(ISBN: 0-943610-39-7)

THE MARINE ECOLOGY OF BIRDS IN THE ROSS SEA, ANTARCTICA

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ORNITHOLOGICAL MONOGRAPHS NO. 32
PUBLISHED BY
THE AMERICAN ORNITHOLOGISTS' UNION
WASHINGTON, D.C.
1984

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ORNITHOLOGICAL MONOGRAPHS

This series, published by the American Ornithologists' Union, has been established for major papers too long for inclusion in the Union's journal, *The Auk.* Publication has been made possible through the generosity of the late Mrs. Carll Tucker and the Marcia Brady Tucker Foundation, Inc.

Correspondence concerning manuscripts for publication in the series should be addressed to the Editor, Dr. Mercedes S. Foster, USFWS, National Museum of Natural History, Washington, D.C. 20560.

Copies of *Ornithological Monographs* may be ordered from the Assistant to the Treasurer of the AOU, Frank R. Moore, Department of Biology, University of Southern Mississippi, Southern Station Box 5018, Hattiesburg, Mississippi 39406. (See price list on back and inside back covers.)

Ornithological Monographs, No. 32, x + 97 pp.

Editor of AOU Monographs, Mercedes S. Foster

Special Reviewers for this issue, John P. Croxall, British Antarctic Survey, Cambridge, England; Peter A. Prince, British Antarctic Survey, Cambridge, England; George E. Watson, Division of Birds, National Museum of Natural History, Washington, D.C.

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First received, 21 April 1982; accepted 27 October 1982; final revision completed, 10 August 1983

Issued February 23, 1984

Price $9.00 prepaid ($8.00 to AOU members).

Library of Congress Catalogue Card Number 84-70267

Printed by the Allen Press, Inc., Lawrence, Kansas 66044

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INTRODUCTION

In the present study we attempt to explain the factors that determine seabird occurrence and distribution in the Ross Sea during summer. Originally, the study was designed to illuminate the at-sea ecology of Adélie Penguins (*Pygoscelis adeliae*) in the Ross Sea, as a complement of intensive studies on the species' breeding biology. However, data were gathered on all species. The study was formulated during a period when information was beginning to emerge on how oceanographic factors affect seabird distribution (see below), and thus we analyzed the occurrence of seabirds in the Ross Sea and northward into the South Pacific Ocean with reference to oceanographic features, the location of productive areas where food is likely abundant, the occurrence of ice, and the location of breeding sites. We attempt to show in a semi-quantitative manner how all these factors are integrated to produce the observed patterns of seabird distribution.

In the last 20 to 30 years, and mostly in the last decade, as a by-product of the "golden age" of oceanographic and fisheries research, a few marine ornithologists have conducted quantitative studies of seabirds at sea. As a result of these recent efforts, the importance of Murphy's (1936) early work on the oceanography of seabird distributions has become very clear. At last we are following his lead in earnest, and in so doing we are discovering that birds perceive the ocean in terms much more specific than merely "wet" or as a provider of food (Brown 1980). Ashmole (1971), Watson et al. (1971), and Watson (1975) summarized the marine distributions of seabirds by broad climatic zones of surface water. Others, such as Szijj (1967) and King (1970), noted a relationship between the distributions of certain species and more narrowly-defined ranges of sea surface temperatures. Brown et al. (1975), Ainley (1976), Pocklington (1979), Brown (1980), and Ainley and Boekelheide (1984) extended this idea to types of water defined narrowly by temperature and salinity. Ainley (1977) noted that other physical properties of the ocean, for example, turbidity as a function of phytoplankton density (the "blue" [clear] water vs "green" [turbid] water of Murphy 1936), could also limit species' distribution.

Based on this recent body of work, it must be recognized that seabirds occur in habitats much more precisely defined than previously thought. To varying degrees, depending on species, seabirds probably occur in waters of oceanographic types specific to a species or a group of species. Classifying each seabird species according to the oceanographic properties of its preferred habitat is a task that has hardly begun. Yet such a classification will help to explain many of the "unusual" occurrences of species in specific regions. So little is now known about the oceanographically-defined habitats or preferred water types of seabirds, that the word "vagrant" (e.g., Watson 1975) must be applied with extreme care to individuals somewhat removed from the currently understood range of a species.

Confounding the idea that seabird occurrences are specific to oceanographic water types are the species that undertake long movements. For example, the Sooty Shearwater (*Puffinus griseus*) annually migrates back and forth across the tropics and subtropics between the southern subpolar waters where its breeding islands lie, and the northern subpolar waters where it molts and spends most of its nonbreeding period. Another example is the Wandering Albatross (*Diomedea exulans*), a species that nests on islands in subpolar or warm polar waters, but that frequents waters well into the subtropical zone.

Identifying the oceanographic habitats to which birds such as these are adapted can come about only after their oceanographic preferences and marine ecologies are studied in detail.

Also confounding our understanding of the marine distributions of seabirds is the fact that within their specific ranges, species are not evenly distributed. One factor that causes seabirds to concentrate in certain areas is breeding; they must stay within range of nesting colonies and nests to feed and care for their young. This idea has been appreciated for a long time; at times it has even dominated our conception of factors controlling seabird distributions (e.g., the "inshore" vs "offshore" concept of Wynne-Edwards 1935). When seabirds are encountered at what seem to be unusually long distances from nesting areas, the obvious question is the breeding status of the individual(s), a subject about which information is often lacking. For breeding Mottled Petrels (*Pterodroma inexpectata*), "within range" of nesting sites can mean a few thousand kilometers (Warham et al. 1977; Ainley and Manolis 1979), but for the Adélie Penguin with its reduced long-range mobility, "within range" is less than 200 kilometers (see p. 24).

Another factor that accounts for the uneven occurrence of seabirds within their specific oceanographic environments is the patchy distribution of their food. During breeding, species may fly to areas of high food availability some distance from nesting areas; nonbreeding individuals occur in these areas too, but would also potentially be free to exploit food sources farther from nesting sites. Physical oceanographic processes, which act to integrate shorter-term atmospheric phenomena, are usually directly or indirectly responsible for concentrations of potential prey through enhancement of productivity in certain areas (see review in Brown 1980).

The broadly-defined distributional patterns of seabird species are qualitatively well known for the open water areas of the Antarctic during late summer and fall, and we are fortunate to have the summaries by Watson et al. (1971) and Watson (1975). The Antarctic Convergence, which is the northern boundary of the Antarctic, and the presence or absence of pack ice, are generally considered to be the prime factors affecting the large-scale distribution of birds in Antarctic waters. The restricted latitudinal occurrences of seabirds in southern, high latitude waters, and the general effect of ice on species' occurrences, are also reflected in more recent studies of seabirds at sea in the Antarctic (e.g., Kock and Reinsch 1978; Griffiths et al. 1982; Thurston 1982; Ainley and Boekelheide 1984). Quantitative observations on species' more specific habitat preferences, however, are rather sparse for the Antarctic. Information on smaller-scale patterns of abundance is, thus, also rare, and factors determining distributions are poorly known. Pack ice exerts a strong influence on the localized occurrence of seabirds, as the few existing quantitative studies show (Cline et al. 1969; Erickson et al. 1972; Ainley et al. 1978; Zink 1978, 1981), but its influence may have been somewhat over-estimated in studies where other physical and biological factors were not considered (Ainley and Jacobs 1981).

METHODS

CENSUSES

Cruises were made aboard U.S. Coast Guard cutters (USCGC, = ice breakers) as listed below. Dates encompass periods when the ships were within the study area (Figs. 1, 2) and are divided into early summer (15 December to 4 January) and late summer (16 January to 21 February) periods. Before the present study, systematic observations of seabirds this far south were virtually non-existent for early summer because of the heavy sea ice. Ships and dates of early summer cruises are: USCGC *Northwind,* 15 December, 1976 to 4 January, 1977, and 19 December, 1979 to 2 January, 1980; and USCGC *Burton Island,* 23 December to 29 December, 1977. Late summer cruises were made on USCGC *Burton Island,* 16 to 19 and 22 to 26 January, 1977; and USCGC *Glacier,* 2 to 21 February, 1979. Counts were made from the ice breakers' bridge wings where eye level was about 16 m above the sea surface. Counts were made for 30 min of every hour that the ship traveled at speeds exceeding 6 knots during daylight (which was more or less continuous). The ships cruised at a maximum 10–12 knots in open water. Each half-hour census was equivalent to one transect. Transects were not made when visibility was less than 300 m, but rarely was visibility other than excellent. We censused only birds that passed within 300 m of the side (forequarter) of the ship on which we positioned ourselves to experience the least glare. Transect width was determined using the sighting board described by Cline et al. (1969) and Zink (1981). Ship's position, up-dated hourly, was determined by satellite navigation. The distance traveled during each half-hour transect, multiplied by the transect width, provided the area of the strip samples; dividing bird numbers by this area gave an estimate of density. Birds that followed or circled the ship were counted only if they initially flew to it from the forequarter being censused. Even so, each such bird was counted as only a 0.25 individual in the total count to partly compensate for the fact that the bird likely approached the ship from at least a kilometer away. Binoculars (8×) were used to sweep the outer part of the census strip visually about once every 1–2 min to insure that storm-petrels and other birds on the water were not underestimated. We also scanned carefully for swimming penguins.

Ice conditions during each transect were recorded according to World Meteorological Organization format. Since the ice breaker generally followed the path of least resistance through heavy pack ice, we always estimated ice concentration just outside of each 300 m wide transect, i.e., from 300 m to 800 m, which gave a better approximation of overall ice conditions. Immediately after each half-hour transect, sea surface temperature was measured with a bucket thermometer, and a sample of water was collected for measurement of salinity (except on USCGC *Burton Island* 1977 when a salinometer was not available). The vertical temperature profile of the water column was measured periodically on most cruises by other researchers (see Ainley and Jacobs 1981). These profiles were useful for locating such features as the Polar Front and the Antarctic Slope Front. Whenever the ship stopped, water clarity was measured with a secchi disk. When in transit,

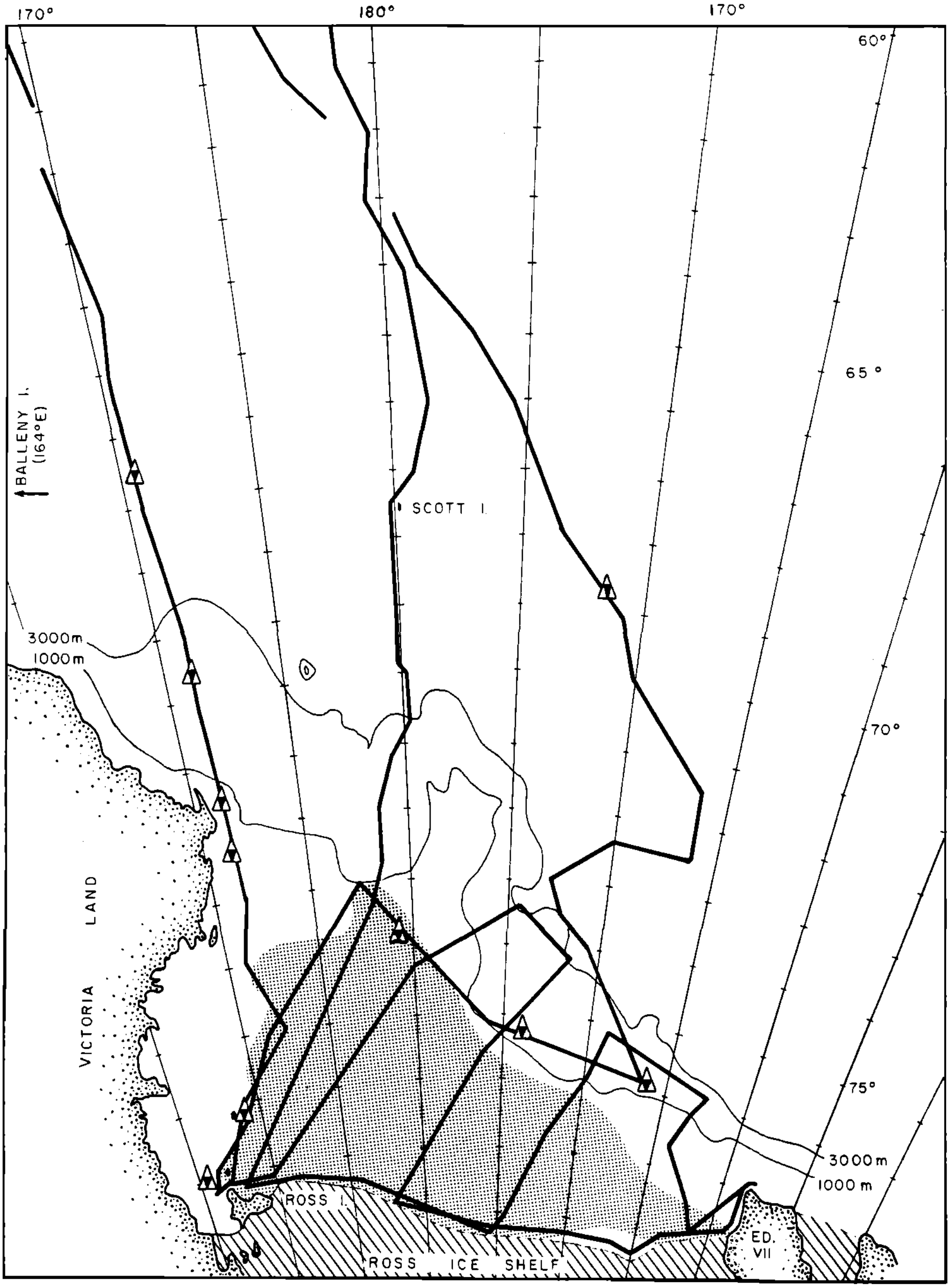

FIG. 1. Cruise tracks between 15 December and 4 January; triangles indicate collecting localities, and shading indicates the area of algal bloom.

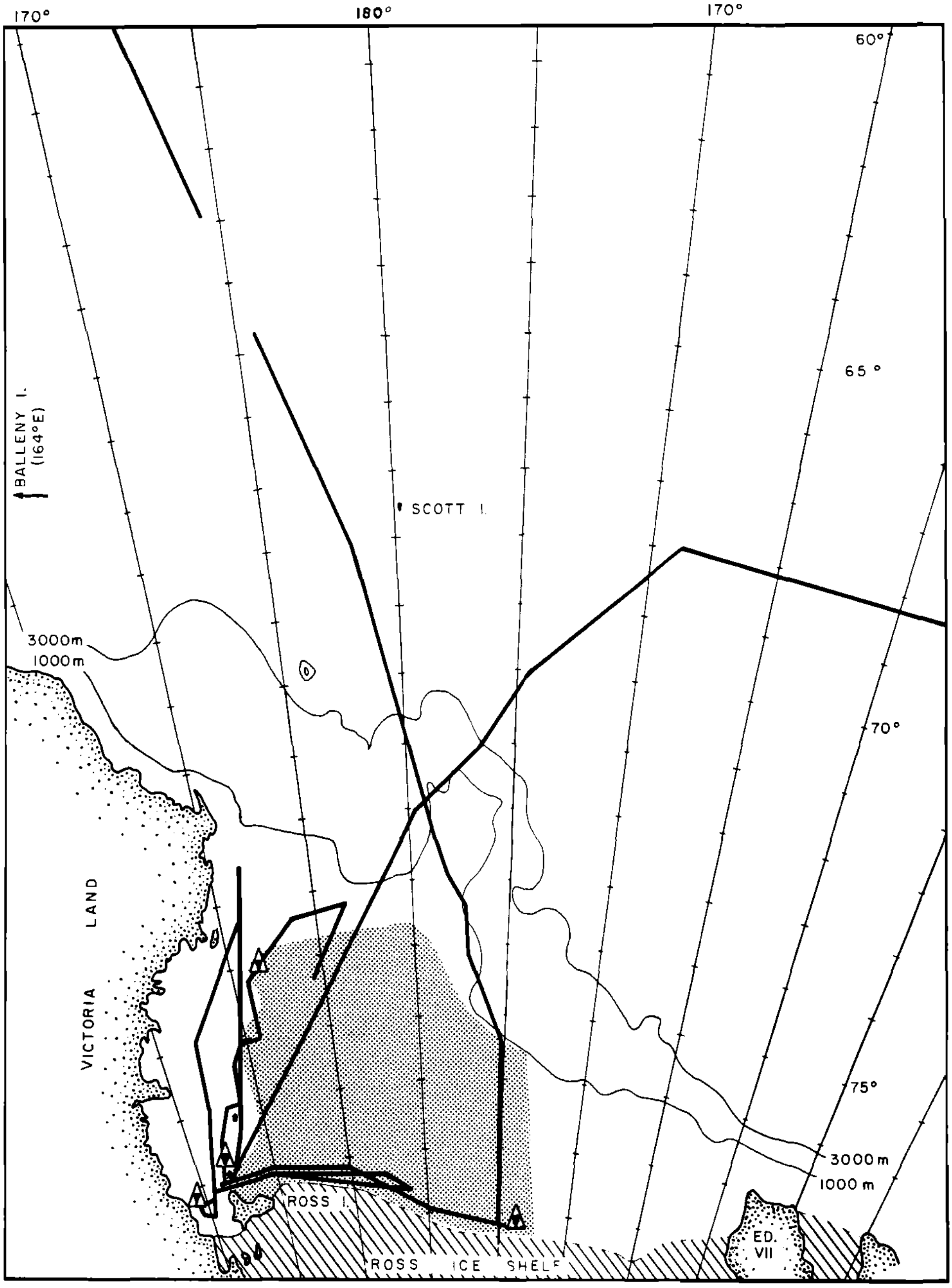

FIG. 2. Cruise tracks between 16 January and 21 February; triangles indicate collecting localities, and shading indicates the area of algal bloom.

we noted water color (green vs blue) as an indirect indication of gross changes in relative clarity.

POPULATION ESTIMATES

For each species, density estimates in each half hour transect were plotted on separate charts of the Ross Sea. Cruise tracks had been plotted on these charts which were drawn from Hayes and Davey (1974: polar stereographic projection). From visual inspection for each species, we then drew lines around zones having densities of consistently similar orders of magnitude. These lines, "isobirds," are analogous to the lines connecting similar sea surface temperature readings plotted on a map, isotherms. The data themselves determined the levels of magnitude of density estimates used to define each zone. Our choice of the level of magnitude for zones varied from species to species and was affected strongly by a species' overall abundance. For example, for a rare species we might distinguish between zones of 0.5 and 0.2 birds/km^2, whereas for a more abundant species, we might distinguish only between 5.0, 1.0, and 0.1 birds/km^2. For each zone delimited by an "isobird" line, we averaged all density estimates contained therein to derive an overall density for that zone. These zones of different densities were then plotted on charts (similar to those mentioned above) to show species' distributions. We did this only for early summer cruises in the Ross Sea and those portions of the South Pacific Ocean immediately adjacent to it because coverage of the study area during late summer was neither as even nor as thorough (e.g., compare Fig. 1 with Fig. 2), and because our transect coverage farther north was rather sparse. This procedure produced a more integrated picture relating species distribution to environmental factors and breeding sites. Breeding sites are shown on all early summer charts.

For many species, the distribution charts were used to estimate total population in the Ross Sea during December. This was done by determining the area of each density zone and multiplying by its respective overall average density, and then by adding the results for all zones. The area of zones was determined with a polar planimeter. For penguins, whose numbers and age structure are fairly well known, population size was determined by summarizing published estimates of breeding populations at rookeries which are fairly well known for the Ross Sea region. Total populations of penguins were then estimated by adding estimates of the number of nonbreeders at rookeries and at sea to estimates of the number of breeding adults (see later accounts of penguin species). Trying to estimate total penguin numbers from charts of at-sea densities would have been much less satisfactory than for other species because during December, a majority of penguins remains at rookeries for many days, the length of the stay being related to age, sex, and breeding status of the individual (Ainley et al. 1983). It was not possible to adjust population estimates of penguins observed at sea to these rookery attendance patterns, and, therefore, population estimates based on at-sea densities could not be made for penguins.

Had it been possible to estimate penguin numbers on the basis of at-sea estimates, we would have been able to compare population sizes estimated from at-sea densities with those estimated from censuses at rookeries. Complex, extended periods of rookery attendance, however, are not typical of petrels and skuas, which fast for only a few days at a time. We therefore believe that population estimates based on at-sea densities, adjusted for birds attending nests, are more valid for these species than for penguins. In the case of the South Polar Skua (*Catharacta maccormicki*) an estimate of rookery populations was available for comparison with our estimate of population size based on at-sea density. Using at-sea densities, we estimated 13,500 birds, and using rookery counts, we estimated 17,450 birds. Thus, at least for this species, the two methods produced results that were fairly close and certainly of the same order of magnitude (see South Polar Skua account for more details).

The methods we used to derive density estimates have been employed rather extensively in modern investigations of seabird occurrence at sea. According to Powers (1982), who recently reviewed and compared various seabird census methods, among the various methods that have been used, the one we used results in the most accurate assessments of the relative abundance of seabird species. Our method of treating individuals obviously attracted to ships is more conservative than the method Powers (1982) used. As pointed out by Powers, factors relating to ship and observer affect the comparability of census results. We anticipated these factors and controlled for them as follows: (1) census platforms (= ice breakers) were virtually identical on all cruises and, in addition, because all ships were ice breakers, effects of switching between fishing and nonfishing vessels did not influence our census results as has happened with some other studies; (2) height of observers above the water was always the same; (3) ship speed did not vary greatly—peak speed was only 12 knots, and we did not census when moving at speeds less than 6 knots; (4) observer variability was not important because one observer (DGA) was present on all cruises and actually participated in about two-thirds of all censuses, and only two other observers (EFO and RJB) participated in the other censuses; (5) perhaps fortuitously, the weather on all cruises in the Ross Sea was ideal (relatively calm with a high overcast), and thus we believe we did not even miss swimming penguins; and (6) our coverage of the Ross Sea was thorough, and we visited some areas enough times (as many as four) to be confident that the patterns of occurrence we describe are typical.

To our knowledge, no previous researchers have attempted to extrapolate population estimates from plots of at-sea densities for marine birds. In most parts of the world, however, estimating population size in that way is not necessary because seabird breeding colonies may be surveyed either by air or on the ground. In continental Antarctica, however, only penguin and skua rookeries are accessible; most breeding sites of other very abundant species (for example, Antarctic Petrels, *Thalassoica antarctica,* and Snow Petrels, *Pagodroma nivea*), are virtually inaccessible, if not unknown, given the great expense and extreme effort required for visits to the remote, inland mountain tops where they often nest. From a practical standpoint, it is only through at-sea censusing that the immense numbers of petrels in the Antarctic can be appreciated.

In the species accounts that follow, population and density estimates, and information on body weight (from the field and literature) were used to estimate biomass. Throughout, density estimates are expressed as the means of transects plus or minus one standard deviation.

FEEDING STUDIES

During censuses, a minute-by-minute tally of birds was kept along with information on behavior, molt, and age. Eight feeding behaviors, as defined by Ashmole (1971) and modified by Ainley (1977), were recognized. These were, (1) *dipping*: picking prey from the sea surface or just beneath it while remaining airborne and contacting the water only with the bill; (2) *contact dipping*: like dipping, but touching the water with the ventral surface of the body, thus suspending flight for an instant; (3) *pattering*: a form of dipping in which the bill and the feet, but not the body, contact the water, with the feet being used to push away from the sea surface; (4) *pursuit plunging*: flying into the sea and pursuing prey in subsurface flight; (5) *diving*: submerging from a sitting position at the surface to pursue subsurface prey using the wings or feet for propulsion; (6) *surface seizing*: catching active, live prey at or near the surface while sitting on the surface (the bird may submerge much of its body in reaching for prey); (7) *scavenging*: eating dead prey floating on the surface or lying on ice floes; and (8) *pirating*: chasing another bird to steal its food.

Seabirds were collected at 10 locations on early summer cruises and at four locations on late summer cruises, with the collector positioned in a small boat (locations are listed in Appendix I). We analyzed bird stomach contents in order to determine diet overlap among birds feeding in different habitats. We sampled birds in several representative habitats, including open water with bergs, and water without bergs over the deep ocean, continental slope, and shelf, with and without pack ice. Following the methods suggested by Bradstreet (1980), we collected in localities where more than one species was abundant and where feeding was actually observed to increase the likelihood that species interactions would be apparent. Birds were weighed and alimentary tracts removed within one hour of collection. Stomach contents comprised predominantly of fish were preserved temporarily in 70% ethanol (to stop digestion) until otoliths could be removed, usually within a day or two; contents subsequently were preserved, along with invertebrate samples, in buffered 10% formalin. Gonads and incubation patches were inspected to determine breeding status, and molt was recorded. Most birds were ultimately preserved as skeletons (a few as skins) and deposited in the U.S. National Museum of Natural History.

When studying the prey brought by adults to chicks, one often assumes that adults eat what they feed their chicks. This assumption is fairly safe for birds that feed chicks by regurgitation because, essentially, once the prey are caught and swallowed, they immediately and rapidly begin to digest, and the chicks ultimately receive what remains from the "race" between digestion and the return of the parent to the nest site. The chick usually receives a "soup" and, in the case of many petrels, an oil into which the food has been converted. The digested condition of regurgitated material makes prey identification difficult; in addition, it is necessary to assume that all prey are digested with equal speed, which is not always the case (see below).

In studies where stomach contents have been identified, some researchers have analyzed separately items contained in the gizzard and items in the proventriculus, or they have not bothered with gizzard contents. We sorted gizzard and stomach contents separately but ultimately combined the data from both for several reasons. First, in virtually all cases, gut contents progressed in degree of digestion, from fresh in the esophagus, through various stages of maceration in the proventriculus, to slower digesting material in the gizzard, rather than proventriculus and gizzard contents being clearly different. In the gizzard we found squid beaks and crustacean exoskeletons, but few otoliths; in the esophagus and proventriculus we found everything from fresh prey to exoskeletons and otoliths, but only a few squid beaks. This indicates that an analysis of items in the proventriculus alone underestimates squid consumption and an analysis of gizzard contents underestimates fish consumption and overestimates squid consumption. In both cases, crustacea are overestimated relative to the other two groups. Most of our collections were made in the morning (ca. 08:00 h), the remainder in the late afternoon or early evening (none late in the evening or at "night"). Prey caught during the darkest hours would be reduced to hard parts in the gizzard by morning; this seems especially likely for squid, which come nearest the surface when light is least intense. Our only observations of birds actually catching squid (n = 3 Mottled Petrels) occurred between 22:00 and 02:00 h. Because of these conflicting biases and an absence of data on relative rates of digestion for different prey, we thought it best to consider each item as equal. Our procedure of including gizzard with proventriculus and esophagus contents is supported by Bradstreet (1980), who summarized information on rates of digestion of fish in alcids. Apparently, otoliths disappear from proventriculus and gizzard contents within 24 h of ingestion and, generally, much more rapidly (even within 1.5 h in some cases; Bradstreet 1980). Presumably, the otoliths disappear even more rapidly from the proventriculus when they pass to the gizzard, where their digestion is completed. In any case, few fish would be detected if only contents of the proventriculus were inspected. In addition, Orr and Parsons (1982) found only otoliths in the gut contents of Ivory Gulls (*Pagophila eburnea*) collected in the morning, even though the birds had been observed feeding on myctophids the previous night. Unfortunately, no observations are available on rate of digestion of squid beaks in bird stomachs.

ENVIRONMENT

The Antarctic Convergence marks the transition between Subantarctic and Antarctic waters. It is the circumpolar region where Antarctic Surface Water sinks below the less dense Subantarctic Surface Water (Fig. 3). Deacon (1937) and Mackintosh (1946) placed it between 57° and 61°S in the South Pacific region north of the Ross Sea during summer. Gordon (1975), calling it the Polar Front, considered it more a zone than a line and placed it between 59.5° and 62.5°S.

One problem in trying to locate the Polar Front, particularly during summer, is that it frequently has no surface manifestation. The front is best defined below but within 200 m of the surface; its northernmost extent is considered to coincide with the 2°C isotherm (subsurface; Fig. 4). Warmer surface waters often extend well south of this feature. Eddies and meanders frequently form and migrate along the front, further complicating the determination of the exact position, or sometimes even, the definition by standard criteria, of the convergence.

The Ross Sea, which is due south of New Zealand, is considered here to lie between Victoria Land and King Edward VII Peninsula on the west and east, and between the Ross Ice Shelf and the 3000 m depth contour on the south and north,

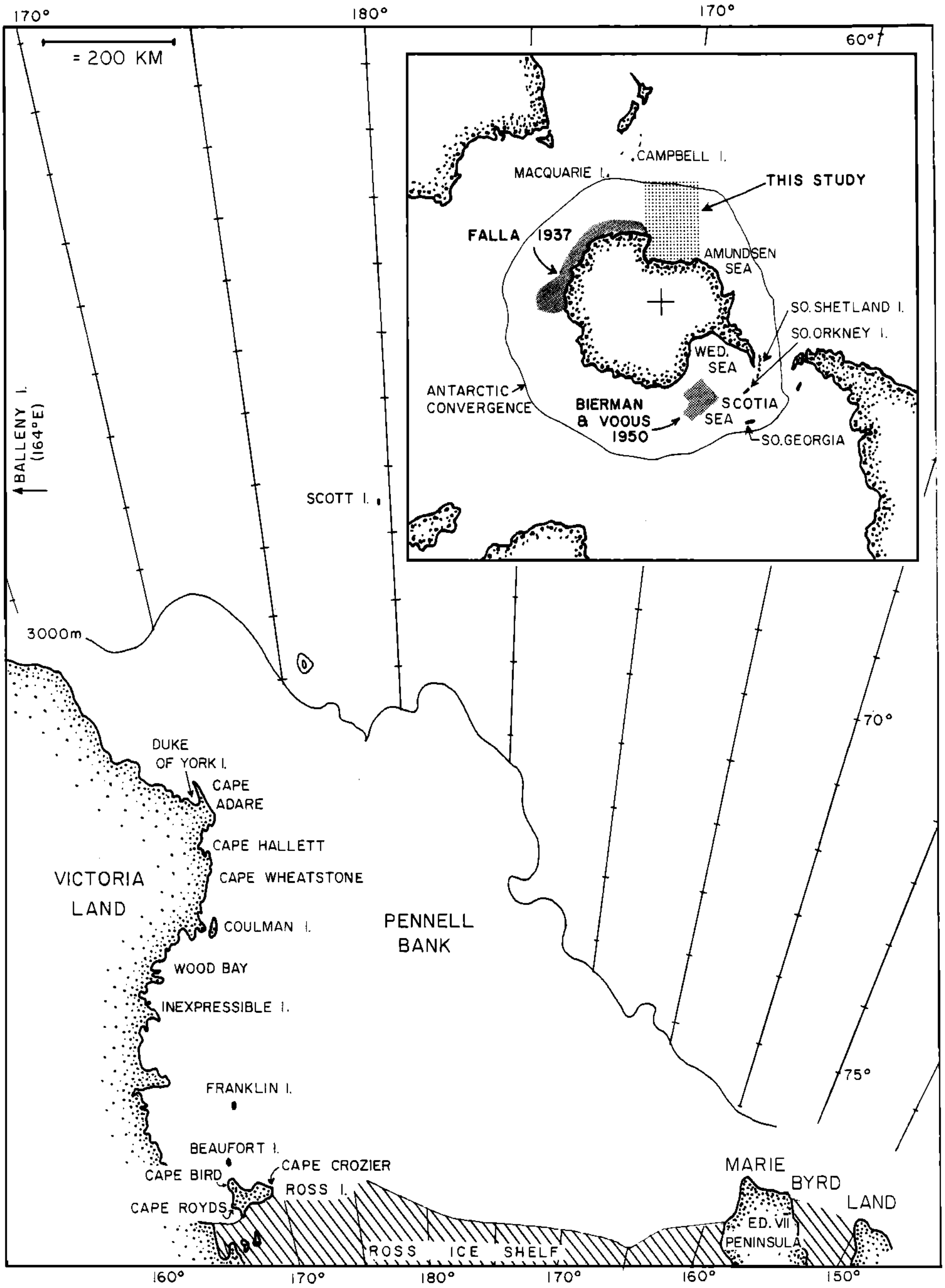

FIG. 3. Ross Sea and Antarctic localities mentioned in the text. In the inset map of the Antarctic, the Ross Sea study area and the study areas of Bierman and Voous (1950) and Falla (1937) are shown by shading.

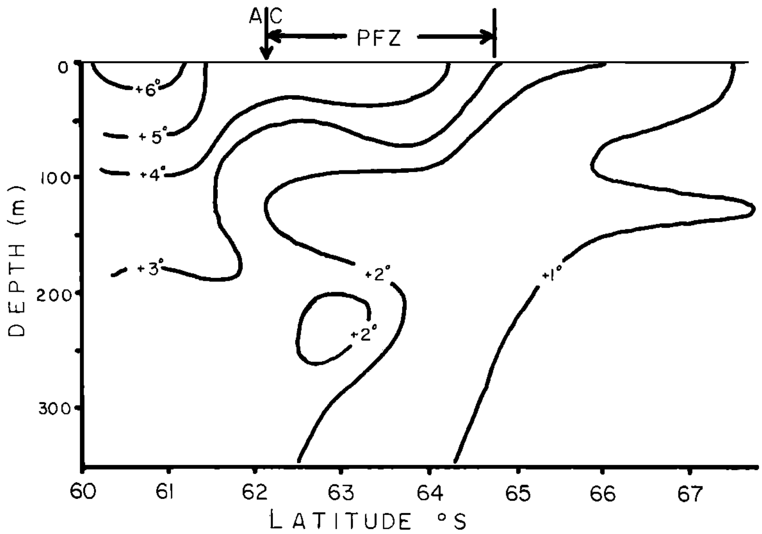

FIG. 4. Temperature profile with depth along the 1979 USCGC *Northwind* track from ca. 60°30′S, 176°30′E to ca. 67°45′S, 174°00′W (Fig. 1). PFZ represents the Polar Front Zone shaded on Figure 6 (waters overlying the 2.0°C isotherm), and AC indicates the position of the Antarctic Convergence as defined by the position of the 2.0°C isotherm 200 m from the surface.

respectively. The 3000 m contour can be taken as the dividing line between the lower continental slope and the deep ocean; bottom topography in the various figures was drawn according to Hayes and Davey (1974). The Ross Sea, thus, is shaped approximately like an equilateral right triangle with a base (Ross Ice Shelf) and a height (Victoria Land coast) of about 880 km each. Using a planimeter, we calculated its total area to be approximately 598,000 km^2. The location of the Ross Sea within the Antarctic, and localities in the Ross Sea mentioned in the text are shown in Figure 3.

Circulation in the Ross Sea is cyclonic, with westerly flow along the ice shelf, northerly flow along Victoria Land, and indications of a southeasterly set near the continental shelf break (shoreward of the 1000 m contour). An opposing current, typical of surface flow along the continental margin of Antarctica (see Sverdrup et al. 1942), sets northwesterly over the continental slope (Ainley and Jacobs 1981: fig. 2).

The Antarctic Slope Front described by Ainley and Jacobs (1981) lies over the Ross Sea continental slope. In the upper 100 m of surface water the front is not apparent, but below the surface layer, increased gradients in physical characteristics between Ross Sea Shelf Water and Circumpolar Deep Water mark its position (Fig. 5). The front generally lies 10 to 55 km seaward of the shelf break (ca. 600 m depth contour), which places it just to the south of the 1000 m contour (see Figs. 6, 7).

The Ross Sea is covered by pack ice during the winter except for intermittent leads and polynyas. The ice extends outward from the coast to beyond Scott Island. In late October a large open water area appears in the southwestern Ross

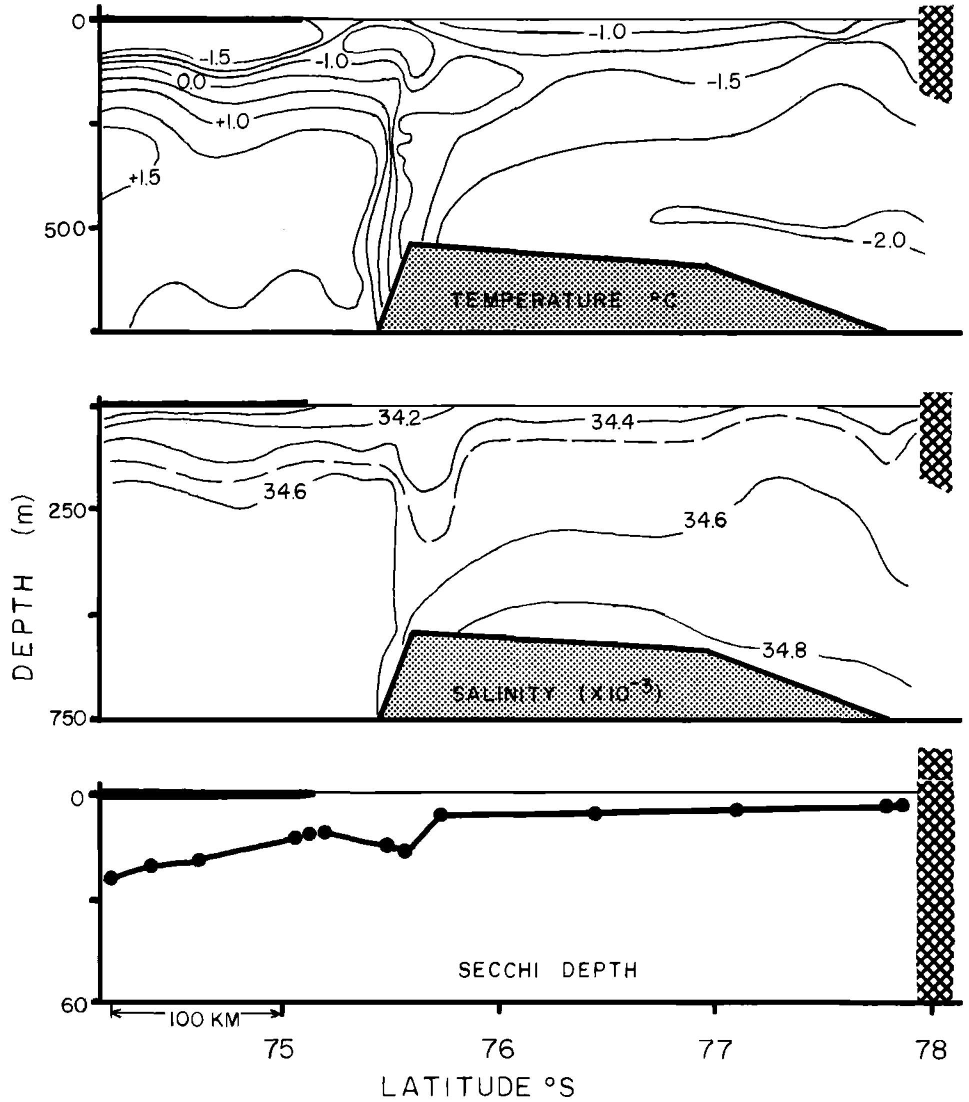

FIG. 5. The Antarctic Slope Front as indicated in the depth profiles of temperature, salinity, and turbidity (secchi depths) along the 1976 USCGC *Northwind* track from ca. 74°10′S, 171°00′W to ca. 77°55′S, 177°30′E (Fig. 1). The Ross Ice Shelf is indicated by cross-hatching at the right, and pack ice, by the thick, dark line at the surface to the left; stippling indicates the Ross Sea continental shelf.

Sea; this continues to widen toward the north and to a lesser extent toward the east (Fig. 8). At the same time, the northern edge of the pack recedes southward. By late summer and fall, pack ice usually remains only along the Victoria Land coast and in a large tongue that extends northwestward from King Edward VII Peninsula (Fig. 9). The western part of the study area away from the coastline is, thus, completely devoid of pack ice by late summer. The pack ice is concentrated in its central part, at 6 to 8 oktas cover, but with its internal leads it is more

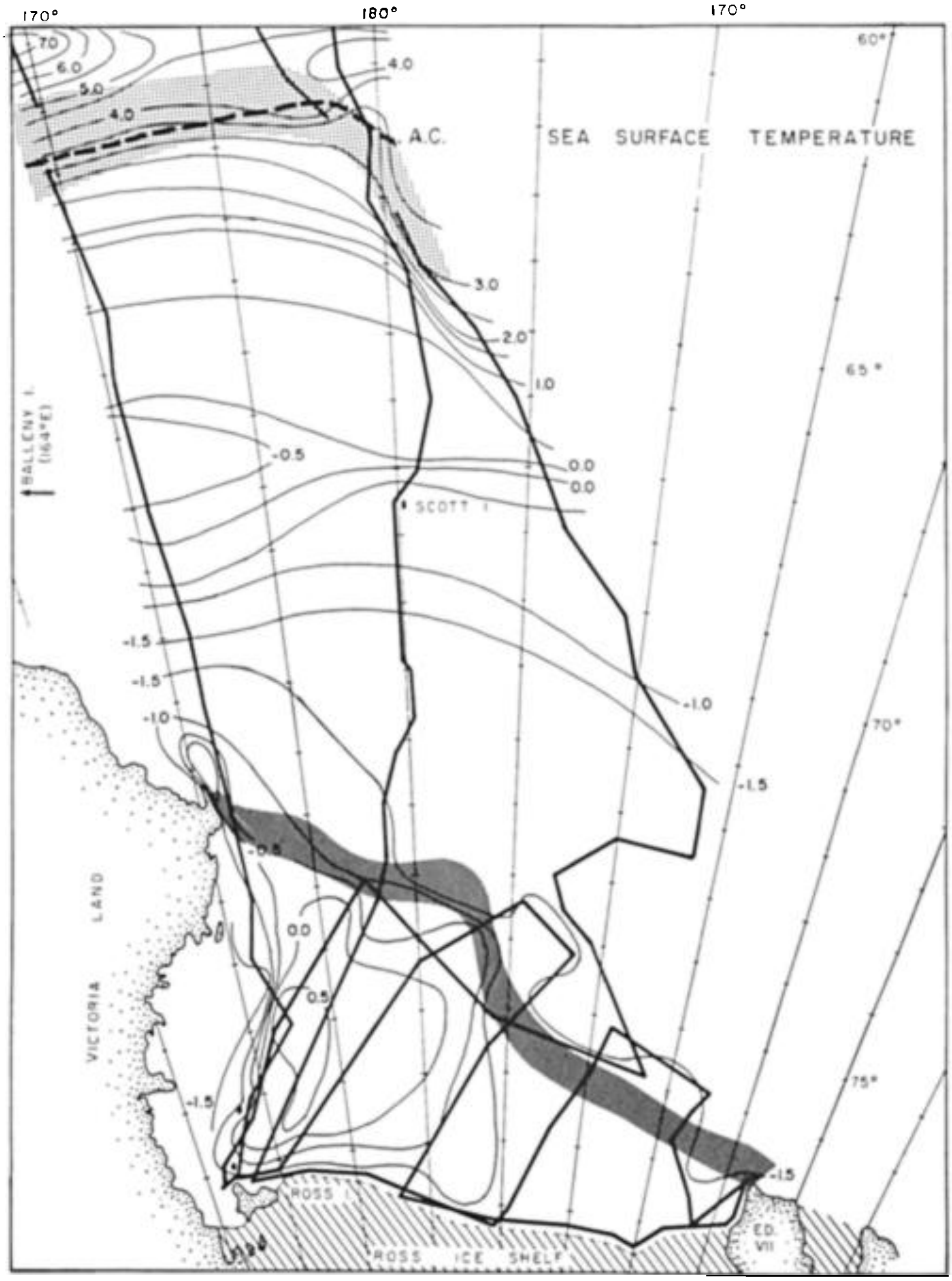

FIG. 6. Sea surface isotherms (in °C) drawn from direct measurements along cruise tracks (heavy unbroken line) of 15 December to 4 January. The position of the Antarctic Convergence (AC) is indicated by a heavy dashed line, and the approximate locations of the Polar Front Zone and the Antarctic Slope Front by light and dark shading, respectively.

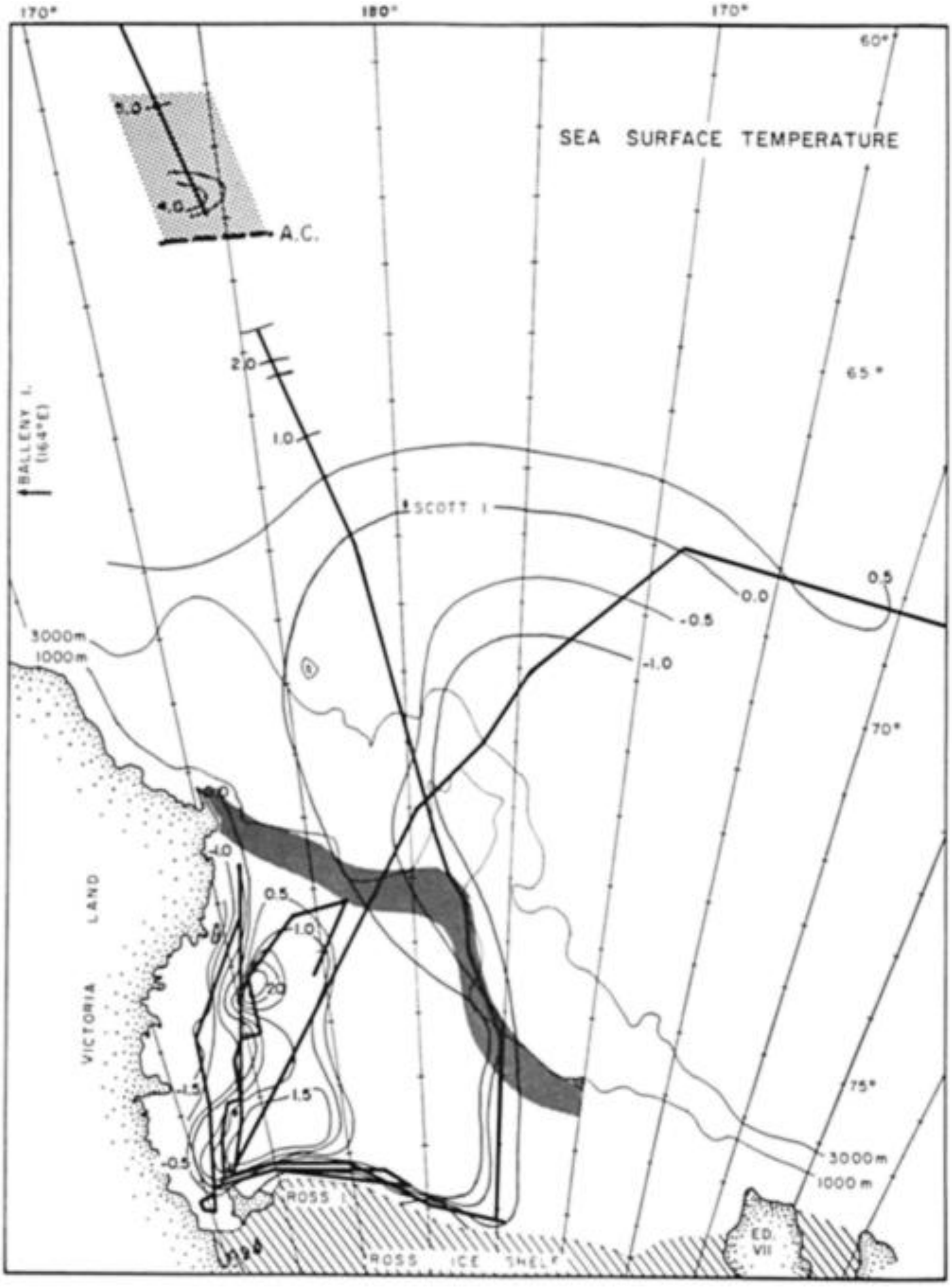

FIG. 7. Sea surface isotherms (in °C) drawn from direct measurements along cruise tracks of 16 January to 21 February; see Figure 6 for explanation of the other features indicated.

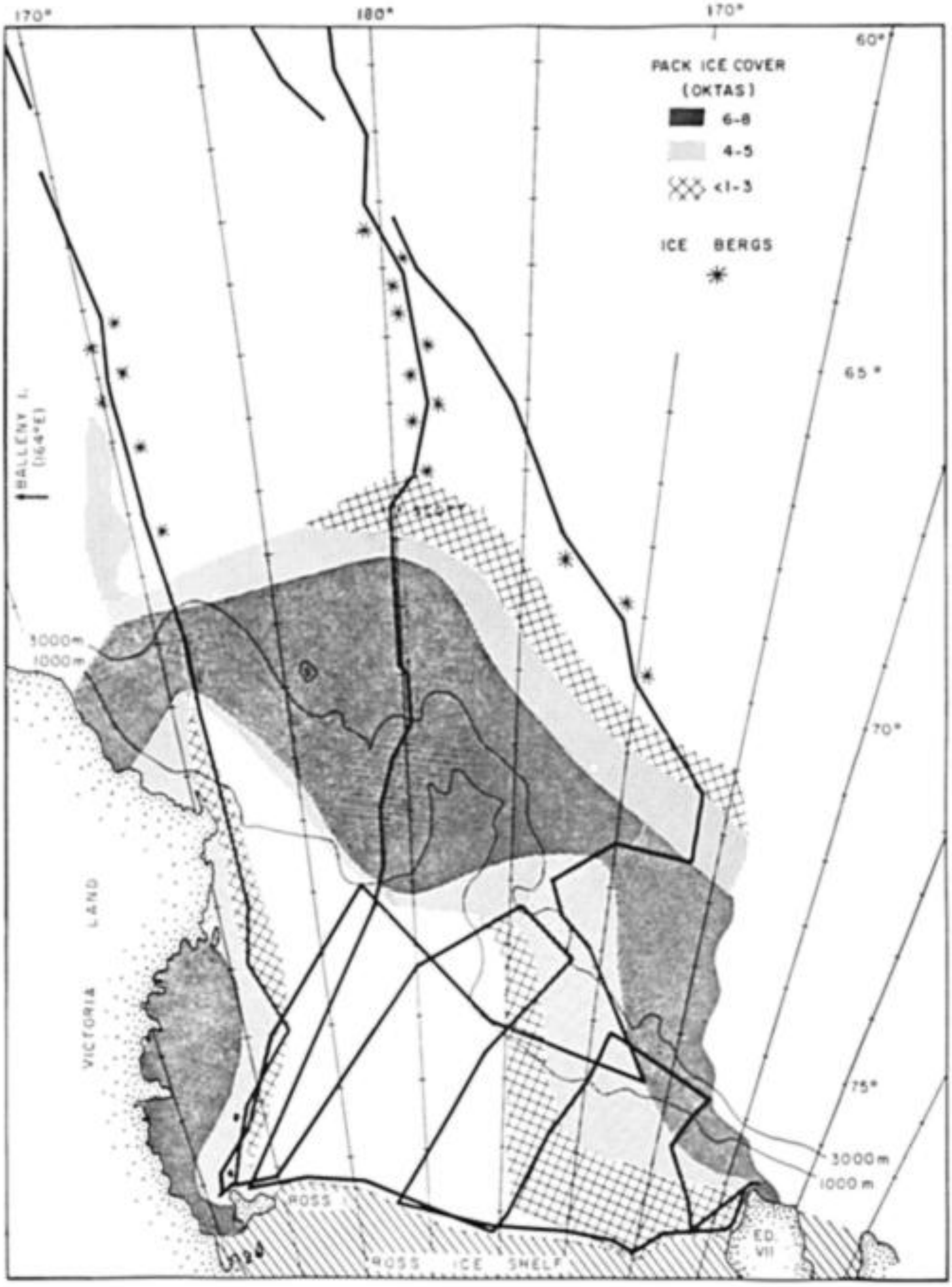

FIG. 8. Ice cover during late December and early January—a composite of satellite imagery and direct observations along cruise tracks.

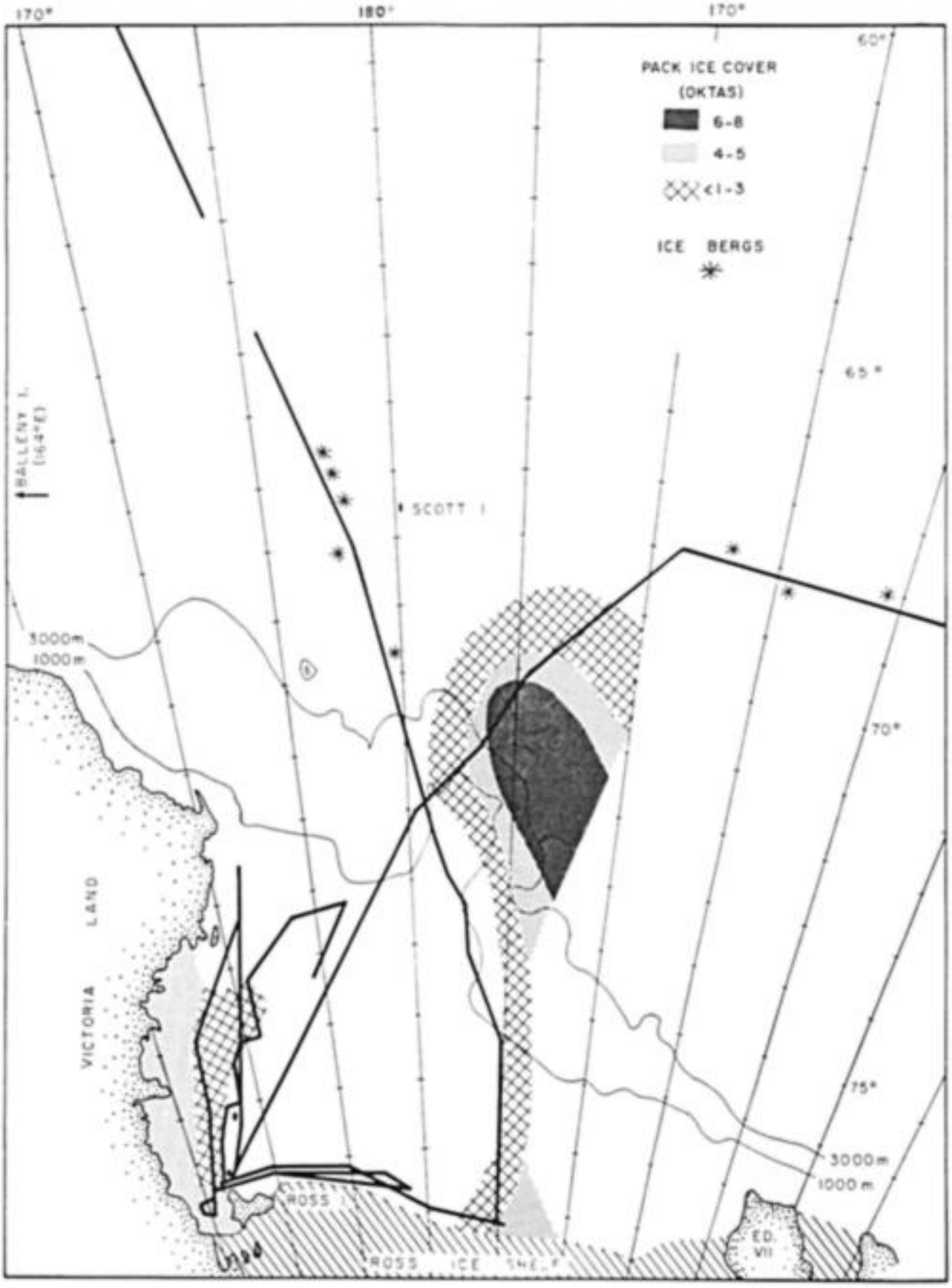

FIG. 9. Ice cover during late January to late February—a composite of satellite imagery and direct observations along cruise tracks.

divergent than the ice pack of the Arctic Ocean. Icebergs were concentrated in a belt extending from about 64° to 68°S; to the south they were less frequent, but grounded bergs were found on the Pennell Bank (74°S, 180°W) and just north of King Edward VII Peninsula (77°S, 158°W).

Surface temperatures declined southward toward the Ross Sea, reaching a minimum below −1.5°C over the continental slope and along the Victoria Land coast (Fig. 6). These low temperatures corresponded to the location of pack ice (Fig. 8), which kept the surface water near the freezing point, ca. −1.9°C at the salinities observed. For the same reason, low temperatures also prevailed next to the Ross Ice Shelf. The warmest temperatures appeared over the western continental shelf. By late January/early February, most temperatures had warmed by at least half a degree, with highs of 2°C over the shelf (Fig. 7). Salinities ranged between 33.8 and 34.2‰ (ppt) north of the shelf, and a band of <34.0‰ water appeared to intrude onto the central shelf (Figs. 10, 11). Salinities were generally lower near the less concentrated pack ice, and highest (>34.5‰) in the region of higher temperature over the western shelf.

An algal bloom, which lasted throughout the summer and fall, colored surface waters over the Ross Sea continental shelf emerald green (El-Sayed et al. 1978; Ainley and Jacobs 1981). A dramatic change in water color from green to blue and an equally dramatic decrease in turbidity over a distance of just a few kilometers indicated the abrupt boundary of the bloom at the slope front (Figs. 1, 2, 5; Ainley and Jacobs 1981). Under the persistent pack ice along Victoria Land (see below), the algal bloom was less intense; it decreased toward the east, as well, in the same direction that pack ice recedes in summer.

SPECIES DISTRIBUTIONS AND NUMBERS

EMPEROR PENGUIN (*APTENODYTES FORSTERI*)

During December, densities of Emperor Penguins were high close to two known breeding colonies in the western Ross Sea, but highest densities were found in an area adjacent to King Edward VII Peninsula (Fig. 12) where the presence of a large undocumented breeding colony has been suspected for some time (Watson et al. 1971, and references therein). The species was distributed in a belt extending from Cape Roget/Coulman Island to King Edward VII Peninsula, roughly coinciding with the continental slope and its overlying pack ice. We were unable to survey adequately the pack ice along Victoria Land, but suspect that relatively high densities of Emperors occur there owing to the several breeding colonies in that vicinity (Table 1; see also Watson et al. 1971: map 1). At distances greater than 300 km from breeding sites, about one-third of all individuals were yearlings (recognizable by their lack of bright colors; Watson 1975); within 300 km, most Emperor Penguins were in adult plumage.

During late summer cruises, we encountered only eight individuals of this species (Fig. 13); all were in pack ice, but our surveys of pack ice areas then were limited. We did, however, find Emperors at the northern edge of the ice pack where we had not found them earlier. One of three at the outer ice edge was a chick of the year. Very low densities of Emperor Penguins, on the order of 0.03/km^2, have been recorded during fall cruises in seasonally residual ice west and east of the Ross Sea (Gilbert and Erickson 1977; Zink 1978, 1981). These authors

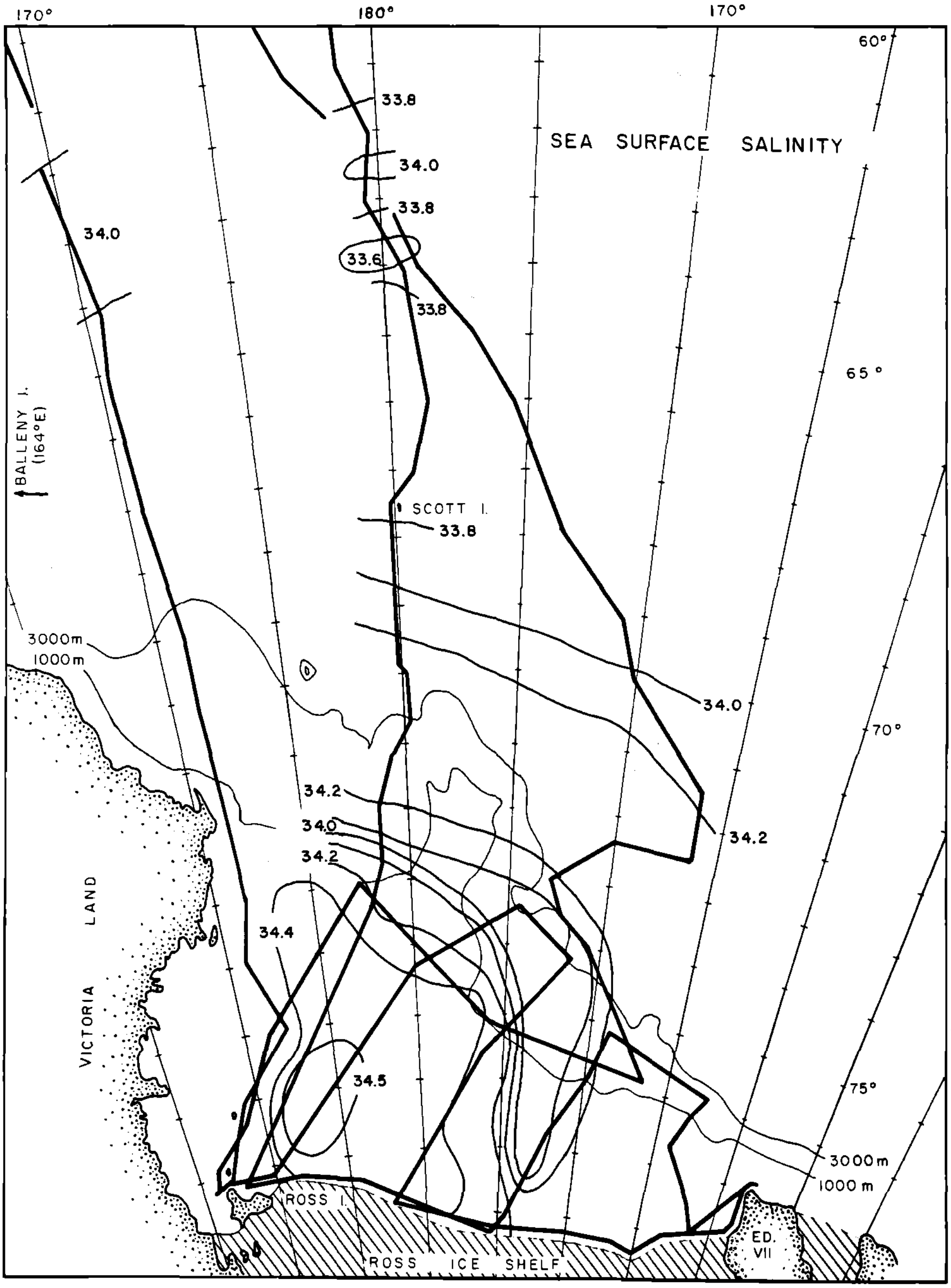

FIG. 10. Sea surface isopleths (‰) drawn from direct measurements along cruise tracks, 15 December to 4 January.

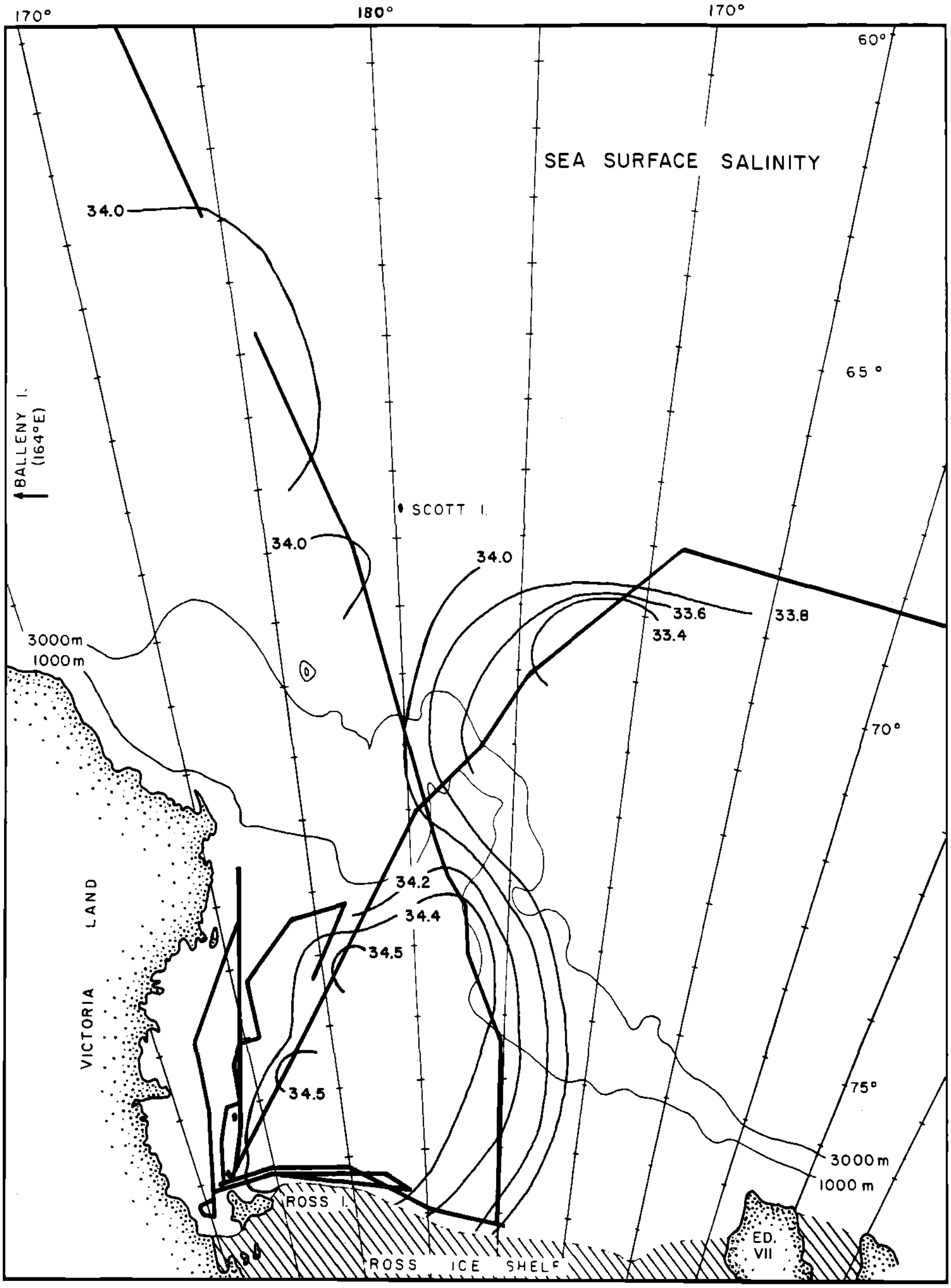

FIG. 11. Sea surface isopleths (‰) drawn from direct measurements along cruise tracks, 16 January to 21 February.

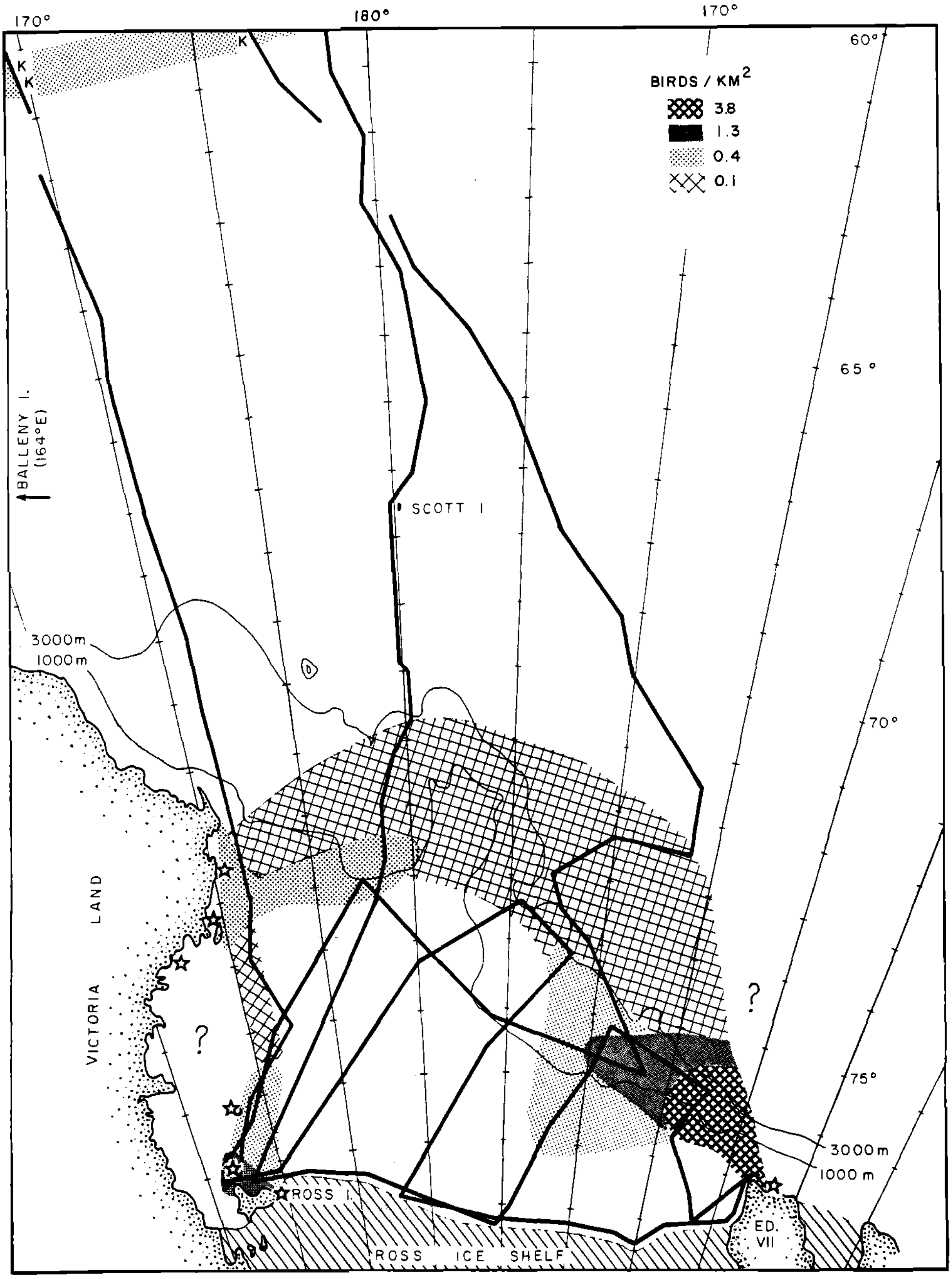

FIG. 12. Distributions of Emperor and King Penguins during early summer; Kings were seen only north of 61°S, and Emperors were seen only south of 70°S. Individual King Penguins are indicated by K's at the upper left. Emperor breeding sites are indicated by stars. Question marks indicate unsurveyed areas.

also encountered a few of these birds in the outer pack ice of the Ross Sea. Thus, Ross Sea Emperor Penguins appear to disperse into pack ice areas during fall (see Stonehouse 1953), but because Emperors remain away from breeding sites for less than three months, it is likely that they do not disperse widely (Bougaeff 1974).

Emperor Penguins definitely prefer pack ice, although we found a few in open waters of the continental slope several kilometers from the ice. The species showed no apparent preference for pack ice of a particular concentration. Cline et al. (1969) noted a preference for ice of sparse concentration in the Weddell Sea, but most of the Emperors they encountered were in ice over the Weddell Sea continental slope (Ainley and Jacobs 1981). Thus, these birds may have been responding more to biological productivity in the water column than to ice concentration.

Ross Sea population.—Counts of Emperors at rookeries along the Victoria Land coast totaled 141,274 breeding birds, which extrapolates to a total population of 227,800 birds including nonbreeding adults (Table 1: localities 1–18). Using the same literature sources, Taylor (1981) derived a much lower estimate of breeding numbers. He conservatively used minimum values from published estimates, whereas we used the maxima, following the argument by Todd (1980) that by late November and December (when all estimates have been made), egg and chick mortality have substantially reduced the ties of many breeders to the colonies. Based on the densities we observed northwestward from King Edward VII Peninsula, we estimated breeding and total populations there to be 70,990 and 114,500 birds, respectively (Fig. 12, Table 1). In the absence of at-sea information, Taylor (1981) arbitrarily chose a figure of 3000 breeders for that site. We believe that the order of magnitude of our rookery estimate, based on the estimate of at-sea densities of Emperors, is more realistic since correspondence between the two estimates is similar to that between comparable estimates near other, known colonies. King Edward VII Peninsula, as a site for a highly productive colony of Emperors, is ideal. Many grounded ice bergs offer protection from the elements as well as from premature breakup of the sea ice on which the species nests, and productive waters of the Antarctic Slope Front are close.

The total population of Emperor Penguins associated with Ross Sea breeding sites was estimated to be on the order of 342,300 birds, all but 17,400 of which were actually within the boundaries of the Ross Sea during December. This gave an overall density for the entire Ross Sea of 0.54 Emperor Penguins per km^2. Because they were concentrated in the ice along the Victoria Land coasts, along the King Edward VII Peninsula, and in the vicinity of the continental slope, but were absent from the open water of the central Ross Sea, the average density in areas where they did occur was about one per km^2. At distances greater than 300 km from nesting colonies, however, they were extremely sparse even where they occurred regularly.

KING PENGUIN (*APTENODYTES PATAGONICA*)

This species was encountered on three of the four cruises passing through the northern edge of the Polar Front Zone: two individuals each on cruises along longitudes 170°E and 175°E, one along 177°E, but none along 180°E (Figs. 12, 13). All were juveniles. Additional individuals were sighted immediately north

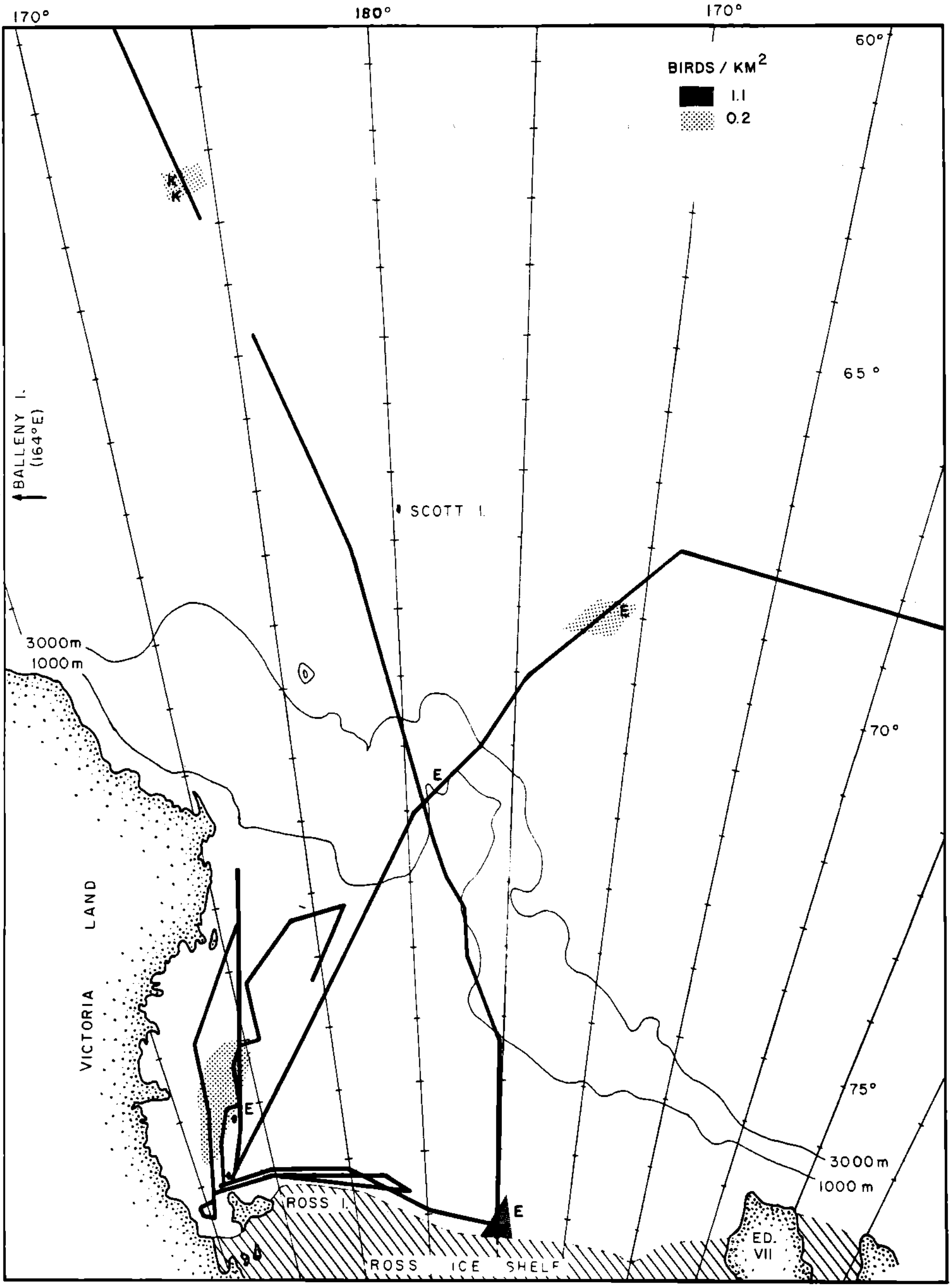

FIG. 13. Occurrence of Emperor (E) and King (K) Penguins along cruise tracks during late summer.

TABLE 1

ESTIMATED NUMBERS OF PENGUINS IN BREEDING POPULATIONS OF THE ROSS SEA

	Emperor Penguin		Adélie Penguin		
Locality	Breeders	Total[a]	Breeders	Total[a]	Source of data on breeders
1. Cape Adare			579,000	933,800	Reid 1962
2. Duke of York I.			2,000	3,200	Austin 1957
3. Possession I.			220,000	354,800	Cranfield 1966a
4. Svend Foyn I.			55,000	88,700	Cranfield 1966a
5. Cape Roget	23,400	37,700			Cranfield 1966a, b
6. Cape Hallett			104,000[b]	167,700	Reid 1964
7. Cape Cotter			80,000	129,000	Cranfield 1966a
8. Cape Wheatstone			3,000[b]	4,800	Cranfield 1966a
9. Cape Jones			1,600[b]	2,600	Cranfield 1966a
10. Coulman I.	100,000	161,300	26,000	41,900	Cranfield 1966a, b
11. Wood Bay			10,000	16,000	Taylor 1964
12. Cape Washington	10,000	16,100			Cranfield 1966a
13. Inexpressible I.			22,000[b]	35,500	Stonehouse 1969a
14. Franklin I.	4,000[b]	6,400	80,000	129,000	Stirling 1969, Stonehouse 1969b
15. Beaufort I.	3,574[b]	5,800	44,000	71,000	Stonehouse 1966, 1969a; Todd 1980
16. Cape Royds			3,200[b]	5,200	Taylor 1962
17. Cape Bird			83,600	134,800	Caughley 1960
18. Cape Crozier	300[b]	500	205,000[b]	330,600	Butler and Müller-Schwarze 1977
19. King Edward VII Peninsula	70,990	114,500			this study
Totals	212,264	342,300	1,518,400	2,448,600	

[a] Based on data in Ainley et al. (1983). About 62% of an Adélie Penguin population participates in breeding; we applied this percentage to Emperors also.

[b] Direct ground counts or counts from aerial photos.

of the Polar Front. The only nesting population anywhere near these transects is at Macquarie Island, about 300 km WNW of the westernmost sighting and over 1200 km NW of the easternmost sighting. The apparent decrease in occurrence from west to east indicates that these penguins may have originated from Macquarie, which also is situated at the northern edge of the Polar Front. King Penguins have not been reported from this area previously, but have been reported from the immediate vicinity of Macquarie Island or the vicinity of several small nesting islands between New Zealand and Macquarie (Watson 1975; Fig. 3).

The sightings in February were about 175 km farther south than those in December, consistent with a slight southwards movement of the Polar Front. Overall densities within the species' area of occurrence were 0.1 ± 0.2 birds/km^2 (n = 15 transects) during both seasons. All individuals occurred where salinities were near 34‰, and sea surface temperatures were 4.5°C (two individuals were actually in a warmer eddy surrounded by 4.5°C water).

ADÉLIE PENGUIN (*PYGOSCELIS ADELIAE*)

This species was recorded only south of the northernmost extent of pack ice. The most important factors affecting its occurrence were the Ross Sea Slope Front, pack ice, and the location of breeding colonies. There were two centers of concentration during the summer, one from Cape Adare to Cape Hallett, then east over the continental slope and pack ice edge, and the other between Ross and Franklin Islands, northward to some extent along the ice edge there, and eastward along the Ross Ice Shelf (Fig. 14). The vast majority of Adélies nesting in the Ross Sea region breed in rookeries concentrated along the Victoria Land coast (Watson et al. 1971: map 3). The extent of the above two concentrations indicates that breeding Adélies range only about 140 km from nesting colonies for food. Based on duration of feeding trips and estimates of swimming speeds, Laws (1977) predicted that Adélies from Cape Crozier could be feeding up to 300 km away, or about twice the distance that they actually travel.

During early summer, Adélies were absent from the open, green water of the central Ross Sea and from the northern part of the ice pack. Thus, during the "reoccupation period" in late December, when rookery populations in the Ross Sea reach their peak (Taylor 1962; Ainley et al. 1978), the entire Adélie population seemed to be contracted toward breeding rookeries. This was true even of yearlings (recognizable by their white chins and throats) which comprised the majority of Adélies in outlying areas (Fig. 15).

In late January and February, Adélies occurred at high densities far from rookery areas in the outer pack ice (Fig. 16) where they had been sparse a month or more earlier. By that time most adults had left the rookeries, and fledglings actually comprised a large proportion of the penguins at sea in the vicinity of nesting areas. The population had, thus, spread out and away from the Victoria Land coast to the residual tongue of pack ice in the eastern Ross Sea, although appreciable numbers still occurred in the remaining Victoria Land pack ice. Large concentrations in the eastern part of the Ross Sea at that time of year were also reported by Zink (1981).

The most important feature affecting Adélie Penguin distribution after the presence of pack ice and proximity to breeding areas, was the Antarctic Slope Front. The higher densities of Adélies extending southeast from Cape Adare in the pack ice over the slope are quite obvious in Fig. 14, as is their absence from pack ice seaward of the slope and in open water south of it. The same pattern of occurrence was apparent in Zink's (1981: fig. 2) autumn study. Adélie Penguins were also numerous at the pack ice edge in the western Ross Sea where steep horizontal gradients in water temperature, salinity, and phytoplankton concentrations during both summer and fall indicated frontal conditions, but of a sort different from those of the slope front (Figs. 1–11).

Several investigators have attempted to relate the densities of Adélie Penguins to pack ice concentration. Adélies were reported to be most abundant where ice concentration was "heavy" in the Weddell Sea (Cline et al. 1969), where it was "light" in the Weddell Sea (Zink 1978), and where it was "heavy" in the Ross Sea (Zink 1981). In the present study we can only confirm that Adélie Penguins prefer pack ice to open water. We observed them in large numbers in open seas in only three situations: (1) the Slope Front near the Pennell Bank, (2) swimming between Cape Crozier at the east end of Ross Island and the pack ice near Franklin Island [observations at Cape Crozier itself also indicate that Adélies with eggs or chicks depart from or return to the rookery in the direction of Franklin Island (S. H. Morrell unpubl. data)], and (3) in late January, swimming in large flocks from Ross Island toward the northeast [this was obviously the mass departure from rookeries of older nonbreeders and failed breeders, a movement known to occur

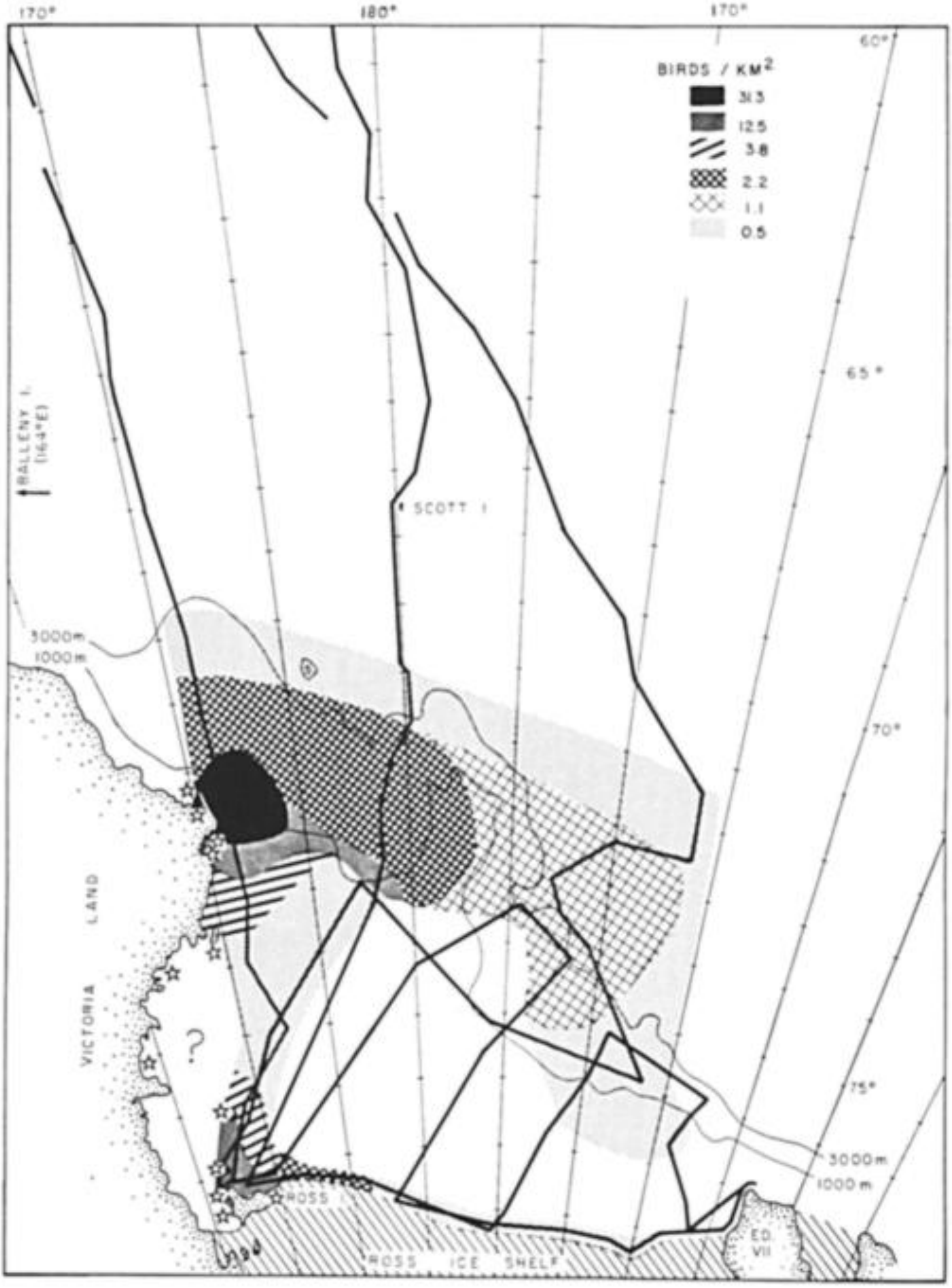

FIG. 14. Distribution of Adélie Penguins during early summer. Breeding sites are indicated by stars; question mark indicates area not adequately surveyed.

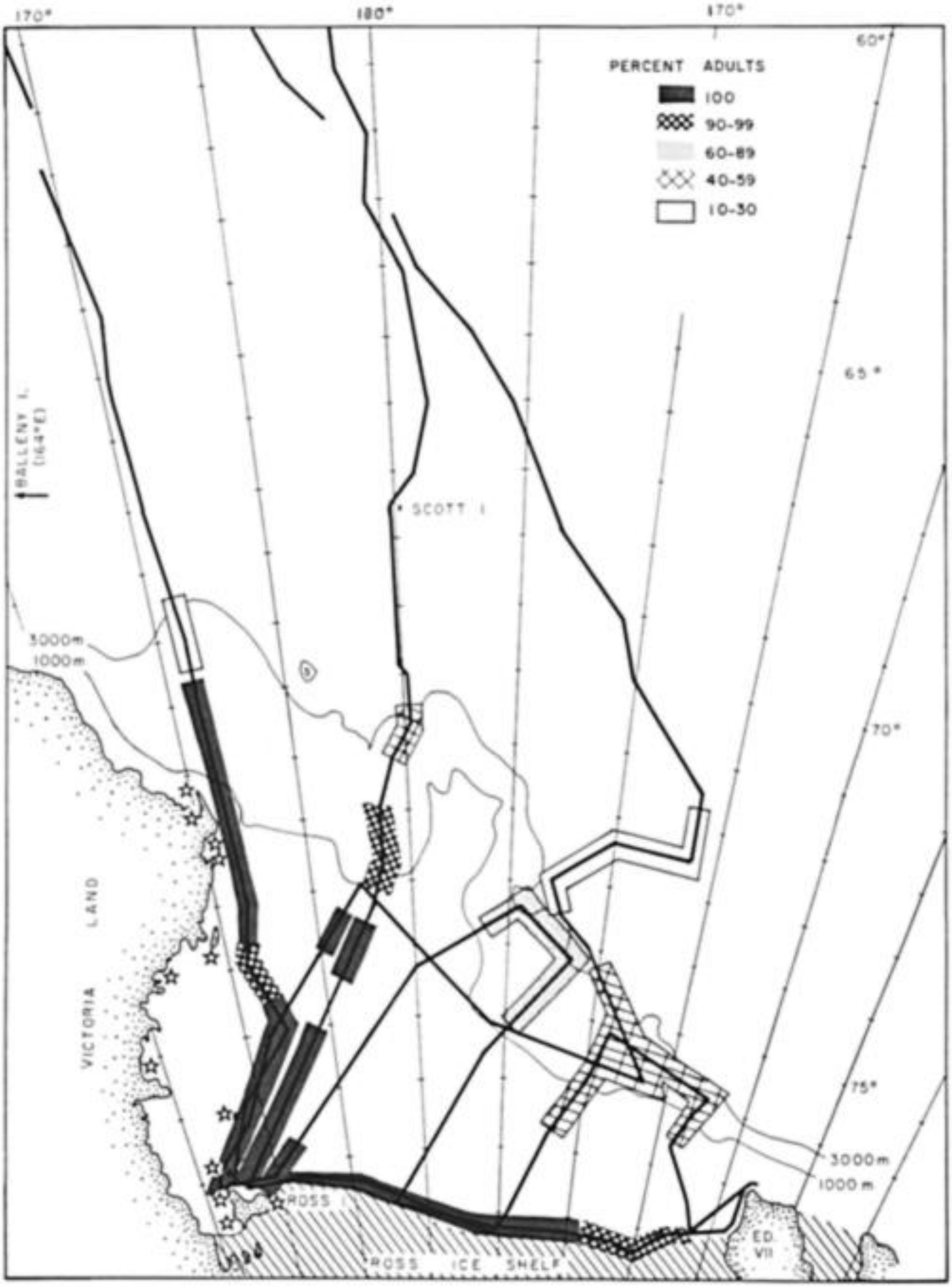

FIG. 15. Proportion of Adélie Penguins in adult plumage (two or more years old) along December cruise tracks; all breeding sites are located along the Victoria Land Coast and are indicated by stars.

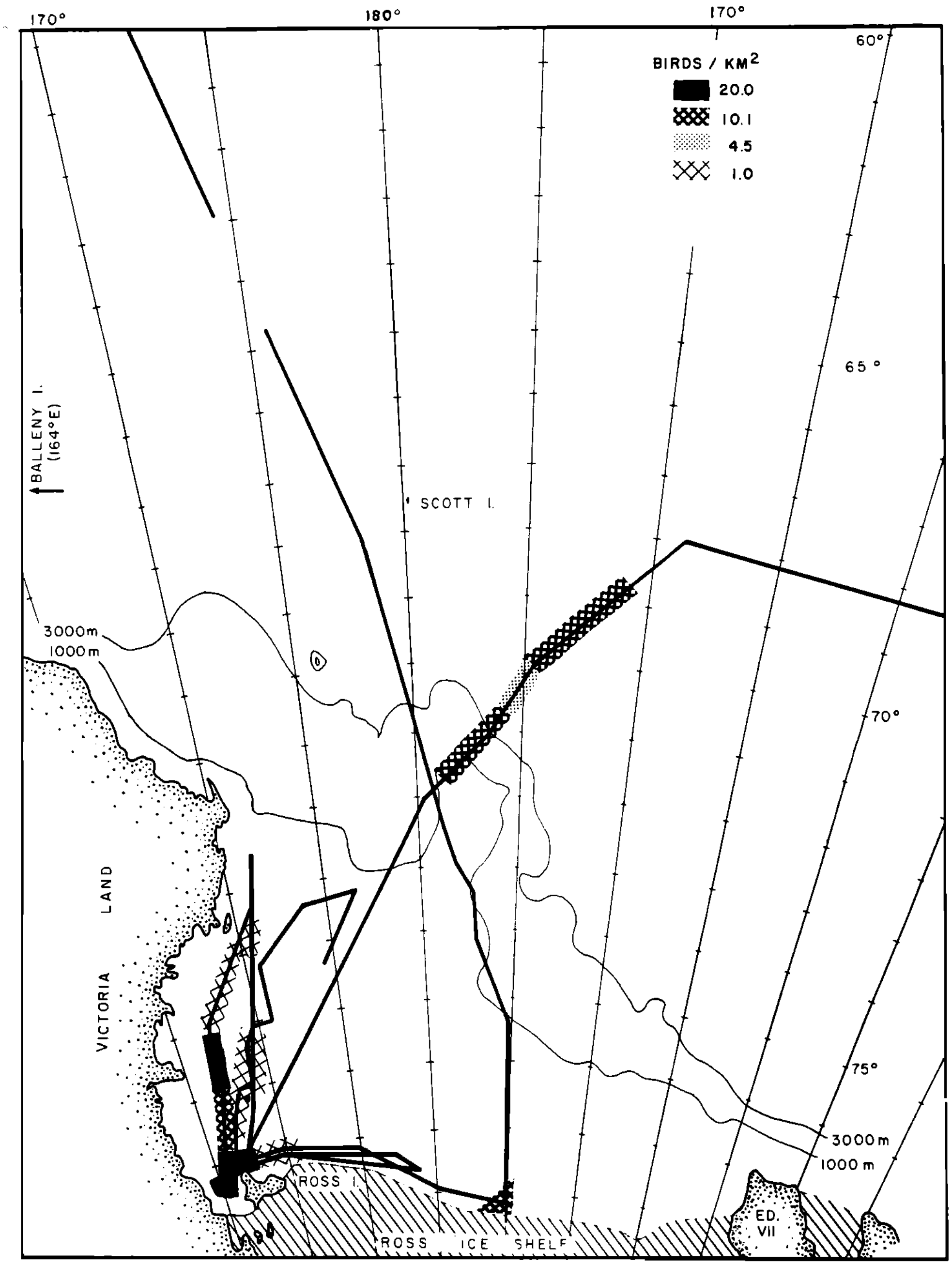

Fig. 16. Occurrence of Adélie Penguins along late summer cruise tracks.

TABLE 2

OCCURRENCE OF ADÉLIE PENGUINS IN RELATION TO ICE CONCENTRATION OVER THE ROSS SEA CONTINENTAL SLOPE BETWEEN 175°E AND 168°W DURING DECEMBER 1976 AND 1979, AND JANUARY 1977

	Oktas of ice cover			
	0	1–2	3–5	6–8
December transects, n	12	14	22	49
Transects with Adélies, %	50	14	64	57
Adélie density (birds/km^2), $\bar{X}$ ± s.d.	0.6 ± 1.0	1.6 ± 4.0	1.1 ± 1.3	1.0 ± 2.5
January transects, n	0	7	14	10
Transects with Adélies, %	—	71	100	80
Adélie density (birds/km^2), $\bar{X}$ ± s.d.	—	3.9 ± 3.6	10.7 ± 7.5	5.8 ± 6.0

at that time (Ainley et al. 1983)]. By swimming northeast, the latter birds intersect the residual pack ice in the eastern Ross Sea.

That Adélies actually prefer ice of a certain concentration, other factors being equal, is doubtful. Comparisons of bird densities and ice concentrations over the continental slope reveal no statistically significant patterns (Table 2). We conclude that the Adélie Penguin prefers pack ice areas to open seas, without preference for pack ice of one concentration over another. Furthermore, the biological activity in the water column beneath the ice is probably more important in determining where in the ice Adélies occur. Very productive oceanic areas particularly near rookeries or pack ice will lure Adélies away from the ice and into open seas.

Ross Sea population.—As a result of many years of exploration, the size and whereabouts of Adélie Penguin breeding populations in the Ross Sea are now fairly well known, and probably better known than for any other area of equal size in the Antarctic. It is surprising that some rookeries, such as the one at Beaufort Island, were unrecorded for many years, even with ships passing within 1 to 2 km several times yearly. It is not surprising that other rookeries are being discovered in less well-traveled areas; for example, two small rookeries were found in Victoria Land (and, as if to confuse matters, another previously reported one could not be found) as late as January, 1982 [P. Harper, G. Hunt, S. Morrell, and J. Sherburne (hereafter, Harper et al.), unpubl. data].

We were unable to survey the pack ice along the Victoria Land coast from Coulman Island to Ross Island adequately. Because of this and the tendency of penguins to remain at rookeries for extended periods (see methods section for discussion), we based our total population estimate on data collected at colonies instead of on density estimates and distributions obtained at sea. Using an estimate of 1.52 million breeding birds and the fact that about 38% of Adélie populations are comprised of nonbreeders (Table 1), about 2.45 million Adélies were associated with Ross Sea breeding populations. Laws (1977) estimated that the Ross Sea Adélie population was comprised of 1.2 million breeding birds. During December, about 2.38 million Adélies were concentrated in the Ross Sea, and about 67,000 individuals resided immediately north of it in the pack ice (mostly yearlings and two-year olds). This represents an overall density of 4.0 Adélies/km^2 in the Ross Sea, although the majority was concentrated in its western half [i.e., densities around 7.4 ± 11.9/km^2 (n = 65 transects) in the western third and about 1.0/km^2 in the eastern two-thirds].

During late summer, the Ross Sea Adélie Penguin population was concentrated in two pack ice areas, one along the southern two-thirds of the Victoria Land coast, and the other northeast of the Ross Sea continental shelf. Densities were about 10.3 ± 11.8 (n = 18 transects) and 8.1 ± 6.0 (n = 24 transects) birds/km^2 in these two Ross Sea areas, respectively. The density of Adélies in the pack ice northeast of the slope thus increased dramatically from December to late January. Gilbert and Erickson (1979) encountered Adélie densities of only 0.02 birds/km^2 during fall in the residual ice pack to the west of Cape Adare, and no Adélies in the ice pack to the east of King Edward VII Peninsula. Zink (1981) also found few Adélies in the latter area, but in the ice pack seaward of the Ross Sea slope, he recorded densities of 5.6 ± 5.1 (n = 15 transects) birds/km^2 during the fall. Adélies probably are most densely concentrated in the fall because the extent of the pack ice is then at its annual minimum (see discussion).

ALBATROSS

Four species occurred in the study area, all of them rare relative to most other avian species present. Light-mantled Sooty Albatross (*Phoebetria palpebrata*) and Black-browed Albatross (*Diomedea melanophris*) were the most abundant during both early and late summer and were the only two that actually occurred within the boundaries of the Ross Sea. Much less abundant were Gray-headed Albatross (*D. chrysostoma*), which also were present during early and late summer, and Wandering and Royal Albatross (*D. exulans* and *D. epomophora*) which were found only during later periods (Figs. 17–20).

Light-mantled Sooty Albatross was the most widespread species of the group. It occurred from the northern edge of the Polar Front south to the −0.5°C isotherm on all four cruise tracks. It was, thus, temperature and not the pack ice edge which seemed more closely correlated with its southern limit. Salinities ranged from 33.8 to 34.0‰. In February the overall density of Light-mantled Sooty Albatross ranged from 0.03 ± 0.08 birds/km^2 throughout most of the western track, but over the continental slope, it increased to 0.15 ± 0.18 birds/km^2; the species was not observed on the eastern track, which passed largely through colder waters. Of two birds collected at 67°37′S on the westernmost track during December, one was probably a breeder (incubation patch bare and gonads enlarged). The closest breeding sites are Campbell and Macquarie Islands, several hundred kilometers to the northwest. Watson et al. (1971), in summarizing records of this species, also recorded it as far south as the Ross Sea continental slope. Siple and Lindsey (1937) reported one individual near the Bay of Whales (east end of the Ross Ice Shelf at 78°S).

Black-browed Albatross occurred from the Polar Front as far south as the 1.0°C isotherm during December, although one isolated individual was encountered where waters were −0.5°C. During February, the species was absent from waters where temperatures were less than about 0.0°C. Density during summer was 0.02 ± 0.05 birds/km^2 (n = 123 transects), and during late summer was 0.06 ± 0.16 birds/km^2 (n = 33 transects). Most individuals were juveniles. Watson et al. (1971) also reported this species as far south as the Ross Sea continental slope.

Only two Gray-headed Albatross were encountered on cruises during December,

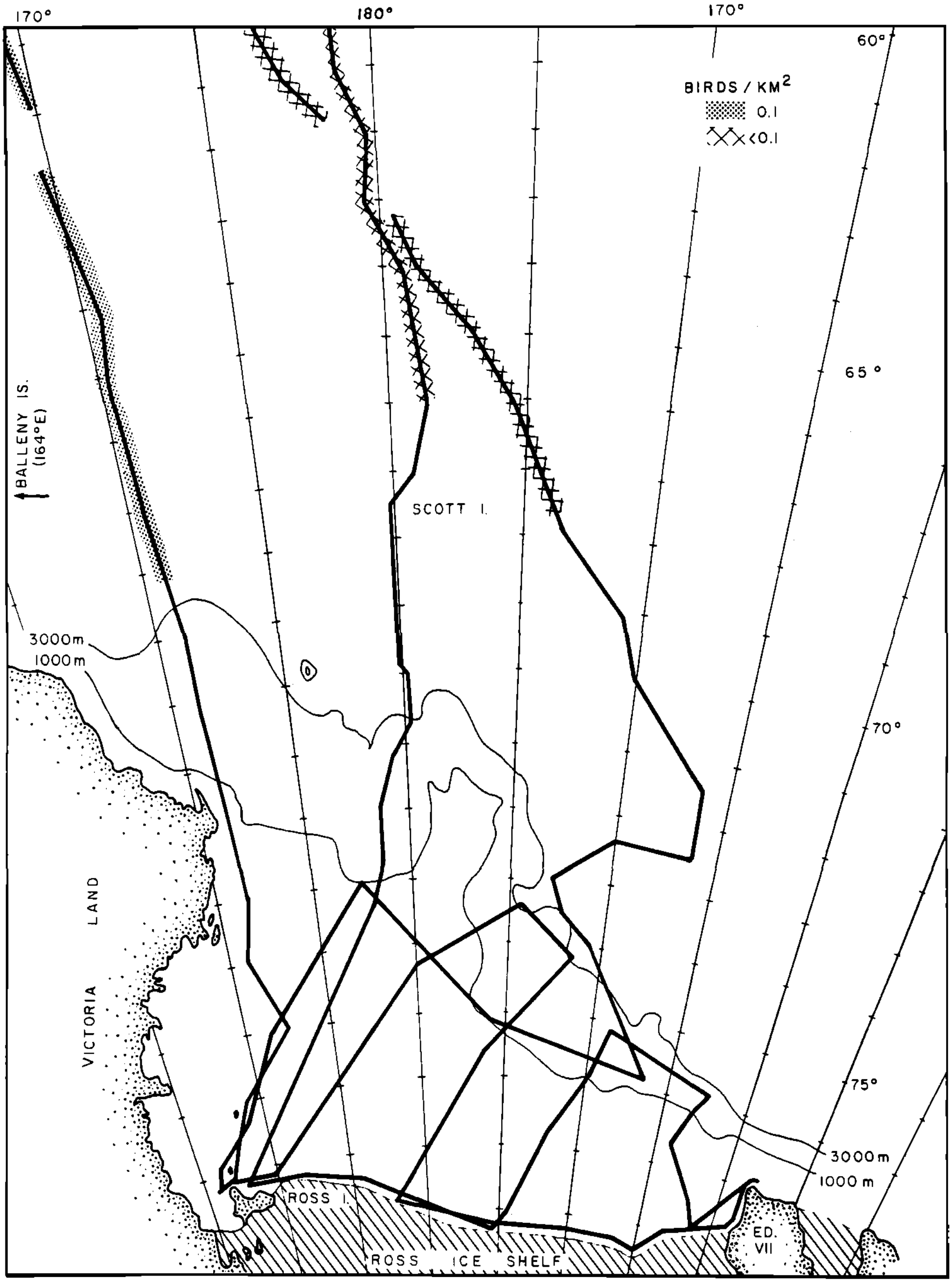

FIG. 17. Occurrence of Light-mantled Sooty Albatross along December cruise tracks.

both at the northern edge of the Polar Front (ca. 60°30'S). Three individuals were seen on the westernmost track during February, all north of 62°S and near the northern edge of the Polar Front. In all instances water temperatures exceeded 4.5°C. In view of this distribution pattern, the two records noted in Watson et al.

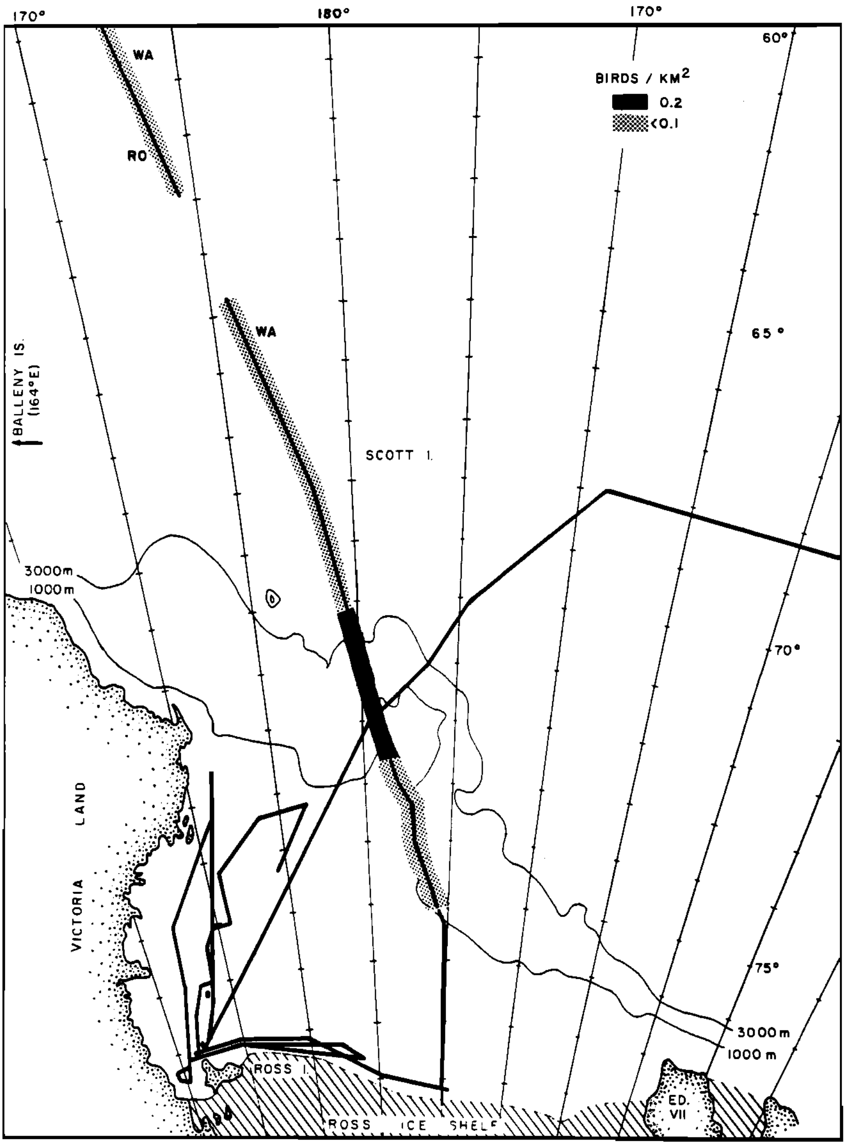

FIG. 18. Occurrence of Light-mantled Sooty Albatross (shading), two Wandering Albatross (WA), and one Royal Albatross (RO) along February cruise tracks.

(1971) of birds near 70°S, are rather interesting. Those two sightings are much farther south than any other records of this species at those longitudes. Because the immature plumage of the Gray-headed is quite similar to that of the Black-browed Albatross, we suspect that those two birds may have been misidentified. Closest breeding areas of the Gray-headed Albatross are at Macquarie and Campbell Islands, several hundred kilometers from the study area.

Two Wandering and one Royal Albatross were sighted during February north of 66°S, where water temperatures exceeded 2.5°C. Watson et al. (1971) reported that Wandering Albatross were frequently observed to about 68°S, and that one individual was seen at 70°S, but it is difficult to evaluate records for this species because individuals are particularly likely to follow ships into waters they would not otherwise enter.

No albatross occurred where pack ice was present. It may be that pack ice, because it dampens sea swells, inhibits albatross flight; normally albatross, in their method of dynamic soaring, employ wind currents deflected upward by swells.

SOUTHERN GIANT FULMAR (*MACRONECTES GIGANTEUS*)

Giant fulmars were encountered as far south as the slope front during December (Fig. 21), and throughout the study area in January and February (Fig. 22), although they were rare compared to most other species. During early summer, they were more abundant over the continental slope (0.02 ± 0.20 birds/km^2, n = 123 transects) than in areas to the north (0.01 ± 0.04 birds/km^2, n = 60 transects). During January/February, their distribution was more uniform, with densities of 0.02 ± 0.06 birds/km^2 from the Polar Front south to the slope front. By that time this species had reached the southern Ross Sea, although in densities much less than 0.01 birds/km^2. Ainley et al. (1978) also reported that this species arrived at Ross Island in late January over a 10-year period. The species demonstrated no preference for open water or for ice in any particular concentration, which is what others have reported also (Zink 1981). However, the fact that these birds do not reach Ross Island until late January may indicate a disinclination to cross a significant belt of ice. Like most species, they were absent from the central Ross Sea. Based on a density of 0.02 birds/km^2 and an area of occupancy of 150,000 km^2, an estimated 3000 giant fulmars were present in the Ross Sea during December; for February the number was about 5000 birds.

All but a few individuals were dark phase, similar to the 1:6::white:dark ratio reported by Zink (1981), and by Ainley et al. (1978) at Ross Island. Two individuals collected in waters of the slope front were both juveniles; one had been banded as a chick at Macquarie Island the previous year. Two young birds captured at Cape Crozier were also banded at Macquarie (Ainley et al. 1978). Watson's (1975) report that the young of this species have a more northerly distribution than adults is not substantiated by these findings or Zink's (1981); in fact, the contrary seems to be true.

SOUTHERN FULMAR (*FULMARUS GLACIALOIDES*)

Like most species in their family, Southern Fulmars in the study area occurred almost exclusively over oceanic waters. Only one individual of 138 seen occurred over the continental shelf, and only eight (6%) occurred over the continental slope during December (Fig. 21).

The species decreased markedly in abundance from west to east during December, consistent with the fact that the closest major nesting colony is at the Balleny Islands (65°S, 165°W) just to the west of the study area. Three other breeding sites lie slightly farther to the west (Watson et al. 1971), and it appears that a few birds nest on Scott Island (Harper et al., unpubl. data). Of all individuals counted, 90% were on the westernmost cruise track, 7% on the central track, and 1% on the eastern track. Seven individuals collected at 66°37′S, 170°32′E (the westernmost track) were breeding adults, and all six individuals collected at 68°41′S, 171°49′W

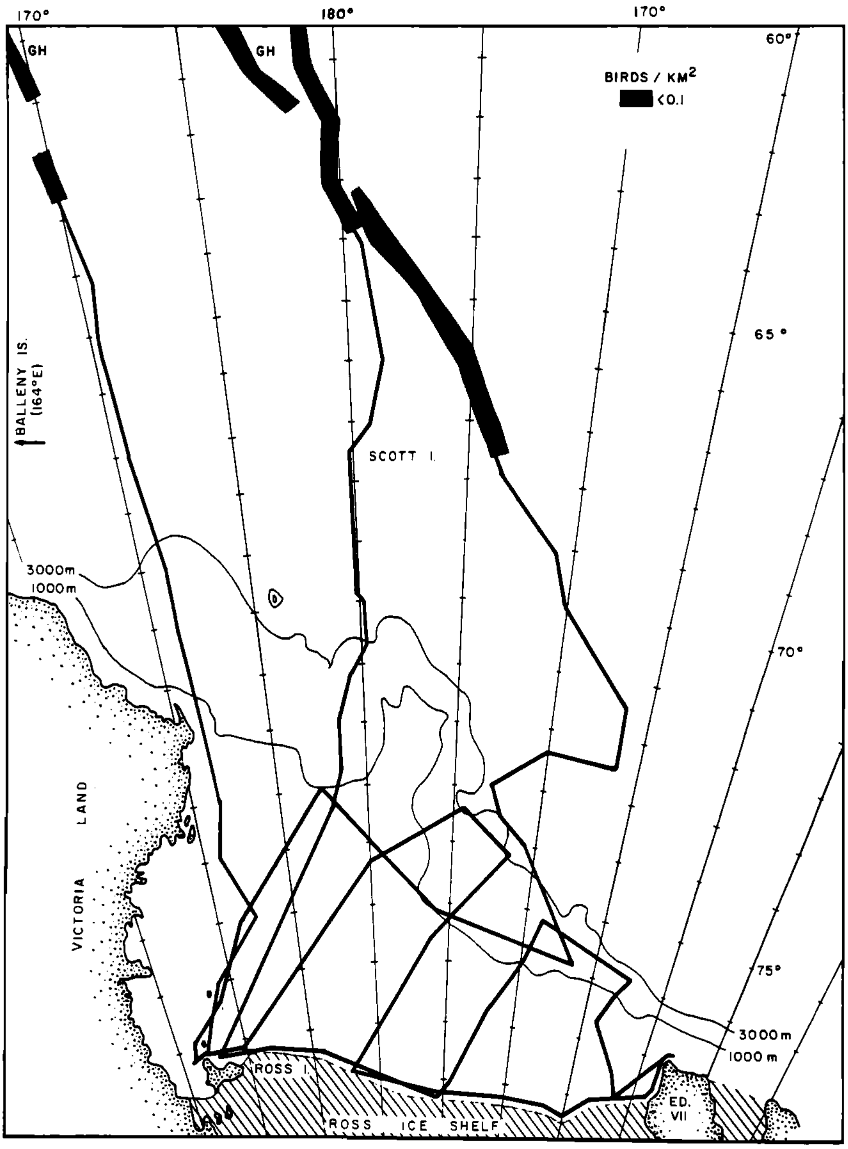

FIG. 19. Occurrence of Black-browed Albatross (shading) and two individual Gray-headed Albatross (GH) along December cruise tracks.

(the easternmost track) were immature nonbreeders. If these individuals were associated with the above mentioned breeding sites, it seems that fulmars may not have to travel more than a few hundred kilometers for food during nesting, but that nonbreeders disperse slightly more widely. Falla (1937) also noted that fulmars tend to concentrate rather close to breeding sites.

All but seven individuals were encountered where waters ranged from +0.5 to −1.5°C, and salinities were low (33.8–34.0‰). These ranges indicate waters strongly affected by pack ice. The species was indeed most abundant in waters adjacent

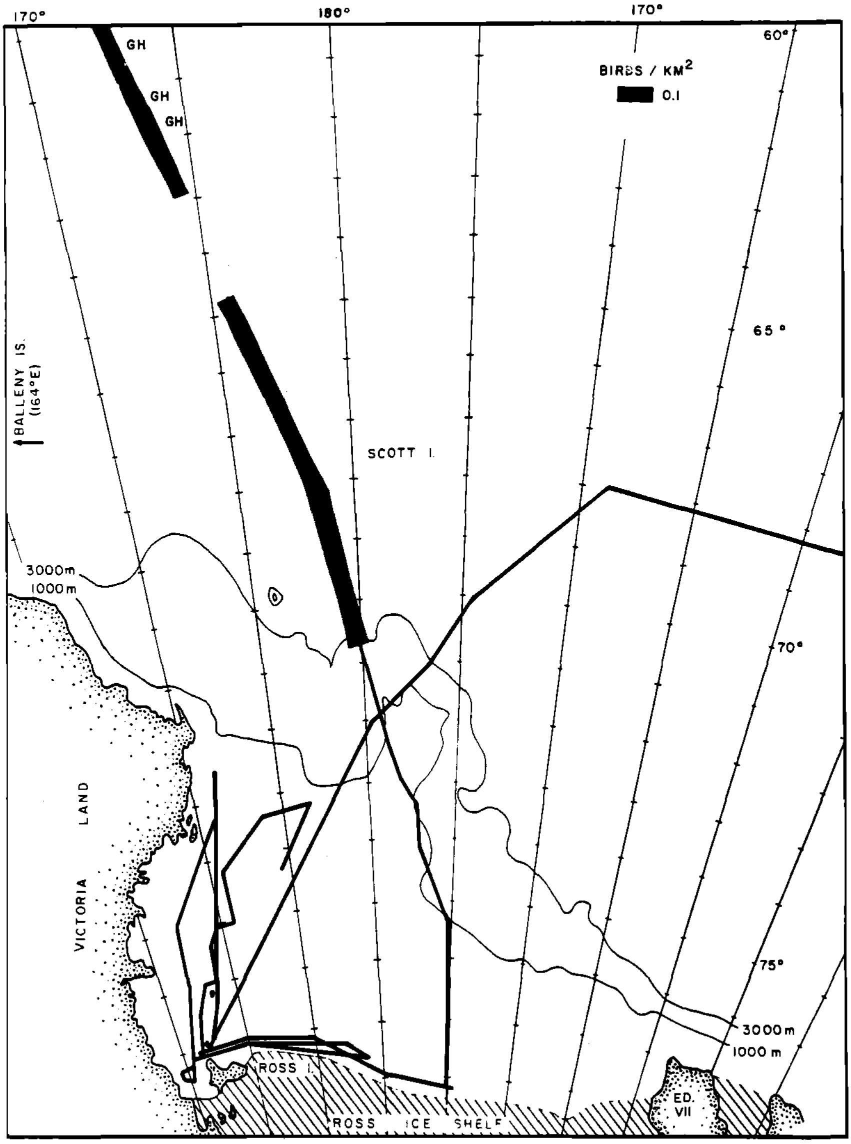

FIG. 20. Occurrence of Black-browed Albatross (shading) and three individual Gray-headed Albatross (GH) along late January and February cruise tracks.

to the pack or within its outer edge, and in fact, was clearly associated with the belt of icebergs in open water just to the north of the ice pack edge (Fig. 8). The rarity of fulmars on the easternmost track may have been due in part to the rarity of icebergs there compared to the other December tracks, and in part to its greater distance from breeding areas. In February, the species' distribution again showed a close coincidence with the occurrence of icebergs (Figs. 9, 22).

Cline et al. (1969), Zink (1978, 1981), Erickson et al. (1972), and we in the present study, found this species to be scarce in pack ice, in contrast to the findings

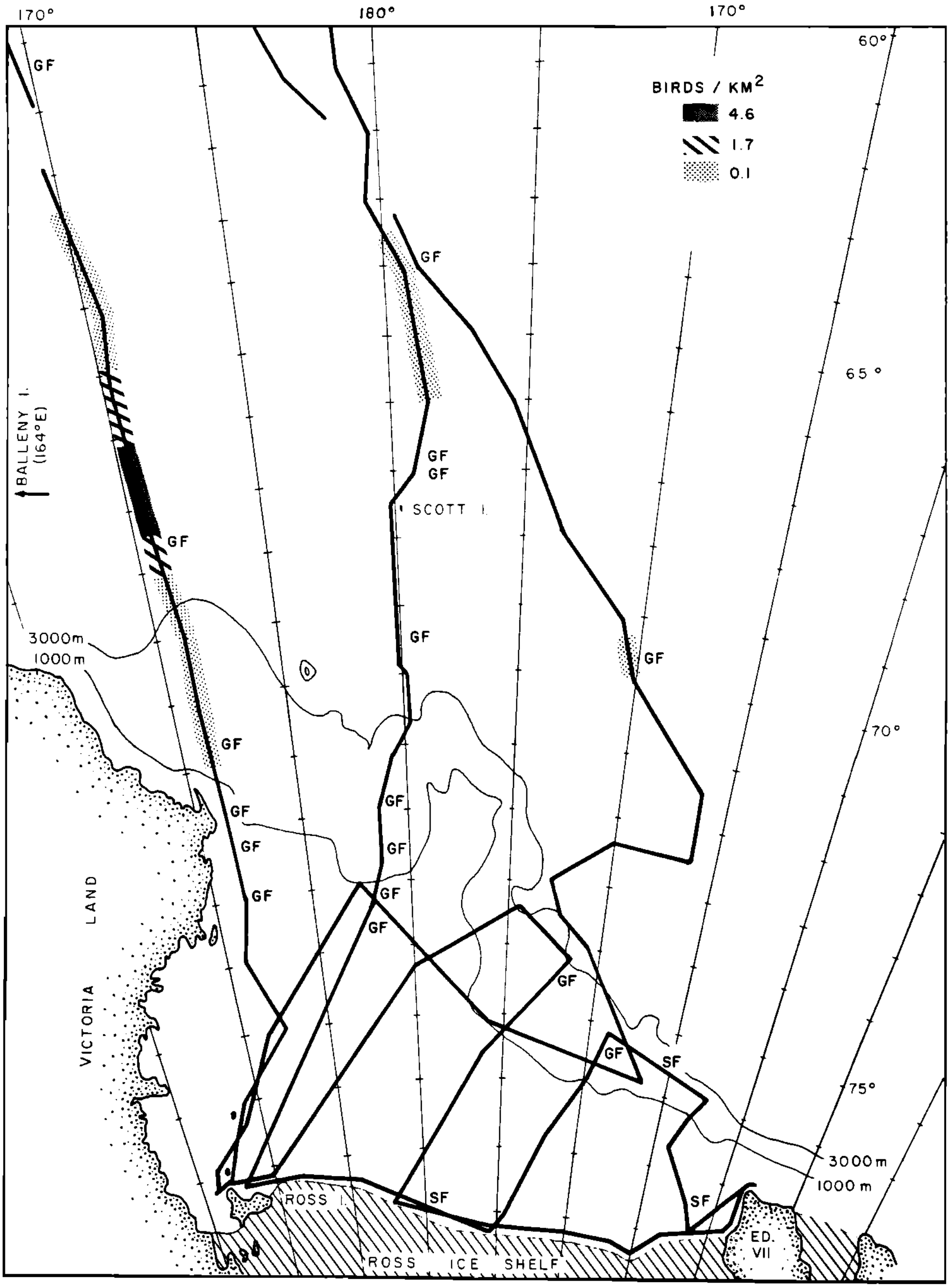

FIG. 21. Occurrence of Southern Giant Fulmars (GF; densities 0.01 to 0.03 birds/km²), and Southern Fulmars (shown by shading; scattered individuals indicated by SF) along December cruise tracks. The latter species breeds on the Balleny and Scott Islands.

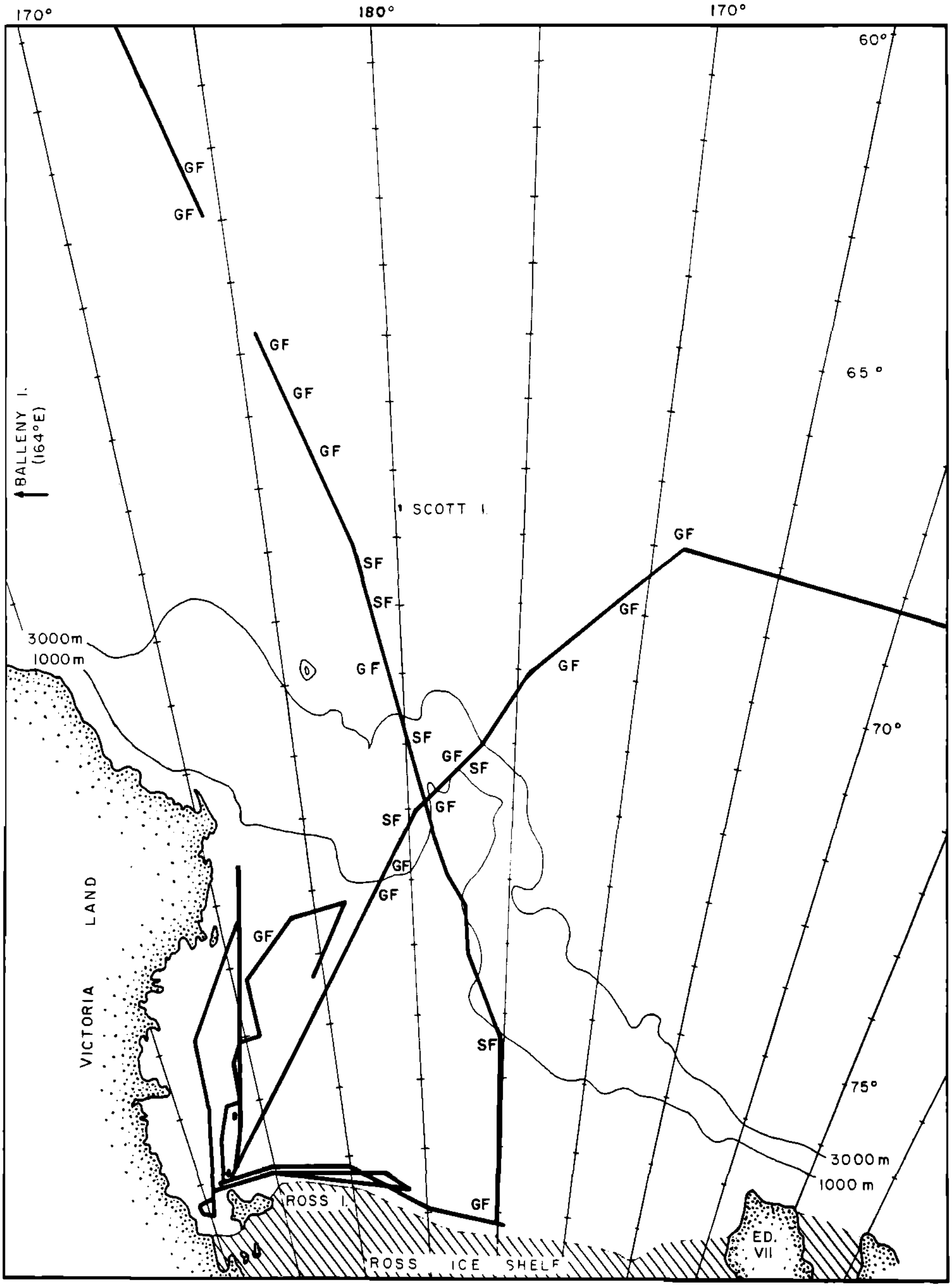

FIG. 22. Occurrence of individual Southern Giant Fulmars (GF, densities of 0.01 to 0.02 birds/km²), and individual Southern Fulmars (SF) along late January and February cruise tracks.

of Johnstone and Kerry (1974). In the area surveyed by the latter authors, however, the species breeds abundantly on the mainland coast where pack ice remains for a relatively long period into summer. Therefore, whether the fulmars were actually frequenting the pack ice there, or merely flying over the ice on their way between rookeries and foraging grounds, remains undetermined. While most authors suggest that the species "avoids" pack ice, we found that it is preferentially attracted to open waters adjacent to the pack, particularly when icebergs are present. Murphy's (1936) conclusion that Southern Fulmars are ubiquitous in the areas of pack ice seems to be true only for the outer edge of the pack.

Ross Sea population.—The species was only incidental in occurrence within the boundaries of the Ross Sea. Its density was much less than 0.01 birds/km^2, and total number of birds during December was no more than 2900. In February numbers may have been even smaller (ca. 2000 birds).

ANTARCTIC PETREL (*THALASSOICA ANTARCTICA*)

This was one of the most ubiquitous species in the study area. It was observed almost everywhere south of 65°S except in the extreme southwestern corner of the Ross Sea. Even there, in the vicinity of Cape Crozier, Ross Island, it is known to occur regularly but in low numbers (Ainley et al. 1978). During December, Antarctic Petrels occurred in high densities within a belt extending northwest from King Edward VII Peninsula (Marie Byrd Land) over the continental slope. The species occurred in extremely high densities, ranging upwards to 306 birds/km^2 over large areas, from about 76°S, 170°W to 73°S, 175°E (Fig. 23). Over vast areas seaward and landward of slope waters, densities dropped to 0.1 birds/km^2. The only known nesting colonies of this species anywhere near the Ross Sea are in the Fosdick and Rockefeller Mountains more than 100 km inland in Marie Byrd Land. The extremely low density of Antarctic Petrels in the western part of the study area during December indicates that the "questionable" breeding colony on the Balleny Islands (Watson et al. 1971) may not, in fact, exist or may be very small.

Both breeding and nonbreeding birds comprised the population over the continental slope, but their relative contributions changed with increasing distance from the slope and from Marie Byrd Land. In slope waters at two localities east of 175°W, 18 of 25 (72%) birds collected were breeders, but farther west at 179°44'E only 2 of 7 (29%) were breeders. In waters seaward of the slope during December, at 68°41'S, 171°49'W and at 66°37'S, 170°32'E, none of eight Antarctic Petrels collected was a breeder.

By late January and February, a large proportion of the Antarctic Petrel population had shifted away from slope waters toward the northeast (Fig. 24). Whereas December densities over deep waters averaged only 0.1 birds/km^2, the average later increased to 7.3 ± 20.61 (range 0.1 to 122.2; $n = 40$ transects). This is a conservative estimate because thousands of Antarctic Petrels roosted on almost every iceberg we passed, and all these were outside of transects due to our cautious captains! The vast majority of these birds were nonbreeders, as was indicated by their advanced stage of wing molt (many with all but the outer three primaries lost) at a time when adults were still feeding chicks. Although densities over the slope were still high (mostly adults, as evidenced by lack of wing molt), levels were reduced from December by the exodus of nonbreeders. Erickson et al. (1972)

and Zink (1981) also recorded high densities of this species east and northeast of the Ross Sea shelf during late January and February. Zink recorded a mean density of 1.3 ± 4.1 and Erickson et al. a mean of 4.3 ± 6.6 birds/km^2.

Virtually all Antarctic Petrels we encountered were in waters colder than 0.5°C; the range of salinities spanned all except the very highest. Highest densities were achieved in areas of open water—frequently coincident with the slope front—but high densities also occurred in areas of pack ice, especially during February. Within the pack ice, regardless of its overall concentration, the species demonstrated a marked tendency to occur over wide leads and polynyas (Table 3). North of the ice pack, Antarctic Petrels frequented areas with icebergs. Our observations support the conclusions of all other authors that Antarctic Petrels are typical of the pack ice habitat, but we must expand this association to include icebergs. Further, the species seemed to prefer open areas near ice to the ice itself (in contrast to the skua, for example).

Ross Sea population.—Using area and density calculations (Fig. 23), we estimate that 3.829 million Antarctic Petrels occurred within the boundaries of the Ross Sea during December. Assuming that the scattered juveniles north of the Ross Sea were part of Marie Byrd Land breeding populations, the total at-sea number of petrels in this population was 3.921 million birds. Making the additional assumption that half the breeding birds were incubating eggs at any one time during December (Watson 1975), then the total number of Antarctic Petrels in the Marie Byrd Land population comes to 5.136 million birds! During December, the overall density of Antarctic Petrels feeding in waters of the Ross Sea was 8.4 birds/km^2, assuming that incubating adults were still living on energy (fat stores) from the Ross Sea. Over the continental slope, where the majority of these birds concentrated, the overall density was 12.7 birds/km^2 (5.028 million/396,509 km^2).

CAPE PETREL (*DAPTION CAPENSE*)

For a species reported to breed on the Balleny Islands (Watson et al. 1971), just to the west of the study area, and on Scott Island (Harper et al., unpubl. data), the low abundance of Cape Petrels was unexpected. Densities along tracks in the western and central part of the study area averaged 0.10 ± 0.30 birds/km^2 (n = 65 transects), but along the eastern track, they averaged only 0.01 ± 0.30/km^2 (n = 22 transects). Either the nearby breeding populations were small, or breeding individuals did not fly far for food. All four birds collected, one at 66°37′S, 170°32′E and three at 68°41′S, 171°49′E, were nonbreeding *D. c. australe.* A total of 21 individuals was recorded on transects; abundance appeared not to change from early to late summer (Figs. 25, 26).

All but six individuals occurred in waters at temperatures of 1.0 to 0.0°C; four occurred at warmer temperatures, and two occurred at lower temperatures (−1.0°C). Only two were encountered in pack ice, both within 40 km of the ice edge, but the large majority was concentrated in areas with numerous icebergs.

SNOW PETREL (*PAGODROMA NIVEA*)

During both early and late summer, the distribution of this species was governed largely by the occurrence of pack ice (Figs. 8, 9, 27, 28). Highest densities occurred within about 350 km of known nesting areas, particularly along adjacent ice pack

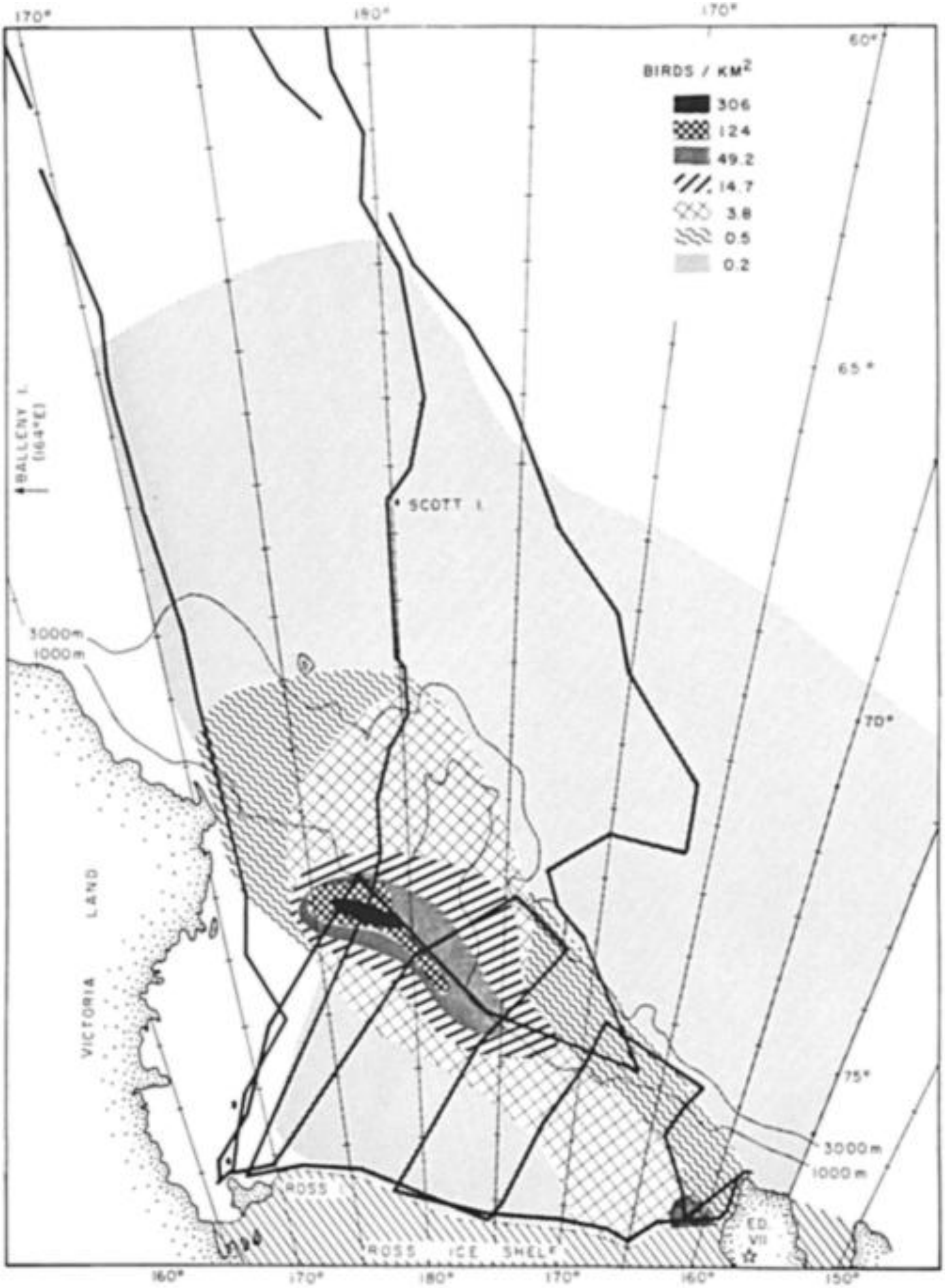

FIG. 23. Distribution of Antarctic Petrels during December. Breeding site is indicated by the star.

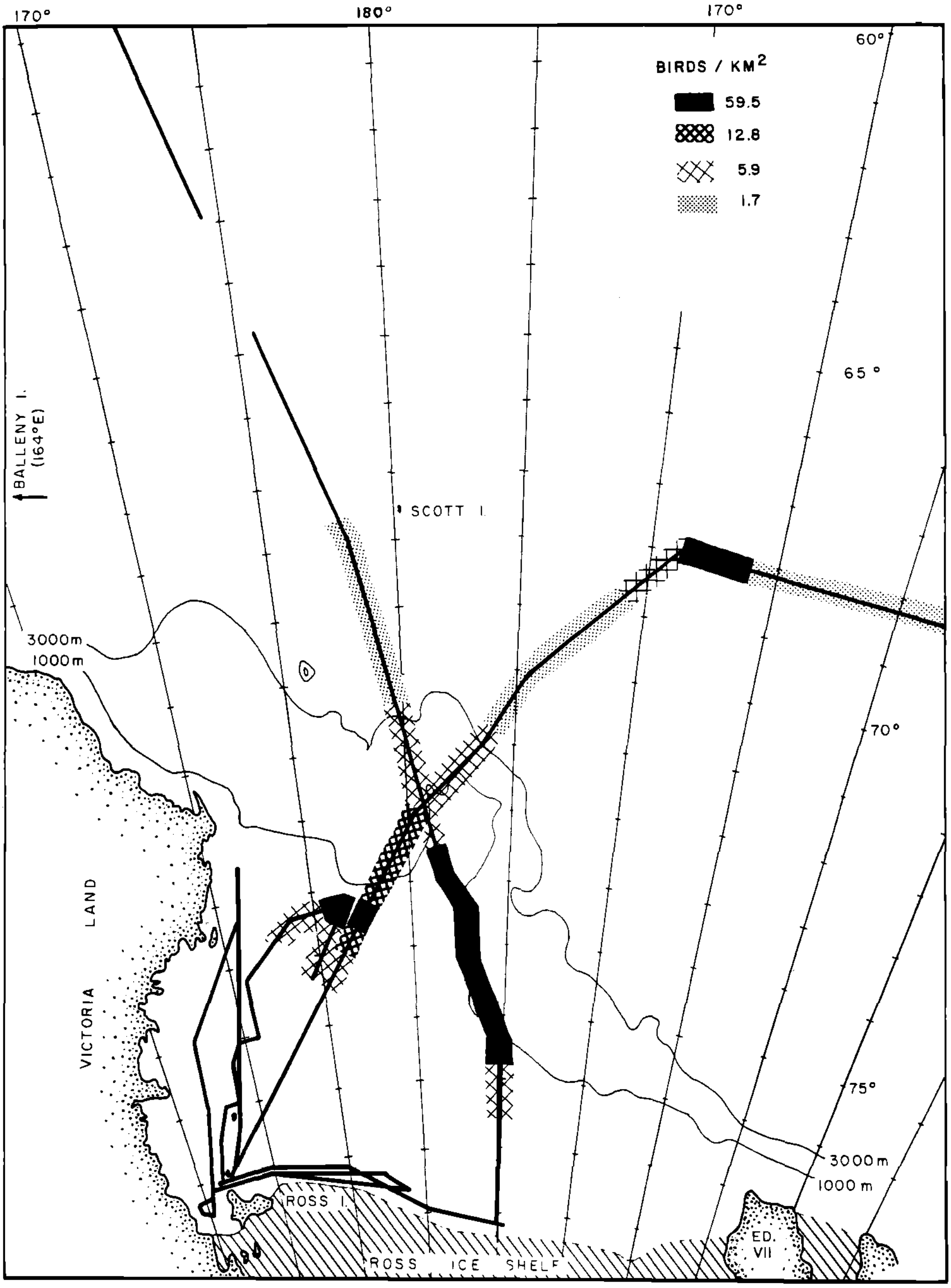

Fig. 24. Occurrence of Antarctic Petrels along late January and February cruise tracks.

edges. Snow Petrels nest on mountain tops in Marie Byrd Land (at least three sites), on Franklin Island, Cape Hallett (two sites), Duke of York Island, the Balleny Islands, and Scott Island (Watson et al. 1971). Relatively high densities also were found in a belt along the continental slope, especially along the edge of

TABLE 3
ASSOCIATION OF BIRDS WITH CERTAIN PACK ICE HABITATS[a]

	Habitat				
	Over ice floe	Over brash ice	At floe lead edge[b]	Over center of lead	No. observ.
Southern Giant Fulmar	20			80	5
Southern Fulmar				100	4
Antarctic Petrel	6	24	32	38	177
Snow Petrel	1	22	65	12	269
Wilson's Storm-Petrel	21	11	17	51	76
Skua	36	18	14	32	22
Arctic Tern		40		60	5

[a] Occurrence among habitats given as percent of total observations.
[b] Within 1 m of floe/lead edge.

the adjacent ice. All Snow Petrels were collected within 350 km of nesting sites; accordingly, 90.2% were breeding birds (n = 41). Individuals of this species seemed to be more dispersed than those of other species during the height of the breeding season, possibly because their distribution was more restricted to open pack ice than was that of the others (see below). Because pack ice does not occur everywhere, Snow Petrels may have to take advantage of all the pack ice available.

The species did not occur in open water except in the vicinity of the Antarctic Slope Front in the western Ross Sea, and to a lesser degree in the vicinity of icebergs near the ice pack. The species' association with pack ice was equalled only by those of Emperor and Adélie Penguins. So close was this association, that breeding by Snow Petrels at such places as South Georgia, or even Scott Island, is enigmatic because parents feeding chicks would have to traverse hundreds, even thousands, of kilometers of open water to find pack ice. In such circumstances Snow Petrels may depend more on icebergs than they would otherwise. The Snow Petrel's close association with ice has been noted by all authors who have written about the marine distribution of this species.

The Snow Petrel showed what appeared to be a clearer preference for ice of certain concentration than any other species we studied. Snow Petrel densities were much lower where ice cover exceeded five oktas than where it was five oktas or less. On the other hand, the pattern was confused somewhat by the species' "habit" of concentrating at the ice pack edge and the fact that the ice was least concentrated at the edge and near the Antarctic Slope Front. The influence of the slope front can be negated somewhat by considering densities in the outer part of the ice pack during February. Where ice cover was less than six oktas, Snow Petrel densities were 1.8 ± 1.3 birds/km^2 (n = 17 transects) except within 20 km of the pack edge, where they jumped to 25.6 ± 15.3 birds/km^2 (n = 12 transects). Snow Petrels may concentrate at the pack edge because productivity is greater there or because preferred feeding situations are more numerous (Ainley et al. 1978). On the other hand, they may merely "accumulate" there when they run out of pack ice and are confronted with open water. These alternatives are explored more fully below.

The species' avoidance of pack ice exceeding five oktas of cover seemed fairly

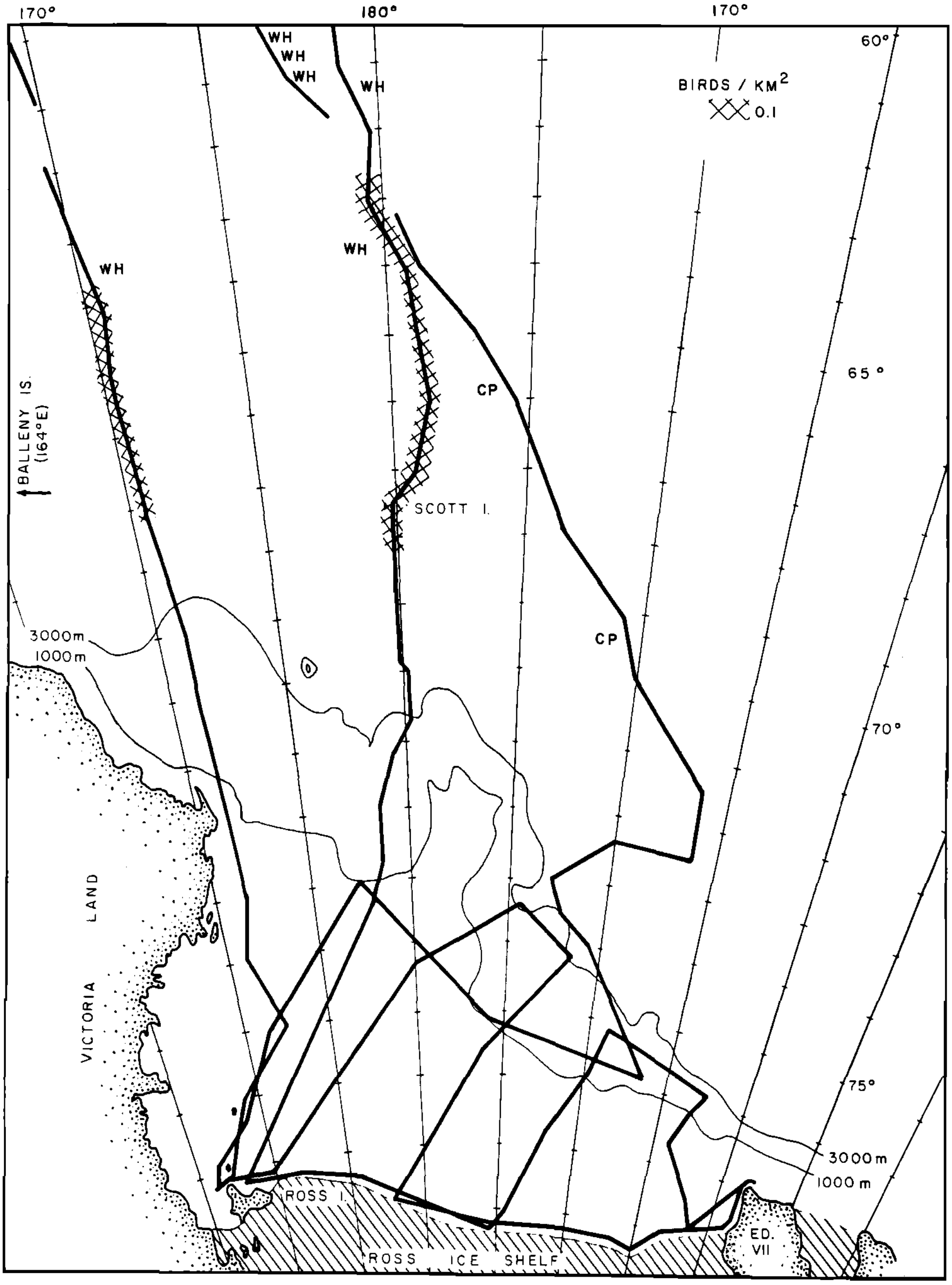

FIG. 25. Occurrence of Cape Petrels (shading) and White-headed Petrels along December cruise tracks (individual Cape Petrels are indicated by CP, and all White-headed Petrels by WH).

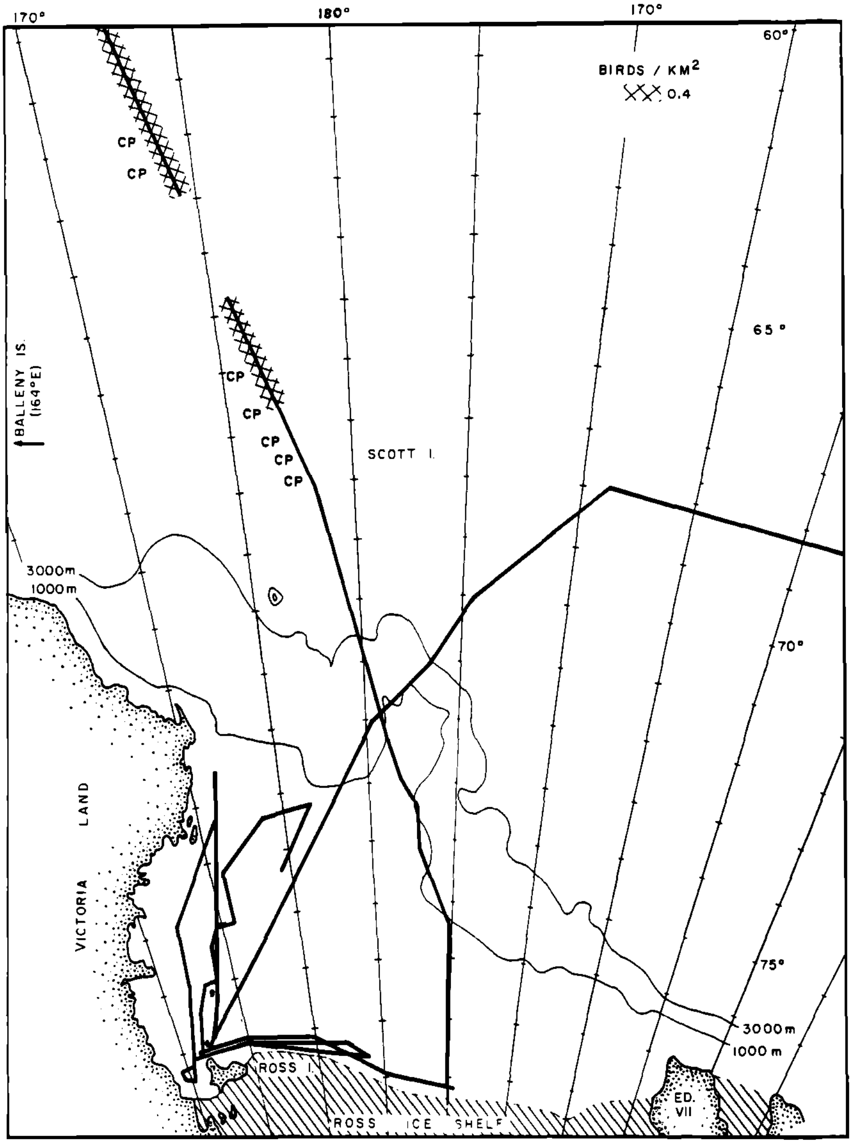

FIG. 26. Occurrence of individual Cape Petrels (CP; overall density was 0.10 ± 0.05 birds/km^2) and White-headed Petrels (shading) along late January and early February cruise tracks.

clear. This may not have been an "avoidance" *per se,* but rather a response to the fact that the amount of ice floe edge is inversely proportional to ice cover, particularly at heavier ice concentrations. Within the pack ice Snow Petrels showed a markedly strong tendency to frequent floe edges (Table 3). Thus, where the pack was more divergent, ice floe edges were abundant, and so were Snow Petrels.

Ross Sea population.—Based on density distributions shown in Fig. 27, we estimated a total population of 1.97 million birds associated with breeding sites on the border of the Ross Sea. This figure includes an adjustment for the fact that

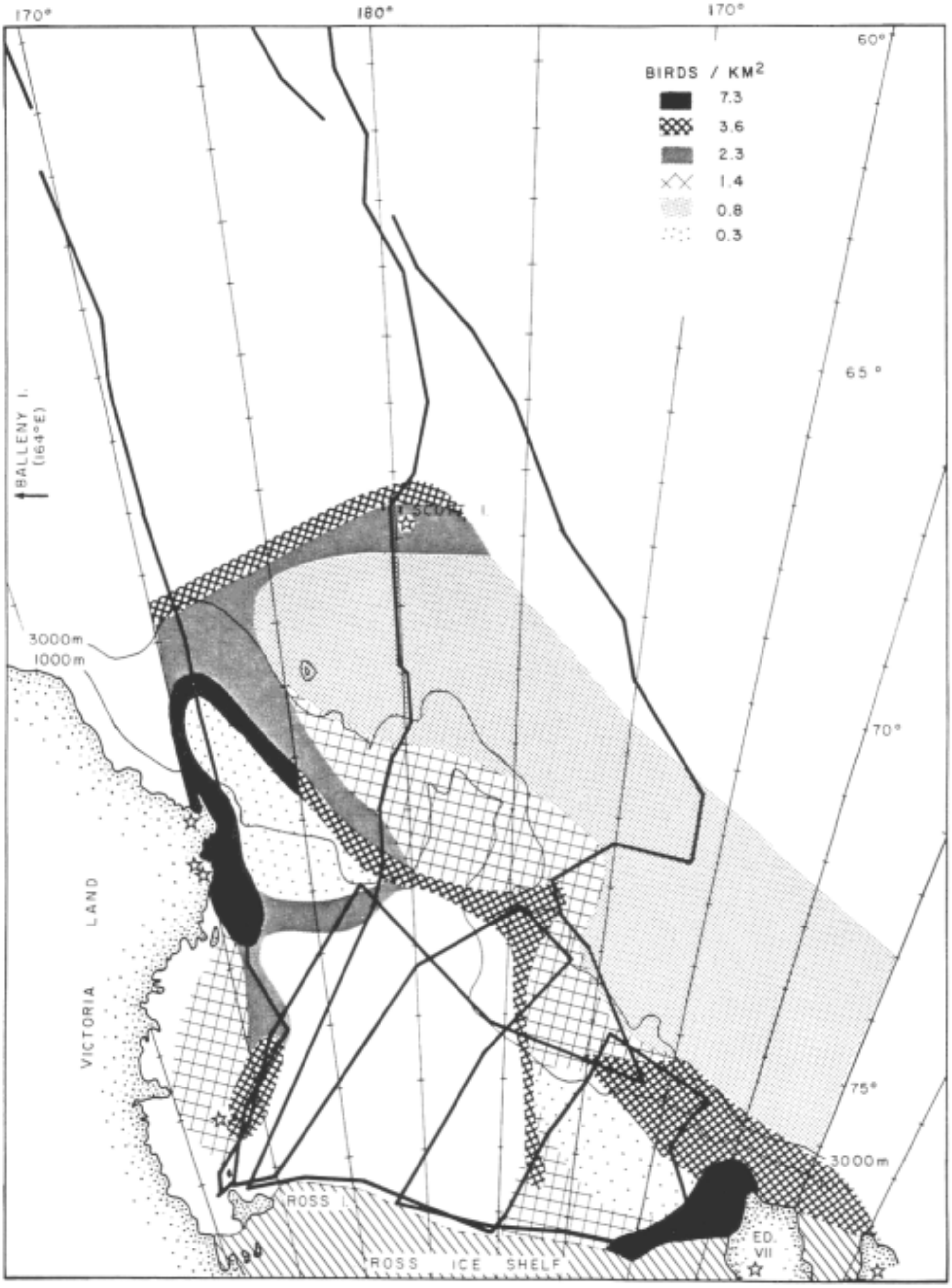

FIG. 27. Distribution of Snow Petrels during December. Breeding sites are indicated by stars.

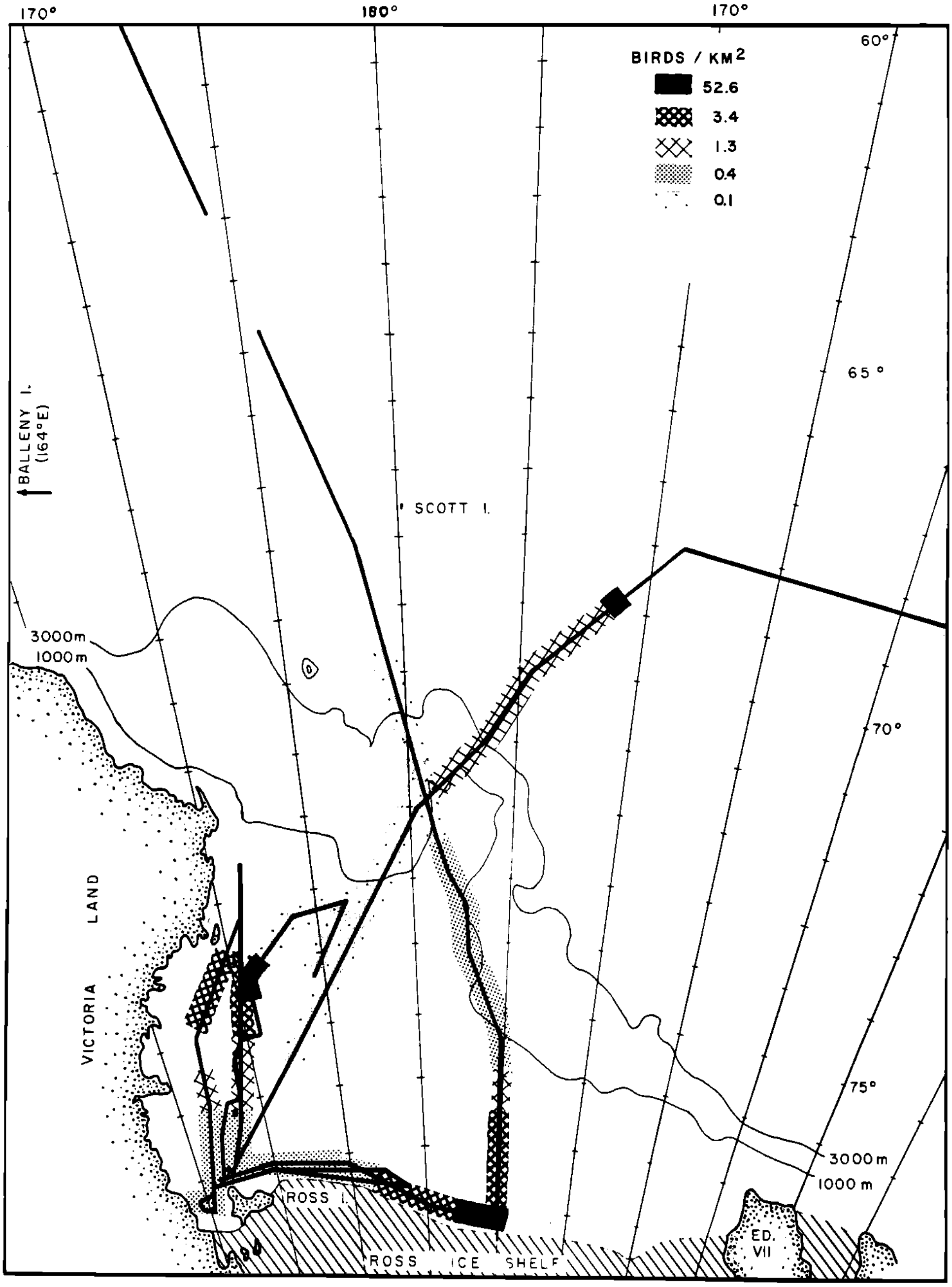

FIG. 28. Occurrence of Snow Petrels along late January and February cruise tracks.

half of the breeding birds, or about 31% of the total population, was incubating eggs at any given time during December (Maher 1962). The species' overall Ross Sea density was 2.7 birds/km^2; it was 3.6 bird/km^2 excluding areas where they did not occur at all.

ANTARCTIC PRION (*PACHYPTILA DESOLATA*)

This species was rather evenly dispersed throughout the northern part of the study area (Figs. 29, 30). During December cruises, prion density in areas of occurrence was 0.6 ± 1.2 birds/km^2 (n = 101 transects); during February it was 0.3 ± 0.7 (n = 30 transects). Antarctic Prions occurred as far south as the −0.5°C isotherm; not surprisingly, they occurred farther south in the late summer than in the spring. The one individual in early February at 72°49'S was a long distance from the next closest one.

The absence of this species during December, 1976, from the vicinity of Scott Island, where it reportedly breeds (Watson et al. 1971), was unexpected. As none was ever seen within pack ice, perhaps the fact that the island was surrounded by ice then explains their absence. Antarctic Prions were not attracted to icebergs or to areas where bergs were concentrated. In fact, the large majority of prions occurred north of the zone of iceberg concentration. Other authors have also noted the preference of this species for open seas. Three prions collected on the easternmost December cruise track at 68°41'S, 171°49'E, were all nonbreeders.

BLUE PETREL (*HALOBAENA CAERULEA*)

A flock of six Blue Petrels was seen at 64°02'S, 179°30'W in December, 1976 (Fig. 29). The area obviously was one of high biological activity. Eight species of seabirds were seen during the transect (some were feeding), and overall numbers were much higher than on the preceding or following transects. The locale was near the southern edge of the Polar Front and just south of the belt of observations shown in Watson et al. (1971). Sea surface temperature was 1.5°C.

WHITE-HEADED PETREL (*PTERODROMA LESSONI*)

This species occurred south to the southern edge of the Polar Front, or to about the 1.5°C isotherm (Figs. 25, 26). The exception was one bird seen in February where sea surface temperature was 0.5°C. Similarly, Nakamura (1982) observed scattered individuals south to the 0.7°C isotherm in the Indian Ocean. Densities during December were 0.04 ± 0.10 birds/km^2 (n = 45 transects), but in February were 0.42 ± 0.44 (n = 26 transects). All birds probably originated from Macquarie and Campbell Islands.

Watson et al. (1971) listed several records as far south as 65 to 70°S in the vicinity of the Ross Sea. This indicates that later in the year the species moves farther south than we observed it.

MOTTLED PETREL (*PTERODROMA INEXPECTATA*)

Mottled Petrel was one of the most abundant avian species in the northern part of the study area (Figs. 31, 32). During December, densities of this species averaged 0.4 ± 0.4 birds/km^2 (n = 102 transects) from the northern edge of the study area

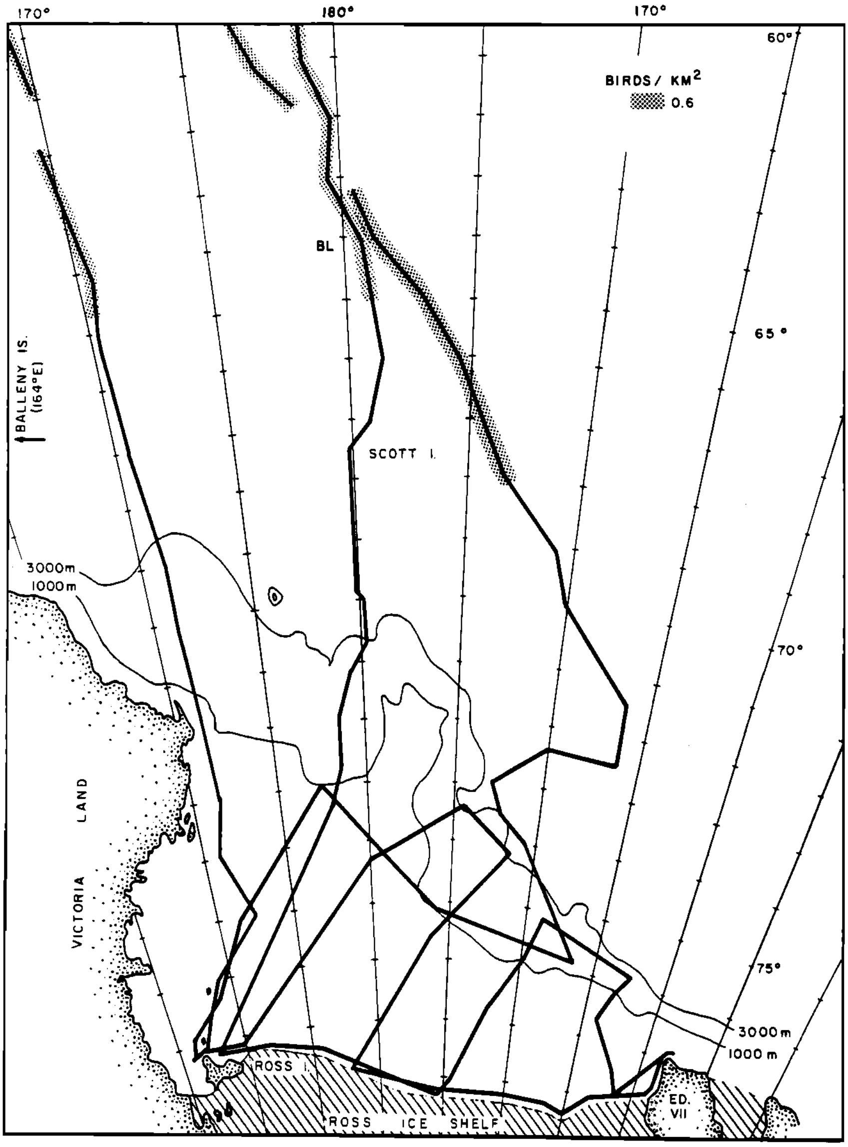

FIG. 29. Occurrence of Antarctic Prions along December cruise tracks. The location of one flock of six Blue Petrels is indicated by BL.

to the edge of the ice pack or the −0.5°C isotherm, whichever came first. Later in the summer, with open water stretching to the edge of the continent, Mottled Petrels occurred as far south as deep oceanic water, pack ice, or the −0.5°C isotherm. Nakamura (1982) also noted that pack ice limited the southward movement of this species. Both Nakamura and we considered Mottled Petrels to be common in Antarctic waters north of the pack ice. Densities of this species in our study area during summer were 0.3 ± 0.3 birds/km^2 (n = 61 transects) north

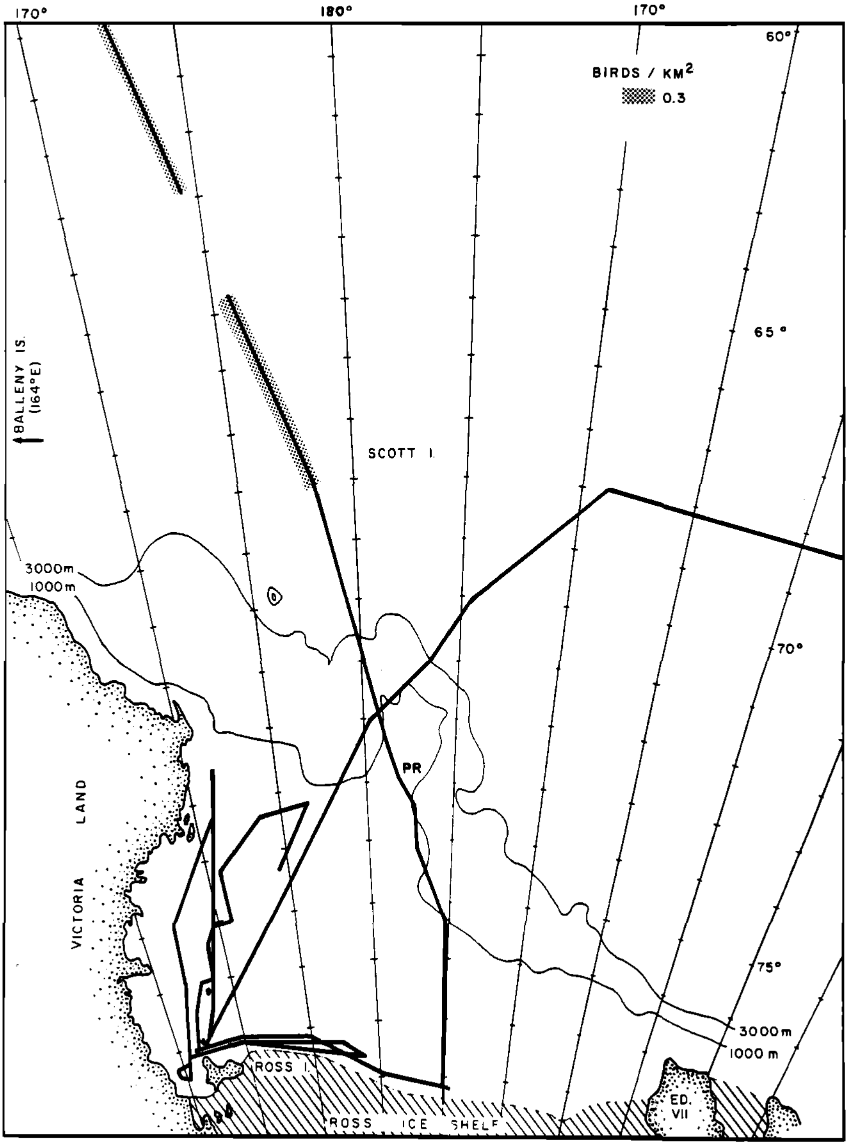

FIG. 30. Occurrence of Antarctic Prions along February cruise tracks. PR indicates an isolated individual.

of 69°S, and 0.05 ± 0.1 birds/km^2 (n = 18 transects) south of there. North of the 4.0°C isotherm during December, the species' density was only 0.1 ± 0.2 birds/km^2 (n = 20 transects), indicating that Mottled Petrels may find Antarctic waters more suitable than Subantarctic waters, the conclusion of Nakamura (1982) also. The occurrence of icebergs did not seem to affect the distribution of this species.

The species is known to nest only on islands just south of New Zealand. Three individuals collected at 68°41'S, 171°49'E in December were all nonbreeders.

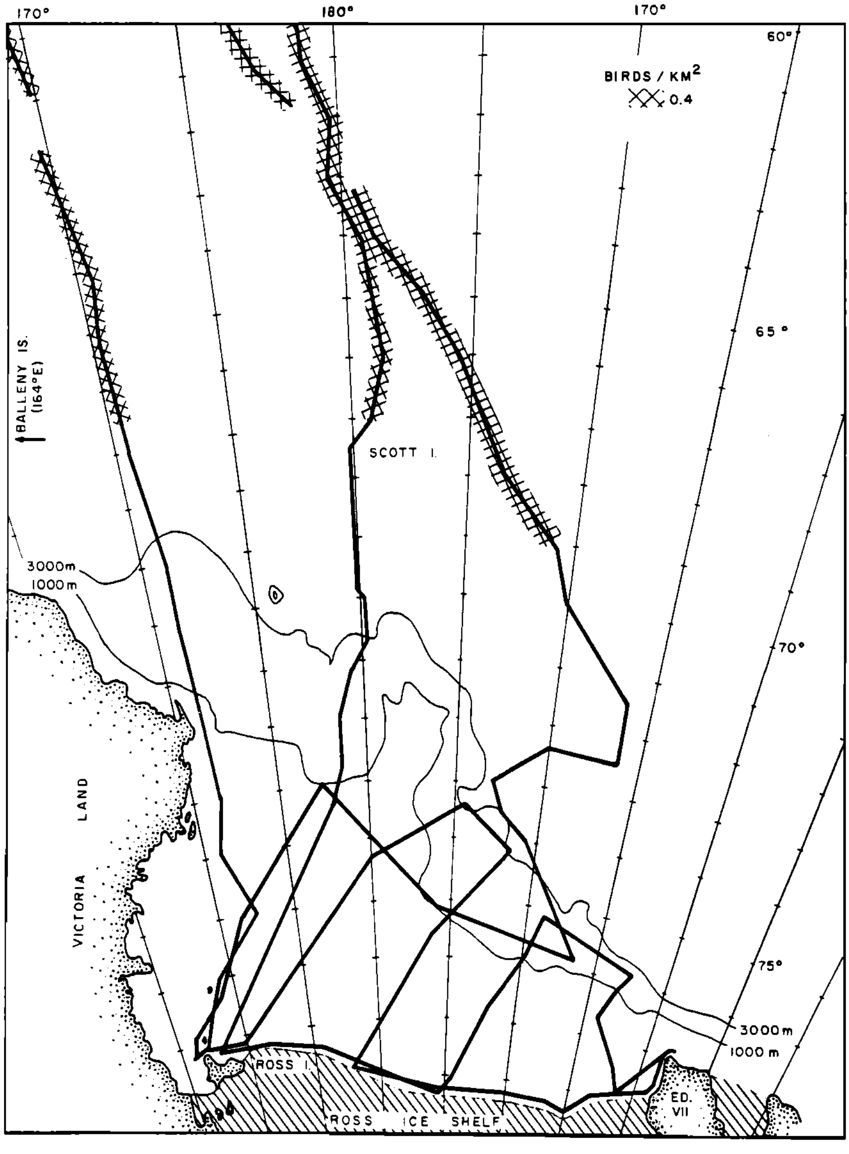

FIG. 31. Occurrence of Mottled Petrels along December cruise tracks.

White-chinned Petrel (*Procellaria aequinoctialis*)

Two individuals were recorded in the vicinity of 61°30'S, 173°30'W in February (Fig. 34). Sea surface temperature was 5.0°C, and the area was obviously productive because King Penguins and high concentrations of Sooty Shearwaters and diving petrels also were present. Watson et al. (1971) reported only a few records of White-chinned Petrels south of 60°S in the region near the Ross Sea.

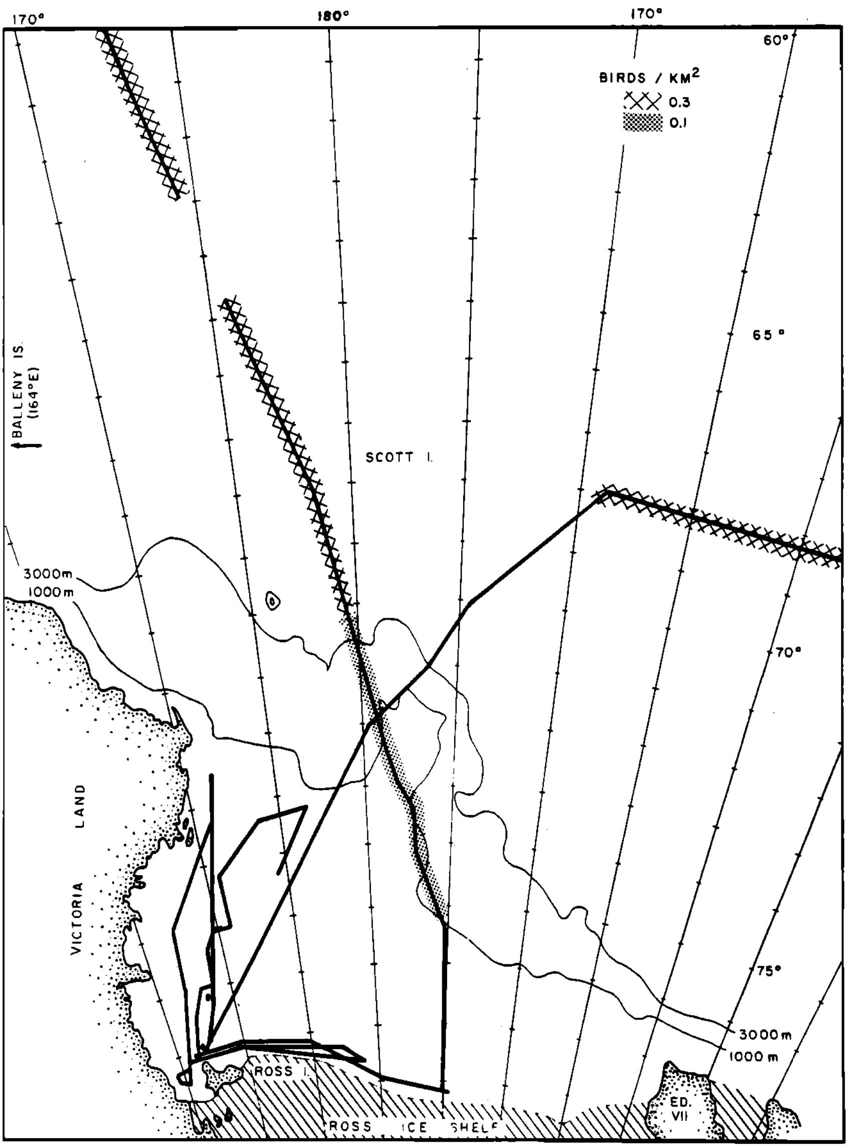

FIG. 32. Occurrence of Mottled Petrels along late January and February cruise tracks.

SOOTY SHEARWATER (*PUFFINUS GRISEUS*)

Throughout the Polar Front region, Sooty Shearwaters were easily the most abundant species. The southern boundary of their occurrence corresponded with the 2.5°C isotherm and the first, widely scattered appearances of icebergs (Figs. 33, 34). During December, the average density was 7.9 ± 18.2 birds/km^2 (n = 32 transects) with single transect densities reaching 87.8 birds/km^2. During February, overall density was similar, at 10.4 ± 23.3 birds/km^2 (n = 24 transects); a

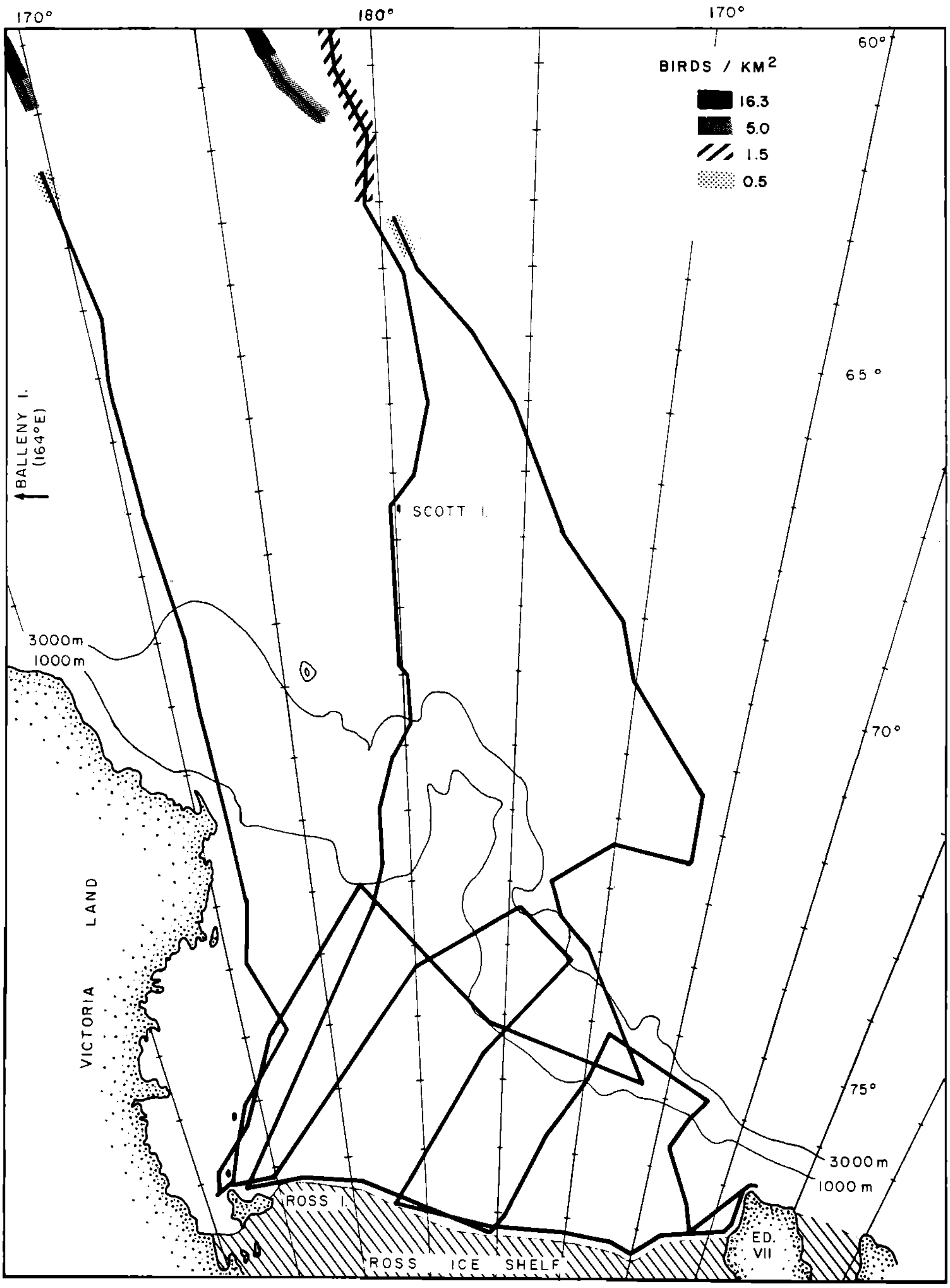

FIG. 33. Occurrence of Sooty Shearwaters along December cruise tracks.

few individuals occurred as far south as the 0.5°C isotherm which also corresponded with the first icebergs.

The closest known nesting areas of this species are at Macquarie Island and the islands just south of New Zealand. The sightings we report extend the southern

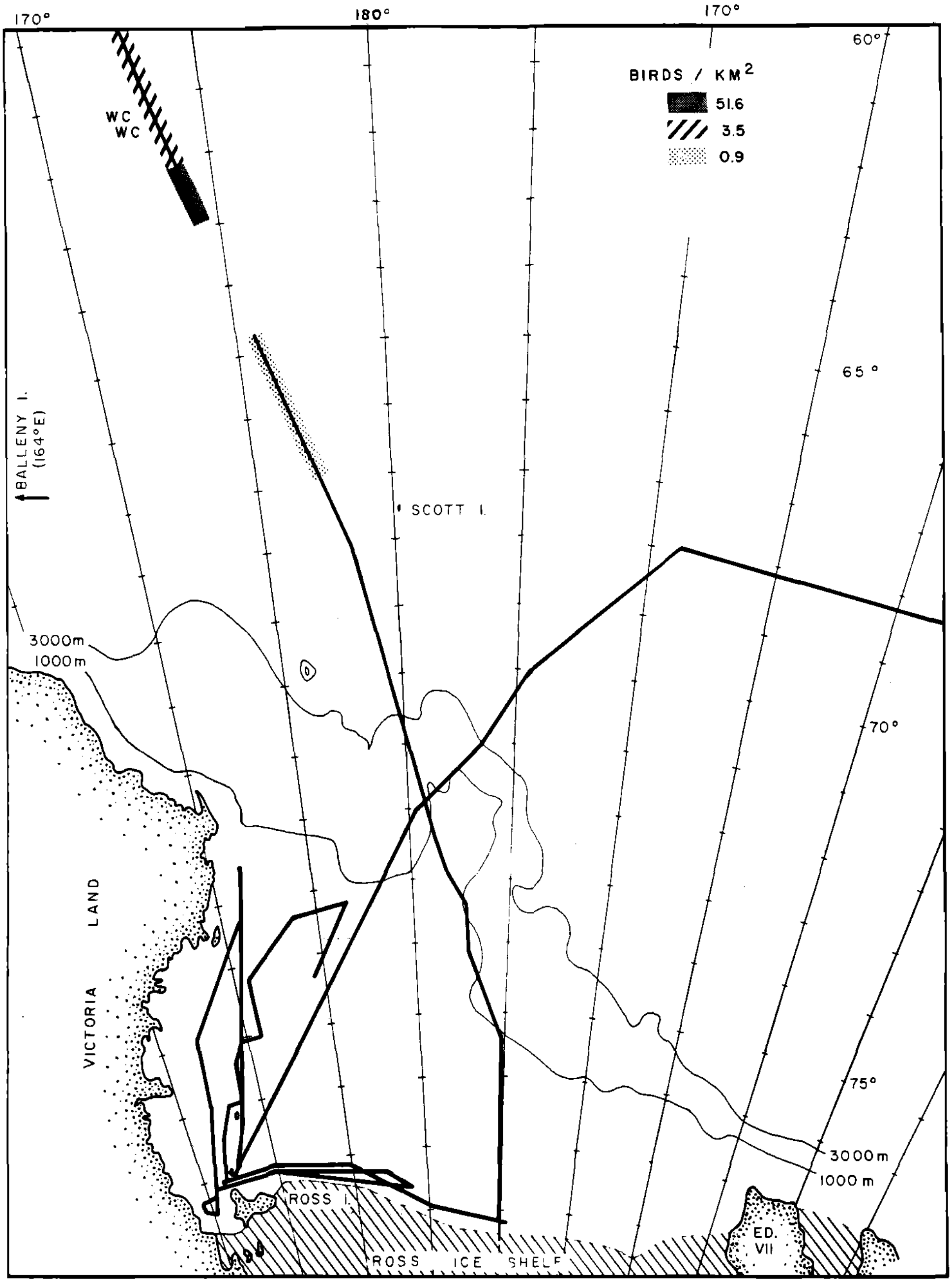

FIG. 34. Occurrence of Sooty Shearwaters (shading) and two White-chinned Petrels (WC) along late January and February cruise tracks.

boundary of this species' range some 650 km farther south in the Ross Sea sector of the South Pacific than was recorded in Watson et al. (1971).

WILSON'S STORM-PETREL (*OCEANITES OCEANICUS*)

The species is reportedly widespread in the world's oceans, but in the Antarctic South Pacific during our studies, it was restricted to within about 750 km of nesting areas; the majority of individuals was closer than 500 km. Breeding sites occur only in the western part of the study area along the northern Victoria Land coast (three sites), and on Scott Island and the Balleny Islands (questionable; Watson et al. 1971). The majority apparently breeds at sites in the vicinity of Cape Hallett and Cape Adare. This species was concentrated from the vicinity of the latter two sites 500 km southeast over the Ross Sea continental slope (Figs. 35, 36). Wilson's Storm-Petrels were much less abundant to the north and south of that zone. East of 175°E, only 63% of birds collected were in breeding condition ($n = 8$), but west of 180° or within 300 km of nesting areas, all were breeders ($n = 24$).

Wilson's Storm-Petrels occurred as far north as the 0.5°C isotherm during both early and late summer, although the northern limit of their occurrence was better defined by the northern edge of the iceberg belt. Compatible with their rather restricted distribution, few occurred in the eastern part of the study area. Zink (1981), Erickson et al. (1972) and Ainley (unpubl. data) also encountered few from that region east to the Antarctic Peninsula. Although icebergs defined the northern limit of the species' distribution, densities dropped sharply within pack ice even over productive waters of the continental slope (Fig. 35). Within the ice pack Wilson's Storm-Petrels frequented areas of light ice cover (generally less than six oktas) and were found more in the centers of wide leads and polynyas than near ice floes or brash (Table 3). This was the only species that occurred in open waters of the central Ross Sea with measurable regularity, albeit at quite low densities (ca. 0.05 birds/km^2). Zink (1981) considered the species to be more typical of open seas.

Ross Sea population.—Measuring areas of known density, and assuming that half of all breeding adults were on nests at any given time during December, we estimated that 419,700 Wilson's Storm-Petrels were associated with nesting colonies in the Ross Sea region (including nonbreeders); the breeding population comprised about 256,000 birds. During December, an estimated 361,700 individuals frequented waters within the boundaries of the Ross Sea for an overall density of 0.6 birds/km^2. Discounting waters where they did not occur, overall density was 1.0 birds/km^2. Densities, numbers, and distributions changed little between December and February.

BLACK-BELLIED STORM-PETREL (*FREGATA TROPICA*)

Within the study area, the distribution of this species complemented that of the Wilson's Storm-Petrel. Black-bellied Storm-Petrels occurred in waters south to about the 0.5°C isotherm, but actually seemed most concentrated within about 100 km of the northern edge of the iceberg belt (Figs. 35, 36). Thus, the two storm-petrels had closely adjoining distributions with very little overlap. In areas where Black-bellied Storm-Petrels occurred, overall density was 0.14 ± 0.29 birds/

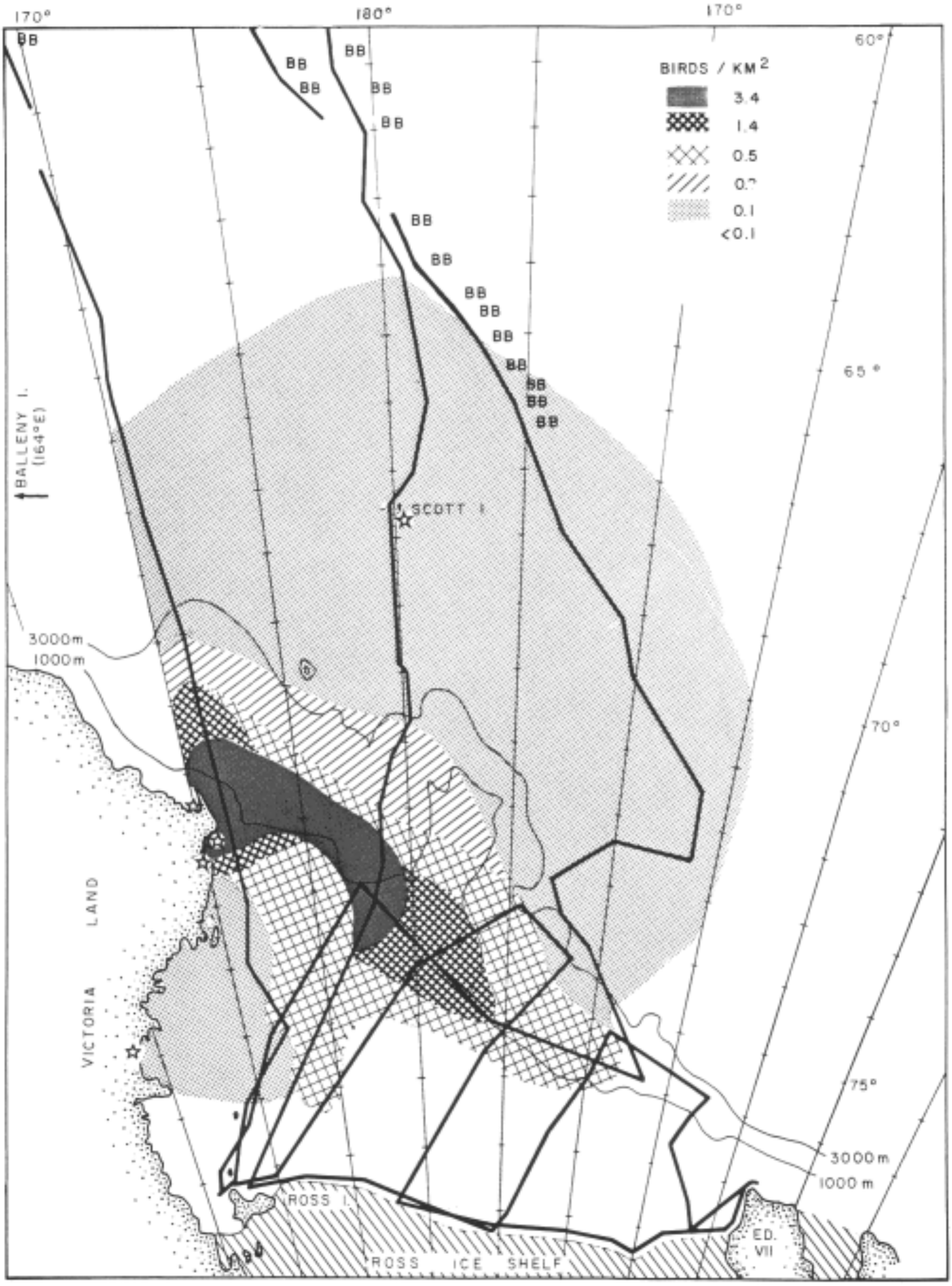

FIG. 35. Distribution of Wilson's Storm-Petrels (shading) and individual Black-bellied Storm-Petrels (BB; densities averaged 0.14 ± 0.29 birds/km²) during December. Breeding sites of Wilson's are indicated by stars.

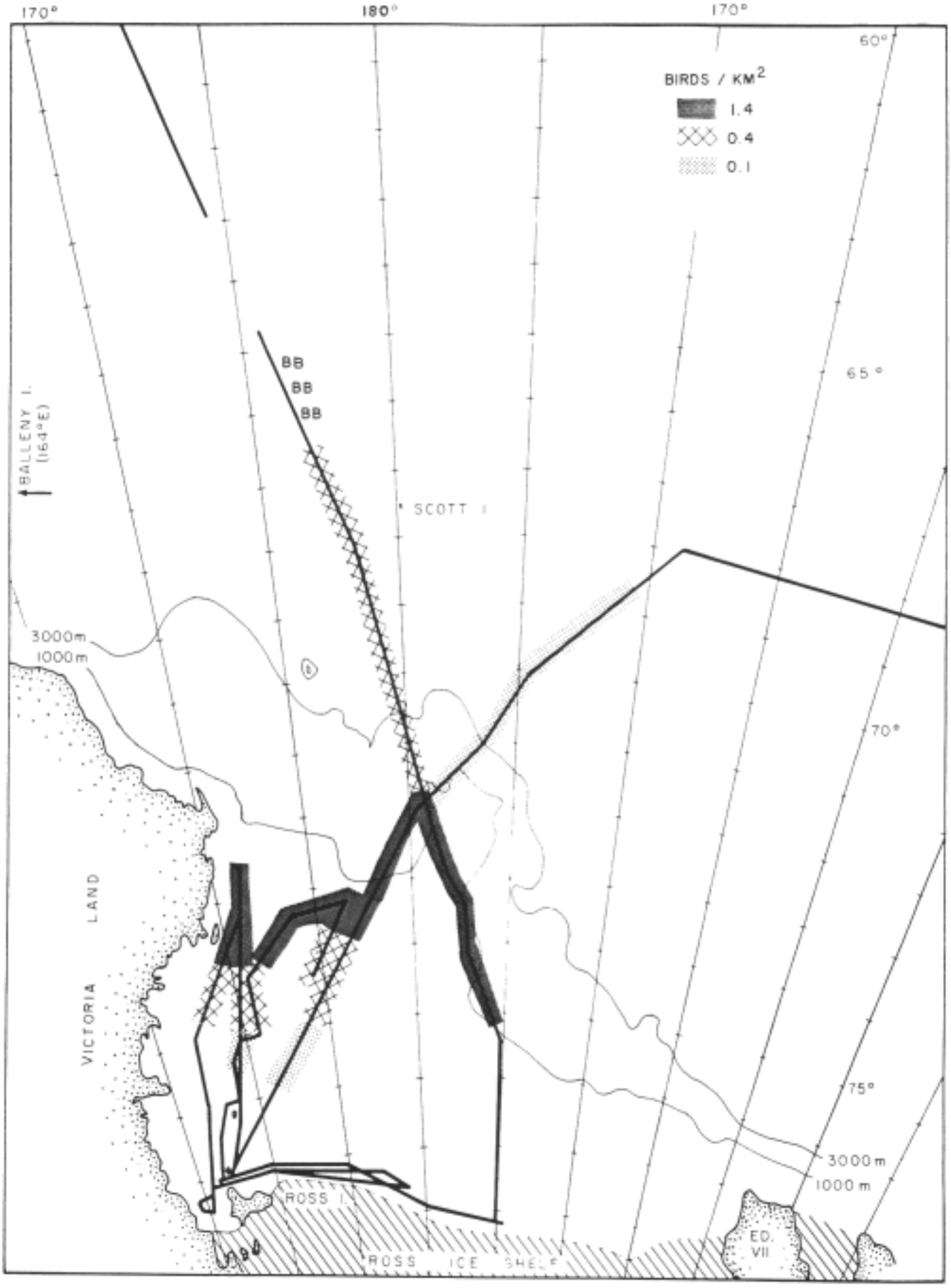

FIG. 36. Occurrence of Wilson's Storm-Petrels (shading) and individual Black-bellied Storm-Petrels (BB; densities averaged 0.16 ± 0.27 birds/km²) along late January and February cruise tracks.

km^2 (n = 43 transects) during December and 0.16 ± 0.27 (n = 20 transects) during February. We recorded the species as far south as 66°30′; Watson et al. (1971) recorded it to about 62°S in the Ross Sea area. The closest known nesting sites are on islands just south of New Zealand.

DIVING PETREL (*PELECANOIDES* SPP.)

Just north of and in the northern part of the Polar Front Zone, diving petrels were encountered rather frequently (Figs. 37, 38). We could not identify them to species. During December, their overall density was 0.16 ± 0.26 birds/km^2 (n = 29 transects), but by February it had jumped to 4.05 ± 3.90 (n = 15 transects). Diving petrels occurred farther south in February than in December. Their southward occurrence ended abruptly at the 3.0°C isotherm in both months. Our southernmost record was 63°40′S; Watson et al. (1971) listed two records south of that in the Ross Sea region. Closest confirmed nesting sites are Macquarie Island and the islands just south of New Zealand (Watson et al. 1971).

BROWN SKUA (*CATHARACTA SKUA*)

Two individuals were sighted over the outer continental slope in the westernmost part of the study area during December (Fig. 39). A nonbreeder was collected over the upper continental slope in that region (73°44′S, 172°18′E) during early January (Fig. 40). The species possibly breeds on the Balleny Islands just outside the western edge of the study area. Brown Skuas on occasion visit Adélie Penguin rookeries as far south as Ross Island (Ainley et al. 1978).

SOUTH POLAR SKUA (*CATHARACTA MACCORMICKI*)

Rather surprisingly, the South Polar Skua was localized in its occurrence during December to a degree exceeded only by the Emperor Penguin (Fig. 39). Except for 13 individuals, 10 of which were riding updrafts along the western two-thirds of the ice cliffs of the Ross Ice Shelf, all skuas occurred within 250 km of breeding areas. The three wayward individuals occurred at 59°59′S, 178°38′E (within the Polar Front), at 68°37′S, 172°30′W, and at 72°30′S, 166°30′W. Later in the summer skuas were only slightly more dispersed, mostly to the east along the Ross Ice Shelf (Fig. 40). Among skuas collected within 50 km of nesting sites, seven of 13 (54%) were breeders; beyond 50 km, all were nonbreeders (n = 9). Thus, even nonbreeding skuas remain relatively close to nesting colonies during the breeding season.

The close association with breeding sites made it difficult to assess the habitat preferences of this species. Even so, it appeared that skuas preferred pack ice over open water. In pack ice near breeding colonies their densities ranged from 0.3 to 0.6 birds/km^2, but in adjacent open water, densities were only 0.1 to 0.2 birds/km^2 (Fig. 39). Within the ice, skuas either stood on floes, or flew and fed in the center of leads (Table 3). Two of the three "wayward" December individuals were in the ice pack. During February, a large feeding flock (n = >75 skuas), the only occurrence of more than one individual a long distance from nesting colonies, was sighted in an area of loose pack ice. Like most other species, skuas avoided the open waters of the central Ross Sea.

Ross Sea population.—By estimating the areas where skuas concentrated in

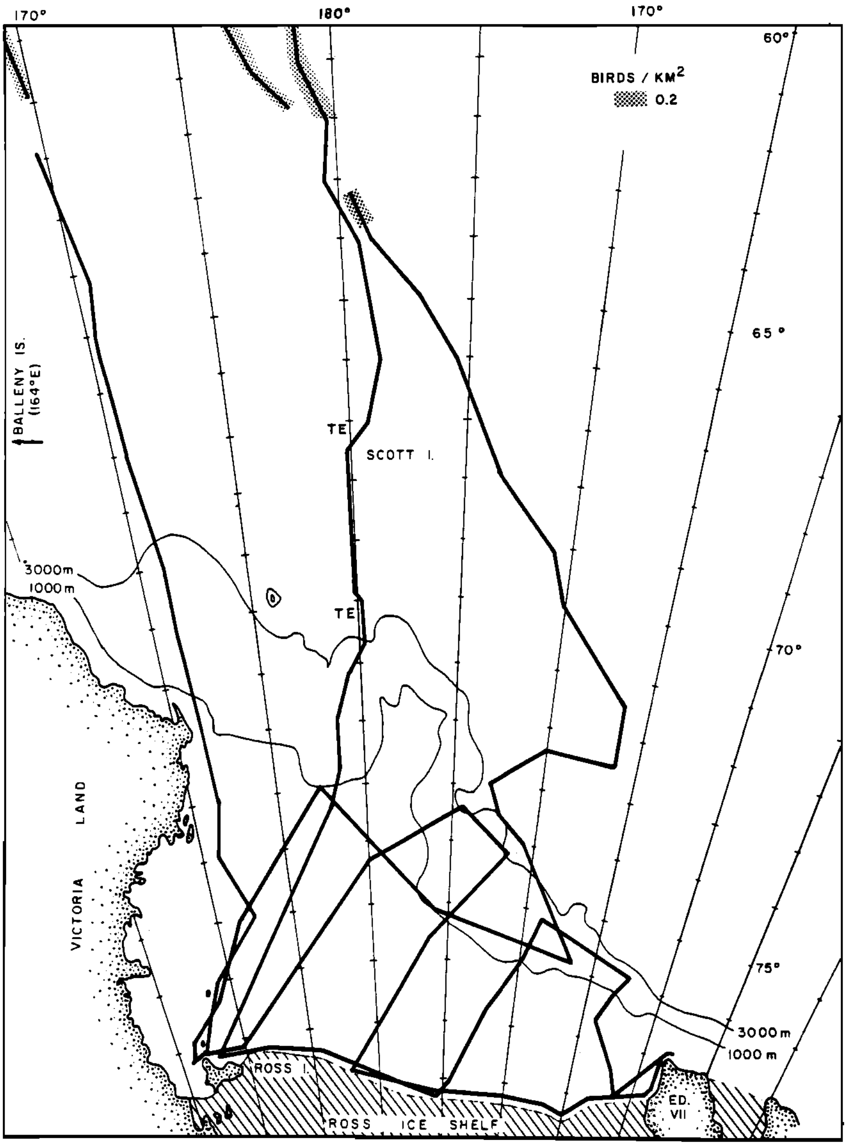

FIG. 37. Occurrence of diving petrels (*Pelecanoides* spp., shading) and two isolated flocks of Arctic Terns (TE) along December cruise tracks.

measurable densities (Fig. 39), and increasing the number by 31% to account for birds attending eggs or small chicks, we estimated a Ross Sea population of about 13,500 skuas. This estimate may be conservative because a small portion of skua breeders remain continually on land during December and January to feed within penguin rookeries.

South Polar Skuas nest at a minimum of 50 localities within the bounds of the Ross Sea. Many of these nesting sites were discovered or censused for the first

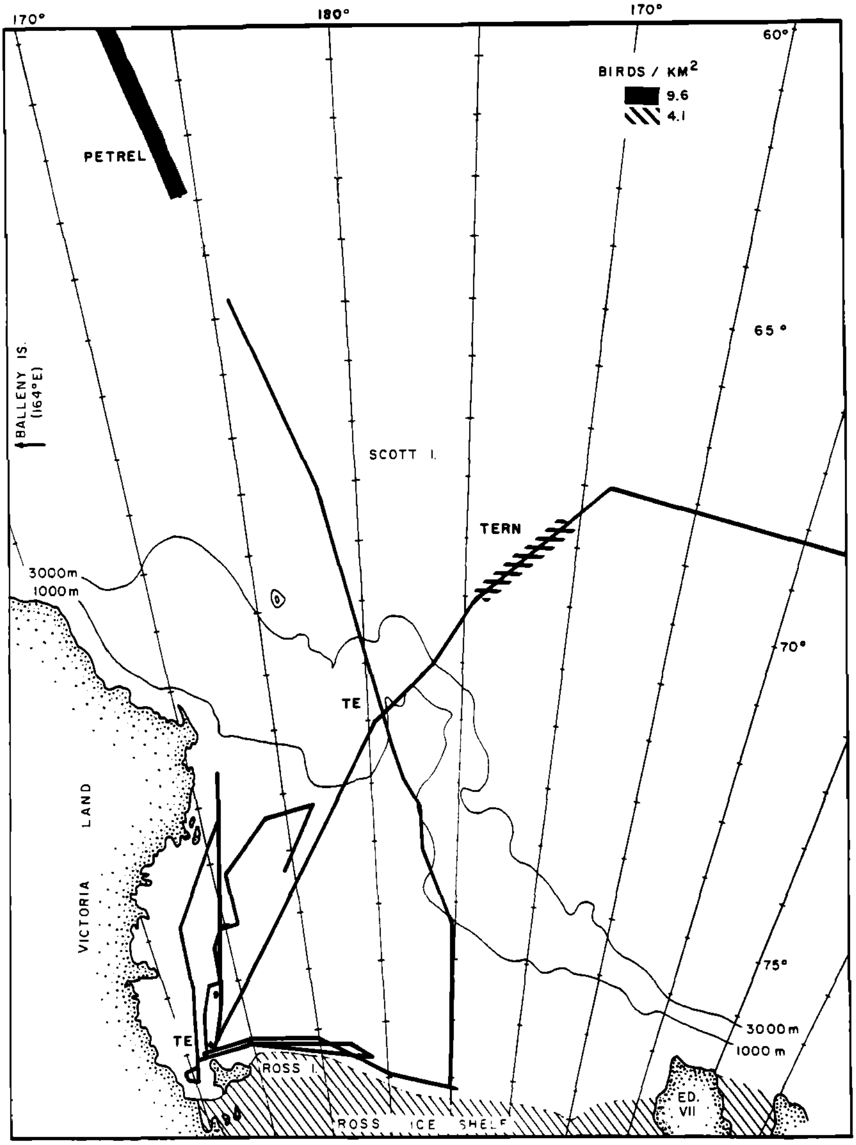

FIG. 38. Occurrence of diving petrels (*Pelecanoides* spp.) and Arctic Terns along late January and February cruise tracks; isolated tern flocks are indicated by TE.

time in the 1981–1982 and 1982–1983 austral summers (Ainley, unpubl. data; Watson et al. 1971 list only 15 breeding sites). From this survey we estimated a minimum of 6141 pairs of skuas breeding in the Ross Sea, an estimate that should be fairly accurate. Based on counts at Cape Adare (Reid 1962), Cape Hallett (Reid 1964), and Cape Crozier (Wood 1971), 82% of the skuas frequenting nesting localities are breeders, but skuas do not begin to visit rookeries until two to three years old (Wood, Ainley and Ribic, unpubl. data). Therefore, an appreciable

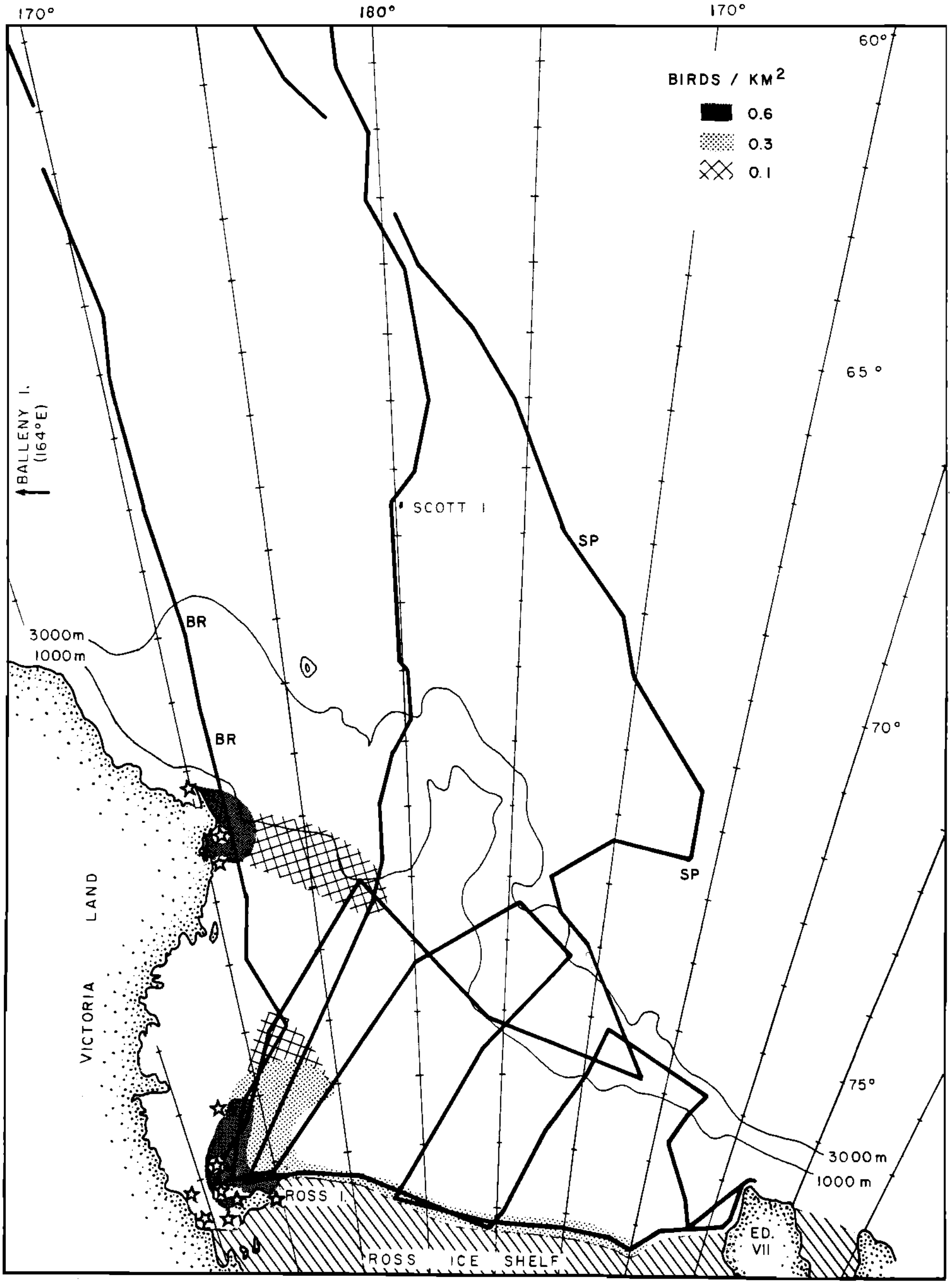

FIG. 39. Distribution of skuas during December. Shading indicates areas of concentration for South Polar Skuas; SP indicates individual South Polar, and BR, individual Brown Skuas. Breeding sites including ≥100 pairs of South Polar Skuas are indicated by stars.

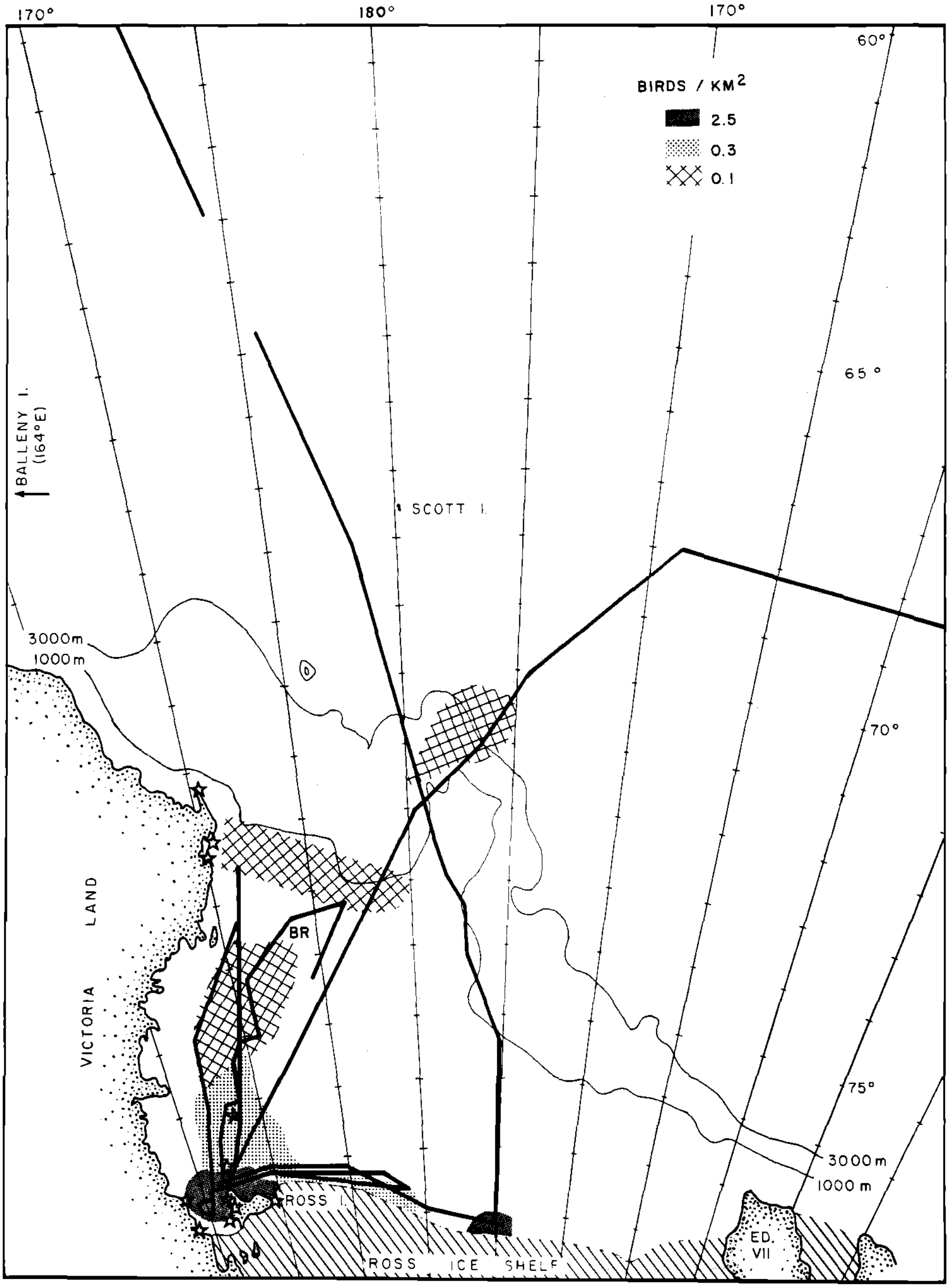

FIG. 40. Occurrence of South Polar Skuas (shading) and an individual Brown Skua (BR) during late January and February. Breeding sites including ≥100 pairs of South Polar Skuas are indicated by stars.

number of skuas must remain at sea (in the vicinity of nesting colonies) during the breeding season. We estimate that nonbreeders comprise about 30% of the skua population. Using the total number of breeding pairs and this percentage, we calculated a total Ross Sea population of about 17,550 birds. This estimate is quite close to the one derived from at-sea densities and is probably accurate to within 1000 birds unless our estimate of the proportion of nonbreeders is grossly in error. Skuas occurred in the Ross Sea at an overall density of 0.03 birds/km^2. Most were concentrated in the south.

ARCTIC TERN (*STERNA PARADISAEA*)

During December, we encountered a flock of four Arctic Terns at the outer edge of the ice pack (67°30′S, 180°W) and another flock of five over the continental slope within the pack interior (70°20′S, 179°40′W). In late January and February, however, we observed many more Arctic Terns in the outer 100 km of the ice pack (Figs. 37, 38). Density within this region of loose pack ice was 9.58 ± 8.26 birds/km^2 ($n = 9$ transects). We observed no terns after moving away from the pack edge; most birds were in heavy wing molt and were sitting on ice floes. In addition, a flock of four terns was observed over open water of the continental slope (71°55′S, 179°30′W), and another flock that size was observed near the edge of loose pack ice at 76°59′S, 166°56′E, probably the southernmost record for the species.

Zink (1981) summarized other reports of Arctic Terns. Most authors have noted the species' preference for loose pack ice at the edge of the ice pack. The species is supposedly most abundant in the Weddell Sea, but we observed it at sustained densities equivalent to those densities measured in the Weddell Sea and much higher than those reported from other areas. Because regular bird observations have been carried out on only a few ship cruises into the Antarctic ice pack, it may be premature to hypothesize where this species is most abundant.

FEEDING BEHAVIOR

Emperor Penguins regularly dive to depths of 200 m and Adélie Penguins to depths of about 30 m in pursuit of prey (Kooyman 1975). Penguins catch only one organism at a time (Zusi 1975), but how many they catch per dive is not known. An Emperor can stay submerged for about 20 min, but an Adélie submerges for only 3 min per dive (Kooyman 1975).

The two species of penguins tended to feed only at certain times of day (Fig. 41). This was determined by noting the proportion of penguins in the water as opposed to on ice floes in areas where ice was present, and by assuming that when in the water, the penguins were feeding. The proportion of Emperor Penguins in the water was lowest in the early morning (00:00–05:00 h) and rose to a peak at mid-day (09:00–14:00 h), whereas the proportion of Adélie Penguins in the water was consistently high in the early morning (03:00–05:00 h) and declined in the late morning through the late afternoon (09:00–15:00 h). Statistical testing of these relationships indicates that the proportion of penguins in the water was indeed dependent on time of day (Emperor, $G = 115.6$ and Adélie, $G = 110.3$; 77 d.f., $P < .005$). There was, thus, little overlap in the periods when the two species were in the water.

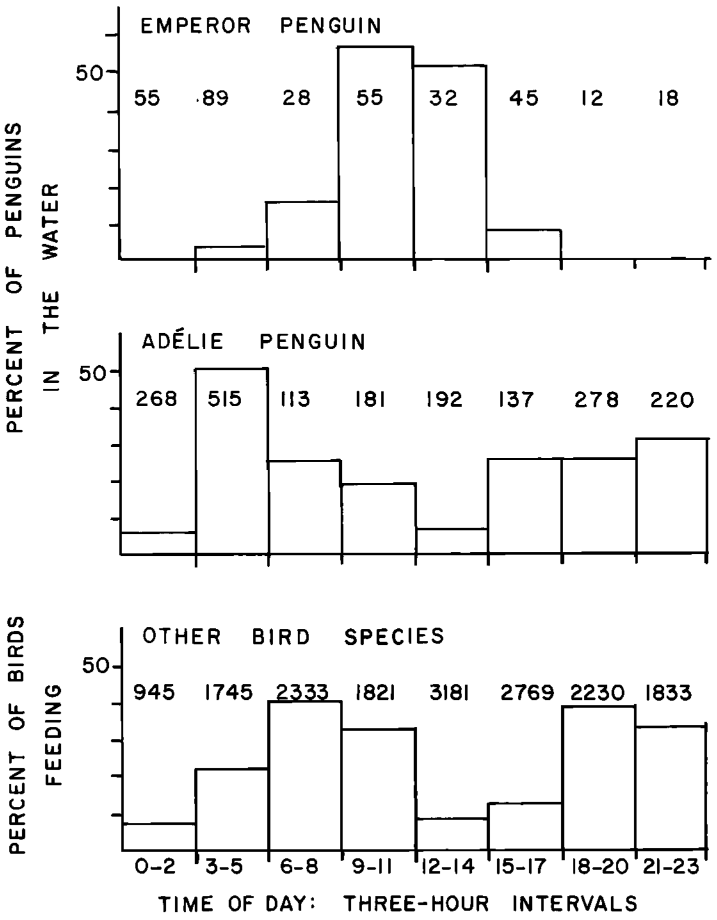

FIG. 41. Daily patterns of feeding in Antarctic seabirds. Patterns revealed by the percentage of penguins observed in the water, as opposed to on ice floes, within areas where floes were present, and the percent of individuals of all other avian species feeding compared to the total observed. Numbers over or within columns are the total number of individuals observed in respective time periods.

The only other seabirds we observed diving after prey were Antarctic and Snow Petrels (Table 4). Some form of dipping was used extensively by many species, ranging from 32% of observations of feeding for South Polar Skuas, to 47% for Antarctic Petrels, 92% for Snow Petrels, 97% for Wilson's Storm-Petrels, and 100% for Black-bellied Storm-Petrels. In the last two species almost all dipping took the form of pattering, but in Antarctic Petrels and skuas it took the form of contact dipping. Only Snow Petrels fed to a large extent by true dipping, and as a result, their contact with the water was much briefer than that of the Antarctic Petrels or skuas. The larger Southern Fulmar and Light-mantled Sooty Albatross (not shown in Table 4 because we were unable to compile observations of them feeding in Antarctic waters) were the only species that fed appreciably by surface seizing; other species, such as Antarctic and Mottled Petrels, used surface seizing

TABLE 4

FEEDING BEHAVIORS OF ANTARCTIC SEABIRDS

	Percent of Observations									
Species	Dip	Contact dip	Patter	Pursuit plunge	Dive	Surface seize	Scavenge	Pirate	Total no. obs.	Percent near ice[a]
Southern Fulmar						100			6	0
Antarctic Petrel	7	40		20	6	21	3	3	71	11
Snow Petrel	35	55	2		4	4			55	69
Mottled Petrel				67		33			3	0
Wilson's Storm-Petrel	9	14	74			3			35	11
Black-bellied Storm-Petrel			100						9	0
South Polar Skua		32				27	23	18	22	4

[a] Feeding in water within 1 m of ice floes.

to a lesser degree. Only Antarctic and Mottled Petrels and Sooty Shearwaters (not in Table 4) fed by pursuit plunging. Scavenging and pirating were used by skuas more than by other species. When pursuit plunging, Antarctic Petrels typically remained submerged 3–4 sec and, thus, probably reached a depth of at least a few meters. In general, it appeared that the extent and amount of time in contact with the water increased with body size. More than any other species, Snow Petrels captured prey close to ice (Tables 3, 4).

Birds capable of aerial flight showed a periodicity in their feeding activity similar in pattern to that of the Adélie Penguin ($G = 1513.3$, d.f. $= 7$, $P < .005$). Periods of peak feeding extended from 06:00 to 11:00 h and 18:00 to 23:00 h, based on 16,847 sightings of birds other than penguins (Fig. 41). Only in open waters near the shelf break did Antarctic seabirds feed to a great extent during "mid-day"; otherwise, most feeding activity occurred when light intensity was low. This was expected since zooplankton and micronekton, along with their nektonic predators, migrate toward the surface when light intensity is least, that is at night. Cloud cover also affects this response to some degree. Except in the vicinity of Ross Island and the southern Victoria Land coast, skies were almost always overcast throughout this study; all observations of feeding seabirds were made under such conditions.

The different temporal pattern of feeding exhibited by Emperor Penguins may reflect the extreme depths to which they can dive (Kooyman 1975). They may not have to wait for prey to migrate to the surface during the dark hours of the day, as other avian species must. Not having to feed during dark hours should also reduce the Emperors' contact with predatory leopard seals (*Hydrurga leptonyx*), which tend to rest on ice floes during midday (Ainley, pers. obs.). If this speculation is correct, it may indicate that Emperor Penguins are more vulnerable to leopard seal attack than are Adélie Penguins. Adélies certainly swim much faster and are more maneuverable than Emperors.

TROPHIC RELATIONS

The trophic relations of seabirds are exceedingly intricate. Not only has the subject received little attention, but most of the available seabird trophic studies either concern single species or a restricted portion of the year. The large majority of trophic studies has been based on food brought to chicks, with little consideration of where, how, or when the prey were caught. Belopolskii (1957), Ashmole and Ashmole (1967), Pearson (1968), Croxall and Prince (1980a), and Harrison et al. (1983), all of whom based their work on food brought to chicks, are the only investigators that have examined trophic relations within entire and discrete seabirds communities. Among the studies, the only one conducted in the Antarctic was that of Croxall and Prince (1980a).

We too studied trophic relationships during the chick feeding period; feeding habitat and means of prey capture, however, were determined. In addition, we simultaneously sampled breeding and nonbreeding individuals of several species in the seabird communities frequenting the various feeding localities.

DIET COMPOSITION

Seabird samples were separated according to origin from oceanic (Table 5), continental slope (Table 6), or continental shelf waters (Table 7). In oceanic habitats just north of the Ross Sea, crustacea and squid predominated numerically in the diets of most species. In continental slope waters the numerical importance of crustacea increased even more, and fish replaced squid to some extent. In continental shelf waters fish and crustacea predominated, and squid numbers were negligible. Trends in frequency of occurrence were generally consistent with average numerical composition (Tables 5, 6, 7), a fact expected more of bird diets in polar waters than in tropical waters where the number of available prey species is greater and perhaps even more patchy in occurrence (see Ashmole and Ashmole 1967; Harrison et al. 1983).

The diet of individual species changed in a fashion consistent with the general community patterns. As examples, Antarctic Petrels ate many euphausiids and a few squid in oceanic waters, but ate euphausiids, squid, and a few fish in continental slope waters. Snow Petrels ate euphausiids and squid in oceanic and continental slope habitats, but ate mostly fish over the continental shelf. Skuas ate fish and squid in continental slope waters, but ate mostly fish over the shelf. Although samples were small, only the Adélie Penguin showed little change in diet, eating one species of euphausiid over the continental slope and switching to another species of euphausiid over the continental shelf. The few Adélies sampled in the present study, however, had diets almost identical to the large numbers of penguins sampled by Emison (1968) that had been feeding in waters over the continental shelf in the western Ross Sea and to those sampled by Volkman et al. (1980) that had been feeding near the South Shetland Islands.

When we analyzed diets by weight of prey consumed instead of number or occurrence frequency, the importance of various prey changed (Table 8). Such an analysis, of course, depends upon the accuracy with which hard-part measurements predict the original size and weight of prey (Tables 9, 10). In oceanic and continental slope habitats, squid became much more important than other prey for most seabirds; in shelf habitats fish predominated to an even greater degree. Only the diet of the Adélie Penguin remained dominated by euphausiids. In the more extensive Adélie collections made by Emison (1968), fish during one year contributed only 4% of the diet by number, but up to 39% by weight; in the next year, fish contributed 8% by number, but weight composition was not determined. Thus, fish are sometimes important as prey even to the Adélie Penguin.

TABLE 5

AVERAGE NUMBER OF PREY ITEMS AND THEIR FREQUENCY OF OCCURRENCE IN STOMACHS OF SEABIRDS COLLECTED AT DEEP OCEAN LOCALITIES[a]

Bird species	Crustacea[b]			Cephalopods[b]				Fish[b]	$\bar{X}$ no. items per stomach
	1	2	3	4	5	6	7	8	
Light-mantled Sooty Albatross 2[c]	20/100 (100)								20.0
Southern Fulmar 13	29/69 (85.8)	0.1/10 (0.3)		1.6/69 (4.7)	1.9/77 (5.6)	1.1/62 (3.3)	0.1/23 (0.3)		33.8
Cape Petrel 4	1.0/100 (52.6)				0.3/25 (15.8)	0.3/25 (15.8)	0.3/25 (15.8)		1.9
Antarctic Petrel 7	6.0/71 (78.9)			0.7/57 (9.2)	0.9/43 (11.8)				7.6
Snow Petrel 3	5.7/100 (95.0)				0.3/33 (5.0)				6.0
Mottled Petrel 3	2.7/100 (17.5)		0.3/33 (1.9)	1.0/33 (6.5)	5.7/67 (37.0)	1.7/33 (11.0)	3.7/100 (24.0)	0.3/33 (1.9)	15.4
Antarctic Prion 3	7.3/100 (100)								7.3

---

[a] Average number of prey items/percent of stomachs in which item was present; in parentheses, percent composition based on total number of prey items.

[b] Prey species: 1 = *Euphausia superba*; 2 = unidentified lysianasid; 3 = pasapheid; 4 = *Gonatus antarcticus*; 5 = *Psychroteuthis glacialis*; 6 = *Galiteuthis glacialis*; 7 = unidentifiable species; 8 = *Pleuragramma antarcticum*.

[c] Number of birds sampled.

TABLE 6

AVERAGE NUMBER OF PREY ITEMS AND THEIR FREQUENCY OF OCCURRENCE IN STOMACHS OF SEABIRDS COLLECTED AT CONTINENTAL SLOPE LOCALITIES[a]

	Crustacea[b]				Cephalopods[b]			Fish[b]		Other[b]	$\bar{X}$ no. items per stomach
Bird species	1	2	3	4	5	6	7	8	9	10	
Adélie Penguin 2[c]	694/100 (99.0)	3.0/100 (0.4)	1.0/100 (0.1)					1.0/100 (0.1)			701.0
Southern Giant Fulmar 2	30/50 (92.3)				0.5/50 (1.5)	0.5/50 (1.5)	1.0/50 (3.0)			0.5/50 (1.5)	32.5
Antarctic Petrel 32	12.2/81 (85.9)	<0.1/19 (1.4)		0.2/9 (1.4)	0.3/31 (2.1)	<0.1/6 (0.7)	0.1/19 (0.7)	1.0/53 (7.0)		0.1/3 (0.7)	14.2
Snow Petrel 30	11.5/93 (95.3)	<0.1/10 (1.6)		0.1/10 (0.8)	0.2/10 (1.6)						12.2
Wilson's Storm-Petrel 28	1.4/64 (46.7)	0.2/21 (6.7)	0.1/4 (3.3)		0.1/4 (3.3)		0.8/50 (26.7)	<0.1/4 (3.3)	<0.1/4 (3.3)	0.2/25 (6.7)	3.0
Skua 4				0.8/50 (34.8)				1.0/50 (43.5)	0.5/25 (21.7)		2.3

[a] Average number of prey items/percent of stomachs in which item was present; in parentheses, percent composition based on total number of prey items.

[b] Prey species: 1 = *Euphausia superba* (also *E. crystallorophias*, 2.0/1.0, 0.3% for Adélie Penguins); 2 = unidentified lysianasids, including mostly small (1 cm) *Orchomene* spp. but also a large (4–5 cm), unidentified species, eaten by single Antarctic and Snow Petrels; 3 = other crustacea; 4 = *Gonatus antarcticus*; 5 = *Psychroteuthis glacialis*; 6 = *Galiteuthis glacialis*; 7 = unidentifiable species; 8 = *Pleuragramma antarcticum*; 9 = other fish (*Lampanyctus* sp. for Antarctic Petrel and *Manaenolepis* sp. for skuas); 10 = other prey (polychaetes for Antarctic Petrels and storm-petrels, penguin scraps for giant fulmars).

[c] Number of birds sampled.

TABLE 7

AVERAGE NUMBER OF PREY ITEMS AND THEIR FREQUENCY OF OCCURRENCE IN STOMACHS OF SEABIRDS COLLECTED AT CONTINENTAL SHELF LOCALITIES[a]

Bird species	Crustacea[b]				Cephalopods[b]			Fish[b]		Other[b]	$\bar{X}$ no. items per stomach
	1	2	3	4	5	6	7	8	9	10	
Adélie Penguin		3971/100	6/100	2/67					0.3/33		3990.3
3[c]		(99.6)	(0.2)	(0.1)					(0.1)		
Snow Petrel		0.3/14				<0.1/14	<0.1/5	3.1/14	0.1/14		3.7
21		(8.1)				(2.7)	(2.7)	(83.8)	(2.7)		
Skua	<0.1/5	0.8/25	0.1/5		<0.1/5		<0.1/5	1.3/50	0.5/25	0.3/30	3.3
20	(3.0)	(24.2)	(3.0)		(3.0)		(3.0)	(39.4)	(15.2)	(9.1)	

[a] Average number of prey items/percent of stomachs in which item was present; in parentheses, percent composition based on total number of prey items.

[b] Prey species: 1 = *Euphausia superba*; 2 = *E. crystallorophias*; 3 = small lysianasid (*Orchomene* spp.); 4 = other crustacea including 2.0/0.7 hyperids; 5 = *Gonatus antarcticus*; 6 = *Psychroteuthis glacialis*; 7 = unknown squid; 8 = *Pleuragramma antarcticum*; 9 = other fish (*Lampanyctus* sp. in Snow Petrel); 10 = penguin scraps.

[c] Number of birds sampled.

Certain species of prey predominated regardless of the predator species. At least seven species of crustacea were eaten, but the numbers of most were negligible compared to *Euphausia superba* in oceanic and slope waters, and *E. crystallorophias* in shelf waters. The pattern for fish was the same; although four species were eaten, the vast majority was *Pleurogramma antarcticum.* Squid use was slightly more diverse. In numerical importance, *Psychroteuthis glacialis* was first, *Gonatus antarcticus* a fairly close second, and *Galiteuthis* sp. (probably *glacialis*) a distant third.

DIET OVERLAP

We used the numerical composition of prey in diets to calculate Morisita's Indices (Horn 1966) as measures of diet overlap among seabird species. A total of 38 diet comparisons were made. In 16 comparisons, the overlap index was greater than .95, and in 22 comparisons the index was less than .85. Based on this frequency distribution of index values, we decided that an index ≥.95 indicated a similar diet and an index ≤.85 indicated a dissimilar diet. Seven seabird species were sampled (n = 35 birds total) at three oceanic localities; the diets of most species overlapped extensively (Table 11). Exceptions were the Cape and, especially, the Mottled Petrels whose diets showed little overlap with other species. Six species were sampled (n = 98 birds total) at five continental slope localities; the diets of all species except the Wilson's Storm-Petrel and South Polar Skua were similar (Table 12). Finally, at four continental shelf localities, three species were sampled (n = 44 birds total), and the diets of all three were dissimilar (Table 13). In oceanic waters the Cape and Mottled Petrels, the two species with diets different from the other species sampled in that habitat, ate more squid than all other species sampled in the study. Correspondingly, the two species did not occur in waters of the slope and shelf where the importance of squid as seabird prey was, in general, rather low. The South Polar Skua had a diet different from other species in both the shelf and slope waters where it was sampled. Its diet was similar only to that of the Snow Petrel in shelf waters; Snow Petrels consumed fish only in the latter habitat, but skuas ate fish in both areas.

In general, within the same habitats all species ate the same size euphausiids (Appendices II, III). Almost all those eaten in oceanic habitats were adult *Euphausia superba*; juvenile *E. superba* were found only in the stomachs of prions. Prince (1980) also found that the Antarctic Prion fed extensively on smaller, immature *E. superba* instead of the larger adults. Thus, the diet of prions in our sample differed more from the diet of other seabirds than the overlap indices indicate. In slope habitats, subadult *E. superba* may have been more numerous than individuals of other age classes since more were consumed there than in the oceanic areas; even the tiny Wilson's Storm-Petrel (Table 14, Appendix II) ate euphausiids as large as those eaten by the much larger Snow Petrel. In shelf habitats of the Antarctic, the most common euphausiid is *E. crystallorophias,* which, as an adult, reaches a length less than half that of *E. superba*; all seabird species sampled ate the same size *E. crystallorophias* (Appendix III).

The squid eaten by seabirds were much larger than the crustacea eaten, and large enough so that to some extent the size of the prey taken was related to the size of the seabird predator (Table 14, Appendix IV). This was more apparent for the squid *Gonatus antarcticus* than for *Psychroteuthis glacialis,* indicating that

TABLE 8

Estimated Average Prey Composition, by Weight, of Stomach Contents of Seabirds from Localities of the South Pacific Ocean and Ross Sea[a]

	Deep ocean[b]			Continental slope[b]				Continental shelf[b]			
Species	C	S	F	C	S	F	O	C	S	F	O
Adélie Penguin				509.4 (97.7)		12.0 (2.3)		840.6 (99.9)		0.8 (0.1)	
Light-mantled Sooty Albatross	14.6 (100)										
Southern Giant Fulmar				21.9 (22.6)	72.0 (74.3)		3.0 (3.1)				
Southern Fulmar	21.2 (6.4)	311.6 (93.6)									
Cape Petrel	0.8 (2.9)	27.0 (97.1)									
Antarctic Petrel	4.4 (3.9)	114.5 (96.3)		10.4 (17.4)	39.4 (65.8)	10.0 (16.7)	0.1 (0.2)				
Snow Petrel	4.2 (34.4)	8.0 (65.6)		9.9 (36.8)	17.0 (63.2)			0.5 (1.1)	3.5 (8.3)	38.4 (90.6)	
Mottled Petrel	2.1 (0.7)	321.6 (98.4)	3.0 (0.9)								
Wilson's Storm-Petrel				1.2 (36.3)	1.5 (45.5)	0.5 (15.2)	0.1 (3.0)				
Arctic Tern	3.7 (100)										
South Polar Skua					120.0 (86.0)	19.5 (14.0)		0.3 (0.8)	8.0 (21.0)	28.8 (75.6)	1.0 (2.6)

[a] Diet composition expressed by weight in grams; percent composition given in parentheses. Data extrapolated from Tables 5, 6, 7, 9, 10.

[b] C = crustacean, S = squid, F = fish, O = other.

TABLE 9

AVERAGE LENGTHS AND WEIGHTS OF SQUID EATEN BY SEABIRDS[a]

	Gonatus antarcticus			*Galiteuthis glacialis*		
Bird species	DML ± s.d.	Weight ± s.d.	n	DML ± s.d.	Weight ± s.d.	n
Southern Fulmar	18.0 ± 2.5	125 ± 25	22	18.0 ± 3.0	36 ± 10	13
Antarctic Petrel	18.0 ± 3.0	125 ± 35	10			
Snow Petrel	14.0 ± 6.0	66 ± 80	4			
Mottled Petrel	10.5 ± 4.5	33 ± 35	3	14.0 ± 3.0	26 ± 15	5
South Polar Skua	20.5 ± 3.5	150 ± 75	4			

[a] Dorsal mantle length (DML), in cm; weight, in grams. Values obtained by comparing lower rostral length (LRL) of squid beaks (Appendix IV) to regressions against weight and DML in Clarke (1980). Too few weight and rostral length data are available for *Psychroteuthis glacialis* to allow estimates of sizes and weights of those eaten by seabirds; a beak of this species with LRL of 0.4 cm, midway in the range of sizes taken by Antarctic seabirds, was from a squid with a DML = 12.8–13.1 cm (Clarke 1980).

the available range of sizes of the latter species was, perhaps, more restricted than that of the former (see also Table 9). Seabirds ate too few *Galiteuthis* sp. to generalize in this way, but some data indicate that it also is smaller than *Gonatus antarcticus* (Table 9, Appendix IV). The Southern Fulmar, Antarctic Petrel, and skuas ate *Gonatus antarcticus* of similar size; the smaller Snow and Mottled Petrels ate smaller squid of that species. Mottled Petrels took smaller *P. glacialis* than did fulmars, Antarctic Petrels, or Snow Petrels. The sizes of *P. glacialis* eaten by the latter three seabirds overlapped extensively, especially among birds sampled at the same localities. Fulmars took larger *Galiteuthis* sp. than did Mottled Petrels. The squid taken by Wilson's Storm-Petrels were the smallest although some overlapped in size with those eaten by Mottled Petrels. Judging from beak size and color, most squid eaten by storm-petrels were larval, and few could be identified. The frequency distributions of squid beaks, sorted by lower rostral length, was related somewhat to the sizes of the birds we sampled (birds were grouped into four size categories, Fig. 42), but the overall distributions of squid beak sizes exhibited almost no overlap with the size taken by sperm whales (Clarke 1980). This indicates that unlike some seabirds in the Scotia Sea (Clarke et al. 1981), the birds sampled in the present study were not taking squid from whale vomit. It is interesting that over the continental slope, seabirds took a disproportionately

TABLE 10

AVERAGE LENGTHS AND WEIGHTS OF THE FISH, *PLEURAGRAMMA ANTARCTICUM*, EATEN BY SEABIRDS IN THE ROSS SEA AND SOUTH PACIFIC OCEAN[a]

	Standard length ± s.d.	Weight ± s.d.	n
Antarctic Petrel	14.2 ± 2.7	17.6 ± 3.3	40
Snow Petrel	12.2 ± 3.5	11.2 ± 3.2	94
Mottled Petrel	16.8	28.5	1
Skua	17.2 ± 2.8	3.5 ± 5.6	45

[a] Standard length, in cm; weight, in grams. Values obtained by comparing diameters of fish otoliths (Appendix V) to regressions against fish length and weight (H. DeWitt, unpubl. data).

TABLE 11

MORISITA'S INDEX OF OVERLAP IN THE DIETS OF SEABIRD SPECIES IN OCEANIC HABITATS[a]

Species	Species (A)	(B)	(C)	(D)	(E)	(F)
Light-mantled Sooty Albatross (A)						
Southern Fulmar (B)	.985					
Cape Petrel (C)	.778	.851				
Antarctic Petrel (D)	.959	.991	.870			
Snow Petrel (E)	.997	.993	.808	.975		
Mottled Petrel (F)	.282	.362	.693	.423	.322	
Antarctic Prion	1.000	.985	.640	.959	.997	.282

[a] Index ranges from 1 (= complete overlap) to 0 (= no overlap); based on data from Table 5.

greater number of the larger squid of each species than they did in oceanic areas (Appendix IV), but the biological significance of this is unknown.

Fish were taken mostly by skuas, Snow Petrels, and Antarctic Petrels. Almost all of the fish found in the bird stomachs were *Pleuragramma antarcticum,* a species that dominates the midwater fish fauna of the Ross Sea (DeWitt 1970; DeWitt and Hopkins 1977). Emison (1968) also noted the importance of this fish to Antarctic seabirds. The birds sampled in the present study ate *P. antarcticum* similar in length to the squid that they caught (Tables 9, 10). The size of avian fish predators overlapped less than the size of squid predators, and not surprisingly, the size of fish taken overlapped less than the size of the squid taken (Appendix V).

In the only instance in which we observed a tight feeding flock comprised of more than one species, Snow Petrels and South Polar Skuas were catching *P. antarcticum.* In this instance the petrels caught fishes as large as those caught by skuas (judging by eye). The Snow Petrels, however, were unable to fly away quickly with these large fishes or to consume them before gaining the notice of skuas. The skuas pirated the large fishes but not the small ones which the petrels ate quickly. This was confirmed by stomach analyses showing little overlap in the size of the

TABLE 12

MORISITA'S INDEX OF OVERLAP IN THE DIETS OF SEABIRD SPECIES IN CONTINENTAL SLOPE HABITATS[a]

Species	Species (A)	(B)	(C)	(D)	(E)
Adélie Penguin (A)					
Southern Giant Fulmar (B)	.996				
Antarctic Petrel (C)	.989	.996			
Snow Petrel (D)	.999	.999	.995		
Wilson's Storm-Petrel (E)	.721	.760	.777	.747	
South Polar Skua	.001	0.000	.009	.065	0.000

[a] Index ranges from 1 (= complete overlap) to 0 (= no overlap); based on data from Table 6.

TABLE 13

MORISITA'S INDEX OF OVERLAP IN DIETS OF SEABIRD SPECIES IN CONTINENTAL SHELF HABITATS[a]

	Species	
Species	(A)	(B)
Adélie Penguin (A)		
Snow Petrel (B)	.095	
South Polar Skua	.389	.739

[a] Index ranges from 1 (= complete overlap) to 0 (= no overlap); based on data from Table 7.

fishes eaten (locality 11, Appendix V). In areas where no mixed feeding flocks of these two species were observed (in hundreds of hours of observation), the sizes of the fishes eaten by skuas and Snow Petrels overlapped much more. On three occasions we observed Snow Petrels hauling large fishes onto ice floes before consuming them. Snow Petrels were also able to eat large squid, and in fact, the squid in their diet had a larger range of sizes than the squid eaten by any other bird (Fig. 42). The close association with ice and the white (cryptic) color of Snow Petrels may be adaptations that allow them to eat large prey, undisturbed by other, larger birds.

SYNTHESIS AND DISCUSSION

COMMUNITY COMPOSITION

Three distinct communities of species were recognizable in Antarctic waters of the South Pacific and Ross Sea. The community having least overlap with the others was that of highest latitudes and the pack ice (Table 15). The chief components were Emperor and Adélie Penguins, Antarctic and Snow Petrels, and South Polar Skuas; minor species included Wilson's Storm-Petrel, which would have been considered a major component were it not for its distinct preference for open water, Southern Giant and Southern Fulmars, and, for a short time at the periphery of the habitat, Arctic Terns. The species composition of this com-

TABLE 14

BILL SIZES OF SEABIRDS FROM THE SOUTH PACIFIC OCEAN AND ROSS SEA[a]

Species	Sample	Culmen length	Bill depth
Giant Petrel	1 ♂, 1 ♀	95.5	35.8
South Polar Skua	4 ♂♂, 3 ♀♀	69.4 ± 1.9	19.3 ± 0.7
Adélie Penguin	1 ♂, 2 ♀♀	62.7 ± 1.9	18.1 ± 0.4
Southern Fulmar	4 ♂♂, 2 ♀♀	60.1 ± 2.4	18.1 ± 1.0
Antarctic Petrel	19 ♂♂, 11 ♀♀	54.0 ± 2.2	15.7 ± 0.9
Cape Petrel	1 ♂, 2 ♀♀	41.8 ± 1.9	14.8 ± 2.9
Mottled Petrel	1 ♂, 2 ♀♀	39.7 ± 1.4	14.6 ± 2.8
Antarctic Prion	1 ♂, 2 ♀♀	39.5 ± 1.5	13.2 ± 0.4
Snow Petrel	11 ♂♂, 12 ♀♀	36.2 ± 1.9	9.9 ± 0.7
Wilson's Storm-Petrel	12 ♂♂, 11 ♀♀	18.8 ± 1.2	5.0 ± 0.4

[a] Body weights, as an indication of overall size, are given in Table 20; culmen length = chord of culmen, and bill depth = depth at anterior edge of the nares. Measurements in mm, $\bar{X}$ ± s.d.

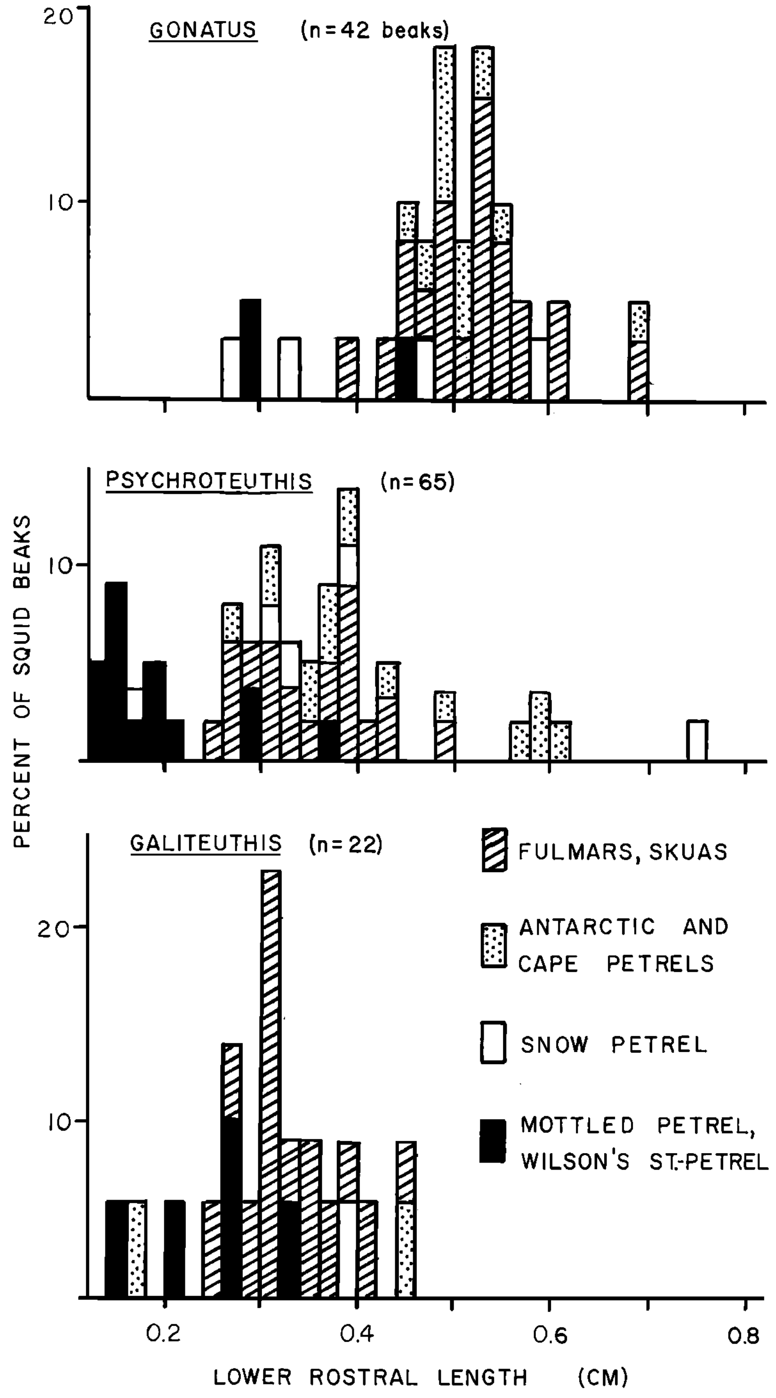

FIG. 42. Size distribution of squid beaks (lower rostral length, cm) in the stomachs of Ross Sea seabirds. Bars indicate the proportion of beaks, with the indicated rostral length, in the stomachs of birds of four size-ranges (Tables 14, 20).

TABLE 15

DISTRIBUTIONS AND HABITAT PREFERENCES OF SEABIRDS IN THE ANTARCTIC SOUTH PACIFIC OCEAN AND ROSS SEA, DECEMBER TO FEBRUARY

Species	Distributional limits		Preferred habitat	Density (no./km^2 ± s.d.) in preferred habitat[a]	
	Northern[b]	Southern		December	February
Emperor Penguin	Pack ice	Continent	Pack ice	1.00 ± 1.21	1.00 ± 1.21
King Penguin	Subantarctic	4.5°C	Open sea; Polar Front	0.10 ± 0.25	0.10 ± 0.13
Adélie Penguin	Pack ice	Continent	Pack ice	7.45 ± 11.8	10.31 ± 11.68
Wandering Albatross	Subantarctic	2.5°C	Open sea; Polar Front		<0.01
Gray-headed Albatross	Subantarctic	4.5°C	Open sea	<0.01	<0.01
Black-browed Albatross	Subantarctic	0.0°C	Open sea	0.02 ± 0.05	0.06 ± 0.16
Light-mantled Sooty Albatross	Subantarctic	−0.5°C	Open sea; bergs	0.04 ± 0.08	0.04 ± 0.08
Southern Giant Fulmar	3.0°C	Continent	Open sea; pack ice; bergs	0.04 ± 0.15	0.02 ± 0.04
Southern Fulmar	0.5°C	−1.5°C	Open sea; pack ice; bergs	1.09 ± 1.50	0.10 ± 0.12
Antarctic Petrel	Bergs	Continent	Pack ice; bergs	8.59 ± 15.51	4.33 ± 20.61[c]
Cape Petrel	Subantarctic	0.0°C	Open sea; bergs	0.08 ± 0.25	0.08 ± 0.25
Snow Petrel	Pack ice	Continent	Pack ice; bergs	3.60 ± 2.52	7.09 ± 4.41[c]
Antarctic Prion	Subantarctic	−0.5°C	Open sea; bergs	0.64 ± 1.22	0.36 ± 0.70
Blue Petrel	Subantarctic	Polar Front	Open sea; Polar Front	<0.01	<0.01
White-headed Petrel	Subantarctic	1.5°C	Polar Front	0.04 ± 0.10	0.42 ± 0.44
Mottled Petrel	Subantarctic	−0.5°C	Open sea; bergs	0.45 ± 0.47	0.34 ± 0.30
White-chinned Petrel	Subantarctic	5.0°C	Open sea		<0.01
Sooty Shearwater	Subantarctic	Bergs	Open sea	7.90 ± 18.26	10.41 ± 23.33
Wilson's Storm-Petrel	0.5°C	Continent	Open sea; pack ice; bergs	0.99 ± 2.10	0.99 ± 2.10
Black-bellied Storm-Petrel	Subantarctic	0.5°C	Open sea; Polar Front	0.16 ± 0.26	4.05 ± 3.90
Diving Petrel	Subantarctic	Polar Front	Open sea; Polar Front	0.16 + 0.26	4.05 ± 3.90
Brown Skua	Subantarctic	Open sea	Open sea	<0.01	<0.01
South Polar Skua	Pack ice	Continent	Pack ice	0.06	0.06
Arctic Tern	Pack ice	Pack ice	Loose pack ice	0.34 ± 0.76	9.58 ± 8.26

[a] Densities do not include recently fledged chicks.

[b] Subantarctic in this column means the species occurs as far north as subantarctic waters occur.

[c] Density greatly underestimated due to large numbers of birds roosting on ice bergs (out of transects).

munity, as we observed it from ships at sea, differed only slightly from the composition described by Ainley et al. (1978) from land at Cape Crozier, Ross Island, in the extreme southwestern Ross Sea. Those authors included the giant fulmar as a major species (it was scavenging at the penguin rookeries) and also included the rare Chinstrap Penguin (*Pygoscelis antarcticus*), Brown Skua, and Southern Black-backed Gull (*Larus dominicanus*) as minor species (present, like the giant fulmar, mainly when seas were free of ice). The chief component species of this community as observed in the present study are year-round residents of the pack ice; the minor ones are not. Species in this community frequented open waters cooled by pack ice to temperatures below 2.0°C, particularly if icebergs were relatively abundant. The ice community was dominated in numbers by Antarctic Petrels, and in biomass by Adélie Penguins (see below).

The penguins and Snow Petrel are the most obligatory associates of pack ice. So highly pagophilic are they that their breeding distributions are probably affected not just by the existence of suitable nesting habitat, but by the existence of pack ice near nesting areas throughout the breeding season. This is most obvious for Emperor Penguins, which actually nest on sea ice, and least obvious for Snow Petrels. While Adélie Penguins will cross relatively long distances of open water to reach the ice pack, Snow Petrels seem to do so much less readily. Furthermore, Adélies, but not Snow Petrels, have the ability to fast for long periods, thereby reducing the necessity to frequent open water and also actually increasing the range they can travel through open water. As pointed out by Ainley et al. (1983), however, when the ice pack moves too far away from nesting localities, even Adélies reduce their rate of visits to rookeries.

Comparison of the areas of residual pack ice in the Antarctic (Gilbert and Erickson 1977: map; plus the southern Victoria Land coast of the Ross Sea) with the known breeding distribution of Snow Petrels (Watson et al. 1971), reveals the close tie between nesting areas and residual pack ice. The existence of this tie perhaps indicates why the population of Snow Petrels at South Georgia is so small (Croxall and Prince 1980a). The only ice usually anywhere near South Georgia during the breeding season is glacial in origin and, thus, limited. The breeding population reported at Scott Island by Watson et al. (1971), like the one at South Georgia, is small (Harper et al., unpubl. data), probably because waters surrounding the island are usually free of pack ice from late December to April.

A second community of Antarctic seabirds occupied cold waters north of the pack ice, particularly those waters where icebergs occur. The most characteristic member of this community was the Southern Fulmar. Other species were the Wilson's Storm-Petrel, the Antarctic Petrel, and the Mottled Petrel. Minor species included Light-mantled Sooty Albatross, Southern Giant Fulmar, Cape Petrel, Snow Petrel, and Antarctic Prion. Except for the Antarctic Petrel, members of this community were less restricted to their habitat than the pack ice community was to its habitat. Many "berg zone" species, however, did not venture into the pack ice except to reach nesting sites, as in the case of Southern Fulmars. All of these species except the Mottled Petrel, Light-mantled Sooty Albatross, and the Southern Giant Fulmar nest on the Balleny and/or Scott Islands, which are surrounded by pack ice during winter and early spring and are within the concentrated berg zone the remainder of the year. As pointed out in the species accounts, some of these species, particularly albatross and giant fulmars, may avoid extensive pack ice because the ice dampens sea swells, and this makes dynamic soaring difficult.

The third avian community in Antarctic waters of the South Pacific was the most diverse and consisted of Subantarctic species that move across the Polar Front. The most widespread species were the Black-browed Albatross, Light-mantled Sooty Albatross, Southern Giant Fulmar, Cape Petrel, Antarctic Prion, Mottled Petrel, Sooty Shearwater, Black-bellied Storm-Petrel, and Brown Skua. Other species restricted more to the north were the King Penguin, Wandering, Royal, and Gray-headed Albatross, White-chinned, Blue, and White-headed Petrels, and diving petrels. The King Penguin and White-headed Petrel may have preferred the waters of the Polar Front Zone.

The species in the last community, along with a few species of penguins, are numerically the most important members of the Subantarctic avifauna (Watson et al. 1971). If islands existed near the Polar Front in the South Pacific, as they do in the South Atlantic and Indian Oceans, we would certainly have been able to include other penguins in the above list. So characteristically Subantarctic is the above list (including the penguins not seen) that the importance of the Antarctic Convergence as an avifaunal barrier may be less than formerly theorized. Kock and Reinsch (1978), on the basis of three cruises in the South Atlantic and Scotia Sea, expressed similar reservations about the Antarctic Convergence. Apparently, the Convergence is no more an avifaunal barrier than any equal drop in water temperature elsewhere in the world (Ainley and Boekelheide 1984). It would, however, be of great interest to study the avifauna within the Polar Front Zone at those few places and times when the Convergence is so sharp that manifestations of it can be detected at the surface (S. S. Jacobs, pers. comm.).

The oceanographic barrier across which the least overlap in species occurred was the edge of the ice pack (or even concentrated icebergs). The effects of ice on the occurrence of avian species in the Antarctic was illustrated inadvertently by Mougin (1975: fig. 40) who showed that during late summer and fall (Mougin had no early summer data), many species cross the Polar Front much farther south than they do during winter, and enter colder waters. In our opinion, this range extension presumably has most to do with the retreat of the ice pack away from the Polar Front Zone and to a much lesser degree with the Convergence moving slightly south.

FACTORS AFFECTING SEABIRD OCCURRENCE

Within the oceanographic habitats of the three seabird communities described above, birds were not equally abundant, but were concentrated by breeding activities and by ocean areas of high productivity. Our best data on this come from the high latitude/pack ice community.

We discovered that the entire population of most major high latitude species, as well as minor ones such as Southern Fulmar and Wilson's Storm-Petrel, were somewhat contracted toward their respective breeding areas during the breeding season, especially the egg and early chick periods, leaving large areas of seemingly suitable habitat vacant. Some species showed this pattern more strongly than others. The penguins and South Polar Skua showed it the most; the Southern Fulmar, Antarctic Petrel, and Wilson's Storm-Petrel showed it to a moderate degree, and the Snow Petrel showed it least. Such a distribution is expected for breeding birds, older nonbreeders that visit rookeries regularly, and, late in the breeding season, younger nonbreeders making initial exploratory visits to rookeries. It is not obvious why the very youngest nonbreeders, which do not visit rookeries, also remained near breeding areas.

Young birds may inadvertently go along with the flow of the majority toward breeding areas, and some of these young birds may even find themselves at nesting areas. For example, this may explain why two- and even one-year-old Adélie Penguins visit rookeries briefly (sometimes for only a matter of hours or minutes) after journeying in a flock across great distances of open water (Ainley et al. 1983). Rookery visitation patterns of Adélie Penguins are closely linked to age (Ainley 1975; Ainley et al. 1983). With an increase from one to six years, individuals progressively increase the number and duration of visits and visit progressively earlier each year. Because this visitation pattern is so precise, Ainley (1975) hypothesized that increasing hormone levels and their entrainment to environmental cues are involved. It could be that the movement toward breeding areas of the youngest Adélies, the ones that do not even visit rookeries, is an incipient migration in response to slight elevations in hormone levels. The hormone levels of young Adélies, as indicated by the degree of morphological maturity of young birds, probably are not high enough to cause them to accumulate the fat required for the fast of longer visits (Ainley 1975).

Whatever the immediate cause, young birds would not move toward breeding areas if it were disadvantageous (Ainley et al. 1983), and remaining associated with adults at sea for as long as possible could be advantageous if young penguins (or other birds) learn from example. Rookery experience as a youngster is advantageous for later breeding, but the majority of one- and two-year-olds does not go ashore. While young penguins may not be able to accumulate the fat reserves needed for visits, that they do concentrate closer to nesting areas and are abundant in areas where breeding adults are feeding, indicate that intraspecific competition for food near nesting areas during the breeding season is not an important limiting factor to these breeding populations. The fact that other species also concentrate near their respective breeding sites indicates this is true for them as well. For the Snow Petrel, the species that disperses most widely from breeding areas, it appears that the amount of feeding habitat may be more critical than the amount of available food (see p. 41). Furthermore, the broad overlap in the respective feeding areas of different species indicates that interspecific competition has not resulted in a segregation of feeding areas among Ross Sea seabirds.

Ashmole (1963) hypothesized that food availability during the breeding season was a major factor controlling population sizes in tropical oceanic seabirds because the concentration of birds forced to remain in the vicinity of islands by the duties of nesting exerted pressure on food to the limits of its availability. A corollary of his idea was that young, nonbreeding birds should avoid these concentrations. Because we found that entire populations (birds of all ages) in the Ross Sea were contracted toward breeding areas, the hypothesis may not be applicable to the high latitude Antarctic. That is consistent with the generally-held concept that food is much more patchy and less available for seabirds in tropical oceanic than in polar waters, especially those of the Antarctic.

The other factor that tended to localize seabirds in the Ross Sea was the Antarctic

Slope Front. The concentration of birds at oceanographic fronts, because of the increased availability of food, is becoming increasingly apparent to marine ornithologists (reviewed by Brown 1980). While it is widely appreciated that upwelling along continental slopes greatly increases the productivity of adjacent waters in many places, this phenomenon has, until recently, escaped the attention of marine biologists studying the Antarctic (Ainley and Jacobs 1981). Unlike continental slope fronts elsewhere, the Antarctic Slope Front is not manifest in gradients of physical properties near or at the surface, perhaps because of the homogenizing effects of sea ice formation and melting in combination with the great depths of the Antarctic continental shelves. The nature of the linkage between subsurface upwelling, manifest only to within about 100 m of the surface, and increased productivity in overlying surface waters has yet to be studied along the Antarctic Slope Front. Earlier data indicated that micronekton, especially krill, may be concentrated in surface waters in the vicinity of the Ross Sea slope (Marr 1962). With no knowledge of coincident frontal activity, Marr hypothesized that high concentrations of *Euphausia superba* at the Ross Sea slope were primarily the result of the younger life stages being physically stopped, transported upward, and concentrated at the continental slope in their passive movement in Circumpolar Deep Water. If primary productivity is enhanced in the Antarctic Slope Front in the Ross Sea, on the other hand, being stopped there certainly would not be disadvantageous to krill. The links between physical and biological factors at the slope front, given the importance of the area to vertebrates (seals and whales, besides birds; Ainley 1984), are in need of further study.

Also in need of further study are the factors responsible for the major phytoplankton bloom in waters over most of the Ross Sea continental shelf and the factors that keep the bloom confined there. Certainly, surface circulation, the slope front, and pack ice must be involved. The virtual absence of birds (and marine mammals; Ainley 1984) from shelf waters, except in the pack ice along the Ross Sea's western margin where birds are abundant, and the abundance of birds along the northern edge of the shelf indicate indirectly that nutrient transfer from the primary (phytoplankton) level to higher trophic levels is not occurring within the bloom but is occurring at the bloom's periphery. Furthermore, the extremely high densities of birds at the northern edge of the shelf (and bloom) indicate that the Antarctic Slope Front, which is also present there, probably enhances the energetic link between trophic levels.

Community Biomass

A statement frequently made in recent Antarctic literature is that the Antarctic bird community as a whole is dominated by penguins which have been estimated by various authors to comprise 90% by biomass and 60% by number of all species (e.g., Everson 1977; Prévost 1981). These estimates are based on combined counts of breeding birds at localized areas. The total number of penguins is relatively well known because these birds are easy to count in colonies and because the few areas suitable for their nesting are also the best sites for human habitation. The numbers of other species, however, are mostly guesses because many nest cryptically and in areas inaccessible to humans; an appreciable portion of the nesting colonies of such species as Snow Petrels and Antarctic Petrels is probably yet to be discovered.

TABLE 16

NUMBERS AND BIOMASS OF SEABIRDS IN THE ROSS SEA DURING DECEMBER AND EARLY JANUARY

Species[a]	Breeding population	Total population[b]	No. in Ross Sea[c]	Density in Ross Sea (No./km^2)	Body wt. (kg)[d]	Biomass in Ross Sea (kg/km^2)[c]
Emperor Penguin	212,264	326,200	308,800 (3.2)	0.52	32.50	16.900 (42.8)
Adélie Penguin	1,518,400	2,448,600	2,380,000 (24.5)	4.00	3.88	15.520 (39.3)
Southern Giant Fulmar			3,000 (<0.1)	0.01	3.98	0.040 (0.1)
Southern Fulmar			2,900 (<0.1)	0.01	0.84	0.008 (<0.1)
Antarctic Petrel	3,921,000	5,136,600	5,045,200 (51.8)	8.44	0.74	6.246 (15.8)
Snow Petrel	1,221,400	1,970,000	1,614,000 (16.6)	2.70	0.27	0.729 (1.8)
Wilson's Storm-Petrel	256,000	419,700	361,700 (3.7)	0.61	0.05	0.031 (0.1)
Brown Skua			30 (<0.1)			
South Polar Skua	12,282	17,550	17,550 (0.2)	0.03	1.33	0.040 (0.1)
Total, summer population	7,141,346	10,318,650	9,733,180	16.32		39.514

[a] Includes only species present during December and early January.

[b] Does not include chicks.

[c] Percent of total given in parentheses.

[d] Data from collected specimens except for the two penguins, whose weights are from Prévost (1961) and Ainley and Emison (1972).

Our best estimates of the number and biomass of seabirds during summer in the Ross Sea, which encompasses 11.1% (40° of longitude) of the circumference of Antarctica, are presented in Table 16. In December, when breeding species are most concentrated in the Ross Sea, two penguin species comprise 27.7% of the numbers but 82.1% of the biomass. By number, the avian community is dominated by the Antarctic Petrel, which contributes 51.8% of the total. How representative the summer composition of Ross Sea bird communities is of other areas in the Antarctic or of other seasons is not easy to assess because only penguin numbers can be estimated with confidence. The Bellingshausen and Amundsen Seas together extend across 70° of longitude (19% of the Antarctic circumference) and, second to the Ross Sea, are the best surveyed for birds (Erickson et al. 1972; Zink 1981; Ainley, unpubl. data). In those seas, penguins were encountered infrequently, but Antarctic and Snow Petrels were common. Thus, the relative frequencies of birds in the Ross Sea (Table 16) may be representative of these areas as well. Judging from maps in Watson et al. (1971), the biomass composition of seabird communities in oceanic waters north of these seas is also similar to those north of the Ross Sea, particularly during fall, winter, spring, and early summer when the pack ice has driven all but the high latitude, pagophilic species near to or north of the Convergence. The addition of Adélie Penguin fledglings to the community probably would compensate during winter for the loss of most Emperor Penguins that remain near rookery areas.

Our estimate of the total biomass of adult seabirds in the Ross Sea during late December is 39.51 kg/km^2 (Table 16). Chicks and recent fledglings of Emperor Penguins and chicks of other species are estimated to contribute an additional 4.96 kg/km^2 (Table 17). This gives a total biomass of birds deriving resources from the Ross Sea of 44.47 kg/km^2 during early summer. The figure is much

TABLE 17
NUMBERS AND BIOMASS OF SEABIRD CHICKS AT ROSS SEA BREEDING LOCALITIES DURING LATE DECEMBER AND EARLY JANUARY

Species	No. breeding pairs	No. chicks[a]	Chick weights (kg)[b]	Biomass (kg/km^2)
Emperor Penguin	106,155	37,154	20.00	1.24
Adélie Penguin	759,200	911,040	2.00	3.05
Antarctic Petrel	1,960,500	1,568,400	0.22	0.58
Snow Petrel	610,700	488,560	0.08	0.07
Wilson's Storm-Petrel	128,000	102,400	0.01	0.01
South Polar Skua	6,141	4,913	0.40	0.01

[a] Based on 35% survival to fledging for Emperors (see Todd 1980 and references therein), 1.2 chicks still alive per breeding pair of Adélies, and 0.8 chicks still alive for breeding pairs of other species as of the first week of January.

[b] Estimated weight in the first week of January, by approximating chick size relative to adult size at that time [see Table 16 for adult weights; see also growth studies by Prévost (1961), Taylor and Roberts (1962), Le Morvan et al. (1967), and Mougin (1968)].

higher than Laws' (1977) estimate of 25.0 kg/km^2. He used a more indirect method of calculation in which the feeding range of breeding penguins was important. Had he used the newly revised, more accurate estimate of Adélie Penguin feeding range that we present in this report, his biomass estimate would have doubled, and would be more similar to our estimate.

Laws (1977) proposed that his estimate of 25 kg/km^2 represented the annual maximal bird concentration; he also proposed a decrease to about 4 kg/km^2 in winter. We believe, however, that our late December estimate of biomass (44 kg/km^2) is not representative of the period when birds are most concentrated in the Ross Sea region. Rather, a number of factors should combine to increase bird densities later, say in February and March. First, by that time fledglings of most species have gone to sea; second, adults have left breeding colonies and most, having a strong tendency to associate closely with or near pack ice, concentrate in the vicinity of the ice pack; and third, the ice pack is at its minimum area in February–March. Thus, in the few areas of residual pack ice, bird biomass is probably several times greater than the December estimate. Since three or four species of abundant pack ice seals (Gilbert and Erickson 1977), as well as some whales, also concentrate in the areas of residual ice, fall may be the period when birds and mammals exert maximal pressure on marine resources in pack ice areas. Whether or not that pressure is significant depends on food availability in late February and March. The fact that baleen whales reach peak numbers in the Antarctic during the period January through April (Mackintosh and Brown 1956) may indicate that food availability is at its maximum then *or,* that the whales may be responding to the amount of open water which also is maximal at that time (in effect indirectly increasing the availability of food to whales). Nevertheless, Laws (1960) hypothesized that food was limiting for whales during summer, as evidenced by the geographic and temporal segregation of whales by size and breeding status. According to Marr (1962), that part of the euphausiid population available to avian and mammalian predators reaches its annual maximum midway through summer (January–February), and slightly later in the more southerly Ross Sea area. By March, abundance begins to decline rapdily as adults, spent in spawning, die, and others are cropped by predators.

If food supply is limiting to Antarctic bird populations, then the important question is, at what season? Several points raised earlier indicate that food supply reaches a maximum during late summer, but bird and pinniped populations may be at that time disproportionately concentrated relative to overall food availability by the limited extent of the ice pack. On the other hand, by fall, when the area of pack ice begins to increase allowing birds and pinnipeds to disperse (assuming that prey are also dispersed), the size of the krill (euphausiid) population—which is the foundation of the food web–has been reduced significantly. Most whales leave the Antarctic then, but pinnipeds and the vast majority of high latitude birds remain (except the storm-petrels, which are relatively insignificant ecologically). Evidence presented by Ainley et al. (1983) indicates that the critical period for Adélie Penguin survival occurs sometime between February and October, but that does not sufficiently narrow the period in question. Because Antarctic Petrels are restricted rather narrowly to waters between −2.5 to 2.0°C from December to April (Kock and Reinsch 1978; this study) but disperse to occupy waters of −2.5 to 4.0°C during July to September (Szijj 1967), food availability may be less during the latter period. The ice pack, at its maximal extent then, may further reduce the availability of food to birds. A similar pattern of expanding habitat use during winter is evident for the Southern Fulmar and Cape Petrel (Mougin 1975: fig. 40). The extremely rapid molt of Southern Fulmars, Antarctic Petrels, Snow Petrels, and Arctic Terns, during which they become almost flightless (Bierman and Voous 1950; Parmelee 1977), is testimony to a reliable food source during February. In addition, the rapid molt in these birds may be an adaptation "anticipating" the low availability of food later in the fall or in the winter.

This discussion, which certainly contains much conjecture, leads to the question of interest to many Antarctic ecologists, as to whether cropping of krill by whales during summer limits Antarctic bird populations. For many researchers, this has been a working assumption (e.g., Sladen 1964; Conroy 1975; Laws 1977; Trivelpiece and Volkman 1979). Important factors that should be considered, before we restrict ourselves to that hypothesis, however, are the degree to which food availability for birds during winter is affected by pack ice cover, and the degree to which it is affected by predators cropping krill during summer.

TROPHIC INTERACTIONS

It is generally agreed that krill (primarily *Euphausia superba*) is the mainstay of seabird diets in the Antarctic, a point summarized most recently by Laws (1977: 424–425). How this conclusion was reached is not clear, but it no doubt had its roots in the pioneering studies of Falla (1937) and Bierman and Voous (1950). Since then, except for studies of breeding birds at South Georgia (Croxall and Furse 1980; Croxall and Prince 1980a, b), of penguins at Cape Crozier (Emison 1968) and in the South Shetlands (Volkman et al. 1980), and of birds in the present study, little information on diet has been systematically collected. The results of our study indicate that fish and squid are more important than has generally been thought. A closer look at Falla (1937), Bierman and Voous (1950), and even Emison (1968), adds support for our findings.

One must realize, however, the difficulties in comparing different studies. Falla (1937) only presented data on frequency of occurrence by major prey type (euphausiid, other crustacea, squid, fish, etc.), and Bierman and Voous (1950) only presented data on frequency of occurrence and numerical importance of prey. More recent studies are much easier to compare, because, as advised by Ashmole and Ashmole (1967), they present seabird diets in three ways: frequency of occurrence of prey (i.e., the proportion of stomachs in which each prey occurs), and numerical and weight compositions of the diet. Standard data collection techniques, however, are still lacking, and some methods employed can critically alter results (c.f. Bradstreet 1980). In almost all studies, euphausiid eyes and squid lower beaks have been counted, but fish components have been analyzed in several different ways. Some researchers have counted whole crania, others, eye lenses, and others, otoliths. The latter may be the best method for counting fish for several reasons: (1) otoliths are more comparable to squid beaks and to euphausiid hard parts, especially eyes (Bierman and Voous 1950; our observation), in the length of time they remain in stomachs; (2) otoliths are more resistant to digestion than are fish crania and eye lenses; and (3) otoliths are species-specific in shape and can also provide a good estimate of fish size and weight (e.g., Table 10). Unfortunately, many investigators preserve stomach samples in formalin, which readily dissolves otoliths but not euphausiid eyes or squid beaks. Thus, evidence of fishes in the gray mass characteristic of bird stomach contents has no doubt been overlooked or destroyed.

We compared the occurrence frequency of prey in seabird stomachs among Falla (1937), Bierman and Voous (1950), and the present study, for the five species of birds common to the three studies and collected in relatively large numbers (Table 18). These studies were conducted in the South Indian Ocean in the early 1930's (Falla), in the eastern Weddell and southeastern Scotia Seas in the late 1940's (Bierman and Voous), and in the Ross Sea in the late 1970's (this study; Fig. 3). The sites, thus, are separated widely by longitude, but all lie in Antarctic seas of high latitude. Results of the three studies agree closely and can be summarized as follows. Euphausiids were eaten frequently by the Antarctic Petrel, squid by the Southern Fulmar and Cape Petrel, euphausiids and squid equally by the Wilson's Storm-Petrel (with other crustacea fairly close), and fish frequently by the Snow Petrel. The few differences in results among these studies were as follows. In the southern Indian Ocean (Falla 1937), Southern Fulmars and Cape Petrels ate no euphausiids, and Antarctic Petrels ate other crustacea species with greater frequency than the results of the other two studies showed. In the eastern Weddell and southern Scotia Seas (Bierman and Voous 1950), Snow Petrels ate squid and fish more frequently than elsewhere, and in the Ross Sea (present study) Wilson's Storm-Petrels ate euphausiids more frequently than at the other localities. In some cases, small sample sizes may account for these differences.

A comparison of diet compositions of four species was also possible based on data from Bierman and Voous (1950) and the present study. Applying weight data from the present study to numerical abundance, and assuming approximate constancy in size of prey eaten (one study to the next), we compared diet compositions based on both the average number and average weight of each prey type per stomach (percent of each prey). These comparisons also established agreement in results (Table 19). Based on number, euphausiids were overwhelmingly the predominant prey of three Antarctic seabirds (Southern Fulmar, Antarctic and Snow Petrels), and undoubtedly these were the type of results that led to the

TABLE 18

FREQUENCY OF OCCURRENCE OF PREY IN THE STOMACHS OF FIVE SEABIRD SPECIES COLLECTED AT SEA: A COMPARISON OF THREE STUDIES[a]

	Sample[b]	Falla (1937)	Bierman and Voous (1950)	This study	Weighted $\bar{X}$ percent
Southern Fulmar	n	8	10	13	
	E	0	50	69	45
	C	38	30	8	23
	S	50	100	100	87
	F	13	20	0	10
	O	13	20	0	10
Antarctic Petrel	n	14	28	39	
	E	50	64	77	68
	C	43	14	8	14
	S	43	46	46	46
	F	21	36	41	36
	O	14	29	5	15
Cape Petrel	n	3	17	4	
	E	0	35	100	42
	C	0	6	0	4
	S	67	88	75	83
	F	0	24	0	17
	O	33	59	0	46
Snow Petrel	n	17	17	54	88
	E	71	35	59	57
	C	18	35	7	15
	S	35	65	24	34
	F	12	95	39	72
	O	12	12	0	5
Wilson's Storm-Petrel	n	7	2	28	37
	E	14	0	61	49
	C	20	50	29	30
	S	20	100	54	51
	F	0	0	7	5
	O	20	0	18	19

[a] Proportion (expressed as percent) of stomachs sampled in which each prey was present.

[b] n = number of bird stomachs sampled; E = euphausiid, C = other crustacea, S = squid, F = fish, O = other prey.

generally accepted conclusion that euphausiids are the primary component of bird diets in the Antarctic. Based on weight of prey, however, the importance of squid increased markedly, and the importance of euphausiids and fish became equal in the Southern Fulmar, Antarctic and Cape Petrels. Squid was probably not quite as important relative to the other prey as these results indicate because the use of squid beaks in stomach content analyses over-estimates squid consumption (see Methods). Nevertheless, these results indicate that squid and fish are major dietary components for these Antarctic seabirds, and that euphausiids are relatively less important than was generally thought earlier. Emison (1968) also pointed out the importance of fish to Antarctic seabirds, especially when the weight composition of diets is considered. The great discrepancy possible when conclusions about diet composition are drawn from numerical as opposed to weight data has been stressed by Bradstreet (1980) for Arctic seabirds.

TABLE 19

MEAN NUMBER AND MEAN TOTAL WEIGHT OF EACH PREY IN THE STOMACHS OF PETRELS COLLECTED AT SEA: A COMPARISON OF TWO STUDIES[a]

	Sample[b]	Bierman and Voous (1950)	This study	Weighted $\bar{X}^c$	$\bar{X}$ percent
Southern Fulmar	n	10	13	23	
	E	3.0/2.9	29.0/28.4	17.7/17.3	81/6
	S	3.5/232.0	4.7/311.6	4.2/277.0	19/94
	F	<0.1/0.4	0/0	0/0.2	0/<0.1
	Total	6.5/235.3	33.7/410.0	21.9/294.5	
Antarctic Petrel	n	28	39	67	
	E	5.4/5.3	11.1/10.9	8.7/8.6	85/9
	S	1.0/91.6	0.9/82.4	0.9/86.2	9/82
	F	0.2/1.4	0.8/5.6	0.6/3.8	6/9
	Total	6.6/98.3	12.8/98.9	10.2/98.6	
Cape Petrel	n	17	4	21	
	E	1.1/1.1	1.0/1.0	1.1/1.1	28/1
	S	3.2/105.6	0.8/26.4	2.7/90.5	69/97
	F	0.1/1.4	0/0	0.1/1.1	3/2
	Total	4.4/108.1	1.8/27.4	3.9/93.1	
Snow Petrel	n	17	54	71	
	E	0.4/0.4	6.8/6.7	5.3/5.2	60/10
	S	1.3/31.2	0.6/14.4	0.8/18.4	9/34
	F	7.4/82.9	1.3/19.6	2.8/30.9	31/57
	Total	9.1/114.5	8.7/35.7	8.9/54.6	

[a] Weights of prey, for both studies, were extrapolated from the average weight of items determined in the present study; the three center columns give the average number of prey/the average total weight of prey per stomach.

[b] n = number of bird stomachs sampled; E = euphausiid, S = squid, F = fish.

[c] Diet composition based on the weighted average of results from both studies.

[d] Percent contribution of prey to each bird's diet based on the weighted averages from the column to the left.

We, thus, have two different conclusions about the importance of various prey, but based on the nutritional (energy) value of prey, one is superior to the other. If we approximate the amount of energy required each day for each species and then convert those energy needs into wet weight of euphausiids, squid, or fish, it is obvious that euphausiids are a poor choice of food (Tables 9, 10, 20). For example, to sustain itself, an Antarctic Petrel would have to catch over 200 euphausiids, compared to only two squid or about 10 fish (Tables 9, 10, 20). Referring back to data on prey size and assuming that an Antarctic Petrel contact dipped or pursuit plunged (which are vigorous activities) for each prey item (a pretty safe assumption), it would obviously be advantageous for it to eat the larger prey on a catch-per-unit effort basis. However, because euphausiids are probably more available than fish or squid as prey, Antarctic seabirds may eat them more often than the more nutritious alternatives.

Another major conclusion of this study, then, is that squid and fish are important prey for most Ross Sea birds during summer (Table 8). The indirectly supporting results obtained by Falla (1937) and Bierman and Voous (1950), the two studies most similar in technique to this one, indicate that this conclusion can probably be applied to seabirds in other Antarctic seas of highest latitudes. A possible exception to this general conclusion is the Adélie Penguin which not only feeds heavily on euphausiids (Emison 1968; Volkman et al. 1980), but is anatomically adapted to catch small schooling prey as opposed to larger ones such as squid

TABLE 20

ESTIMATED WET WEIGHT OF EUPHAUSIIDS, SQUID, OR FISH NEEDED BY ANTARCTIC SEABIRDS TO MEET DAILY ENERGY REQUIREMENTS AT 0°C AMBIENT TEMPERATURE

Seabird species	Body wt. ± s.d. (g)[a]	Existence energy (kcal/day)[b]	Total energy (kcal/day)[c]	Wet wt. (g) food needed/day[d]			Max wt. (g) stomach contents[e]
				E	S	F	
Adélie Penguin	3876 ± 100 (34)	346.1	484.5	495	505	289	378
Light-mantled Sooty Albatross	2875 ± 60 (2)	295.4	413.6	422	431	246	21
Southern Giant Fulmar	3975 ± 46 (2)	350.4	490.6	501	511	292	30
Southern Fulmar	839 ± 48 (13)	153.5	214.9	219	224	128	70
Cape Petrel	454 ± 54 (4)	111.0	155.4	159	162	93	5
Antarctic Petrel	735 ± 100 (31)	143.6	201.0	205	209	120	35
Snow Petrel	272 ± 27 (39)	84.6	118.4	120	123	70	14
Antarctic Prion	150 ± 5 (3)	61.7	86.4	88	90	52	5
Mottled Petrel	385 ± 38 (3)	101.9	142.7	146	149	85	5
Wilson's Storm-Petrel	46 ± 4 (29)	33.0	46.2	47	48	28	3
South Polar Skua	1326 ± 139 (23)	196.0	274.4	280	286	163	60

[a] Data for Adélies are from Ainley and Emison (1972) for December; remainder from this study. Number of birds weighed is given in parentheses.

[b] Based on the equation $M = 4.337\ \mathrm{Wt.}^{0.53}$ (Kendeigh 1970); values comparable to those summarized by Croxall (1982).

[c] Wiens and Scott (1975) increased existence energy by 40% to allow for flight, swimming, etc. in seabirds; the figure, however, is a guess.

[d] E = euphausiids (4.9 kcal/g dry wt., 0.2 g dry to 1.0 g wet wt.), S = squid (4.8 kcal/g dry wt., 0.2 g dry to 1.0 g wet wt.), F = fish (5.6 kcal/g dry wt., 0.3 g dry to 1.0 g wet wt.; ratios based on references in Wiens and Scott (1975), but the resultant estimates of food requirements do not take into account differences in efficiency of digestion of different prey (thus, amounts required are underestimated, not necessarily equally for each food type).

[e] Data from this study; no stomach was entirely full; see Croxall and Prince 1980a: table 7.

and fish (Zusi 1975). Nevertheless, fish do at times comprise a significant portion of the Adélie's diet (Emison 1968). At lower latitudes, diets of the Chinstrap Penguin and crested penguins (*Eudyptes* spp.) are similar to that of the Adélie. The preponderance of squid and fish in the diets of the larger Gentoo, Emperor, and King Penguins is well known (Kooyman 1975; Zusi 1975).

Quite different from the diets of seabirds at high latitudes, it seems, are those of seabirds breeding at South Georgia Island, which is situated in the northern Scotia Sea, at the northern limits of the Antarctic. In fact, the marine avifauna of South Georgia (Croxall and Prince 1980a: table 3) and the northern Scotia Sea (Kock and Reinsch 1978) is largely Subantarctic. There is little overlap in species between South Georgia and higher latitude areas, and because of this, the diets only of the Cape Petrel and Wilson's Storm-Petrel can be compared among the various studies (actually the data in Croxall and Prince for these two species are from breeding birds at Signy Island, in the southern Scotia Sea). Based on weight, these two species ate euphausiids almost exclusively (!) while feeding chicks, which was also true of all other South Georgia species except the six largest ones: King Penguin, three albatrosses, and two giant fulmars. These data, however, were based on food regurgitated to chicks (no gizzard samples), and samples were preserved in formalin. Therefore, techniques and, perhaps, results are not closely comparable to those in the present study (nor to Falla 1937, nor Bierman and Voous 1950), but they do indicate the importance of euphausiids as prey of many seabirds, and not just the smaller penguins, in the Scotia Sea. The results of the South Georgia study are consistent with the fact that euphausiids, especially the large *Euphausia superba,* are far more abundant in the vicinity of South Georgia and in the Scotia Sea, in general, than elsewhere in the Antarctic (Marr 1962).

At high latitudes the Adélie Penguin is the only avian species that comes close to being a food "specialist." This is due to anatomical constraints (Zusi 1975) but ultimately is probably due to the Adélie's relatively limited ability to search for prey. Like all penguins, because of the high energetic cost of swimming and the time constraints of supplying food to chicks, the Adélie requires reliable food sources in the areas where it occurs and especially near where it nests (see also Boersma 1978; Crawford and Shelton 1978). Aerial species can cope with more patchily-occurring prey because they can search much more ocean, much more rapidly than can penguins (Ainley and Boekelheide 1984). Even the Emperor Penguin may be better off than the Adélie in searching for food, because it can dive to far greater depths than the Adélie (Kooyman 1975). Thus, much more of the water column and much more habitat is potentially available to it for exploitation. Adélies may feed primarily on euphausiids because they constitute the most reliably available shallow-depth prey in range of nesting sites. For less obvious reasons, nonbreeding Cape Petrels and Mottled Petrels seem to rely more heavily on squid, and South Polar Skuas, regardless of breeding status, more heavily on fish, than other birds of approximately similar size. Otherwise, within the same habitats and, more importantly, the same localities during summer, Antarctic seabirds have extremely similar diets (Tables 5–7, 11–13). When species segregate ecologically, it is by feeding method, the size of the largest prey, or microhabitat preference. Based on the broad overlap in diets, we suggest that food abundance may not be a limiting factor to high latitude Antarctic bird populations during summer. Further study is, of course, needed.

ACKNOWLEDGMENTS

We wish to thank the officers and crews of the USCG icebreakers *Northwind* (1976 and 1979), *Burton Island* (1976 and 1977), and *Glacier* (1978) for their indispensable assistance. United States Antarctic Research Program personnel from the National Science Foundation and Holmes and Narver, Inc., particularly A. F. Betzel and M. A. Lanyon, helped to coordinate our logistic needs. A. Amos, G. Divoky, and S. Jacobs provided assistance and guidance on various cruises; L. Karl designed software for our shipboard computer entry of census data and assisted in its analysis by computer. J. Fitch identified all otoliths, and P. Slattery identified crustacean prey. Squid beaks were identified by DGA at a squid identification workshop held at the Marine Biological Association Laboratory, Plymouth, England in June 1981; M. R. Clarke and M. J. Imber were particularly helpful in that effort. H. DeWitt provided unpublished regressions of otolith size against fish length and weight. S. Jacobs provided unpublished data on temperature/depth profiles along various cruise tracks. Through his detailed criticisms, and those of J. P. Croxall and M. S. Foster, the manuscript was improved considerably. O'B. Young and E. Tuomi helped immensely in the preparation of the manuscript.

This project was funded by the National Science Foundation, Division of Polar Programs, Grants DPP-7615358, DPP-7615358 A01, DPP-7820755, 7820755 A01, and DPP-7920796. DGA's attendance at the squid workshop was made possible by a travel grant from the National Academy of Sciences, Polar Research Board. This is Contribution No. 202 of the Point Reyes Bird Observatory.

SUMMARY

Seabirds were censused from icebreakers on six cruises in the Ross Sea and the adjacent South Pacific sectors of the Antarctic Ocean south of 60°S between 1976 and 1980. Birds were counted within 300 m of one forequarter of the ship when ship's speed exceeded six knots (max. 12 knots); censuses were conducted for one-half hour out of every hour when the ship was underway during daylight. Daylight was largely continuous. During early summer, 15 December to 4 January, we made 598 half-hour transects; during late summer, 16 January to 21 February, we made 264 transects. Bird density and biomass were calculated based on these census results. The number of birds in the Ross Sea was calculated for each species based on densities and the area of occurrence. Oceanographic measurements such as sea surface temperature and salinity, the thermal structure of the upper 400 m of water, and water clarity were made at regular, frequent intervals; ice conditions were recorded for each transect. Seabirds were collected at 14 localities to determine diet.

The most clearly defined bird community was associated with pack ice and adjacent open seas influenced strongly by the presence of the pack ice nearby. It was comprised of nine species and was dominated numerically by Antarctic Petrels (52%) and in biomass by Emperor and Adélie Penguins (82%). A second, less well defined community overlapping with the latter was also comprised of nine species and was associated with seas free of pack ice but with abundant icebergs. It was dominated by the Antarctic Petrel. The third community was comprised of 13 species having affinities with the Subantarctic. These birds generally occurred where seas were completely free of ice. It appeared that the Antarctic Convergence is not an avifaunal barrier to the extent previously believed. The presence or absence of ice in the sea influenced species' occurrences to a much greater degree.

Within the pack ice and iceberg zone communities, birds were not evenly distributed. Except for the Snow Petrel, entire populations, including immature nonbreeders, were contracted toward breeding sites in December (the egg-laying/hatching period), but by February populations had dispersed to occupy all available preferred habitat. Populations were also concentrated in areas where ocean productivity was high, especially along the Antarctic Slope Front. Only the Snow Petrel appeared to prefer pack ice of certain concentration over others, and this probably caused its population to be more dispersed than other species. For most pack ice seabirds, the presence of oceanographic fronts, which probably enhanced prey availability in the water column, was more important than ice concentration in determining their occurrence. Within the ice, some species, such as the Snow Petrel, exhibited a marked preference for lead or floe edges, while others, such as the Antarctic Petrel, tended to frequent the centers of leads and polynyas. Southern Fulmars and Mottled Petrels were closely associated with areas of iceberg concentration.

We calculated an overall avian biomass of 44.47 kg/km^2 in the Ross Sea during late summer. Few birds occurred in a large central area over the Ross Sea continental shelf where an intense phytoplankton bloom existed. Thus, actual biomass where birds occurred was double the above figure. We hypothesized that in the fall, seabirds are even more concentrated because the ice pack then reaches its annual minimum, and numbers of birds at sea are augmented by the addition of recently fledged individuals.

Diet overlapped extensively among species. By weight, squid and fish were the dominant prey in all species except the Adélie Penguin which came closest to being an euphausiid specialist. Squid dominated diets of other birds in oceanic habitats, and fish dominated diets in shelf waters. What little trophic segregation existed among species was accomplished through differences in feeding behavior, prey size, and feeding microhabitat.

We hypothesized that if food supply limits the population size of Antarctic seabirds, it most likely does so during winter when prey availability is reduced by maximum pack ice cover, and prey abundance is at its annual minimum.

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APPENDIX I

HABITATS AND LOCALITIES AND THE NUMBERS OF SEABIRDS COLLECTED AT EACH

Deep Ocean (depths >3000 m)

1. Open seas with scattered ice bergs at 66°37'S, 170°32'E (25 December 1977); Light-mantled Sooty Albatross (2), Southern Fulmar (7), Cape Petrel (1), Antarctic Petrel (1).
2. Open seas with scattered ice bergs at 68°41'S, 171°49'W (27 December 1979); Southern Fulmar (6), Cape Petrel (3), Antarctic Petrel (6), Antarctic Prion (3), Mottled Petrel (3).
3. Six oktas pack ice at 69°39'S, 171°09'E (26 December 1977); Snow Petrel (3).

Continental Slope (depths 600–3000 m)

4. Open seas at 75°22'S, 174°52'W (30 December 1979); Antarctic Petrel (12), Snow Petrel (2), Wilson's Storm-Petrel (7).
5. Open seas with scattered ice bergs at 73°59'S, 179°44'W (31 December 1979); Antarctic Petrel (7), Snow Petrel (8), Wilson's Storm-Petrel (3).
6. Four oktas pack ice at 71°32'S, 171°19'E (26 December 1977); Adélie Penguin (2).
7. Seven oktas pack ice near pack edge at 73°44'S, 172°18'E (6 January 1980); Giant Fulmar (1), Snow Petrel (8), Wilson's Storm-Petrel (17), Brown Skua (1), South Polar Skua (2).
8. Three oktas pack ice at 76°01'S, 166°17'W (30 December 1979); Giant Fulmar (1), Antarctic Petrel (13), Snow Petrel (12), Wilson's Storm-Petrel (1), South Polar Skua (1).

Continental Shelf (depths <600 m)

9. Five oktas pack ice near pack edge at 72°17'S, 172°07'E (27 December 1977); South Polar Skua (2).
10. Three oktas pack ice at 76°02'S, 166°20'E (8 January 1980); Adélie Penguin (3), South Polar Skua (5).
11. Five oktas pack ice near pack edge at 76°11'S, 169°11'E (29 December 1977); Snow Petrel (7), South Polar Skua (5).
12. Three oktas pack ice at 77°09'S, 166°13'E (29 December 1977); Snow Petrel (2).
13. Three oktas pack ice at 77°37'S, 165°49'E (13 February 1979); South Polar Skua (4).
14. Three oktas pack ice at 78°12'S, 174°02'W (17 February 1979); Snow Petrel (12), South Polar Skua (4).

APPENDIX II

LENGTHS (CM) OF *EUPHAUSIA SUPERBA* EATEN BY SEABIRDS AT VARIOUS DEEP OCEAN AND CONTINENTAL SLOPE LOCALITIES[a]

	Localities[b]								
Bird species	1	2	3	4	5	6	7[c]	8	1–8
Adélie Penguin						4.0 ± 0.3 3.3–4.7 (60)			4.0 ± 0.3 3.2–4.7 (60)
Light-mantled Sooty Albatross	3.9 ± 0.3 3.5–4.4 (16)								3.9 ± 0.3 3.5–4.4 (16)
Southern Fulmar	4.0 ± 0.4 3.2–4.7 (108)								4.0 ± 0.4 3.2–4.7 (108)
Cape Petrel	4.4 (1)								4.4 (1)
Antarctic Petrel	4.0 ± 0.4 3.2–4.4 (11)	3.8 (1)	3.5 ± 0.5 2.6–4.1 (7)	4.1 ± 0.3 3.5–4.7 (28)			3.4 ± 0.4 2.6–4.1 (36)		3.7 ± 0.4 2.6–4.7 (83)
Snow Petrel			4.0 ± 0.5 3.2–5.0 (12)	3.8	4.0 ± 0.2 3.5–4.4 (27)		3.9 ± 0.3 3.2–4.4 (26)	3.4 ± 0.3 2.6–4.4 (58)	3.7 ± 0.3 2.6–5.0 (124)
Mottled Petrel		4.4 (1)							4.4 (1)
Antarctic Prion		1.9 ± 0.3 1.4–2.3 (9)							1.9 ± 0.3[d] 1.4–2.3 (15)
Wilson's Storm-Petrel							3.5 ± 0.5 2.6–4.4 (14)	2.9 (1)	3.5 ± 0.5[e] 2.6–4.4 (15)

---

[a] Values for each avian species/locality cell are, in descending order, mean ± standard deviation, range, and sample of prey measured (in parentheses).

[b] Specific localities and habitats listed in Appendix I.

[c] Means in this column statistically different; $t = 3.17$, $P < .01$.

[d] Mean statistically different from all others in this column; $t = 8.66$, $P < .01$.

[e] Mean statistically different from means for Adélie Penguin, Light-mantled Sooty Albatross, and Southern Fulmar; $t = 2.0$, $P < .01$.

APPENDIX III

LENGTHS (CM) OF *EUPHAUSIA CRYSTALLOROPHIAS* EATEN BY SEABIRDS AT VARIOUS CONTINENTAL SHELF LOCALITIES[a]

Bird species	Localities[b]				
	9	10	11	14	9–14
Adélie Penguin		2.0 ± 0.4 1.4–2.9 (48)			2.0 ± 0.4 1.4–2.9 (48)
Snow Petrel			2.1 ± 0.4 1.4–2.6 (8)	2.0 (1)	2.1 ± 0.4 1.4–2.6 (9)
South Polar Skua	2.0 ± 0.4 1.4–2.6 (12)	2.0 (1)			2.0 ± 0.4 1.4–2.6 (13)

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[a] Values for each avian species/locality cell are, in descending order, mean ± standard deviation, range, and sample of prey measured (in parentheses).

[b] Specific localities and habitats listed in Appendix I.

APPENDIX IV

SIZE OF BEAKS OF SQUID EATEN BY SEABIRDS AT VARIOUS DEEP OCEAN AND CONTINENTAL SLOPE LOCALITIES[a]

Bird species	Localities							
	1	2	3	4	5	7	8	All
Squid species *Gonatus antarcticus*								
Southern Fulmar	5.3 ± 0.7 4.0–7.0 (12)	5.2 ± 0.5 4.3–5.8 (10)						5.2 ± 0.6[b] 4.0–7.0 (22)
Antarctic Petrel	7.0 (1)	5.1 ± 0.3 4.7–5.3 (3)		5.0 ± 0.0 (3)	5.0 ± 0.7 4.5–5.5 (2)		5.0 (1)	5.2 ± 0.7[d] 4.5–7.0 (10)
Snow Petrel						4.4 ± 2.2 2.8–6.0 (2)	4.0 ± 1.1 3.3–4.8 (2)	4.2 ± 1.5[b] 2.8–6.0 (4)
Mottled Petrel		3.5 ± 0.9 3.0–4.6 (3)						3.5 ± 0.9[c,d] 3.0–4.6 (3)
Skua						6.1 ± 0.0 (2)	4.5 (1)	5.6 ± 0.8[c] (4)[e]
Squid species *Psychroteuthis glacialis*								
Southern Giant Fulmar				2.9 (1)				2.9 (1)
Southern Fulmar	3.4 ± 0.6 2.5–4.4 (14)	3.5 ± 0.4 2.8–4.0 (10)						3.4 ± 0.5[f,g,k] 2.5–4.4 (24)
Cape Petrel	5.0 (1)							5.0 (1)
Antarctic Petrel		3.5 ± 0.5 2.8–4.0 (4)		5.2 ± 1.1 3.9–5.9 (3)	4.3 ± 1.2 3.2–5.9 (4)		5.0 ± 1.8 3.7–6.2 (2)	4.4 ± 1.2[f,i,j] 2.8–6.2 (13)

APPENDIX IV

CONTINUED

Bird species	Localities 1	2	3	4	5	7	8	All
Snow Petrel			3.2 (1)			6.0 ± 2.3 4.3–7.6 (2)	3.4 ± 1.6 1.9–5.0 (3)	4.0 ± 1.7[h] 1.9–7.6 (8)[l]
Mottled Petrel		1.9 ± 0.6 1.4–5.2 (15)						1.9 ± 0.6[g,h,i] 1.4–5.2 (15)
Wilson's Storm-Petrel				2.2 ± 1.1 1.5–3.0 (2)				2.2 ± 1.1[j,k] 1.5–3.0 (2)
Squid species *Galiteuthis glacialis*								
Southern Giant Fulmar							3.3 (1)	3.3 (1)
Southern Fulmar	3.4 ± 0.6 2.5–4.6 (12)	3.8 (1)						3.4 ± 0.6[m] 2.5–4.6 (13)
Cape Petrel		1.8 (1)						1.8 (1)
Antarctic Petrel				3.9 (1)				3.9 (1)
Mottled Petrel		2.5 ± 0.7 1.5–3.3 (5)						2.5 ± 0.7[m] 1.5–3.3 (5)

---

[a] For localities see Appendix I; data expressed here for each avian species/locality cell are, in descending order, mean length (mm) of the lower rostrum (LRL) of the beak ± standard deviation, range, and sample of beaks measured (in parentheses). In the "All" column, entries having similar superscripts (footnotes) were compared statistically.

[b] $t = 2.383$, $P < .05$.

[c] $t = 3.268$, $P < .05$.

[d] $t = 3.488$, $P < .01$.

[e] Sample includes one beak (LRL = 5.5 mm) from locality 9 (Appendix I).

[f] $t = 3.580$, $P < .01$.

[g] $t = 8.439$, $P < .01$.

[h] $t = 4.373$, $P < .01$.

[i] $t > 4.373$, $P < .01$.

[j] $t = 2.429$, $P < .05$.

[k] $t = 3.028$, $P < .01$.

[l] Sample includes one beak (LRL = 3.9 mm) from locality 12 (Appendix I) and one beak (LRL = 3.3 mm) from locality 14 (Appendix I).

[m] $t = 2.730$. $P < .05$.

APPENDIX V

SIZE OF OTOLITHS OF THE FISH, *PLEURAGRAMMA ANTARCTICUM*, EATEN BY SEABIRDS AT VARIOUS LOCALITIES[a]

Bird species	Localities									All
	2	4	5	7	8	11	12	13	14	
Antarctic Petrel		1.6 ± 0.3 1.0–2.0 (22)	1.7 ± 0.3 0.8–2.0 (15)		1.7 ± 0.5 1.4–2.2 (3)					1.6 ± 0.3^{b,c} 0.8–2.2 (40)
Snow Petrel				1.8 (1)	1.8 ± 0.0 (2)	1.4 ± 0.4^{d} 0.6–2.2 (39)	1.6 ± 0.4 0.6–2.0 (19)		1.4 ± 0.4 0.8–2.0 (38)	1.4 ± 0.4^{c,e} 0.6–2.2 (94)
Mottled Petrel	1.8 (1)									1.8 (1)
South Polar Skua				2.0 ± 0.2 1.8–2.4 (4)		1.9 ± 0.2^{d} 1.6–2.2 (31)		1.8 ± 0.4 1.2–2.0 (5)	1.4 ± 0.8 0.8–2.2 (5)	1.9 ± 0.3^{b,e} 1.2–2.4 (45)

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[a] Specific localities listed in Appendix I; data expressed here for each avian species/locality cell are, in descending order, mean largest diameter (mm) of otoliths ± standard deviation, range, and sample of otoliths measured (in parentheses). In the "All" column, entries having the same superscript (footnote) were compared statistically.

[b] $t = 4.602$, $P < .01$.

[c] $t = 2.838$, $P < .01$.

[d] $t = 6.351$, $P < .01$.

[e] $t = 7.438$, $P < .01$.

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