and feeding-method classes. These trophic arrangements are preliminary and provisional, because there is a dearth of quantitative information on the diets of seabirds during the non-breeding, pelagic phases of their life-cycles. Nevertheless, the analyses do yield ecological patterns potentially useful in comparing communities of seabirds in different oceanic regions and in generating hypotheses concerning the roles of seabirds as predators in the Southern Ocean.

METHODS

Seabirds were recorded during seven separate cruises of the M.V. S.A. Agulhas in 1979 and 1980 (Fig. 2). All birds flying past the moving ship (mean speed = 24km/h) and sitting on the water in a 1km-wide transect were counted during 3 005 10-minute observation periods (Part 1). The ship usually arrived at islands (Prince Edward-Marion, Tristan-Gough and Bouvet) and Antarctica in the early morning, and departed from them in the afternoon. Hence, observations of seabirds were not made within approximately 250km of land.

Avian community structure is described in terms of species richness (total number of species at a particular observation station), Shannon-Wiener species diversity index ($HI = -\Sigma p_i \log_{10} p_i$ where p_i is the proportion of the i^{th} species in the community at a particular observation station), abundance (total number of all birds at an observation station) and biomass (total live-weight of all birds at an observation station). Four diet and six feeding classes are recognized (Appendix 1). I define omnivores as species not easily classified as plankton-, cephalopod- or fish-eaters.

RESULTS AND DISCUSSION

General diversity

The study area contained a high total number (42) of volant species which were dispersed widely, as indicated by the relatively low mean species richness per observation station (Table 6). Neritic zones, and particularly those in which

Table 6: Species richness (numbers of species) and abundance (numbers of individuals) of seabirds in regions.

Region	Species richness			Abundance		Observation period	Source
	Mean	Maximum	Total	Mean	Maximum		
North Atlantic							
pelagic	5.5/7.7h	12/8.7h	22+	16.5/h	230/h	Sept-Oct	Harris & Hansen 1974
offshore			6	5.1/10min		Feb-March	Brown 1979
offshore			15+	4120.4/h		June-Aug	Joiris 1976
South Atlantic							
pelagic	6.9/9h	16/10.8h	31+	24.9/h	97/h	Sept-Nov	Harris & Hansen 1974
pelagic	12.3/4.9h	15/4h	24	156/h	2543.3/h	Mar-April	Jehl *et al.* 1979
offshore	9.5/3.9h	10/2h	19	295.5/h	4361.5/h	June-Aug	Jehl 1974
offshore	5.9/station	14/station	33	58.2/station	1149.0/ station	Whole year	Abrams & Griffiths 1981
North Pacific							
offshore	18.3/7.4h	23/8h	25	767.7/h	2557.2/h	April-Oct	Wahl 1975
offshore	5.2/2h	6/h	17	7601.5/h	133333.3/h	June-Sept	Arnold 1948
South Pacific							
pelagic	5.9/day	11/day	26	37.6/day	80/day	July-Sept	Szijj 1967
pelagic	6.7/8.8obs	11/3obs	37	16.9/obs	162/obs	Dec-Feb	Ozawa *et al.* 1968
offshore	10.1/2h+	16/2h+	25	139.7/h	788/h	May-July	Jehl 1973
North Indian							
pelagic			12	12.9/h	96/h	Jan,Feb & May	Gill 1967
South Indian							
pelagic			23	16.5/h	255/h	Feb-June	Gill 1967
Southern Ocean	3.3±1.8/10min	14/10min	42	27.4±140.5/10min	4298/10min	Whole year	This study

upwelling occurs, generally contain greater avian species diversity per unit area than pelagic environments (Table 6, Jespersen 1930). Thus, species richness and abundance on the continental shelves of south-western Africa (Abrams & Griffiths 1981) and south-eastern Arabia (Bailey 1966), are higher than those in our area (Table 6). The continental shelf of Argentina, however, supports an only slightly higher species richness, but lower abundance (Cooke & Mills 1972, Jehl 1974, Linkowski & Rembiszewski 1978), probably due to the low incidence of upwelling in the area (Murphy 1936).

The relatively low mean species richness and high abundance in our area (Table 6) are due in part to a few observations of large aggregations of single species, and the presence of three island groups and two nearby continents. The apparently lower avian abundance in the South Pacific (Szijj 1967) may reflect a paucity in breeding stations in that area.

Trophic structure

Plankton-eaters, taking mainly crustaceans, comprised 51% of the total abundance but only 22% of the total biomass of seabirds (Table 7). They are mainly prions and the Blue Petrel (Appendix 1), and they feed mainly as surface-seizers and surface-filterers (Table 8). However, the high abundance (Appendix 1) of the Blue Petrel (the only surface-seizer in the plankton-eating group), observed at relatively few stations, heavily biased the correlation between diet and surface-seizing. Reanalysis after $\log_{10}$ transformation of the data emphasized the association between planktivores and surface-filterers, and decreased the importance of surface-seizers (Table 8).

Table 7: Percentage food-type composition of the avifauna in the African sector of the Southern Ocean. Absolute total figures are given in parentheses. See Appendix 1 for ordering of species.

	Abundance (75 779)	Biomass (39 662 kg)
Planktivores	51.0	22.3
Cephalopod-eaters	23.2	49.3
Piscivores	3.3	3.3
Omnivores	22.5	25.1

Table 8: Coefficients of correlation (r) between food-type and feeding-method groups in seabird assemblages in the African sector of the Southern Ocean. Underlined values indicate categories which together define trophic groups of seabirds. Figures in parentheses are correlation coefficients between $\log_{10}$ transformed groups.

FEEDING METHOD	FOOD TYPE			
	Plankton	Cephalopods	Fish	Mixed
Surface-seizing/ scavenging	.786 (.190)	.009 (.338)	.007 (.135)	.229 (.730)
Surface-filtering	.553 (.845)	-.008 (.153)	.013 (.043)	-.033 (-.094)
Plunging	-.006 (-.011)	.000 (.073)	.040 (.114)	-.011 (-.049)
Pursuit-plunging/diving	-.022 (.112)	.999 (.491)	.069 (.539)	-.009 (.049)
Dipping/pattering	.001 (.063)	.003 (.050)	.718 (.293)	.010 (.061)
Piracy	-.002 (-.012)	-.003 (.018)	-.008 (-.004)	-.009 (.005)

Cephalopod-eaters made up 23% of the total abundance and, being mainly large-bodied albatrosses (Diomedeidae) and the Greater Shearwater (Appendix 1), accounted for 49% of the total avian biomass (Table 7). Log_{10} transformation of the data decreased the numerical importance of this species (Table 9). Most (71%) individuals were Greater Shearwaters, classed as pursuit-plungers (Appendix 1). However, $\log_{10}$ transformation revealed the importance of surface-seizing in the group as a whole (Table 8).

Piscivorous species were low in abundance and biomass (Tables 7 & 9). Only two of the five species recorded are breeding residents. Two are Holarctic migrants (Appendix 1). Excepting the Sooty Shearwater, which is a pursuit-plunger, dipping into the surface water layer is the predominant feeding method of the piscivores (Table 8).

Omnivorous feeders, employing mainly surface-seizing and scavenging (Table 8), accounted for 23 and 25% of the avian abundance and biomass, respectively (Table 7). The Antarctic Petrel, Kerguelen Petrel and Softplumaged Petrel were the most abundant species. Kleptoparasitic species (Stercoraridae) were represented poorly (Appendix 1).

Spatial distribution

Analysis of the birds' distribution in relation to longitude, showed that abundance was greatest at about 12°W and 36° E (Fig. 11). These peaks were dominated by Greater Shearwaters (78%) and prions (93%), respectively. Most of the Greater Shearwaters were at five stations at which flocks of up to 4 200 birds were observed sitting on the water. The area east of 35° E included only seven observation stations. Nothing more can be said about

Table 9: Coefficients of correlation (r) between food-type groups, bird species richness (BSR), bird species diversity (BSD), abundance (numbers of individuals) and biomass (live-weight of individuals) of seabirds in the African sector of the Southern Ocean. Figures in parentheses are correlation coefficients between $\log_{10}$ transformed food-type groups and community indices.

	BSR	BSD	Abundance	Biomass	Plankton	Cephalopods	Fish
BSD	.829 (.843)	1.000					
Abundance	.098 (.635)	-.097 (.273)	1.000				
Biomass	.110 (.664)	-.037 (.387)	.883 (.832)	1.000			
Plankton	.032 (.390)	-.121 (.094)	.557 (.712)	.136 (.420)	1.000		
Cephalopods	.086 (.621)	-.034 (.513)	.798 (.375)	.979 (.632)	-.004 (.125)	1.000	
Fish	.117 (.294)	.061 (.125)	.087 (.215)	.072 (.223)	.001 (-.004)	.055 (.213)	1.000
Mixed	.036 (.355)	-.012 (.302)	.135 (.438)	.117 (.404)	-.023 (-.061)	-.010 (.034)	.015 (.016)

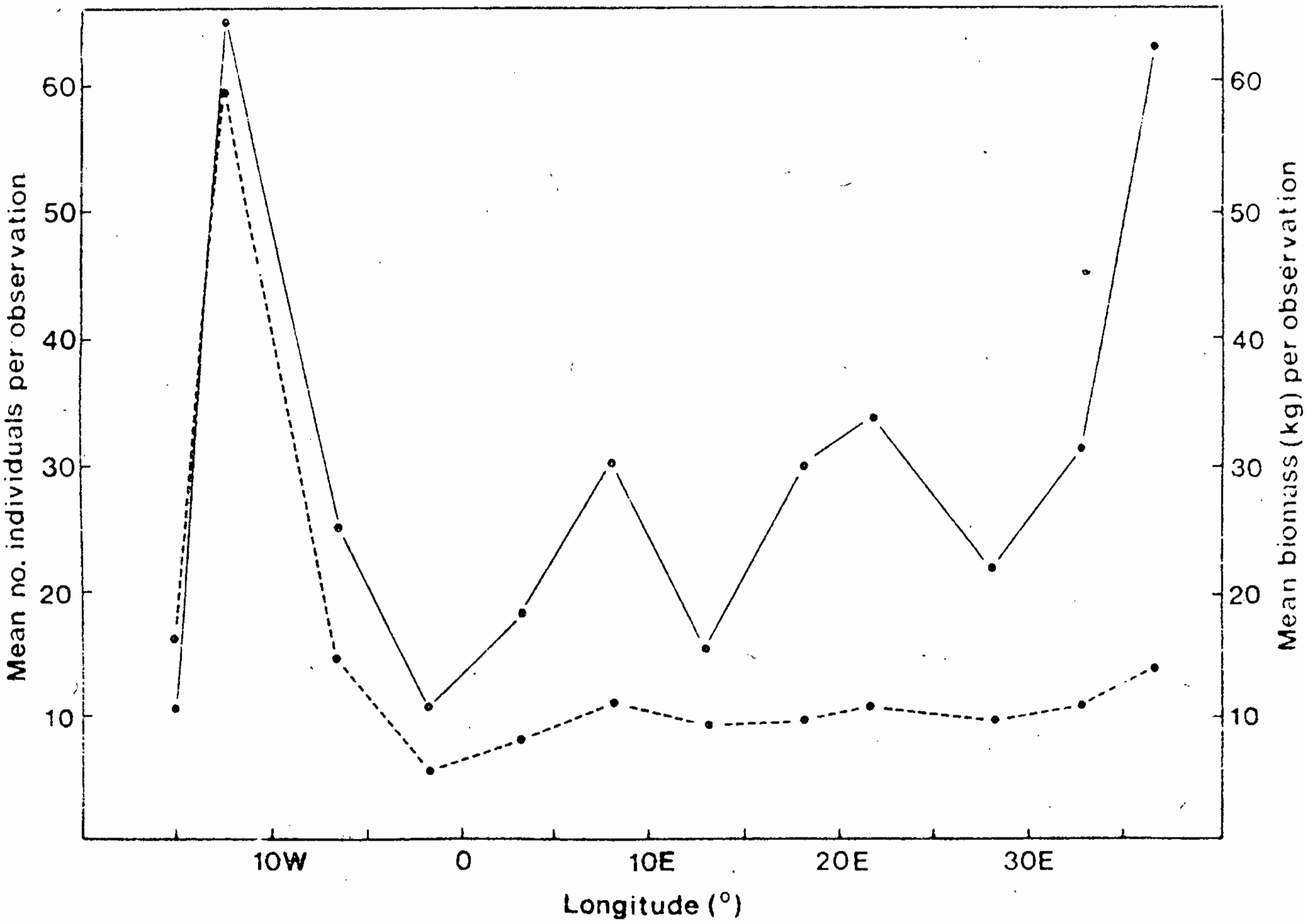

FIGURE 11. Longitudinal distribution of total abundance (continuous line) (F = 0.88, p = 0.4763) and total biomass (dashed line) (F = 1.29, p = 0.2704) of seabirds in the African sector of the Southern Ocean

these super-abundant concentrations of birds, because of the limited number of surveys of the areas in which they were encountered.

Species richness, species diversity, abundance and biomass of pelagic seabirds were not distributed randomly with respect to latitude (Figs 12 & 13). Mean species richness and diversity peaked at the Subtropical and Antarctic convergences (Fig. 12). Maximum species richness (11.0) and diversity (2.16) were recorded during an observation at the Subtropical Convergence. Maximum abundance and biomass occurred in the vicinity of the Subtropical and Antarctic convergences, respectively (Fig. 13). In the rest of the study area there were fewer than 20 birds on average per observation station, with the lowest abundance (7.2 individuals) occurring near the African continental shelf in the warm Agulhas Current.

Relatively large birds were abundant near the Subtropical Convergence, so that total avian biomass was greatest there, whereas smaller birds predominated in the community near the Antarctic Convergence (Fig. 14). Mean bird mass (and size) increased slightly in areas of sea-ice (Fig. 14).

The varying distribution of large and small birds reflects the occurrence of the two dominant trophic groups in the study area. Cephalopod-eaters, dominating avian abundance north of the Subtropical Convergence, decreased southwards to very low numbers near the Antarctic continent (Fig. 15). Planktivores, also numerous near the Subtropical Convergence, were especially abundant near the Antarctic Divergence (Fig. 15). Our current knowledge allows only speculative explanations for the apparently disjunct distribution of small and large birds.

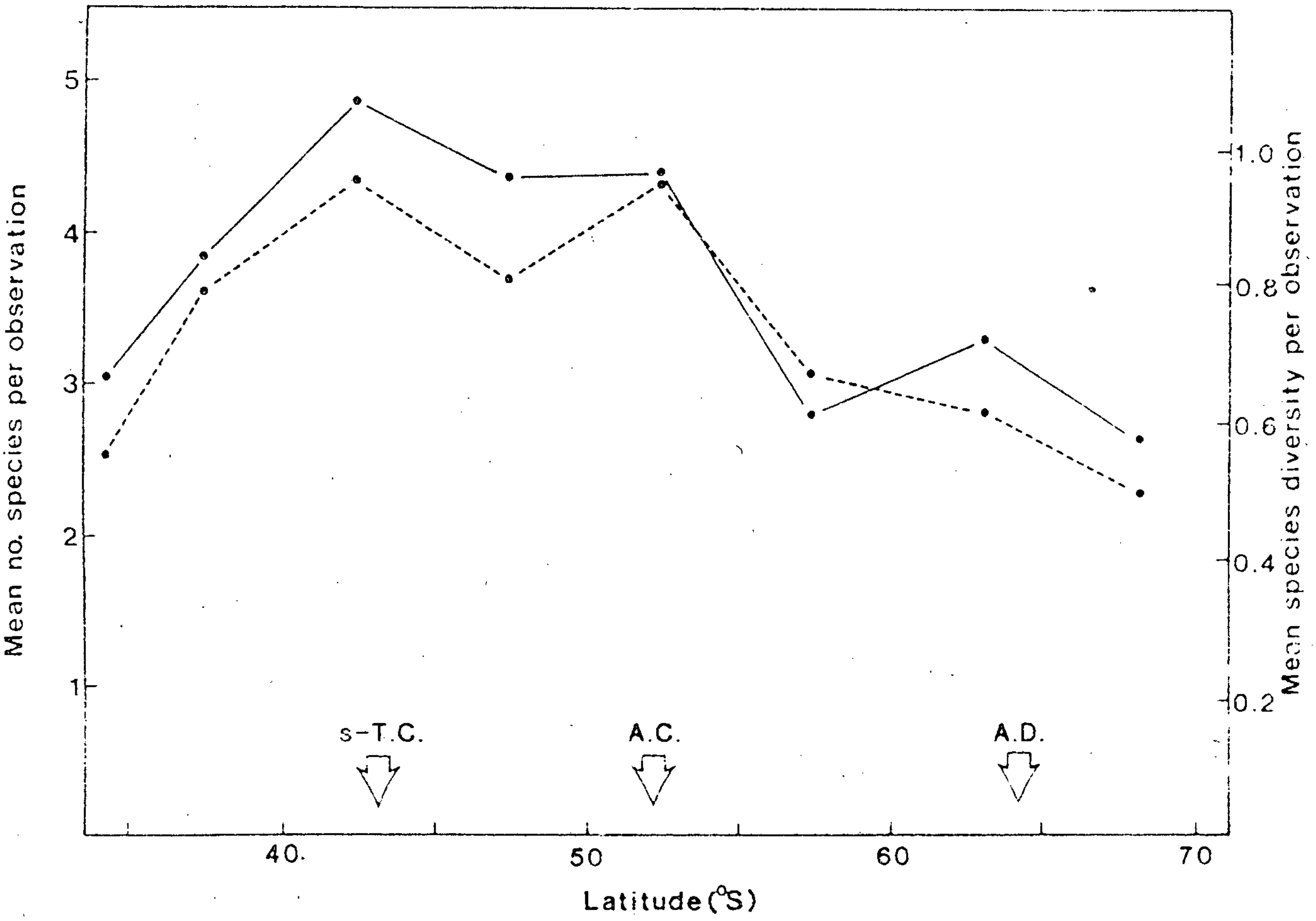

FIGURE 12. Latitudinal distribution of species richness (dashed line) ($F = 68.42$, $p < 0.0001$) and species diversity (continuous line) ($F = 28.83$, $p < 0.0001$) of seabirds in the African sector of the Southern Ocean. Approximate annual positions of the sub-Tropical Convergence (s-T.C.), Antarctic Convergence (A.C.) and Antarctic Divergence (A.D.) are shown

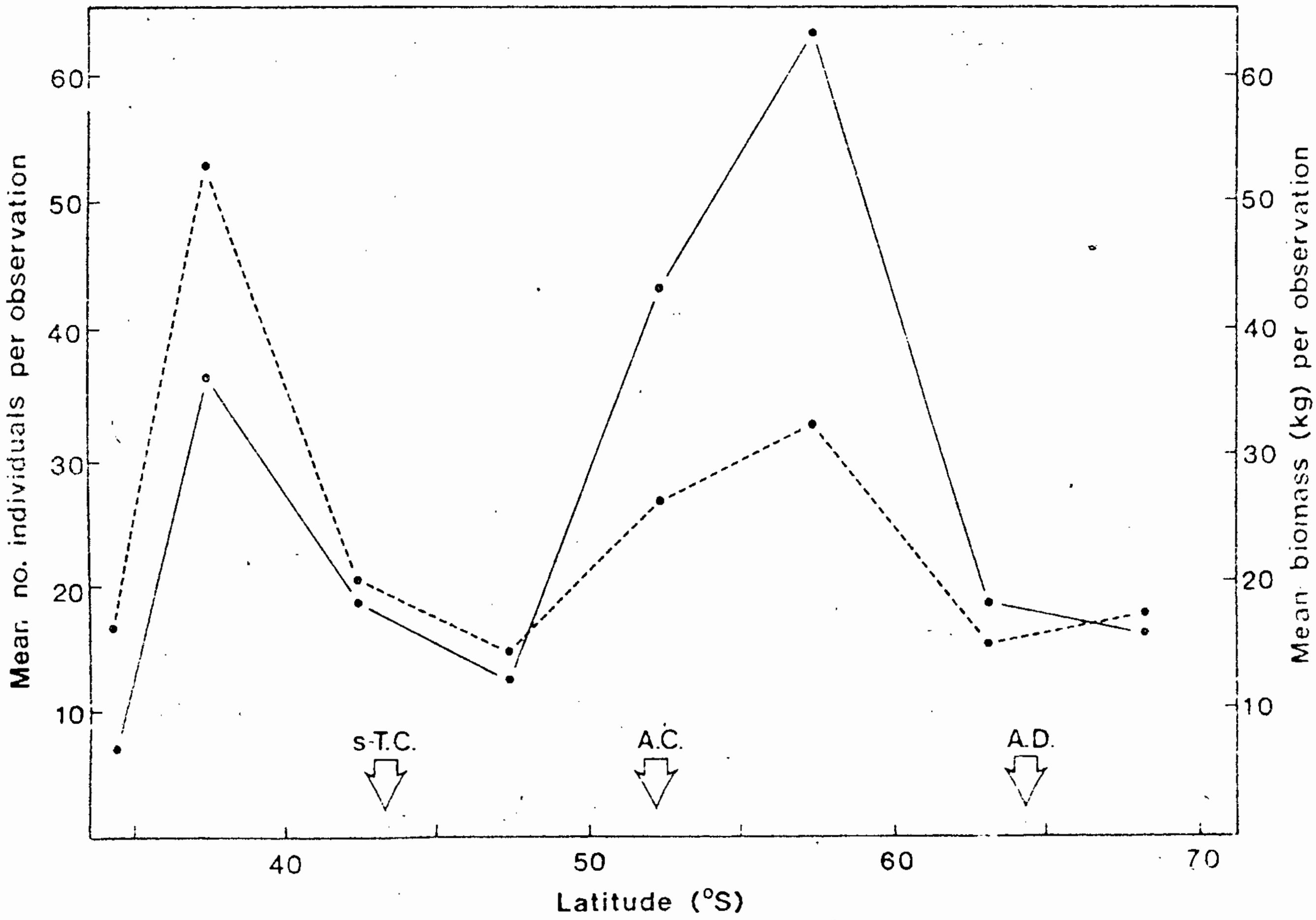

FIGURE 13. Latitudinal distribution of total abundance (continuous line) (F = 7.26, p = 0.0001) and total biomass (dashed line) (F = 3.36, p = 0.0181) of seabirds in the African sector of the Southern Ocean

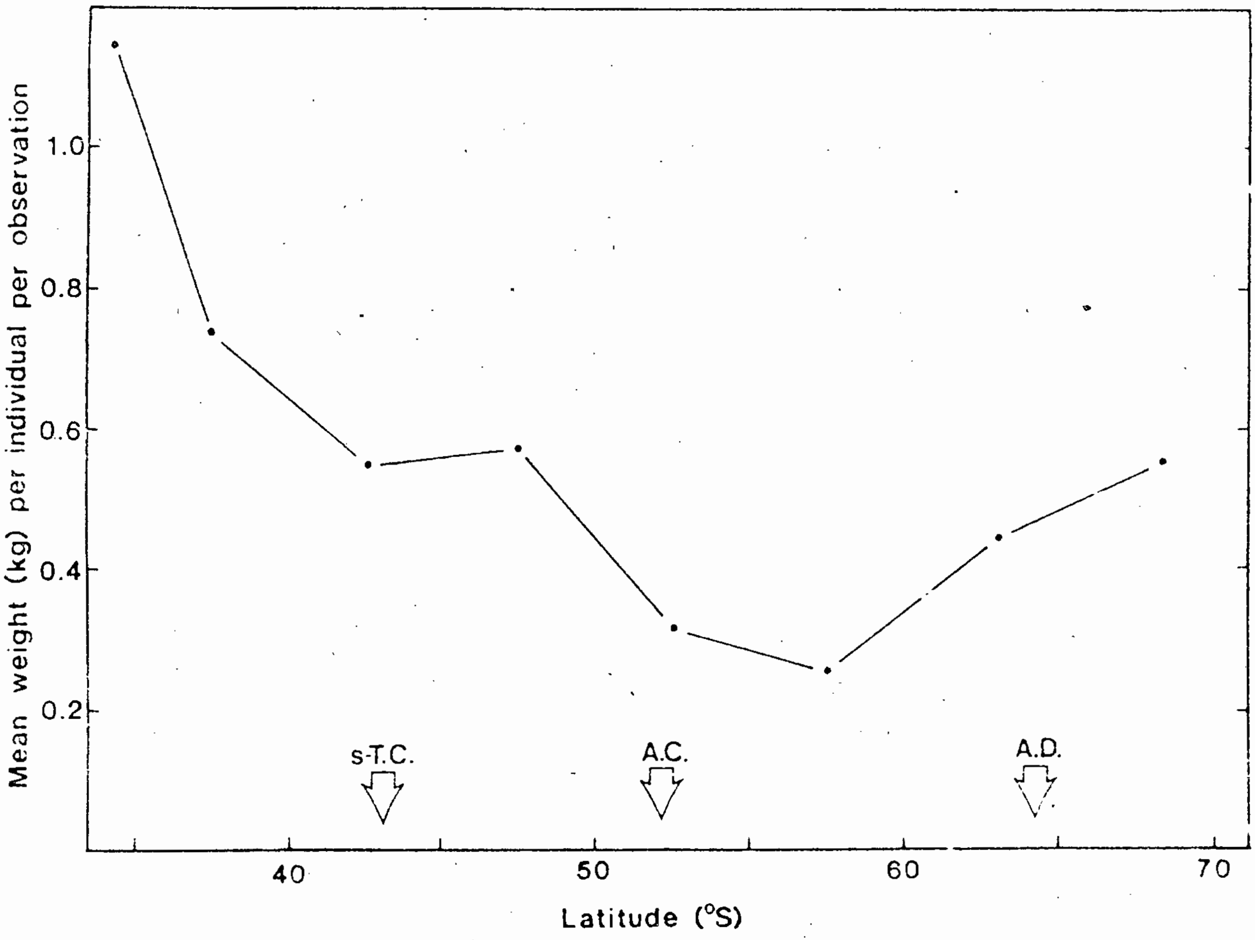

FIGURE 14. Latitudinal distribution of mean mass of individual birds ($F = 43.63$, $p < 0.0001$) in the African sector of the Southern Ocean

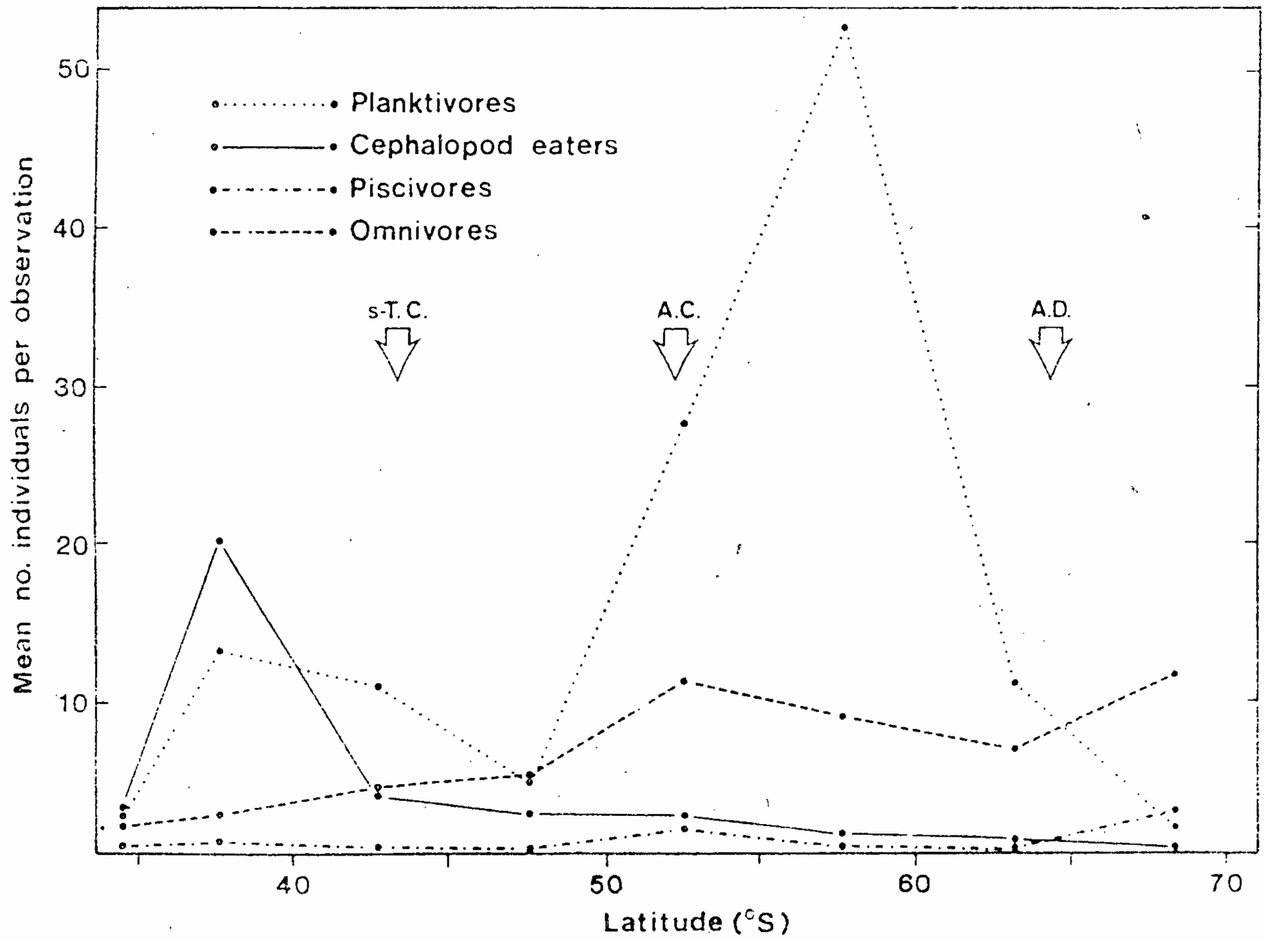

FIGURE 15. Latitudinal distribution of planktivores ($F = 6.45$, $p < 0.0001$), cephalopod-eaters ($F = 3.75$, $p = 0.0106$), piscivores ($F = 1.16$, $p = 0.3245$) and omnivores ($F = 14.68$, $p < 0.0001$) in the African sector of the Southern Ocean

Large birds generally have lower metaboloic rates and take larger prey than small birds (Schoener 1974). Large seabirds can fast for longer than small ones when breeding and moulting (Croxall 1982). Thus, large seabirds, potentially, are equipped to survive on irregularly occurring food sources (Ashmole & Ashmole 1967). Smaller birds must feed more frequently and, therefore, must have a reliable food source that allows feeding at regular intervals. The pattering flight (Withers 1979) of the smallest pelagic seabirds, the stormpetrels (Oceanitidae), appears to be an adaptation for almost continual feeding on abundantly available, small organisms at the air-sea interface. Such presumably reliably locatable, or renewable, concentrated sources of small food particles apparently are found mainly in areas where the planktivores were most abundant. Thus, the highest biomass of mesoplankton (excluding euphausiids) occurs in the region of the Antarctic Convergence between 48° S and 53° S (Foxton 1956). Concentrations of the Antarctic krill (mainly <u>Euphausia superba</u>), the biomass of which may equal the total biomass of all the other zooplankton (Holdgate 1967), occur in our study area in the vicinity of the Antarctic Divergence (Marr 1962, Makarov <u>et al</u>. 1970), where the density of zooplankton on the surface of the sea tends to be high (Fig. 3).

Very little is known about the distribution and abundance of cephalopods in the Southern Ocean, but their populations apparently are large (Everson 1977). Many species occur at the surface of the sea only during darkness (Roper & Young 1975). In high latitudes the short nocturnal periods during summer might reduce the availability of cephalopods to surface-feeding predators. Other cephalopod-eaters, such as whales and penguins, apparently are less affected, because of their ability to dive deeply.

The abundance of omnivorous birds increased steadily from the African continental shelf to peak at the Antarctic Convergence and in the pack-ice (Fig. 15), where plankton- and cephalopod-eaters were least abundant. Only the Snow Petrel, Antarctic Petrel and Arctic Tern (a piscivore), and presumably penguins (Prévost 1981), were abundant in the pack-ice. The presence of ice can affect seabirds in many ways (Divoky 1979). Although representatives of three orders of seabirds (Procellariiformes, Sphenisciformes and Charadriiformes), each foraging very differently, co-occur in areas of Antarctic pack-ice (Watson 1975), the ice generally precludes the presence of soaring Procellariiformes which are unable to become air-borne in the confined patches of open water, and therefore are unlikely to feed there (Part 5).

Piscivorous birds were abundant only in the highest latitudes (Fig. 15), where Arctic Terns were recorded in flocks of up to 213 birds sitting on ice floes. Epi- and meso-pelagic fish appear to be generally uncommon except in the vicinity of land masses and the ice-shelf (Everson 1981). There are no large populations of surface-schooling pelagic fish in the Antarctic zone (Everson 1981). The majority of fish species are bathypelagic or benthic (Andriashev 1965) and therefore are not readily available to predatory birds.

Temporal distribution

The mean number of bird species per observation was lower in the austral summer (3.17) than in winter (3.96). This probably reflects the summer concentrations of adults at breeding localities both in the study area and elsewhere in the Southern

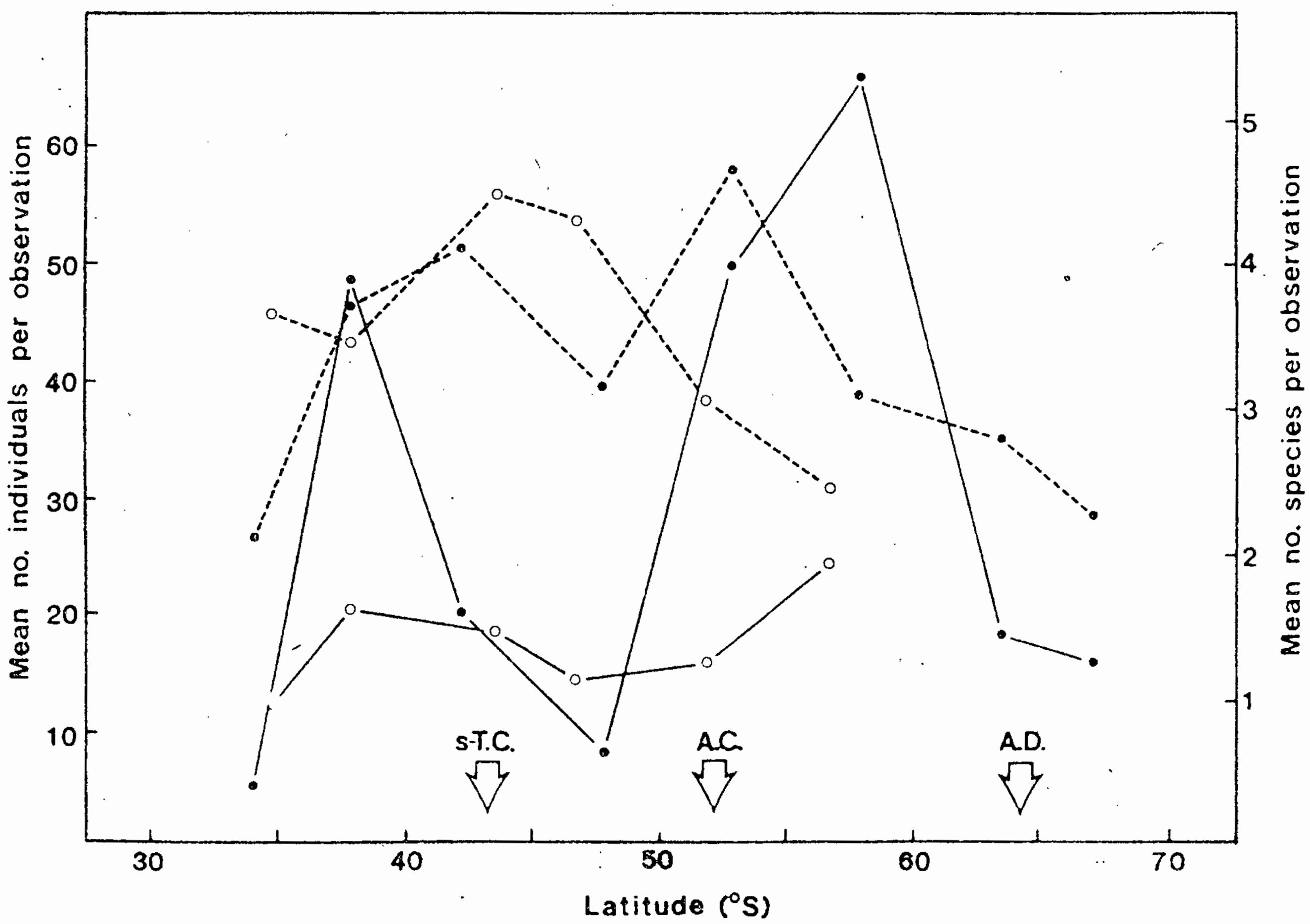

FIGURE 16. Latitudinal distribution of total abundance (continuous lines) and species richness (dashed lines) of seabirds during the austral summer (October - March) (dots) and winter (April September) (open circles) in the African sector of the Southern Ocean

Ocean. Breeding birds with short foraging ranges would have largely escaped observation, because we made very few observations near land. The presence in summer of Holarctic migrants is almost restricted to the continental waters of southern Africa.

Mean total abundance was higher in summer (28.3) than in winter (17.7). In winter, the birds, mostly released from their breeding stations, are wholly pelagic, resulting in a relatively uniform distribution of abundance (Fig. 16). Moreover, mean abundance in winter is reduced farther by the accumulation in the Benguela Current region of Southern Ocean species (Cooper & Dowle 1976, Abrams & Griffiths 1981).

CONCLUSIONS

1. At any one time and place in the African sector of the Southern Ocean, the avifauna is characterized by relatively few species which occur relatively abundantly.

2. Avian community indices (BSR, BSD, abundance and biomass) vary spatially and temporally with maximum values found in areas of environmental anomalies reputedly associated with high biological activity.

3. Planktivores are the most abundant birds, and dominate in the Antarctic zone, whereas cephalopod-eaters are dominant in terms of biomass and occur mostly in the Subtropical zone.

PART 4

RELATIONSHIPS BETWEEN THE DISTRIBUTION OF PELAGIC SEABIRDS AND SELECTED ABIOTIC FEATURES OF THE SOUTHERN OCEAN

ABSTRACT

The effect of five abiotic features (water temperature, air temperature, depth of ocean, wind strength and weather condition) on four indices and four trophic groups of the avifauna of the African sector of the Southern Ocean is investigated. None of the features shows strong linear association with the seabirds. However, seabirds do show significant preferences for specific ranges of the features. The types of physical environments in which each of the trophic groups are found most abundantly appear to suit the birds' feeding and flight capabilities.

INTRODUCTION

Pelagic avifaunas have been described broadly for different oceanic regions characterized by particular sets of abiotic features (Murphy 1936, Shuntov 1974). More deterministic approaches have shown, with varying success, associations between seabirds and distance from shore, salinity, air and water temperatures, barometric pressure and wind strength (Bailey 1968, 1971, Sanger 1970, Manikowski 1971, Cooper & Dowle 1976, Pocklington 1979, Abrams & Griffiths 1981, Ainley & Jacobs 1981). Combinations of oceanographic and meteorological features have also been investigated as possible determinants of seabird dispersion (Pocklington 1979, Abrams & Griffiths 1981). Here I report on a preliminary attempt to correlate species richness, diversity, abundance, biomass and numbers of individuals in each of four trophic groups of seabirds with selected features of the abiotic environment in which the species are found. More particularly, I investigate statistical relationships between the distribution of pelagic seabirds (excluding penguins) and water and air temperatures, water depth, wind strength and weather conditions in the African sector of the Southern Ocean.

METHODS

The occurrence of all seabirds passing within 1km of the one side of the moving ship (average speed = 24km/h) was recorded in 10-minute periods during seven cruises of the M.V. S.A. Agulhas from April 1979 to April 1980 in the African sector of the Southern Ocean (Fig. 2). Surface-water and air temperatures, depth, wind strength and weather conditions (coded from 1: best, to 6: worst) were recorded also for 2 546 observations. These data were analysed for linear correlation (Sokal & Rohlf 1969) with bird species richness (BSR = numbers of species), bird species diversity (BSD = Shannon-Wiener index), total abundance (numbers of individuals), total biomass (live-weight) and numbers of individuals in each of four principal food-class groups, namely plankton, cephalopods, fish and mixed (Appendix 1). A principal components factor analysis was employed to identify subsets of the abiotic features which, in turn, were correlated with the seabird indices and groups.

RESULTS & DISCUSSION

Bird species richness and diversity, total abundance and biomass, and all four trophic groups of birds showed weak linear associations with surface-water and air temperatures, water depth, wind strength and weather conditions (Table 10). The high correlation between BSR and BSD (Table 9), and their parallel distributions (Fig. 12) suggest that these two indices associated similarly with the environment. Both BSR and total abundance are used in the calculation of BSD. Since the association between BSR and BSD is stronger than that between abundance and BSD (Table 9), it appears that total abundance was distributed among the species at a particular observation station fairly evenly, and that relatively large single-species flocks were rare. Thus, BSR and BSD are treated as more or less equal below.

Water temperature

Species richness was distributed normally about a mode at 8 - 10°C water temperature (Fig. 17). The lowest numbers of species were associated with the coldest (areas of sea-ice) and warmest

Table 10: Coefficients of correlation (r) between five abiotic features, and bird species richness (BSR), bird species diversity (BSD), abundance, (numbers of individuals) and biomass (live-weight of individuals), and four trophic groups of seabirds in the African sector of the Southern Ocean. Figures in parentheses are correlation coefficients between $\log_{10}$ transformed abiotic features and the avian indices and trophic groups.

	Water temperature	Air temperature	Depth	Wind strength	Weather
BSR	.038 (.014)	.110 (.075)	-.154 (-.098)	.030 (.037)	-.030 (-.038)
BSD	.043 (.030)	.092 (.074)	-.126 (-.102)	.116 (.108)	-.003 (-.003)
Abundance	-.012 (-.148)	-.002 (-.117)	-.026 (-.020)	-.032 (-.038)	-.021 (-.060)
Biomass	.025 (-.006)	.039 (-.133)	-.066 (-.133)	-.010 (-.007)	-.002 (-.062)
Planktivores	-.041 (-.155)	-.032 (-.073)	.054 (.106)	-.051 (-.075)	-.050 (-.060)
Cephalopod-eaters	.034 (.240)	.048 (.325)	-.058 (-.155)	-.007 (.037)	.007 (-.049)
Piscivores	-.009 (.123)	-.059 (.045)	-.078 (-.099)	-.022 (-.041)	-.031 (-.086)
Omnivores	-.099 (-.200)	-.123 (-.265)	-.049 (-.046)	-.004 (.092)	.024 (.096)

(influence of the Agulhas Current) waters. More than 3.5 species per observation were associated with water temperatures typical of the Subantarctic range (Fig. 17). Total abundance and biomass were lowest at the highest water temperatures, and highest between 10 and 12°C with sharp decreases below this level (Fig. 17). In areas of sea-ice (water temperatures below about 4°C) total numbers and biomass were lower than farther north. Many of these birds were observed sitting on sea-ice. The association of abundance and biomass with water temperature (Fig. 17) shows that smaller birds relatively were more abundant in cold waters.

Planktivores tended to be associated with two regimes of water temperature: below 4°C and around 13° C (Fig. 18). Cephalopod-eaters were most abundant between 10 and 12°C. Piscivores and omnivores were only numerous in areas with water cooler than 0 and 4°C, respectively, although the latter were present throughout the range of water temperatures observed (Fig. 18).

Air temperature

Air temperature and water temperature were associated strongly with one another (Table 11). The highest numbers of species were found at air temperatures between 2.5 and 15°C (Fig. 19). A slight increase in BSR occurred at both extremes of the temperature range, a trend not apparent in the case of water temperature (Fig. 17). Total abundance and biomass both had three peaks at approximately -9, 3, and 14°C (Fig. 19). These findings suggest that air temperature has a stronger association with the distribution of seabirds than water temperature. However, well-insulated, volant species are unlikely to be affected directly much by air temperature. Also, air temperature is

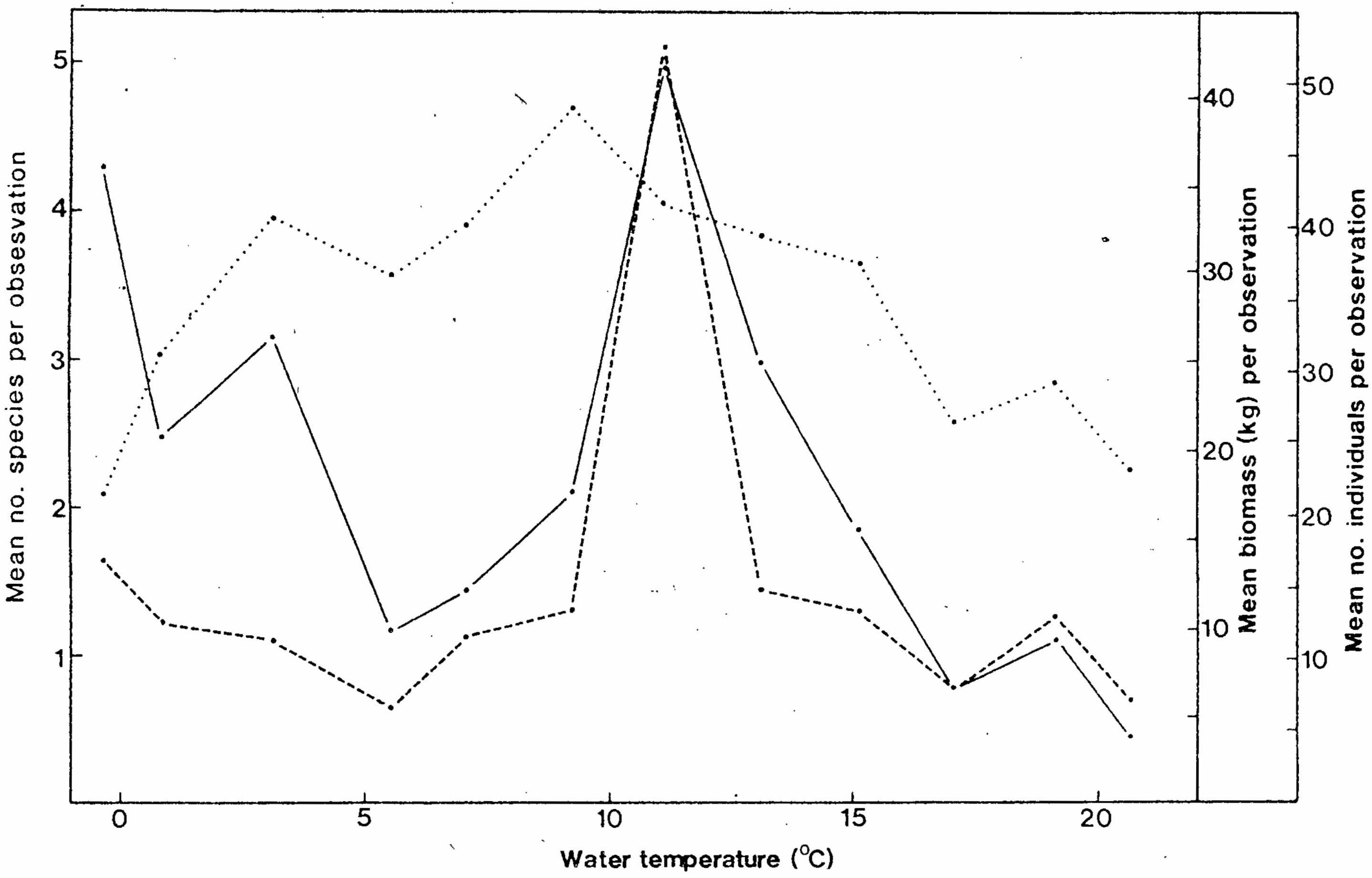

FIGURE 17. Occurrence of species richness (dotted line) (F = 33.72, p < 0.0001), total abundance (solid line) (F = 2.06, p = 0.0198), and total biomass (dashed line) (F = 2.44, p = 0.0049) in relation to surface-water temperature in the African sector of the Southern Ocean

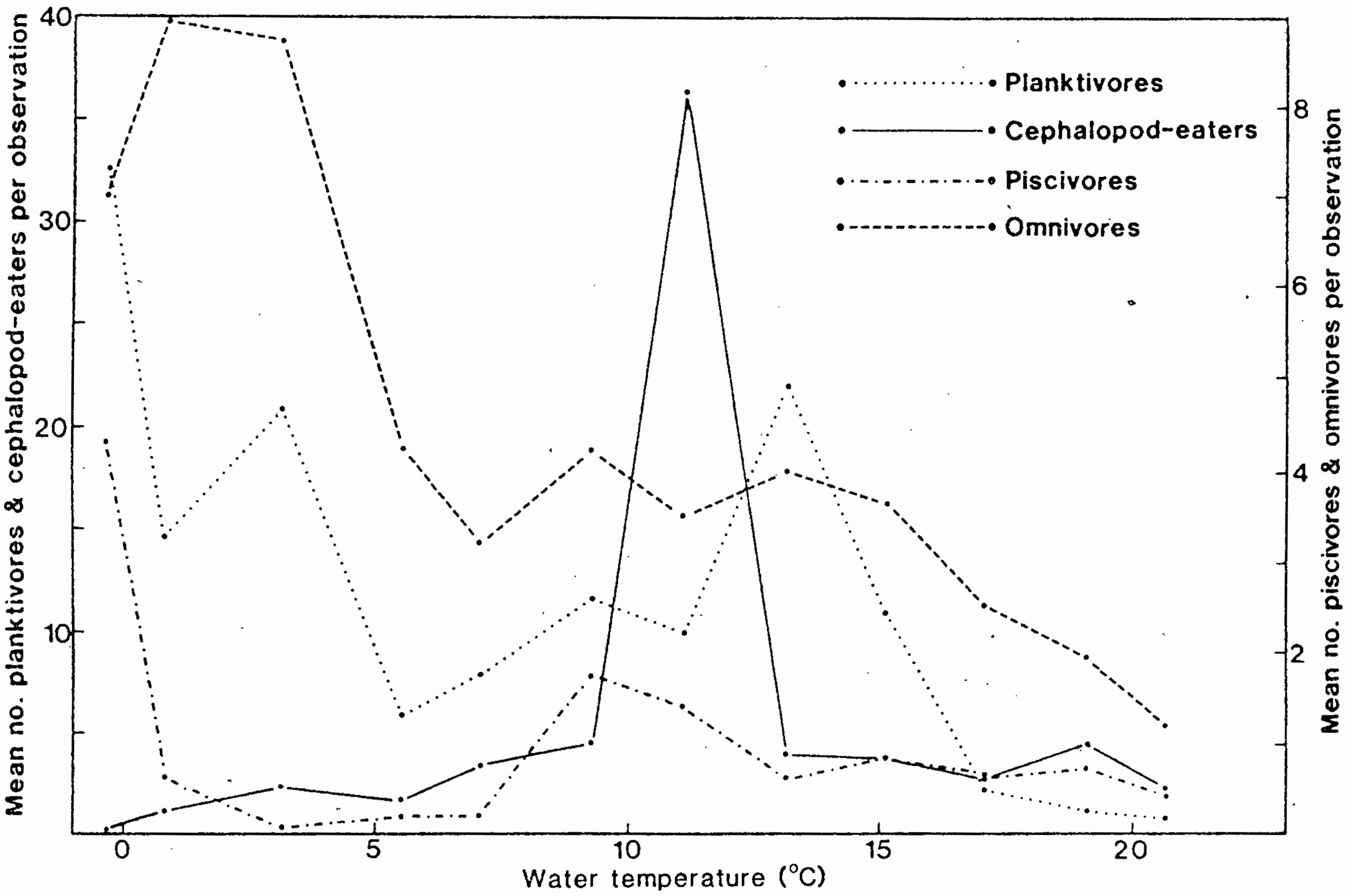

FIGURE 18. Occurrence of planktivores (F = 1.95, p = 0.0293), cephalopod-eaters (F = 2.54, p = 0.0035), piscivores (F = 7.02, p < 0.0001), and omnivores (F = 4.33, p < 0.0001) in relation to surface-water temperature in the African sector of the Southern Ocean

Table 11: Coefficients of correlation (r) between abiotic features in the African sector of the Southern Ocean.

	Air temperature	Depth	Wind strength	Weather
Water temperature	0.900	-.069	.018	-.233
Air temperature	1.000	-.076	-.028	-.186
Depth		1.000	-.117	-.043
Wind strength			1.000	.124
Weather				1.000

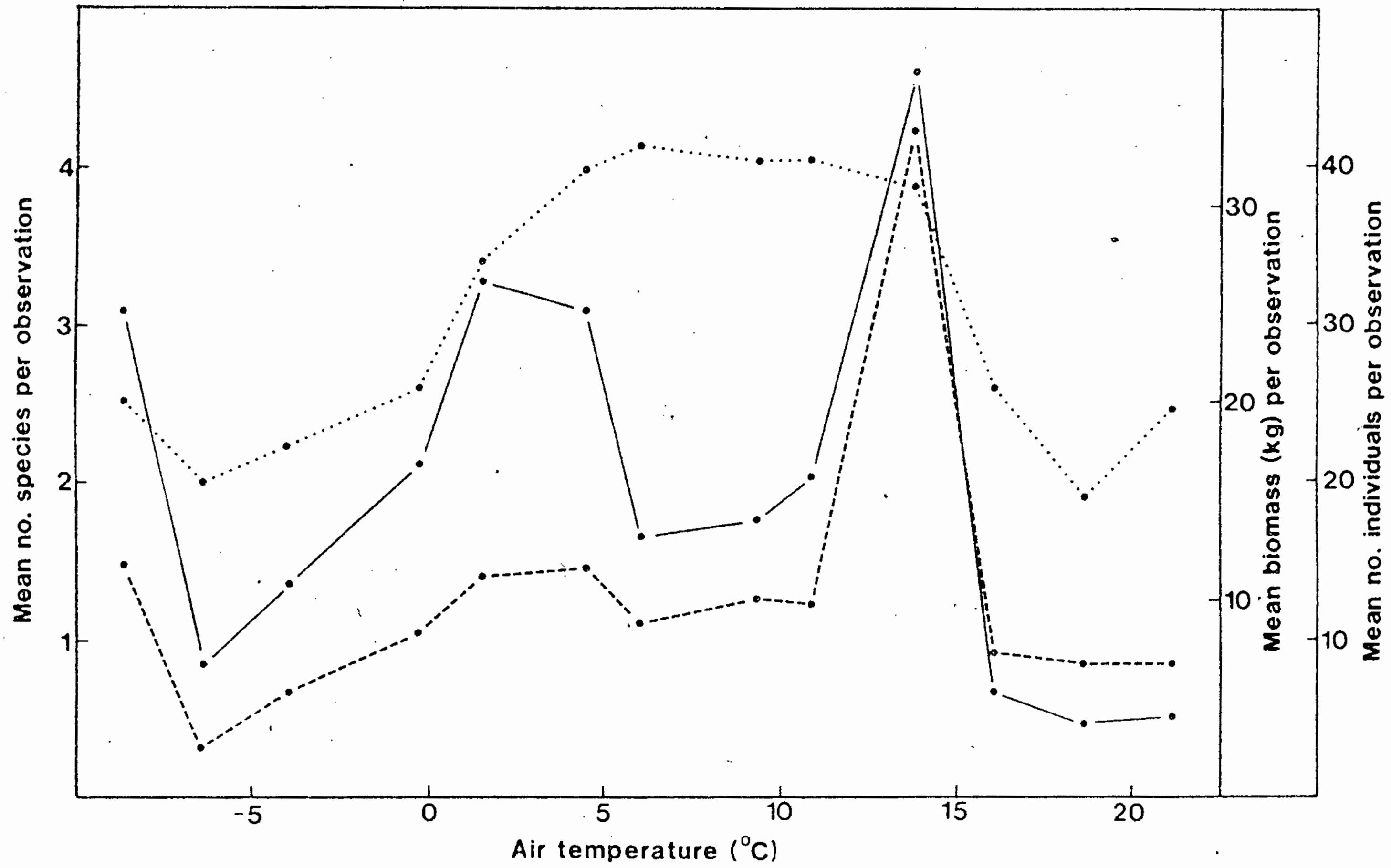

FIGURE 19. Occurrence of species richness (dotted line) ($F = 40.89$, $p < 0.0001$), total abundance (solid line) ($F = 2.09$, $p < 0.0147$), and total biomass (dashed line) ($F = 1.92$, $p = 0.0280$) in relation to air temperature in the African sector of the Southern Ocean

dependent on the incidence of wind, its direction and the prevailing surface-water temperature. Relatively small birds were more numerous in cold air temperatures. Planktivores were most abundant around 2°C, but also had a noticeable peak between 12.5 and 15°C, where the majority of cephalopod-eaters were also found (Fig. 20). Piscivores were only numerous in the lowest air temperatures. Omnivores were numerous here also, but occurred frequently around 2.5°C as well, decreasing above and below this value. Omnivores showed the strongest correlation (negative) with air temperature (Table 10).

Water depth

Species richness varied little over the range of depths recorded, but increased slightly in relatively shallow waters (Fig. 21). Both abundance and biomass had three peaks (Fig. 21). This makes interpretation difficult, but relatively small birds tended to occur over deeper waters. These small birds are mainly planktivores (Fig. 22) and many feed on Euphausia superba which tend to remain close to the surface of the sea (Bainbridge 1961). Some cephalopods, on the other hand, migrate daily from the ocean bottom, and therefore have to be in shallower waters to be within reach of the surface (Imber & Berruti 1981). This is reflected by the occurrence of cephalopod-eaters in areas of relatively shallow water, and their paucity in deep water (Fig. 22). Piscivores and omnivores occurred over all water depths with the latter especially abundant in areas with depths of about 2 000m.

Wind strength

Low association of all three avain indices with the strongest wind

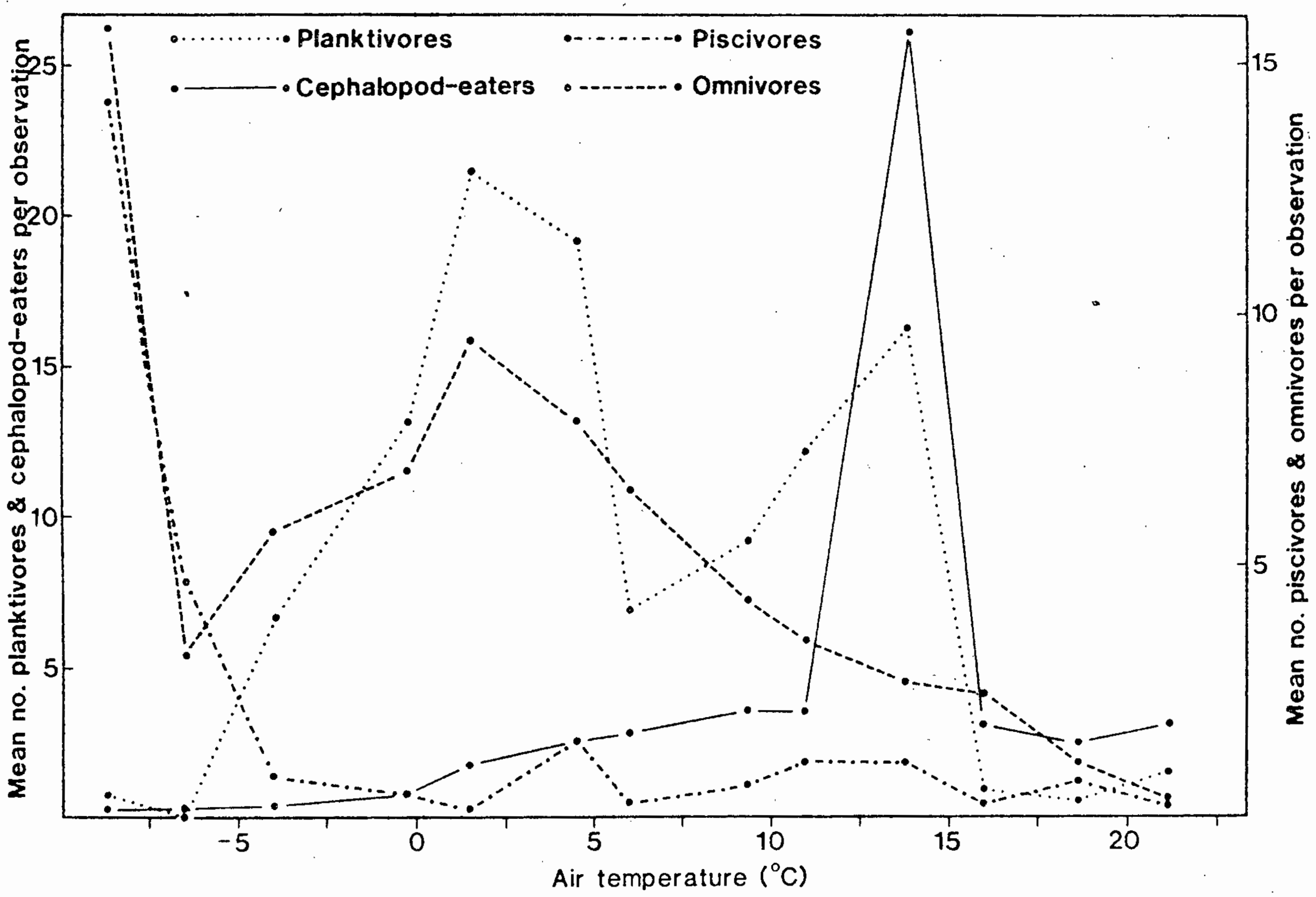

FIGURE 20. Occurrence of planktivores (F = 1.68, p = 0.0649), cephalopod-eaters (F = 1.79, p = 0.0447), piscivores (F = 24.99, p < 0.0001), and omnivores (F = 4.99, p < 0.0001) in relation to air temperature in the African sector of the Southern Ocean

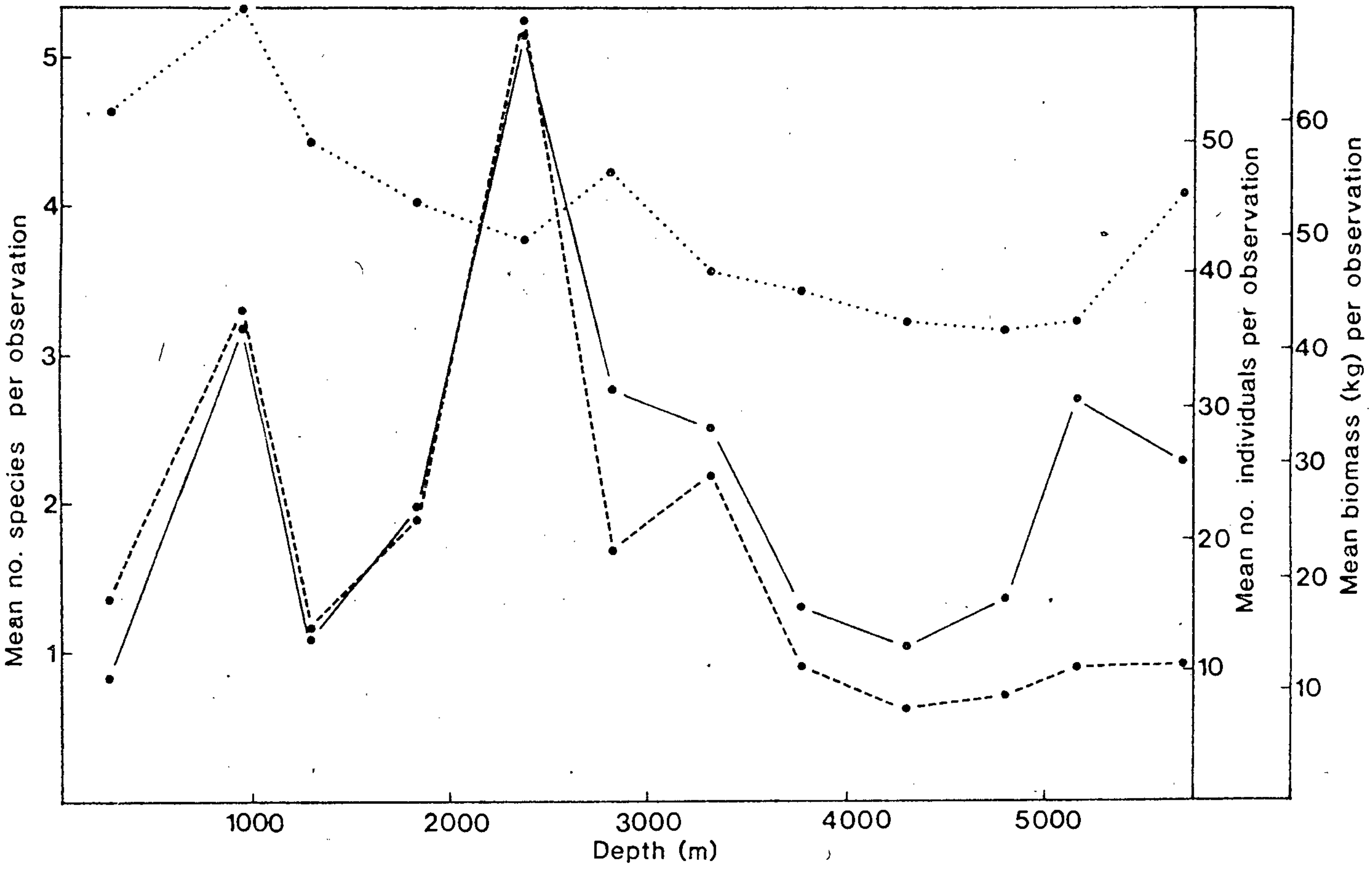

FIGURE 21. Occurrence of species richness (dotted line) (F = 9.49, p < 0.0001), total abundance (solid line) (F = 2.34, p = 0.0073), and total biomass (dashed line) (F = 2.65, p = 0.0022) in relation to water depth in the African sector of the Southern Ocean

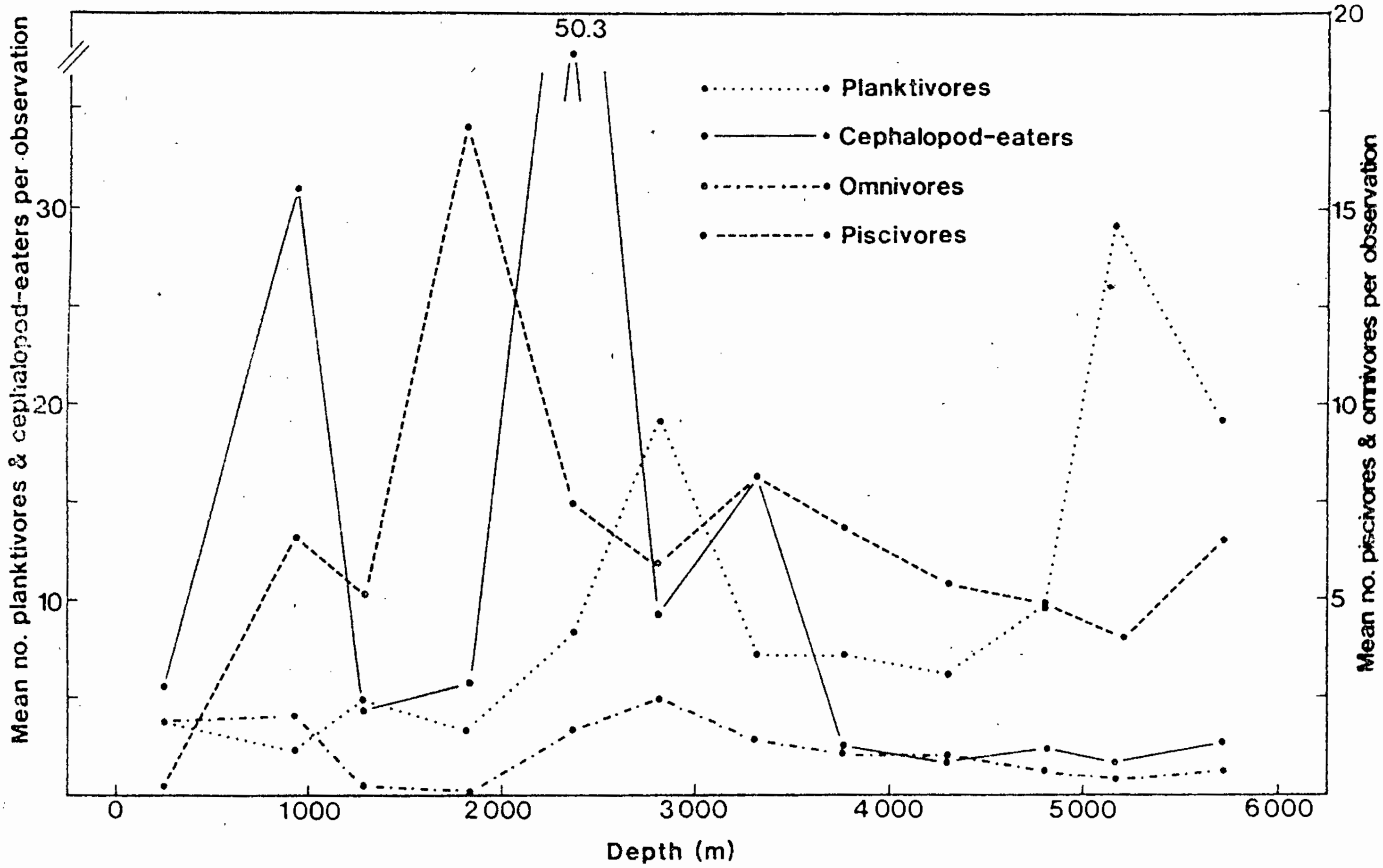

FIGURE 22. Occurrence of planktivores ($F = 3.64$, $p < 0.0001$), cephalopod-eaters ($F = 2.30$, $p = 0.0083$), piscivores ($F = 2.56$, $p = 0.0031$), and omnivores ($F = 2.34$, $p = 0.0072$) in relation to water depth in the African sector of the Southern Ocean

strengths is evident (Fig. 23). Species richness was distributed bimodally with maxima at wind strengths 0 - 1, and 5 - 6 on the Beaufort Scale. Total abundance and biomass show parallel distributions, although relatively small birds, which rely largely on flapping flight, apparently prefer weak winds. Planktivores, piscivores and omnivores tended to be more abundant in weak winds (Fig. 24), whereas cephalopod-eaters were distributed normally around wind strengths of 4 - 5 on the Beaufort Scale. The large cephalopod-eaters are highly specialized flyers, needing strong, consistent winds for dynamic soaring (Part 5).

Weather conditions

Weather conditions appeared to have little influence on BSR, but the lowest numbers of species occurred in the worst weather (Fig. 25). Both abundance and biomass were lower in worse weather, with smaller species perhaps favouring calmer conditions (Fig. 25). With the the exception of the omnivores, all trophic groups occurred least abundantly in the worst weather (Fig. 26). Omnivores were more numerous in bad weather.

Groups of abiotic features

A principal components factor analysis revealed two subsets of abiotic features (F1 and F2). F1 (λ_1 = 2.025) included, in decreasing order of variance, surface-water and air temperatures and weather, and F2 (λ_2 = 1.260) included wind strength, weather and depth. One might expect F1 to correlate better with the avian indices and trophic groups than the three features separately. However, both F1 and F2 correlated very weakly with the avian variables, albeit with very high statistical significance (Table

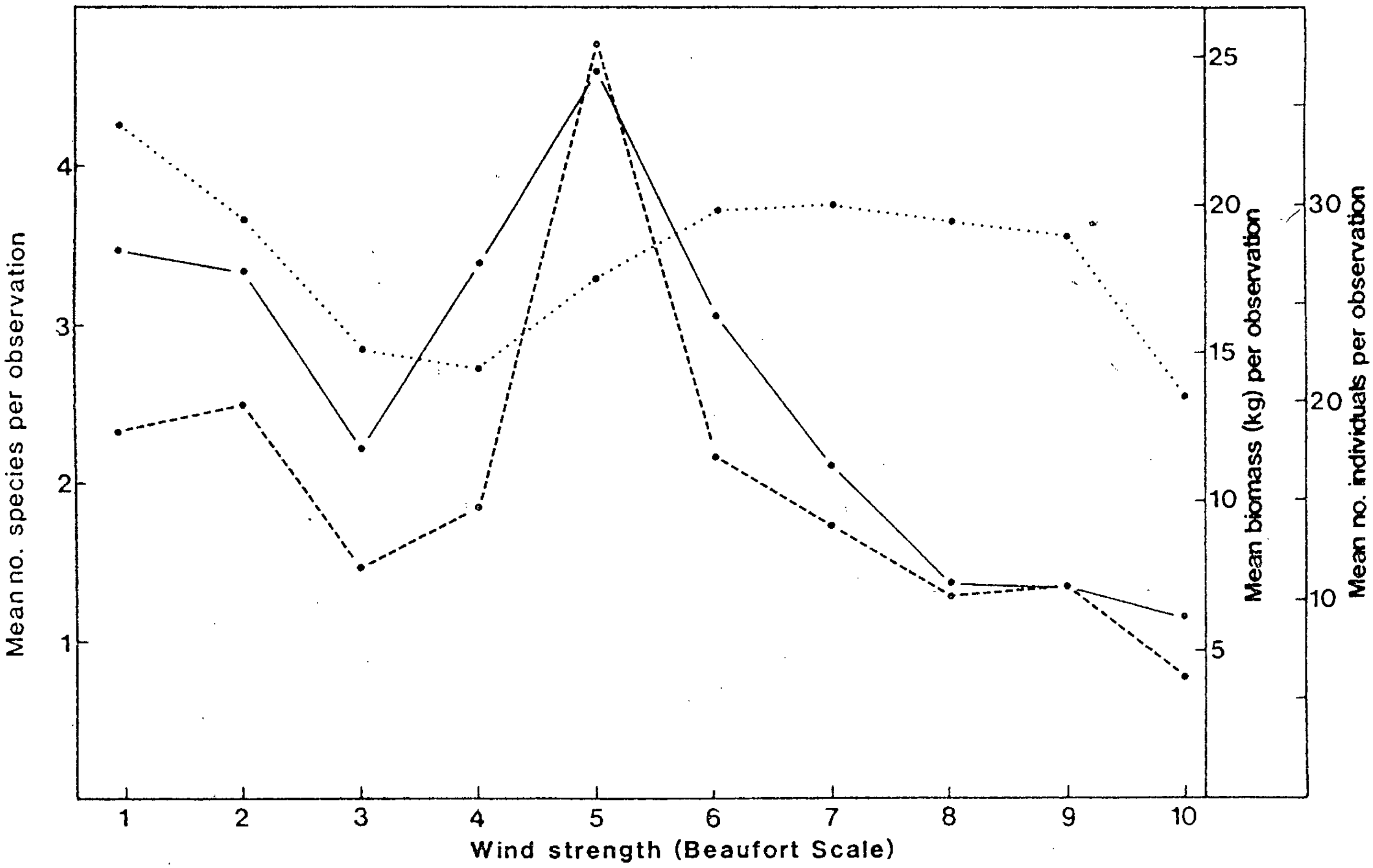

FIGURE 23. Occurrence of species richness (dotted line) (F = 18.32, $p < 0.0001$), total abundance (solid line) (F = 1.18, p = 0.30), and total biomass (dashed line) (F = 1.29, p = 0.24) in relation to wind strength in the African sector of the Southern Ocean

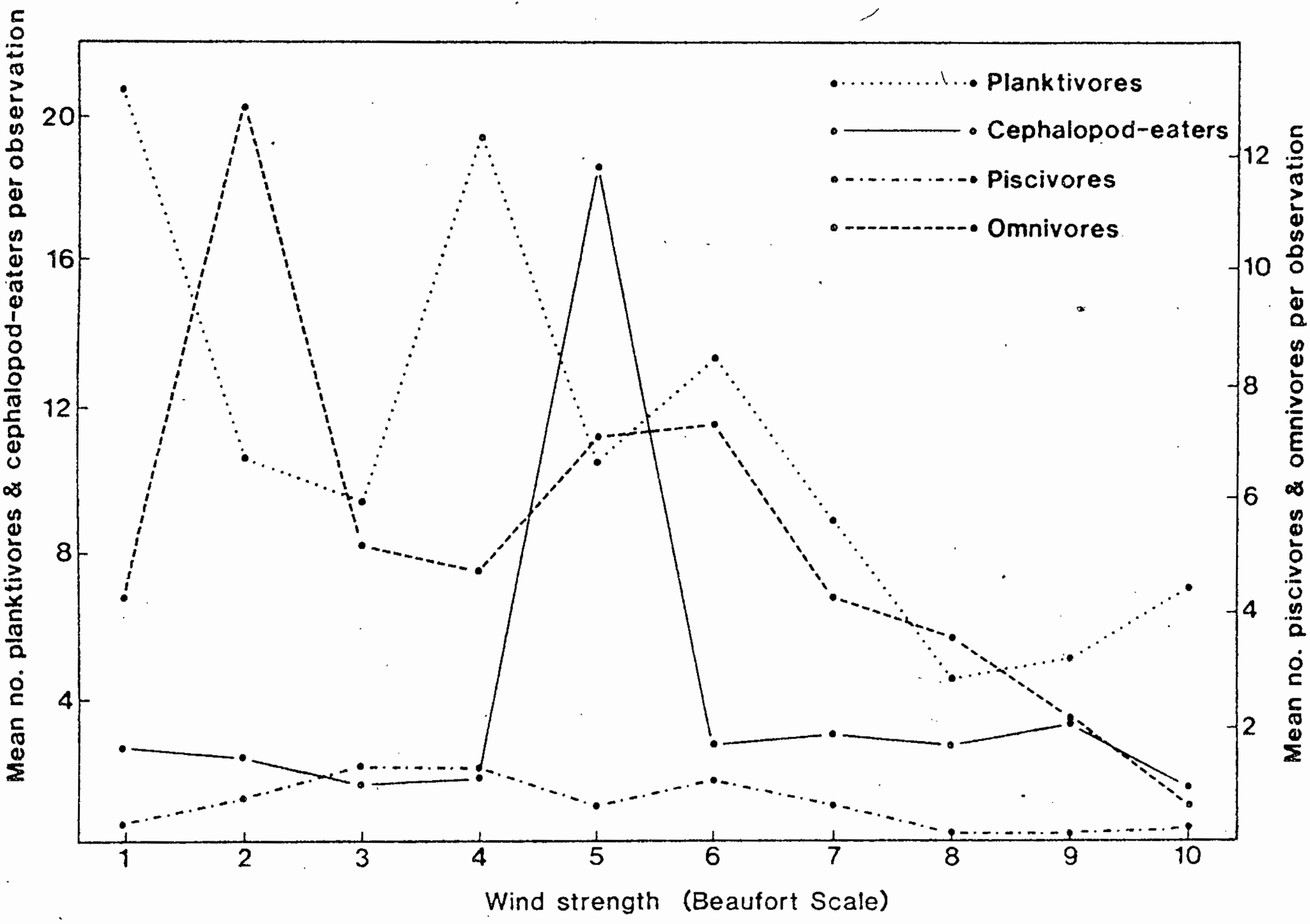

FIGURE 24. Occurrence of planktivores (F = 1.09, p = 0.3378), cephalopod-eaters (F = 1.29, p = 0.2381), piscivores (F = 1.49, p = 0.1463), and omnivores (F = 2.56, p = 0.0062) in relation to wind strength in the African sector of the Southern Ocean

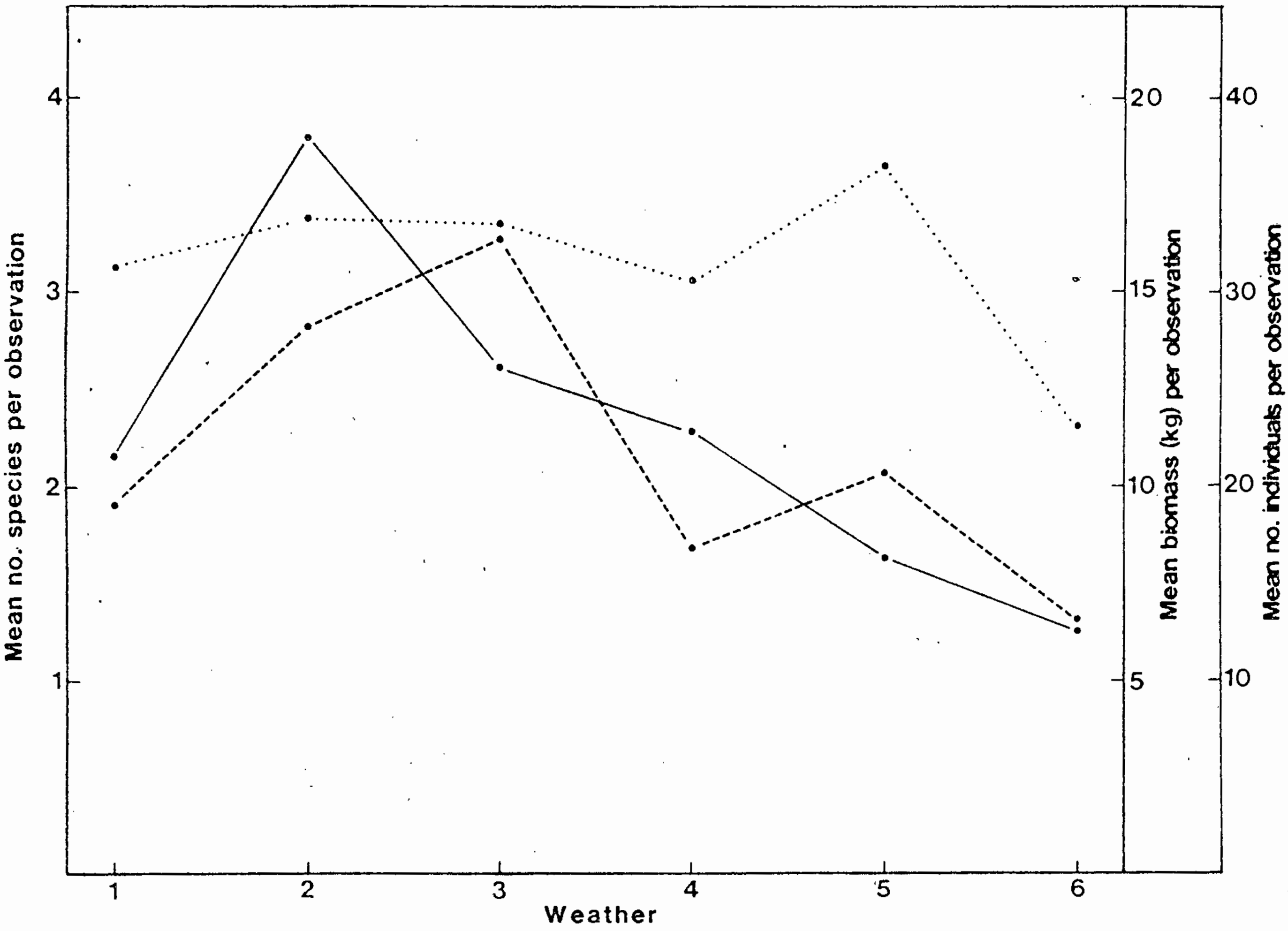

FIGURE 25. Occurrence of species richness (dotted line) (F = 8.60, $p < 0.0001$, total abundance (solid line) (F = 1.03, p = 0.4004, and total biomass (dashed line) (F = 0.34, p = 0.9185 in relation to weather in the African sector of the Southern Ocean

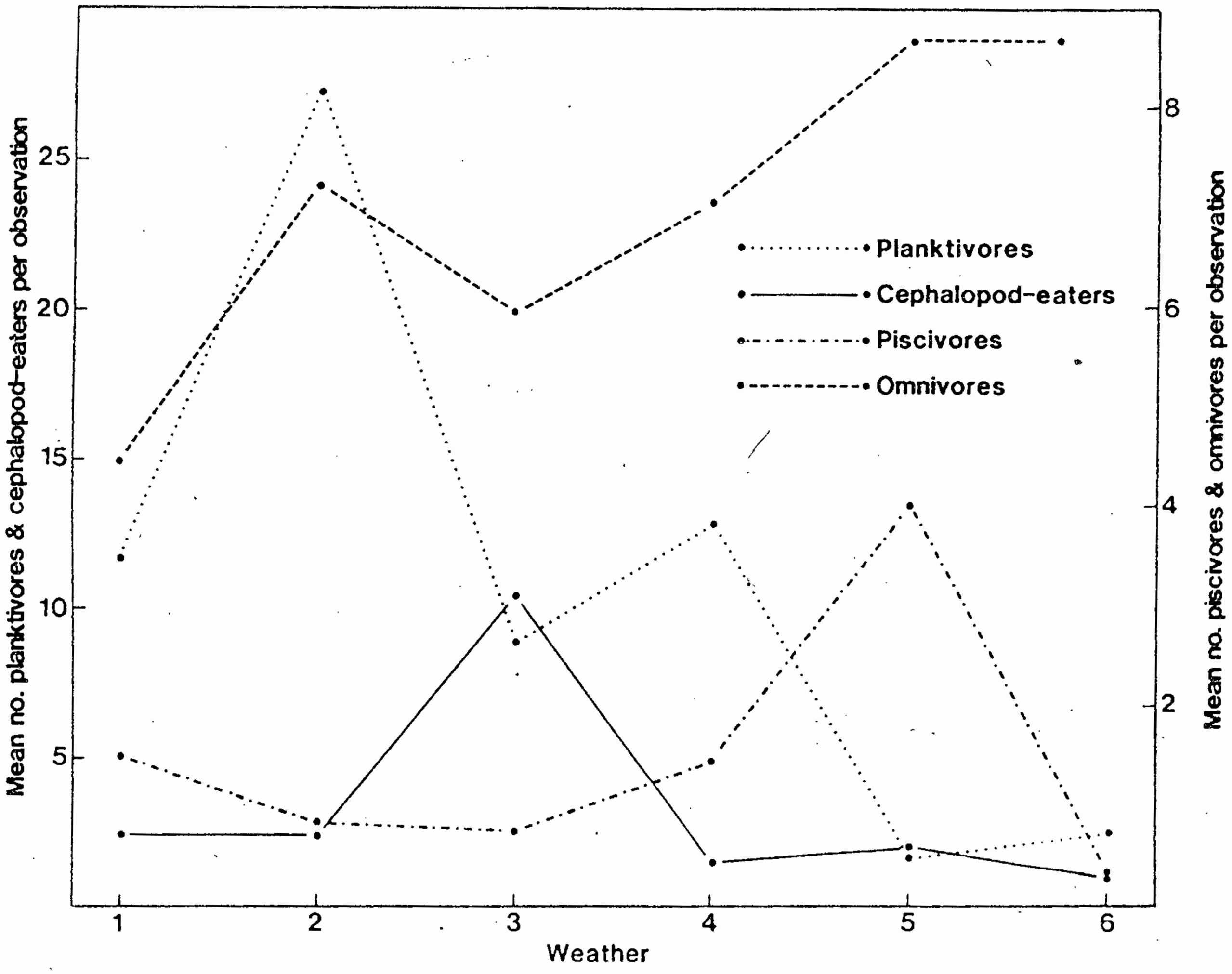

FIGURE 26. Occurrence of planktivores (F = 4.22, p = 0.0003, cephalopod-eaters (F = 0.57, p = 0.7472, piscivores (F = 1.38, p = 0.2199, and omnivores (F = 1.06, p = 0.3839 in relation to weather in the African sector of the Southern Ocean

Table 12: Coefficients of determination (R^2) for statistically significant (F-statistic) relationships of Factor 1 (water and air temperatures and weather) and Factor 2 (depth, wind strength and weather) with avian community indices and trophic groups in the African sector of the Southern Ocean.

	FACTOR 1		FACTOR 2	
	R^2	Significance level	R^2	Significance level
Bird species richness	.030	.001	.024	.001
Bird species diversity	.021	.001	.016	.001
Planktivores	.001	.046	.003	.003
Cephalopod-eaters	.005	.019	.003	.001
Omnivores	.014	.001	.016	.006

12).

CONCLUSIONS

Abiotic features, either independently or collectively, apparently do not determine seabird occurrence linearly. I doubt whether it will be possible to use the physical environment to predict the occurrence, or trophic structure, of seabird communities in time and space on a small scale. Broad-scale patterns may, however, be predicted. For instance, if cold, calm conditions occur over deep water, one would expect to see more planktivores than cephalopod-eaters. The high occurrence of the trophic groups in particular ranges of abiotic features appears to complement the groups' feeding methods and flight capabilities. Until we know more about the relationships of the birds' prey with the physical environment, it will remain difficult to decide whether to attribute seabird occurrence to the physical environment directly, or indirectly to the presence of available prey. Moreover, other factors not immediately obvious to the researcher, may be affecting seabird distribution.

PART 5

RELATIONSHIPS BETWEEN THE DISTRIBUTIONS OF SNOW AND ANTARCTIC PETRELS AND SELECTED ABIOTIC FEATURES IN THE SOUTHERN OCEAN

ABSTRACT

The restriction of Snow and Antarctic petrels to areas of sea-ice, and the concomitant exclusion of albatrosses and other petrels were investigated. Oceanographic and meteorological features are correlated poorly with Snow and Antarctic petrel abundances. Air and surface-water temperatures influence the distribution of sea-ice, rather than the birds directly. The diet of the two species is unspecialized, and feeding is opportunistic. Snow and Antarctic petrels are non-specialized flyers. Their aerodynamic characteristics restrict them to the inconsistent meteorological regime of the Antarctic. The paucity of open water for feeding, unpredictable winds, and the distance to breeding localities exclude most other procellariiform seabirds from the area studied.

INTRODUCTION

Two wind systems characterize the circumpolar Southern Ocean: the strong, regular westerly winds north of the Antarctic Divergence, and a narrow belt of inconsistent easterly winds south of the Antarctic Divergence. Although 14 of the 34 species of procellariiform seabirds in the zone of the westerly winds venture into the southern zone, bordering on Antarctica, only two are resident there throughout the year (Watson 1975). Moreover, these two species, the Snow Petrel and the Antarctic Petrel, are restricted to this zone of low temperatures, unpredictable winds and ice-strewn seas (Watson 1975).

Here I report on an investigation into why Snow and Antarctic Petrels are restricted to areas of sea-ice and, concomitantly, why other petrels (Procellariidae) and albatrosses (Diomedeidae) are excluded from such areas.

METHODS

The distribution of pelagic seabirds in the Southern Ocean was recorded on seven cruises of the M.V. S.A. Aghulas during the period April 1979 to April 1980 (Fig. 27). All birds in a 1km wide transect were counted during a six hour day, split into hourly sessions of 10-minute periods (Part 1). Air and surface-water temperatures, depth, wind strength and the extent of sea-ice (when present) were recorded. Linear regression analysis (Sokal & Rohlf 1969) was used in an attempt to find significant correlations between these abiotic features and the abundance of Snow and Antarctic Petrels.

Twenty-two Snow Petrels and 39 Antarctic Petrels were collected at four stations at sea (Table 13). Oil was drained from the stomach contents, and the identifiable material was separated into crustaceans, fish and cephalopods, and quantified by mass and occurrence. Nine Snow Petrels, 10 Antarctic Petrels and smaller numbers of other species were measured and weighed, permitting computation of the birds' wing loadings and aspect ratios (Pennycuick 1972).

RESULTS

Distribution

Within the area surveyed (Fig. 27), the abundance (numbers of individuals) of procellariiform seabirds tended to be high at the Subtropical and Antarctic convergences in both the austral summer and winter (Figs 28 & 29). The maxima were most evident in winter, during the birds' non-breeding phase, the pattern in summer being masked by concentrations of birds around their breeding islands.

Species richness (numbers of species) was relatively low (Figs 28 & 29). Both abundance and species richness decreased southwards of the northern limits of icebergs, and in areas of ice floes (defined as ice coverage of more than one-tenth) only Snow and Antarctic petrels were numerous (Fig. 30). Only two per cent of all (5 663) Antarctic Petrels recorded were observed north of ice floes. Contrary to Routh (1949) and Holgersen (1957), Antarctic Fulmars and Pintado Petrels were not found around ice floes. They were seen occasionally amongst icebergs, but were numerous only near Bouvet Island where they breed (Watson 1975, Watkins in press). The ubiquitous Wilson's Stormpetrel was the only other procellariiform seen in the ice.

Table 13: Numbers of Snow and Antarctic Petrels collected at four stations in the Southern Ocean.

STATION POSITION	DATE	LOCAL TIME	NO. BIRDS	
			Snow Petrel	Antarctic Petrel
68° 07'S; 09° 11'E	20 Jan. 1980	11h00	2	6
70° 06'S; 02° 47'W	29 Jan. 1980	23h30	4	13
70° 13'S; 02° 58'W	30 Jan. 1980	18h00	7	17
69° 48'S; 03° 33'W	2 Feb. 1980	17h30	9	3

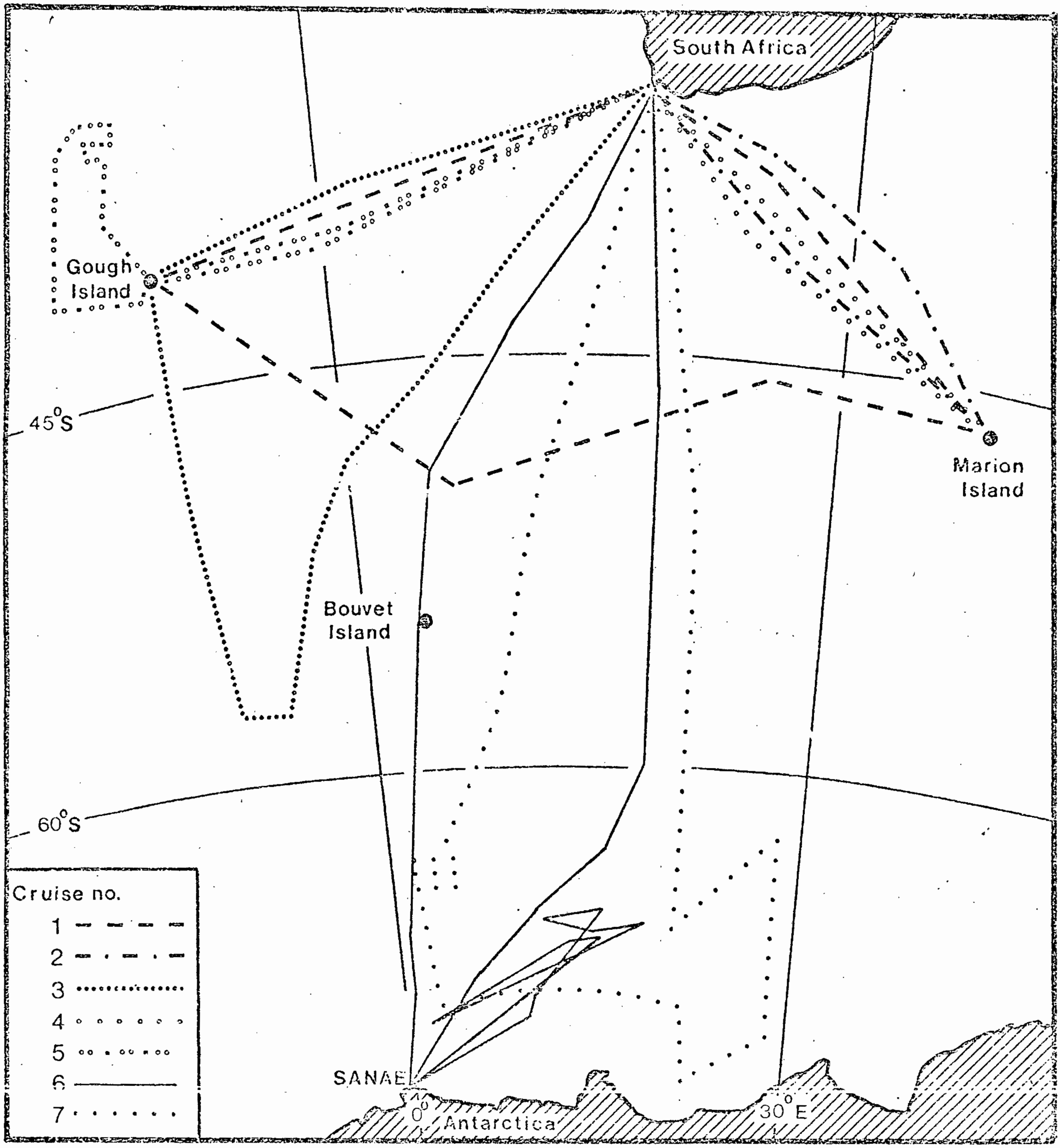

Figure 27. Seven cruise tracks of the M.V. S.A. Agulhas in the Southern Ocean during 30 April - 14 May 1979 (cruise no. 1), 23 May - 13 June 1979 (no. 2), 18 July - 5 August 1979 (no. 3), 7 September - 24 September 1979 (no. 4), 26 October - 16 November 1979 (no. 5), 4 January - 10 February 1980 (no. 6) and 28 February

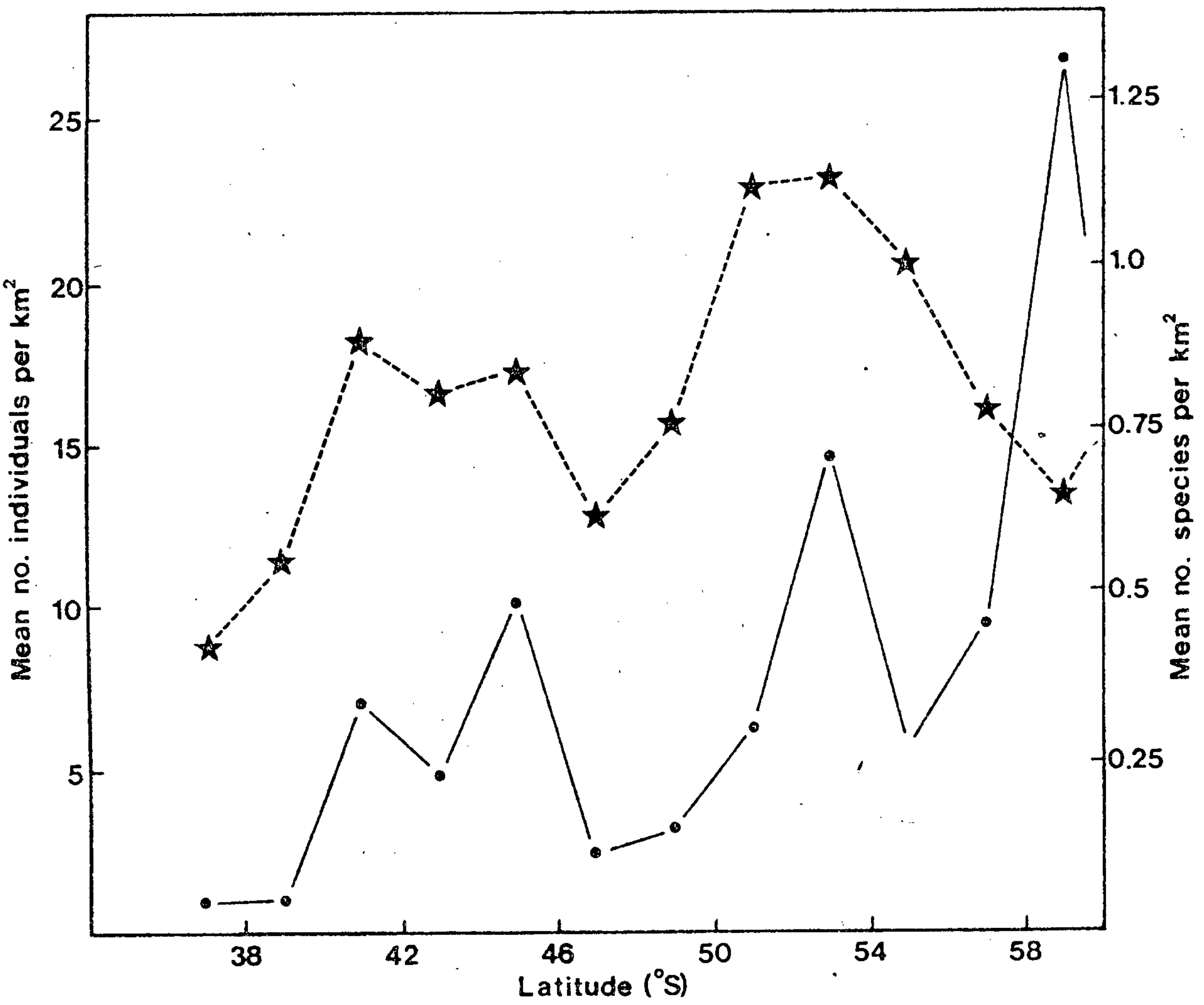

FIGURE 28. Summer distribution of species richness (closed stars) and total numbers (closed circles) of pelagic birds

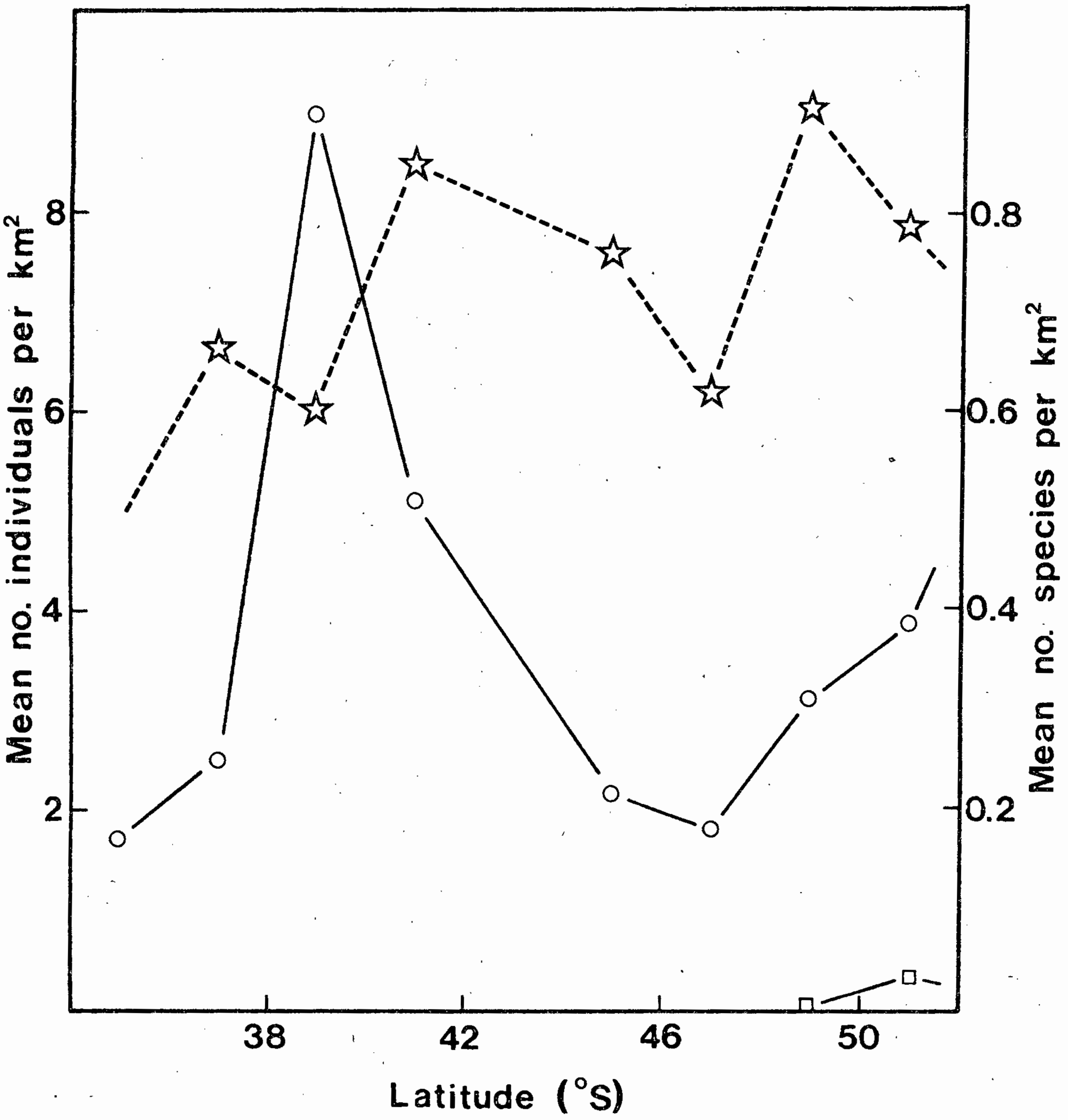

FIGURE 29. Winter distribution of species richness (open stars), total numbers (open circles) of pelagic birds, and northern limit of Antarctic Petrels (open squares)

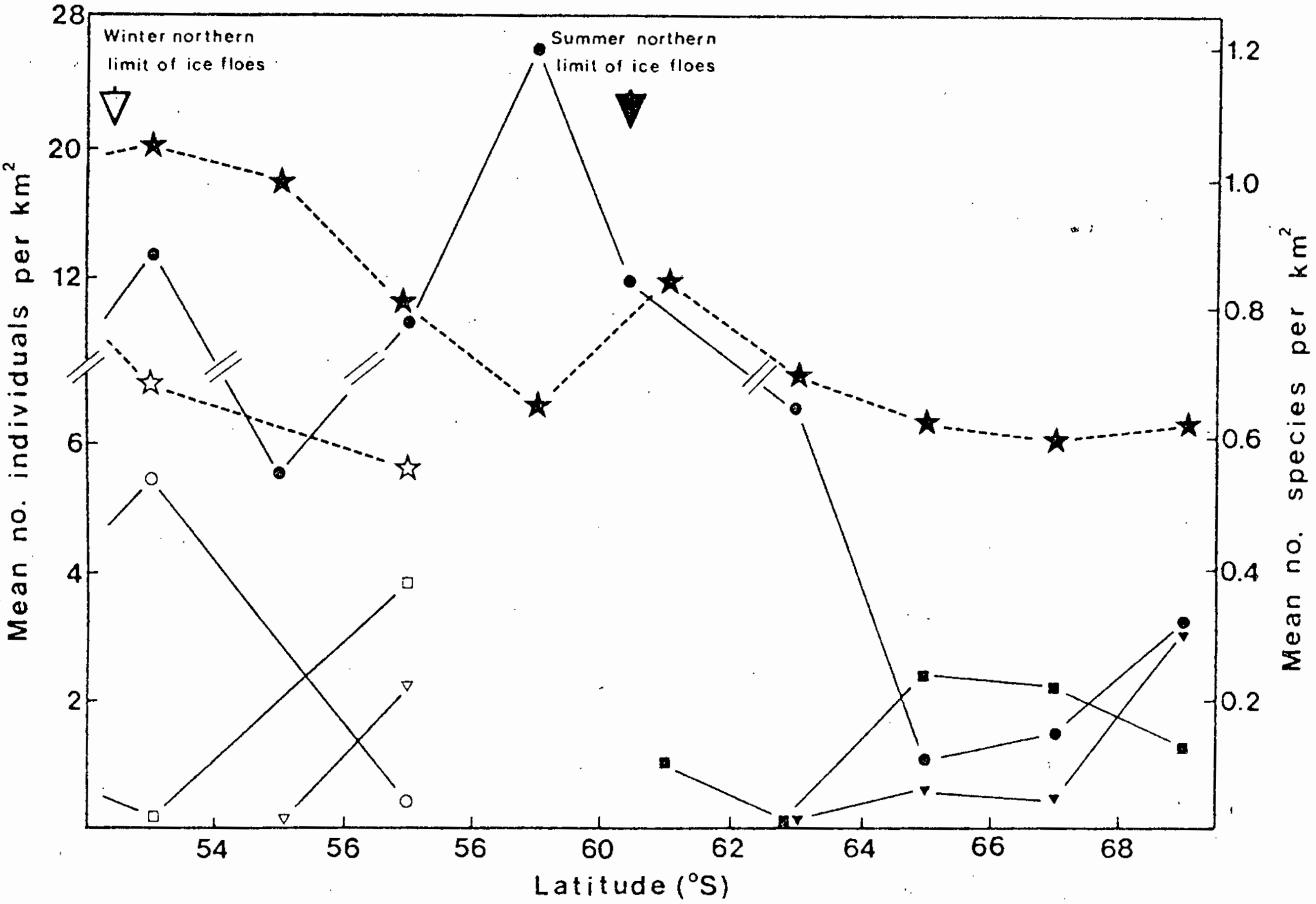

FIGURE 30. Summer and winter distribution of species richness (closed and open starts, respectively), total numbers (closed and open circles, respectively) of pelagic birds, Antarctic Petrels (closed and open squares, respectively) and Snow Petrels (closed and open triangles, respectively)

Seasonal change in the abundance of procellariiforms was most pronounced in high latitudes (Figs 28 & 29), presumably in response to seasonal shifts in the distribution of sea-ice (icebergs and ice floes). Whereas the southerly limits of the seasonal ranges of most species merely were extended and retracted, the summer and winter ranges of the Snow and Antarctic petrels were separated completely (Fig. 30). Oceanographic and meteorological features correlated poorly with the abundance of Snow and Antarctic petrels, respectively (Table 14). However, neither species was found associated with air temperatures above 10°C or water temperatures above 4°C.

Feeding and Food

Snow and Antarctic petrels were observed to feed most often amongst disturbed ice in the wake of the ship. On one occasion both species were noted feeding in association with about 200 Minke Whales <u>Baleanoptera acutorostrata</u>, but it was not possible to determine the petrels' prey. The birds were also observed scavenging the remains of culled Ross Seals <u>Onamatophoca rossi</u>, and taking refuse from the ship.

The masses of stomach contents of Snow and Antarctic petrels were low, averaging 4.1g and 10.3g respectively. Crustaceans, fish and cephalopods constitute approximately equal proportions of the stomach contents of both species (Table 15). Cephalopods occurred in 86% of the Snow Petrels examined, whereas fish occurred in 76% of the Antarctic Petrels.

Thirty-five per cent of the Snow Petrel and 49% of the Antarctic Petrel stomachs contained only one of the three food-classes at a time. All three occurred equally frequently.

Table 14: Correlation coefficients (r) for association of Snow and Antarctic Petrels with air and surface-water temperatures, wind strength and depth.

	Air temperature	Water temperature	Wind strength	Depth
Snow Petrel	-0.123	-0.095	-0.031	-0.087
Antarctic Petrel	-0.079	-0.082	-0.032	-0.046

Table 15: Mean mass (g) and relative frequency of occurrence (%) of prey items in Snow and Antarctic Petrel stomachs. Coefficient of variation (C.V.) = 100 x standard deviation/mean.

Unit of Measure	Species	No. stomachs	Crustaceans		Fish		Cephalopods		Unidentified	
			Mean	C.V.	Mean	C.V.	Mean	C.V.	Mean	C.V.
Mass (g)	Snow Petrel	19	1.3	186	2.1	242	0.6	241	0.1	283
	Antarctic Petrel	34	4.8	303	4.4	150	0.1	217	1.0	476
Occurrence (%)	Snow Petrel	22	73		55		86		32	
	Antarctic Petrel	34	71		76		65		32	

Wing loading and aspect ratio

Albatrosses have high wing loadings and aspect ratios (Fig. 31), features essential for dynamic soaring flight (Pennycuick 1972). The Sooty Shearwater, Cory's Shearwater, Grey Petrel, Whitechinned Petrel and Whiteheaded Petrel have moderate wing loadings and aspect ratios, characteristic of the smaller procellariiforms. These birds are relatively unspecialized flyers, and flap their wings more often than the specialist soarers (pers. obs.).

DISCUSSION

The reported distribution of the procellariiform seabirds considered here follows a generally accepted pattern, with highest abundances encountered at the highly productive Subtropical and Antarctic convergences (Watson 1975). The decrease in species richness and total abundance south of the northernmost icebergs agrees with the findings of Bierman and Voous (1950). The lack of Antarctic Fulmars and Pintado Petrels in the ice is probably a reflection of the vast distance separating the species' nearest breeding station, Bouvet Island. Both Routh (1949) and Holgersen (1957) made their observations in areas in which both of these species breed, explaining why they found the birds farther south than I did.

Many oceanographic and meteorological features have been proposed as determinants of seabird distribution (see Manikowski 1971, Brown <u>et</u> <u>al</u>. 1975). However, combinations of such features are probably more predictive of seabird distribution than isolated features (Pocklington 1979, Abrams and Griffiths 1981), especially south of the Antarctic Convergence where variation in oceanographic conditions is minimal (Szijj 1967). Also, there are

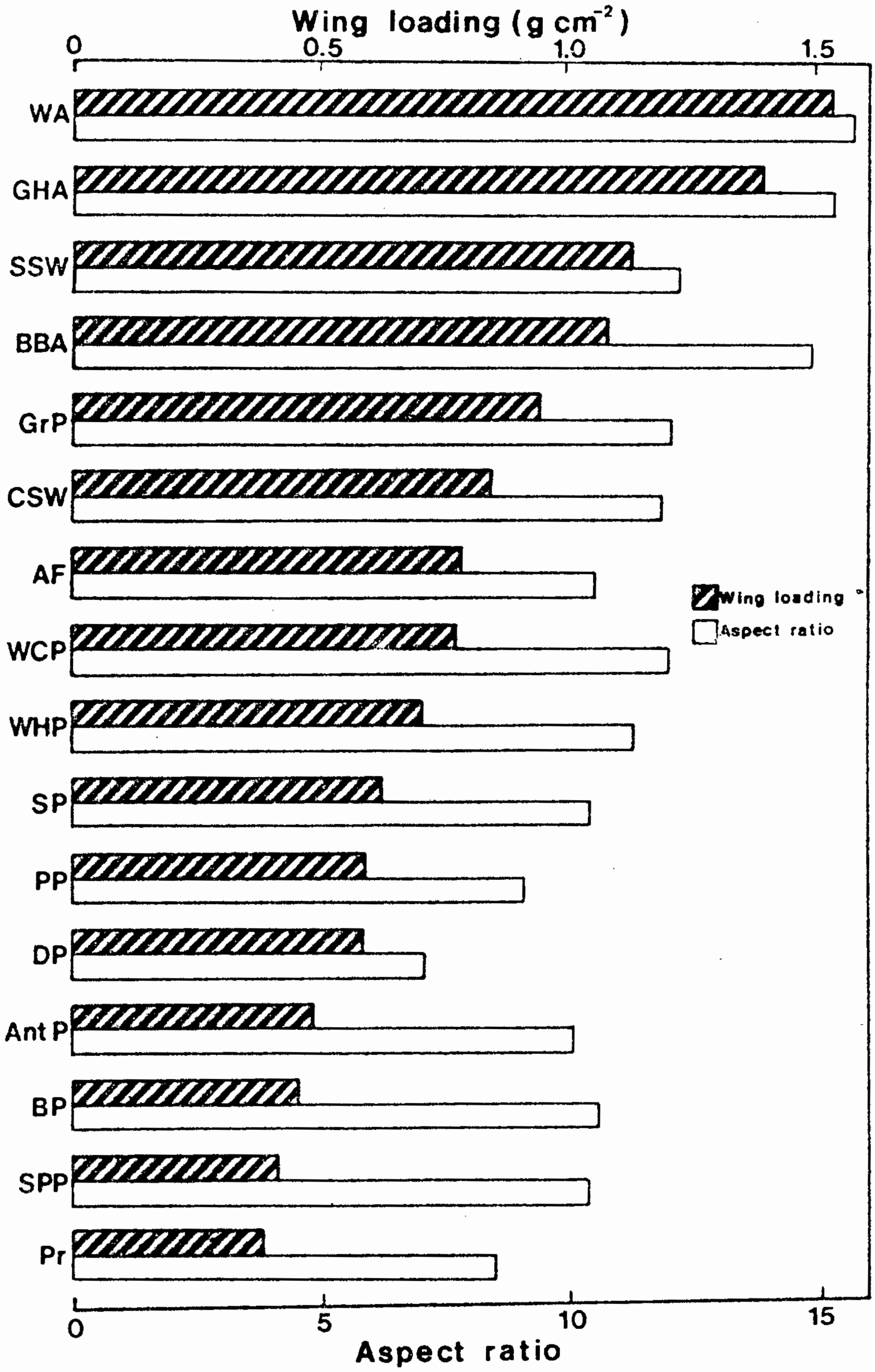

FIGURE 31. Wing loadings and aspect ratios of 16 procellariiform seabirds. Data are my own and from Warham (1977)

many factors intermediate between the birds and their physical environment. These (eg. food) directly affect the birds' distribution and, in turn, are affected by the abiotic environment. Bailey (1972) and Brown (1979) have shown how organic production and subsequent increased food availablilty are more important than the abiotic features promoting these favourable conditions for seabirds. The low correlations between Snow and Antarctic petrels on the one hand, and air and water temperatures, depth and wind strength on the other (Table 14), indicate that these features are of limited deterministic value. However, since my results and those of Szijj (1967) and Shuntov (1974) show that temperature represents a boundary for the northward dispersion of both species, it appears that intermediate factors are affecting the birds' distributions.

The diets of Snow and Antarctic petrels apparently are very variable and contain a large proportion of single prey items, suggesting opportunistic feeding. Crustaceans, fish and cephalopods occurred in more than 50% of the birds of both species, suggesting a lack of diet specialization. Mougin (1975) recorded crustaceans as the most frequent prey type of both species, again pointing to the apparent variablity in the birds' diet.

Many procellariiforms use dynamic soaring as an energetically economical mode of covering the vast expanses of the Southern Ocean. The low wing loadings and aspect ratios of the Snow and Antarctic petrels, and the smaller Procellariidae, are adaptations for buoyant flight, but not for long distance journeys (Warham 1977). The longer time spent flapping, as opposed to soaring, also limits the distance these birds can cover. Wind strength in the

East Wind drift is not as consistent as in the belt of the westerly winds north of the Antarctic Divergence. The easterly winds are characterized by strongly-gusting, katabatic, local air streams (King 1969, French 1974) and high pressure calms (pers. obs.). On windy days icebergs cause turbulence, and disrupt the wind speed gradient necessary for dynamic soaring. More particularly, ice floes inhibit albatrosses which need large, open areas of water in order to take to the air, especially in calm conditions. Most albatrosses and petrels have to alight on the water to seize their prey (Ashmole 1971, Appendix 2). Food is often accessible only in small areas of water amongst ice floes and, therefore, available to those procellariiforms capable of gaining flight within short distances and in weak winds. Thus, flight manoeuvrability and flapping flight are advantageous for feeding in the ice.

Ice floes apparently restrict the use of Antarctic seas to those seabirds (penguins excluded) which can use active flapping flight. The relatively low wing loadings and aspect ratios of Snow and Antarctic petrels apparently have evolved in association with the meteorological environment and ice conditions of the Antarctic. Their non-specialized, but more manoeuvrable, flight is likely to be relatively expensive energetically, restricting their foraging ranges to within the distribution of icebergs. This tends to sustantiate Shuntov's (1974) classification of Snow and Antarctic petrels as neritic-ice, rather than pelagic species. Other species (eg. Pintado Petrel, Antarctic Fulmar) with similar physical characteristics are absent in areas of sea-ice, probably because their nearest breeding stations are relatively far from Antarctica. The harsh winter climate may exclude these species from Antarctic seas during their non-reeding pelagic phase.

CONCLUSION

Snow and Antarctic petrels are restricted to areas of sea-ice by their flight characteristics. Food and oceanographic and meteorological conditions seem not to affect distribution directly. Topographical and meteorological features have promoted flight chracteristics unsuitable for long-distance journeys. The inability of albatrosses and large petrels to use flapping flight, and the considerable distance of the breeding localities of the smaller petrels, largely preclude them from areas of sea-ice.

SYNTHESIS

Seabirds are highly mobile animals. During the non-breeding phases of their lives, free to fend for themselves, pelagic birds apparently wander the ocean in search of food: "seabirds breed where they must and feed where they can" (Murphy 1936). By flying at approximately 30km/h, they probably cover a greater area per unit time than any other group of animals. This mobility makes study of their ecology at sea extremely difficult. Identification of many species is difficult. In particular, the various species of prions and divingpetrels are inseparable unless examined in the hand. Moreover, only the volant species, which comprise only about 35% of the total bird population of the Southern Ocean (Prévost 1981), are detectable from a ship. Penguins are seldom observed but comprise about 90% of the total avian biomass (Prévost 1981, Croxall in press).

To make best use of the limited sampling possible, it is necessary to count consistently accurately. Guide-lines for censusing, as given in Part 1 of this dissertation, should improve the precision of counting, if not the accuracy of the results. Whilst the 10-minute observation period is ideal for the vast areas of the Southern Ocean, shorter periods may be necessary for counting in neritic zones, where the environment changes rapidly over much shorter distances. The actual counting technique should, however, be applicable to all oceanic areas. Counting only those birds crossing an imaginary line perpendicular to the ship's path should aid the observer in deciding whether or not to count a particular individual. This rule also eliminates overestimates due to counting the same area more than once which results when counting within an arc.

Because they are able to fly faster than most ships, seabirds can display a variety of reactions to a ship. Birds following and circling the ship are the most difficult to count, because all individuals (excepting albatrosses and giant petrels) look similar. Only experience will reduce the overestimates due to counting birds close to the ship more than once. Part 2 highlights those species likely to give the most difficulties. Many observers claim that too many birds are missed in a 1 000m wide transect, and suggest 500m or 300m transects. However, it is close to the ship that the effect of the ship is greatest (attraction towards the ship is a more common and more exaggerated reaction than avoidance). I suggest that the degree of overestimation resulting from counting close to the ship only, will be far greater than any underestimation resulting from a 1 000m wide census. Providing that constant concentration is maintained, and powerful binoculars are used (10X magnification with at least a 40mm objective lens is recommended), practically all birds within a kilometre of the ship will be seen, identified and counted. The faster the ship moves, the less time a bird has to react in relation to it, and the closer the observer approaches an instantaneous count. I would seriousely doubt relative abundances assessed from a ship moving slower than 9km/h (5 knots), whilst counts from stationary vessels are useful for intra-specific analyses only.

My study area covered 5 100 000km^2 (by comparison the African continent covers about 29 000 000km^2). The logistical problems inherent in sampling seabirds in this area are immense. My study embraced a total of 167 days spent censusing seabirds from the M.V. S.A. Agulhas, covering an area of 11 720km^2. Thus, only 0.23% of the study area was surveyed. Looking at the problem from another angle, the total of 75 779 individual birds counted during my censuses represents only a small fraction of the total population of the study area. (An exact percentage is not meaningful because some breeding species leave the area (eg. Greater Shearwater), whereas others (eg. Blackbrowed Albatross, Sooty Shearwater), enter it during their pelagic phases.) The Prince Edward islands alone have at least 500 000 breeding birds (penguins excluded) (Williams _et_ _al_. 1979).

The trophic group approach is a means of overcoming the paucity of knowledge on the diet of seabirds away from their breeding localities (Part 3). Although the individual species comprising these trophic groups may be, to varying degrees, generalists, or opportunists, or both, each group as a whole generally takes one principal food-class. The species comprising the trophic groups all use one, or at most two, feeding methods. Therefore, the trophic groups of species were well-defined. Also, the distribution of the groups reflected the presumed distribution of their principal prey (Part 3). The distribution of small and large birds raises interesting questions about the birds' thermoregulatory mechanisms. Are birds immune from low temperatures when they fly? It is surprising that small birds, having a relatively large surface area to mass ratio, are able occur more abundantly in the south than larger birds, which appear to prefer warmer latitudes. Concomitantly, how fast is heat lost through the feet when a bird sits on the water? If heat loss is negligible, then it lends supports to the assumption that larger birds occur in warmer areas because of their prey distribution. We need to acquire more knowledge on seabird metabolic rates, and their responses to air and water temperatures, before more definitive conclusions can be made.

Associations of trophic groups with selected abiotic features of the environment were weak (Part 4). This may be due to the constituent species of a group associating differently with the tested feature (eg. species A increasing in abundance with depth, and species B decreasing). The resulting association would be confusing, with the more abundant species having the most influence. Another reason for the apparent non-linear association of the groups with the environment may be the abiotic data collected. As is shown in Part 5, there may be other features, not measured, that are important associates of overall distribution. Salinity, not recorded because of recurring problems with the salinograph, may be an important determinant or associate of the vertical distribution of plankton because of its effect on water density. Also, short-term fluctuations of those features measured may mask an association with some mean value of the feature. This is most probable with water temperature which was recorded at the surface. Here, under the immediate effect of insolation, wind and air temperature, the temperature is bound to fluctuate much more than the mean temperature for the top 10m layer. However, it is not unreasonable to assume that seabird distribution is associated in some determinable fashion with the physical environment. The two most obvious candidates for testing this type of relationship are the Snow Petrel and the Antarctic Petrel. The two species have limited and well-defined ranges. However, I show (Part 5) that linear correlations of single species with the abiotic features investigated are poor and, therefore, the occurrences of the species are unpredictable. I suspect that if a particular abiotic feature is within the acceptable range of a species' tolerance, individuals will occur there in any numbers, throughout its range. Thus, if water temperature is below 4° C, Snow Petrels will occur: an all-or-nothing effect. This may not apply to all features, and probably not to all species. Birds may be restricted by features not easily measured or not obvious to the observer (eg. the extent of ice coverage was not an anticipated associate of Snow and Antarctic petrel distribution). It is possible that other unforseen features will yield significant correlations with the distribution of other species.

It may be possible to use seabirds as indicators of food resources of potential commercial importance in the Southern Ocean (Part 3), providing that all possible influences of their distribution are investigated. The variety of responses of individual species within the trophic groups to environmental features probably will not allow the groups themselves to be used as indicators, because the patterns are too generalized. We need to attempt the same approach with an appropriate individual species for which we have detailed knowledge of its diet at sea. At present there are no such species. Only penguins appear to have specialized diets, but they cannot be censused from a ship. In our area, the best known at-sea diets are those of the Snow and Antarctic petrels. However, these two species are unsuitable candidates, because they appear to be generalist feeders, their distribution is associated with sea-ice which may mask any association with the occurrence of prey, and they associate positively with ships, thus complicating observer precision and census accuracy. The Kerguelen, Softplumaged and Whiteheaded petrels appear to be likely candidates. The former two are abundant and range over the whole area, the Kerguelen Petrel in the south and the Softplumaged Petrel in the north. They neither follow, nor are attracted towards, ships. Their wheeling, banking flight facilitates their detection, and they are easily identified. Unlike prions, which "mill about" in large flocks, these two species normally are encountered as individuals and they tend to fly in set directions. Thus, they are counted easily. However, detailed analyses of the species' diets at Marion Island (PFIAO unpublished data) suggest that they are also generalists. If this is true of other species as well, the possibility of using birds as indicators seems remote. Whiteheaded Petrels are less numerous and are not so conspicuous. Also, they do not breed in the area which may complicate complementary studies.

I can offer no suggestions on how to investigate the diets of seabirds at sea. In some 200 days that I spent at sea in the Southern Ocean I rarely saw birds actively feeding (Appendix 2), and never encountered conditions under which the collection of birds for stomach analyses was practicable (excepting in areas of sea-ice, where only Snow and Antarctic petrels are abundant).

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Appendix 1: Principal food-type and feeding-method groups, abbreviated vernacular name, status, body-weights and percentage abundance (numbers of individuals) of species observed in the African sector of the Southern Ocean. Food and feeding classification based on data in Ashmole (1971), Appendix 2 and unpublished records taken from the FitzPatrick Institute which also maintains records of bird weights. Status denoted by breeding resident (BR), Southern Ocean migrant (SM) and Holarctic migrant (HM).

FOOD-TYPE	FEEDING METHOD	SPECIES	Abbreviation	Status	Body-weight (kg)	Abundance (%)
Plankton	Surface-filter	*Pachyptila* spp, prions	Pr	BR	0.15	33.59
	Surface-seize/scavenge	*Halobaena caerulea*, Blue Petrel	BP	BR	0.21	13.16
	Pursuit-plunge	*Puffinus puffinus*, Manx Shearwater	MSW	HM	0.48	<0.01
	Dip/patter	*Oceanites oceanicus*, Wilson's Stormpetrel	WSP	BR	0.04	0.28
	Dip/patter	*Oceanodroma leucorhoa*, Leach's Stormpetrel	LSP	HM	0.05	0.05
	Dip/patter	*Fregetta tropica*, Blackbellied Stormpetrel	BBSP	BR	0.06	0.32
	Dip/patter	*Fregetta grallaria*, Whitebellied Stormpetrel	WBSP	BR	0.05	0.03
	Dip/patter	*Pelagodroma marina*, Whitefaced Stormpetrel	WFSP	BR	0.03	<0.01
	Dip/patter	*Hydrobates pelagicus*, European Stormpetrel	ESP	HM	0.04	0.13
	Pursuit-plunge	*Pelecanoides* spp, divingpetrels	DP	BR	0.12	0.35
	Dip/patter	*Phalaropus fulicarius*, Grey Phalarope	Phal	HM	0.03	0.03
Cephalopods	Surface-seize/scavenge	*Diomedea exulans*, Wandering Albatross	WA	BR	8.60	0.66
	Surface-seize/scavenge	*Diomedea melanophris*, Blackbrowed Albatross	BBA	SM	3.50	0.77
	Surface-seize/scavenge	*Diomedea chrysostoma*, Greyheaded Albatross	GHA	BR	3.60	0.25
	Surface-seize/scavenge	*Diomedea chlororhynchos*, Yellownosed Albatross	YNA	BR	2.00	0.17
	Surface-seize/scavenge	*Diomedea cauta*, Shy Albatross	ShyA	SM	4.10	0.29
	Surface-seize/scavenge	*Phoebetria fusca*, Sooty Albatross	SA	BR	2.50	0.25
	Surface-seize/scavenge	*Phoebetria palpebrata*, Lightmantled Sooty Albatross	LMSA	BR	2.70	0.35
	Surface-seize/scavenge	*Fulmarus glacialoides*, Antarctic Fulmar	AF	BR	1.00	0.39

	Surface-seize/scavenge	Daption capense, Pintado Petrel	PP	BR	0.45	0.61
	Surface-seize/scavenge	Pterodroma macroptera, Greatwinged Petrel	GWP	BR	0.58	1.32
	Surface-seize/scavenge	Pterodroma lessonii, Whiteheaded Petrel	WHP	SM	0.75	1.11
	Surface-seize/scavenge	Pterodroma incerta, Atlantic Petrel	AtlP	BR	0.52	0.37
	Surface-seize/scavenge	Procellaria aequinoctialis, Whitechinned Petrel	WCP	BR	1.21	1.40
	Surface-seize/scavenge	Procellaria cinerea, Grey Petrel	GrP	BR	1.03	0.16
	Pursuit-plunge	Puffinus gravis, Great Shearwater	GSW	BR	0.95	14.82
Fish	Surface-seize/scavenge	Calonectris diomedea, Cory's Shearwater	CSW	HM	0.96	0.08
	Pursuit-plunge	Puffinus griseus, Sooty Shearwater	SSW	SM	0.79	1.04
	Dip/patter	Sterna vittata, Antarctic Tern	AntT	BR	0.14	<0.01
	Dip/patter	Sterna paradisaea, Arctic Tern	ArcT	HM	0.13	1.28
	Surface-seize/scavenge	Puffinus assimilis, Little Shearwater	LSW	BR	0.23	0.90
Mixed	Surface-seize/scavenge	Macronectes giganteus, Southern Giant Petrel	GntP	BR	4.10	0.30
	Surface-seize/scavenge	Macronectes halli, Northern Giant Petrel		BR	5.20	
	Surface-seize/scavenge	Thalassoica antarctica, Antarctic Petrel	AntP	BR	0.70	6.59
	Surface-seize/scavenge	Pagodroma nivea, Snow Petrel	SP	BR	0.30	1.60
	Surface-seize/scavenge	Pterodroma brevirostris, Kerguelen Petrel	KP	BR	0.33	6.99
	Surface-seize/scavenge	Pterodroma mollis, Softplumaged Petrel	SPP	BR	0.31	6.84
	Piracy	Catharacta antarctica, Subantarctic Skua	SSk	BR	1.63	0.04
	Piracy	Catharacta maccormicki, Maccormic's Skua	MSk	BR	1.26	<0.01
	Piracy	Stercorarius pomarinus, Pomarine Skua	PSk	HM	0.67	0.03
	Piracy	Stercorarius parasiticus, Arctic Skua	ASk	HM	0.53	0.01
	Piracy	Stercorarius longicaudus, Longtailed Skua	LTSk	HM	0.29	0.01

Greyrumped Stormpetrel Garrodia nereis, Kerguelen Tern Sterna virgata, and Common Noddy Anous stolidus were seen in the area but were not recorded during set observation periods.

Appendix 2: OBSERVATIONS OF PELAGIC SEABIRDS FEEDING IN THE SOUTHERN OCEAN

There is a paucity of direct observations on the feeding habits of pelagic seabirds. These birds spend the greater part of their lives, and feed almost entirely, at sea. Moreover, they feed mainly at night when their vertically migrating prey are at the surface (Imber 1973, Imber & Berruti 1981). Here I summarize observations on natural feeding in the African sector of the Southern Ocean recorded while counting birds on 15 cruises of the M.V. S.A. Agulhas, representing approximately 1 300 hours of observation, during the period April 1979 to September 1981. Censuses were made at all latitudes in the study area. Feeding observations are recorded here in groups of apparent prey (crustaceans, squid, fish), as well as associations with cetaceans, fish and other birds, and are summarized in Table 16. Unless otherwize stated, Ashmole's (1971) terminology is used to describe observed feeding methods. Records of Subantarctic Skua predation are published elsewhere (Sinclair 1980).

Crustaceans as prey

Dense surface swarms of krill (mainly Euphausia superba) were common south of the Antarctic Divergence. Neuston net trawls encountered these krill within 500mm of the surface. The Snow, Antarctic, Kerguelen and Blue petrels, the only species common in this area, showed little obvious interest in these swarms.

Snow and Antarctic Petrels were seen feeding more often than all the other pelagic species together. These birds are restricted within areas of sea-ice (Part 5), where at the height of the

Table 16: Food, feeding methods and feeding associations of 21 seabird species recorded in the African sector of the Southern Ocean during the period April 1979 to September 1981

SPECIES	FOOD				FEEDING METHOD						FEEDING ASSOCIATIONS
	Crustacean	Squid	Fish	Carrion	Surface seizing and scavenging	Surface filtering	Contact diving	Plunge diving	Dipping	Pattering	
Wandering Albatross		X			X						Whales
Blackbrowed Albatross											Whales
Greyheaded Albatross											Whales
Lightmantled Sooty Albatross		X			X						
Giant petrels				X	X						
Antarctic Petrel	X		X		X		X		X	X	Minke whales
Pintado Petrel	X	X	X		X				X		
Snow Petrel	X								X		Minke whales
Prions						X	X		X		Whales, penguins
Blue Petrel							X		X		
Atlantic Petrel		X			X						
Softplumaged Petrel		X			X						
Kerguelen Petrel											Whales
Whitechinned Petrel		X	X		X						Whales
Cory's Shearwater											Tuna
Great Shearwater		X			X						Tuna
Sooty Shearwater											Dolphins
Stormpetrels										X	
Divingpetrels								X			
Arctic Tern			X						X		Minke whales
Common Noddy									X		Penguins

austral summer they experience continuous daylight. As winter approaches, the periods of darkness increase, but this is minimized by the northward shift in the birds' distribution (Part 5). The Antarctic Petrel fed by three methods. Of 14 feeding attempts observed in one hour, eight fed by surface-seizing (always with wings outspread), five fed by "contact diving" (alighting on the water and immediately dipping head underwater, thrusting the wings backward apparently driving the body downwards, and diving up to a depth of 500mm), and one attempted to feed by pattering on the surface. Contact diving appears to be intermediate between pursuit diving, where the bird dives from the water surface, and plunge diving, where the bird dives from the air (Ashmole 1971). The prey observed were pink crustaceans. The surface swarms of krill appeared to be within easy reach of the Antarctic Petrel, but only once was the species seen to dive among these krill, with undetermined success. Snow Petrels and, to a lesser extent, Antarctic Petrels also fed by dipping amongst ice floes broken up by the ship. This feeding method is distinct from pattering (Ashmole 1971) where the feet may be used extensively as an aid to flight (Withers 1979). Whilst no prey was visible, the birds presumably were feeding on herbivorous fauna grazing on the epontic (ice-dwelling) algae which appeared to be abundant (see also Brown 1980). The ship's bow wave often washed krill onto ice floes. Snow Petrels, and once a Pintado Petrel, were quick to seize this krill by hovering momentarily above the ice. Dipping without submerging was the only feeding method seen employed by Snow Petrels, whereas Ashmole (1971) lists surface-seizing and pattering as the chief methods.

Squid as prey

I never saw any bird actually catching a squid. Squid were occasionally seen floating on the surface. It has been suggested (Ashmole & Ashmole 1967, Imber & Berruti 1981) that moribund squid may form a sizeable proportion of a seabird's diet.

Observations of squid being eaten by seabirds were infrequent. Four Pintado Petrels were seen sitting together on the water feeding on a squid approximately 400mm long. It is doubtful that these birds, even collectively, could have killed such a large squid. It was probably moribund or the left-over prey of an albatross or large petrel. An Atlantic Petrel and a Great Shearwater were at different times seen to seize squid (approximately 100mm long) from the surface, only to drop them after flying short distances. One each of the Wandering and Lightmantled Sooty albatrosses, Whitechinned and Softplumaged petrels were observed taking squid by surface-seizing. Squid were not seen to be eaten by either Snow or Antarctic Petrels although this prey type has been found in their stomach contents (Mougin 1975, Part 5).

Fish as prey

No shoals of small fish, as may be seen on the African continental shelf, were seen in the study area. Only four seabird species were seen taking fish.

All Arctic Terns fed by dipping, never submerging totally. Fish (approximately 50 - 70mm long) were the only prey observed. Antarctic Petrels took black and silver fish (about 50mm long) by contact diving, and a Whitechinned Petrel and a Pintado Petrel were seen flying with silvery fish in their bills.

Unidentified prey

Very small prey objects are not likely to be seen by an observer on a moving ship. The prey of prions, Blue Petrels, stormpetrels and divingpetrels were not identified during apparent feeding attempts by these species.

Prions were seen frequently in aggregations of several hundred individuals, but never feeding as a flock at sea. They do, however, feed in flocks in the inshore zone around Marion Island (A. Berruti pers. comm.). Filter-feeding was the preferred feeding method. They occasionally fed by picking up individual prey objects by dipping (especially alongside icebergs where Snow, Antarctic and Blue Petrels also fed), and rarely dived below the surface. By contrast, Blue Petrels were seen contact diving, remaining underwater for up to two seconds with undetermined success.

Most stormpetrels pattered along the surface, apparently feeding continually. This was particularly true of Wilson's Stormpetrel. None was seen to feed by any other method. No prey objects, if indeed they took any, were observed. Similarly, divingpetrels were not seen to capture anything. They were observed flying into waves without any apparent change in flight pattern, maintaining their fast wing beat until disappearing underwater. They also executed a "belly flop", bouncing hard on the water surface whilst flying, but these did not appear to be feeding attempts.

Feeding associations

Associations were recorded when birds took an obvious interest in other animals. Birds associated with mammals, fish and other birds, apparently in anticipation of food. However, feeding was not always observed.

Extremely few marine mammals were observed on the voyages, and then only some were accompanied by birds. Snow and Antarctic petrels and Arctic Terns were seen feeding most actively in association with a school of about 200 Minke Whales *Baleanoptera acutorostrata*. The only prey observed at this time were fish approximately 70mm long, taken by Arctic Terns. At different times Wandering, Blackbrowed and Greyheaded albatrosses, Whitechinned and Kerguelen petrels and prions were seen accompanying unidentified whales. A pair of Killer Whales *Orcinus orca* were followed by 18 individuals of four species, apparently feeding in their wake. Killer Whales were seen frequently at Marion Island but were never accompanied by seabirds, although giant petrels were, on three occasions, seen scavenging on the remains of Southern Elephant Seals *Mirounga leonina* and penguins killed by these whales. Other associations observed were Cory's and Great shearwaters with a school of tuna (see also Ashmole & Ashmole 1967), Sooty Shearwaters with a school of 30 dolphins, and 10 prions with *Eudyptes* penguins. Feeding was not confirmed. At Gough Island, Common Noddies often were seen following and feeding (by dipping) above Rockhopper Penguins *Eudyptes chrysocome*. A similar association between Antarctic Terns and Jackass Penguins *Spheniscus demersus* has been observed in southern African inshore waters (J. Cooper pers. comm.). On none of these occasions was the prey visible.

Concluding remarks

The range of prey taken and feeding methods used suggests that the many pelagic species of the Southern Ocean are, to varying degrees, opportunists. This conclusion is supported by the high abundance of Southern Ocean birds on the trawling grounds off southwestern Africa (Sinclair 1978), where offal, discarded fish and squid are taken during feeding frenzies (pers. obs.).

Diel vertical migration of squid (Roper & Young 1975) and crustaceans (Ashmole 1971) enables Procellariiformes to feed on mesopelagic prey (Imber 1973). A nighttime feeding strategy would be feasible only north of the Antarctic Divergence where there is sufficient darkness. This would explain the lack of feeding observations of species whose distribution lies within these areas. However, in the high latitudes in the austral summer there is no, or only partial darkness. Snow and Antarctic petrels, the two most southerly distributed procellariiforms, therefore have to feed during daylight, at least for part of the year. Any disadvantages for these birds that may arise from the shorter night and possible suppressed vertical migration (Bogorov 1946) would appear to be compensated for by the fauna associated with sea-ice at or near the surface.

The above feeding observations were recorded out of a total of approximately 160 000 birds counted during the censuses. Whilst I do not claim to have all feeding attempts recorded, and therefore hesitate to quantify the data, I am confident that less than 0,5% of all birds seen were foraging. The paucity of direct observations of natural feeding accumulated over such a long period stresses the need for indirect methods of discovering where