

DENSITIES OF ANTARCTIC SEABIRDS AT SEA AND THE PRESENCE OF THE KRILL *EUPHAUSIA SUPERBA*

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ABSTRACT.—The antarctic krill *Euphausia superba* forms abundant, well-organized schools in the waters off the Antarctic Peninsula. Mean avian density is 2.6 times greater in waters where krill schools are present than in waters without krill schools. Seabird density is a good predictor of the presence of krill. Seabird density did not correlate with krill density or krill school depth. Disoriented krill routinely were observed swimming near the surface above submerged schools, providing potential prey for surface-feeding birds.

Responses of seabird species to the distribution of krill schools varied. The small to medium-size procellariiform species were the best indicators of krill schools; large procellariiforms and coastal species were poor indicators. *Pygoscelis* penguins occurred at high densities only in the presence of krill schools. These responses are consistent with the constraints imposed by the metabolic requirements and reproductive strategies of each of these groups.

Krill schools were detected near the sea surface throughout the day. Correlations between seabird density and the presence of krill during daylight hours suggest that diurnal foraging is important to the seabirds of this region. *Received 19 December 1983, accepted 4 December 1984.*

RELATIVELY little is known about the factors influencing the distribution of seabirds in the marine habitat. The past decade has produced a number of studies attempting to correlate patterns of avian abundance and distribution with physical features of the ocean such as currents and convergences, water masses, and temperature-salinity fronts, features presumed to influence the distribution of marine prey. Many such studies have demonstrated broad-scale correlations between these oceanographic features and bird distributions or species assemblages (e.g. Jehl 1973, 1974; Shuntov 1974; Brown et al. 1975; Pocklington 1979; Griffiths et al. 1982; Schneider 1982; Gould 1983).

Recently, however, Ainley and Boekelheide (1983) concluded that the major, classical oceanographic boundaries in the south Pacific do not act as effective distributional barriers for seabirds inhabiting the region. Furthermore, where associations between seabirds and large-scale oceanographic features have been tested statistically, explained variances of seabird numbers have been low (Abrams and Griffiths 1981). Hunt and Schneider (in press) suggest that "fine-scale" patchiness in bird distribution can effectively mask differences at larger scales, e.g. differences between water masses. Patchiness at scales of meters to hundreds of meters is evident for planktonic organisms that sea-

birds depend on directly or indirectly for food (Haurly et al. 1978). These observations suggest that relatively small-scale phenomena, such as local concentrations of prey, may be of major importance in determining the patterns of seabird distribution within the broad limits set by features of the physical ocean.

It is well known that seabirds sometimes aggregate over concentrations of prey (see Brown 1980 for a review). But because the number of potential prey species is often quite large and the movements of prey within the open ocean are complex and difficult to monitor, systematic studies of the influence of prey distribution upon the density and distribution of seabirds in pelagic environments are lacking.

The present study documents the influence of a principal prey species, the krill *Euphausia superba*, on the densities of seabirds in waters off the Antarctic Peninsula. The overwhelming dominance of *E. superba* in this ecosystem and its habit of forming large, well-defined schools (Hamner et al. 1983) facilitated the location of this abundant prey organism by SONAR, providing a uniquely simple system in which distributions of seabirds and their prey could be monitored simultaneously. The relationships between krill distribution, school size, and school depth and the densities of the seabirds comprising this community are examined.

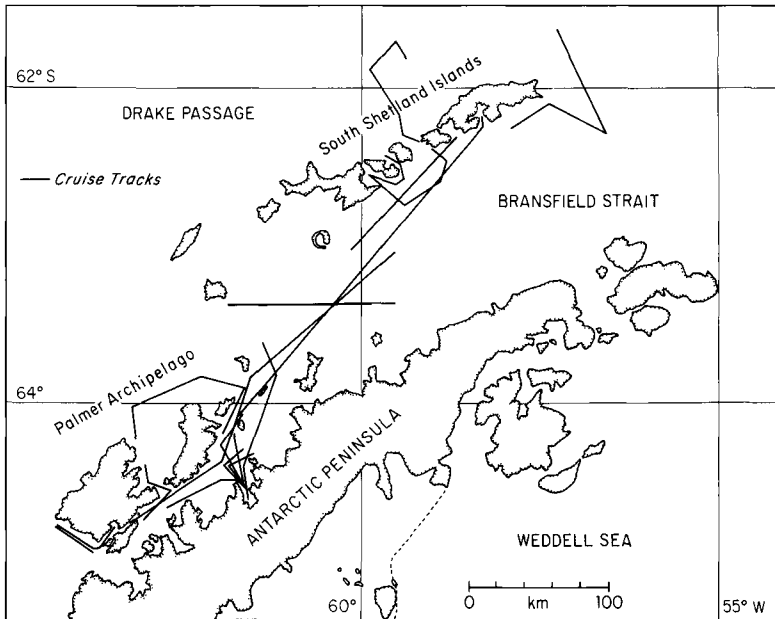


Fig. 1. Map of the northern Antarctic Peninsula and surrounding waters indicating cruise tracks followed during the study.

METHODS

Seabird densities were determined by performing strip transects from the R.V. 'Hero' during 3 cruises between 12 January and 12 February 1983. I performed 226 10-min transects (48 from 12-17 January, 83 from 25-30 January, and 125 from 2-12 February) in the waters to the northwest of the Antarctic Peninsula, including the Bransfield Strait, Gerlache Strait, and Drake Passage (Fig. 1). One 10-min transect was carried out during each 30-min period that the ship was in transit and visibility permitted. Only birds seen within a quadrat defined by a line out from the ship's bow and a second, perpendicular line off the beam out to 300 m were counted. The area of each transect was calculated using ship's velocity, time of travel, and the width of the transect strip, and bird numbers were converted to units of density.

Many antarctic seabirds, including most procellariiforms, skuas, and larids, are inveterate ship followers. Because seabird numbers typically were low, ship followers usually could be recognized and monitored throughout the 10-min census; such individuals were not recorded. However, the presence of a ship may attract such species into the transect limits even if they do not follow, thereby increasing their density artificially. On the other hand, penguins can be quite difficult to detect during a shipboard census, particularly in rough seas, because they float low in the water and may dive upon approach. Thus, density estimates for volant seabirds may be somewhat

elevated and those for penguins somewhat depressed, relative to the true levels.

Euphausiid distribution was monitored via a continuously reading SONAR echosounder that produced discrete, easily recognizable tracings as the ship passed over krill schools. The identity of the organisms producing these tracings was verified by netting within the schools; over 99% of the tracings were attributable to *E. superba*. Several problems are associated with the use of hydroacoustics to monitor prey. First, because the SONAR system used was vertically oriented, only schools directly under the ship were detected. Second, because the transducer was mounted in the ship's hull, the upper 3 m of the water column (the ship's mean draft) were not monitored. Finally, vertical SONAR does not provide an absolute measure of a school's size because it bisects it only in a single plane. However, the frequency with which distinct krill schools appear on the echosounder, as well as their duration, provides an index of the general abundance of krill in the waters covered during a transect. Each transect was assigned a ranking (0-10) corresponding to this apparent prey abundance. A value for krill depth corresponding to the shallowest school detected also was assigned to each transect.

Finally, SCUBA and blue-water diving techniques (Hamner 1975) were used to observe shape and behavioral characteristics of several selected, shallow (10-30 m) krill schools located by SONAR.

TABLE 1. Comparison of avian density and biomass for waters with and without *Euphausia superba* schools.

	Transects without krill schools	Transects with krill schools	Factorial increase	P^a
Mean density (birds/km ²)	8.8	22.8	2.6	<0.001
Mean biomass (kg/km ²)	23.2	45.4	2.0	<0.001
n	56	167		

^a Significance of the difference between means.

RESULTS

Krill schools were present in 167 (75%) of the 226 transects. Mean avian density was 2.6 times greater in waters where krill schools were present, and mean avian biomass was double that found in waters without krill schools (Table 1). The difference between these means was significant in each case (t -test, $P < 0.001$).

When seabird density (all species combined, rounded to the nearest bird/km²) was plotted against the probability that krill schools were present (i.e. the fraction of transects with a given bird density in which krill schools were present), a regular, increasing trend was obvious (Fig. 2). Of the transects where avian density was 1–10 birds/km², 68% also had krill; of those transects with an avian density of 31–40 birds/km², 92% had krill schools. Where observed seabird density was greater than 40 birds/km², krill schools were always present. This suggests that seabirds are effectively concentrating their activities in response to *E. superba*, and that seabird density is a good predictor of krill's presence.

Krill abundance did not correlate with seabird density (Spearman's rank correlation, $P > 0.05$). The presence of large or numerous krill schools in a transect did not necessarily produce high densities of seabirds. Thus, while seabird aggregations are associated with krill schools, waters supporting the highest krill densities do not necessarily support the greatest avian densities. Similarly, no correlation between school depth and bird density was detected (Spearman's rank correlation, $P > 0.05$). Shallow schools did not consistently support higher concentrations of birds than did deeper schools, despite the predominance of surface-feeding birds in most transects.

Of the ten avian species recorded frequently enough to permit statistical analysis, two species, the Southern Fulmar (*Fulmarus glacialis*) and Wilson's Storm-Petrel (*Oceanites*

oceanicus), were found in transects with krill significantly more often than expected by chance alone (Chi-square paired test of association, $P < 0.05$ for each). Both regularly feed on krill during the breeding season. One species, the South Polar Skua (*Catharacta maccornicki*), showed a significant negative association with krill schools ($P < 0.05$). These skuas regularly include krill in their summer diet, but are restricted primarily to coastal waters during this season. The Black-browed Albatross (*Diomedea melanophris*) tended toward a negative association with krill schools, but this tendency was not statistically significant ($P = 0.07$).

Densities of individual species within the seabird community varied in relation to the distribution of krill schools. Three species, Southern Fulmar, Cape Petrel (*Daption capense*), and Wilson's Storm-Petrel, showed clear positive correlations between their densities and the probability that krill were present (Fig. 3). These species are all small to medium-size procellariiforms, pelagic foragers, and take much krill during the breeding season (Table 2). No clear correlation was detected for three other surface-feeding species, Black-browed Albatross, Southern Giant-Petrel (*Macronectes giganteus*), and South Polar Skua (Fig. 4). Although these species all take krill, it is a less important component of the diet than for the Cape Petrel and Wilson's Storm-Petrel.

Because the three common penguin species of the Antarctic Peninsula [Adélie Penguin (*Pygoscelis adeliae*), Chinstrap Penguin (*P. antarctica*), and Gentoo Penguin (*P. papua*)] are often impossible to distinguish at sea, all penguin data were pooled for analysis. While their foraging ranges and specific diets vary (Volkman et al. 1980), this pooling may be justified ecologically because they sometimes travel and forage together in mixed flocks (pers. obs.), and all have diets comprised of 80–99% krill. At low

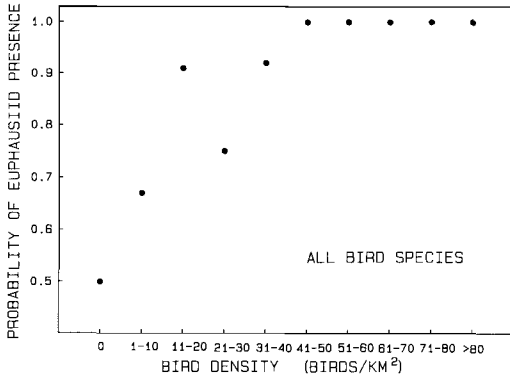


Fig. 2. The probability that *Euphausia superba* schools are present in a given transect as a function of seabird density. Data for all bird species are pooled; values are rounded to the nearest whole bird/km².

penguin densities, no clear correlation was seen between density and the probability that krill schools were present. However, at high penguin densities (>30 penguins/km²) krill schools were always present (Fig. 5). This relationship held whether all penguins observed (foraging, porpoising, and loafing birds) were considered or just those seen making foraging dives.

The following species were observed too infrequently to permit a meaningful plot of density vs. the probability of krill presence: Wandering Albatross (*Diomedea exulans*), Grey-headed Albatross (*D. chrysostoma*), Light-mantled Albatross (*Phoebastria palpebrata*), Snow Petrel (*Pagodroma nivea*), Dove Prion (*Pachyptila desolata*), Blue Petrel (*Halobaena caerulea*), Black-bellied Storm-Petrel (*Fregatta tropica*), Blue-eyed Cormorant (*Phalacrocorax atriceps*), Great Skua (*Catharacta skua lonnbergi*), Southern Black-backed Gull (*Larus dominicanus*), and Antarctic Tern (*Sterna vittata*).

DISCUSSION

SEABIRD DENSITY AND THE PRESENCE OF KRILL

The clear and substantial increase in mean avian density associated with the presence of krill schools lends support to the idea that local phenomena, such as concentrations of prey, strongly influence patterns of avian distribution observed at sea. Three hypotheses could account for the observed correlations: (1) seabirds are locating and preying on krill, thereby

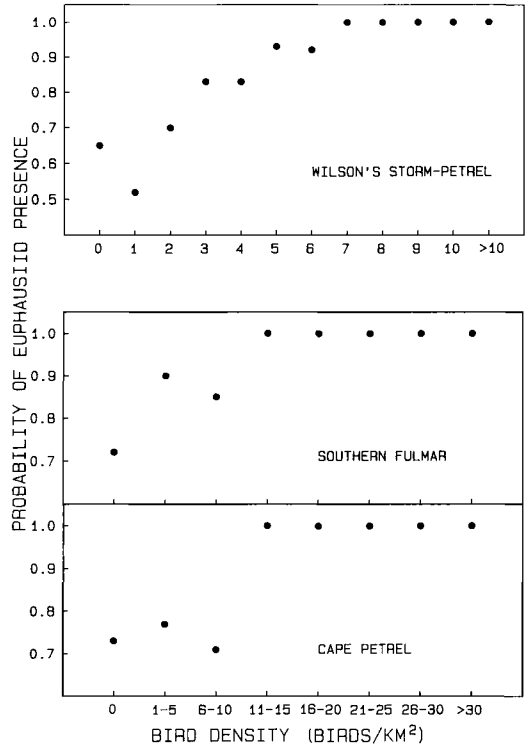


Fig. 3. The probability that *Euphausia superba* schools are present as a function of avian density for three small to medium-size procellariiforms.

concentrating their foraging activities in waters where krill schools occur; (2) seabirds are foraging on nonkrill prey whose distribution is correlated with the distribution of krill; and (3) seabirds and krill are responding similarly but independently to some feature of the environment. While these need not be mutually exclusive alternatives, each will be discussed in turn.

The first hypothesis is supported by the fact that most of the seabird species in the study region (75%) regularly include *E. superba* in their diets, sometimes to the near exclusion of other prey (Table 2). Only 3 of the 20 species recorded during the study take negligible amounts of krill. These species, the Blue-eyed Cormorant, Wandering Albatross, and Great Skua, seldom were recorded during transects, because they are either uncommon in the region (albatross) or restricted to coasts (cormorant and skua). Thus, the majority of birds contributing to density and biomass values were krill feeders. Similarly, Ainley et al. (1984) found euphausiids to be numerically the most important prey for the

TABLE 2. The importance of *Euphausia superba* in the diets of seabirds of the Antarctic Peninsula region.

	Breeding range ^a	Breeding stage ^b	% krill in diet (by wt) ^c	% diet samples with krill ^c	Source of diet data ^d
Species eating mostly krill					
Adélie Penguin	T	C	99.6	100	1
Chinstrap Penguin	T	C	99.6	100	1
Gentoo Penguin	SS, PA, MP	C	85	100 (?)	1
Cape Petrel	SS, PA	C	85	98	2, 3
Snow Petrel	SS, MP	C, I	80	—	2
Dove Prion	NB	—	57	87	4
Blue Petrel	NB	—	75	—	4
Wilson's Storm-Petrel	T	I, C	85	95	5
Species regularly taking krill in lesser amounts					
Black-browed Albatross	NB	—	41	70–92	6
Grey-headed Albatross	NB	—	17	53–69	6
Light-mantled Albatross	NB	—	36	—	7
Southern Giant-Petrel	SS, PA	C	1–21	3–65	8
Species regularly taking krill, importance unknown					
Southern Fulmar	SS, NP	I, C	—	50	9
South Polar Skua	SS, PA, MP	I, C	—	—	10
Southern Black-backed Gull	T	C	—	—	5
Antarctic Tern	T	I, C	—	67	11
Species taking little or no krill					
Blue-eyed Cormorant	T	C	n	5	12
Wandering Albatross	NB	—	<10	—	13
Great Skua	T	I, C	n	—	14

^a Data from Watson et al. (1971). SS = South Shetlands, PA = Palmer Archipelago, NP = northern Antarctic Peninsula, MP = middle Antarctic Peninsula, T = throughout study region, NB = not breeding in study region.

^b Breeding stage of Antarctic Peninsula seabirds during the study period. C = chick rearing, I = incubation.

^c Data derived from samples regurgitated by chicks or adults returning to feed chicks, except in the cases of Southern Fulmar and Antarctic Tern where data refer to stomach contents of birds collected at sea. Dietary information for the penguins, cormorant, storm-petrel, and charadriiform species come from the Antarctic Peninsula; values for the remaining species are from the Scotia Sea (South Georgia or South Orkneys). n = negligible quantities.

^d 1 = Volkman et al. (1980), 2 = Croxall and Prince (1981), 3 = Beck (1969), 4 = Prince (1980a), 5 = Obst (unpubl. data), 6 = Prince (1980b), 7 = Thomas (1982), 8 = Hunter (1983), 9 = Bierman and Voous (1950), 10 = P. Pietz (unpubl. dissertation), 11 = D. Parmelee (unpubl. data), 12 = Schlatter and Moreno (1976), 13 = Croxall and Prince (1980), 14 = Trivelpiece and Volkman (1982).

majority of seabird species in the Ross Sea. However, they estimated that on the basis of weight, squid and fish are much more important than studies from western Antarctica would indicate (Croxall and Prince 1980, 1981). The probable explanation for this difference is the far greater abundance of krill in the Scotia Sea–Antarctic Peninsula region compared with other Antarctic regions (Marr 1962).

Many instances of birds feeding on krill were witnessed during transects. The most impressive event was a mixed-species flock of over 700 birds, including Wilson's Storm-Petrels, Cape Petrels, Southern Fulmars, Southern Giant-Petrels, and Black-bellied Storm-Petrels, feeding on a small school of krill visible at the

surface. Thus, it seems likely that the density of seabirds is correlated with the presence of krill schools.

However, the hypothesis that seabirds aggregate over waters with krill schools to exploit larger, nonkrill prey cannot be dismissed. Many seabirds' prey species, such as squids and fishes, are known to feed on krill (Mauchline 1980). Many of these (e.g. cephalopods and myctophid fishes) are probably most available during the darkest hours, and these interactions would be unlikely to influence the diurnal distributional patterns recorded in this study. Some krill-eating fishes do occur in surface waters during the day, and piscivorous birds prey on them. For example, in March 1984

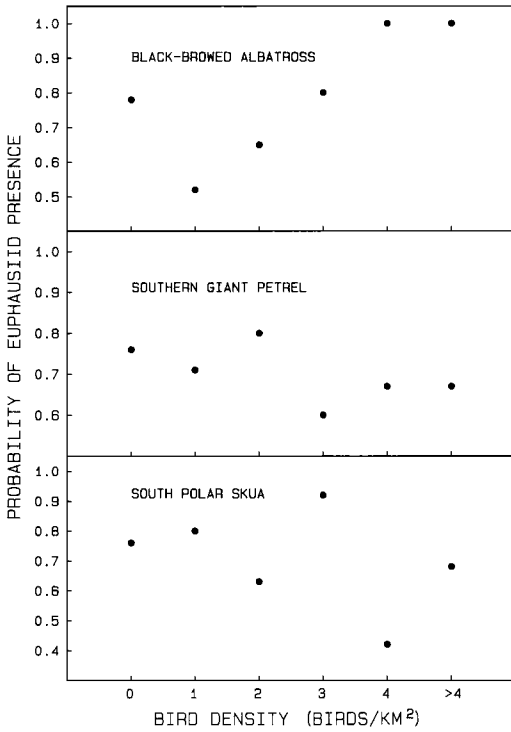


Fig. 4. The probability that *Euphausia superba* schools are present as a function of avian density in two large procellariiforms and the South Polar Skua.

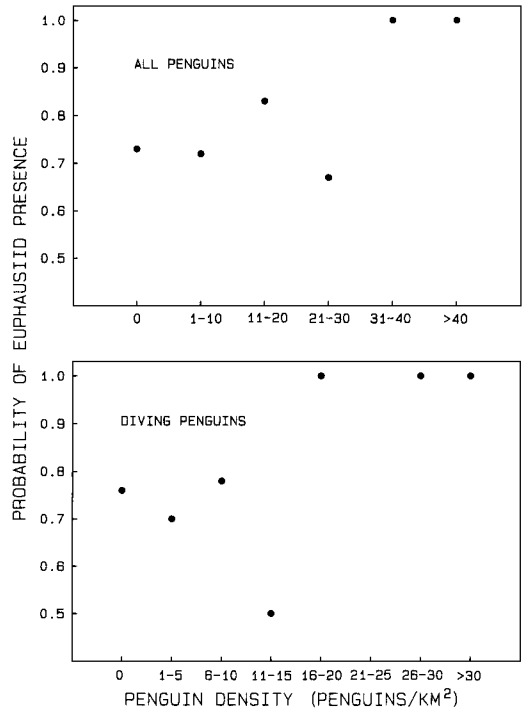


Fig. 5. The probability that *Euphausia superba* schools are present as a function of *Pygoscelis* penguin density. Data for all penguins observed and for feeding penguins only are plotted separately.

I observed large numbers of South Polar Skuas and Southern Black-backed Gulls catching silvery fish, probably *Pleuragramma antarcticum*, amid a large surface krill school. Although the birds were associated with the krill school, they ignored the abundant euphausiids and clearly selected the fish as prey. *Pleuragramma* eats mostly krill (DeWitt and Hopkins 1977), and it is reasonable that its local distribution would be correlated with prey availability.

Finally, the correlation between seabird density and the presence of krill may result from an independent tendency of both to occur in waters of a particular physical/chemical type and not from any trophic interactions. No water temperature or salinity data were gathered during the study, but the dietary information discussed above argues strongly against this hypothesis. Krill schools and bird aggregations were broadly distributed throughout the region covered, rather than being restricted to waters of particular depth, distance from shore, etc. While the factors governing the distribution of *E. superba* are poorly understood, it has

become increasingly clear that these crustaceans are far from the passive, planktonic organisms they once were regarded to be. Krill "swarms" are in fact highly organized schools that orient and travel in set directions, often against the flow of prevailing currents (Kanda et al. 1982). Their behavior includes a set of complex, antipredatory patterns (Hamner et al. 1983).

SEABIRD DENSITY AND KRILL AVAILABILITY

No correlation was found between seabird density and the relative abundance or depth of krill schools. In view of the limitations of the hull-mounted, vertically oriented SONAR, it is difficult to know whether this lack of correlation accurately reflects nature or is merely a methodological artifact. The lack of correlation between seabird density and krill abundance may simply stem from the fact that seabirds are not omniscient. A bird aggregation may begin

when a few birds discover a krill school and grow via social facilitation with a dynamic of its own, regardless of whether a larger school is present nearby.

The lack of correlation between seabird numbers and krill depth also may be a result of the inability to detect schools in the upper 3 m of ocean, the region of particular importance to volant seabirds. However, this limitation cannot account for the strong correlations between the densities of some surface-feeding seabirds and submerged krill schools. Characteristically, krill schools observed while SCUBA diving were centered between 10 and 30 m depth. However, divers regularly encountered individual euphausiids swimming apart from the well-organized school between its upper edge and the ocean surface. These individuals often could be seen from the ship when it was directly over a school. A small fraction of these individuals were whitish and opaque, probably due to disease or damage. The majority appeared normal but were disoriented with respect to the swimming direction of the school. These damaged and disoriented individuals must provide an easy food source for surface-feeding and shallow-diving seabirds, even when the main school is submerged. Thus, the presence of these individuals may account for the increased density of surface-feeding birds associated with submerged krill schools. Isolated euphausiids were rarely encountered during SCUBA dives away from the proximity of schools.

INTERSPECIFIC DIFFERENCES

While the density of seabirds generally correlates with the presence of krill, individual species vary in their responses. The factors contributing to these differences are doubtlessly many and complex, but the specific responses are consistent with aspects of the foraging and reproductive ecology of the various seabird species.

Small-to-medium Procellariiformes.—The best avian indicators of the presence of krill are the Southern Fulmar, Cape Petrel, and Wilson's Storm-Petrel. These are all highly pelagic foragers. Foraging trips may last from 2 to 4 days in the storm-petrel (Beck and Brown 1972; pers. obs.) and up to several days in the other species (Pinder 1966). This mobility permits the foraging bird to search out and exploit waters with

available patches of krill. An individual euphausiid represents a substantial package of energy relative to the overall daily energy budget in these moderate-size species (see below). Although these species are opportunistic feeders and will take a wide variety of food when available, during the antarctic summer they feed heavily upon *E. superba*.

Large Procellariiformes.—The two large procellariiform species common in the study area, the Black-browed Albatross and Southern Giant-Petrel, were not good indicators of krill. Like the smaller procellariiforms, these species are highly pelagic and, owing to their larger size, have even greater fasting abilities. They may remain at sea for 1–3 weeks during the incubation phase of the reproductive cycle; adults of both species forage for 1–4 days while rearing chicks (Tickell and Pinder 1975, Hunter 1983).

These larger species must have much greater absolute daily energy requirements, such that an individual euphausiid represents a relatively minor input of energy. Allometric equations predicting daily energy expenditures of free-living birds (nonpasserines at 0°C, Kendeigh et al. 1977; Walsberg 1983) suggest that the energy requirements of a 4-kg albatross would be 10–15 times greater than that of a 40-g storm-petrel. Using the more conservative equation of Kendeigh et al. to predict daily energy requirements, and assuming an energy content for krill of 4.35 kJ/g wet weight (Clarke 1980) and an assimilation efficiency of 80% for both species, it would take 24 min for a storm-petrel to use the energy assimilable in 1 g of krill (2–4 adult euphausiids) but only 2.4 min for an albatross to use the same quantity. Thus, krill probably provides an attractive food source to large procellariiforms only when it is highly concentrated, as on those infrequent occasions when krill schools surface.

While speculative, this prediction agrees with the observed behavior of procellariiforms. Albatrosses and giant-petrels are adapted for sustained, soaring flight (Pennycuik 1982), and they appear to interrupt their progress to feed infrequently. On several occasions, however, groups of giant-petrels or Black-browed Albatrosses were observed sitting on the water scooping up beakfuls of krill from surface schools. Smaller petrels, on the other hand, fly low over the water, frequently picking or dipping at the surface, and they were observed to

feed on isolated euphausiids surfacing above krill schools as well as on surface schools themselves. The best foraging strategy for the Black-browed Albatross and Southern Giant-Petrel may be to stay on the wing and cover broad areas in search of concentrated prey, rather than to chase disoriented individual euphausiids associated with submerged schools. The albatrosses and giant-petrels appear to depend more heavily upon nonkrill prey than do their smaller relatives (Table 2). Ainley et al. (1984) discuss some advantages of feeding on squid and fish relative to krill for antarctic seabirds.

Coastal species.—Several species recorded during transects are primarily coastal in their distribution during the breeding season. These species undergo frequent incubation exchanges and consequently are limited in their potential foraging ranges. The potential foraging ranges of the four commonest breeding species at Palmer Station, located in the Palmer Archipelago, are presented in Table 3. Of the coastal species, only the South Polar Skua was observed frequently enough to permit analysis of the relationship between krill distribution and skua density. This species showed a negative association with krill, and its density was independent of the probability that krill were present. South Polar Skuas do include krill in their diets; however, the krill probably are taken opportunistically as schools move into waters near the bird colonies or are pirated from other species. Other coastal species, which take little krill, may conform to this opportunistic pattern.

Penguins.—High concentrations of penguins invariably were associated with krill schools, but the probability of schools being present did not increase steadily with penguin density throughout the range of densities observed. Foraging excursions in the *Pygoscelis* species typically last no longer than 12–24 h, depending upon the species (Volkman et al. 1983; pers. obs.). This, coupled with their inability to fly, effectively restricts them to waters near their rookeries. The potential foraging range of the Adélie Penguin at Palmer Station is a fraction of the potential ranges of the volant giant-petrel and storm-petrel, and is in fact more comparable to the restricted range of the South Polar Skua (Table 3). Unlike the procellariiform species, high penguin densities generally were encountered near major penguin colonies; 78% of the transects with penguin densities greater

TABLE 3. Potential foraging ranges of four seabird species of the Antarctic Peninsula region during the chick-rearing phase of reproduction.

Species	Traveling speed (km/h) ^a	Mean foraging-trip duration (h) ^b	Potential range (km) ^c
Adélie Penguin	11.2	11.7	65.3
Southern Giant-Petrel	39.2	23.9	469
Wilson's Storm-Petrel	24.5	60.8	744
South Polar Skua	48.4	~2.0	48.4

^a Adélie Penguin value is for birds porpoising to and from rookeries (Obst and Hamner in prep.), values for the two procellariiforms are ground speeds published in Pennycuik 1982, and value for the skua is from Young 1963.

^b All values are for adults feeding young chicks at Palmer Station in the Palmer Archipelago area. Data for penguin and procellariiforms are from unpublished field studies in 1983–1984 by B. Obst, G. Bartholomew, and K. Nagy. The skua estimate is from P. Pietz (pers. comm.).

^c Traveling velocity \times trip duration/2. This is the distance that would be achieved if 100% of the time away from the nest were spent traveling and the path taken to and from the nest were a straight line.

than 25 birds/km² were within 25 km of a large colony. Foraging behavior was observed in 33% of these transects.

It is tempting to speculate that the relationship between high penguin density and the presence of krill may be the result of a long-term process in which *Pygoscelis* colonies located near waters with dependable krill populations have flourished, while those away from such waters have not. Although the factors controlling patterns of krill distribution are not understood at present, regions of dependably high krill populations do exist. It would indeed be surprising if the geography of penguin breeding has not been influenced by this.

NOCTURNAL FORAGING AND VERTICAL MIGRATION

Imber (1973, 1976) argued that several subantarctic petrel species feed primarily at night, taking advantage of the nocturnal vertical migrations of bioluminescent prey toward the ocean surface. Similarly, Lishman and Croxall (1983) suggested that Chinstrap Penguins feed chiefly at night in shallow krill schools. Because all the transects during this study were performed during daylight, nocturnal forager

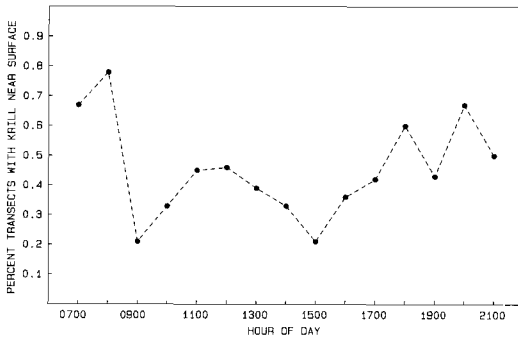


Fig. 6. The percentage of transects in which *Euphausia superba* schools were recorded within 3 m of the sea surface during each hour of the day.

densities were less likely to show correlations with krill distributions.

Euphausia superba is considered to be a vertically migrating species throughout its range (Mauchline 1980, Kalinowski and Witek 1980). However, B. H. Robison et al. (in prep.) found no evidence of a significant vertical migration in krill near the Antarctic Peninsula. I found krill schools throughout the day in the shallowest waters; roughly 42% of all transects had schools within 3 m of the surface. Shallow krill schools appeared to become somewhat less common toward midday but were detected at all hours (Fig. 6). Surface schools were observed during daylight on several occasions during the study. The periods of darkness varied from 3 h in early January to about 5 h in mid-February. The shortness of nights, the presence of krill at or near the surface throughout the day, and the interactions of birds and krill witnessed during daily transects suggest that nocturnal foraging may be less pervasive in seabirds in this region than in communities at lower latitudes. The routine presence of vertically migrating cephalopods and midwater fishes in the diets of many antarctic seabirds (Croxall and Prince 1980, Ainley et al. 1984) is evidence that nocturnal foraging occurs, and *E. superba* may be taken at night as well.

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LITERATURE CITED

- ABRAMS, R. W., & A. M. GRIFFITHS. 1981. Ecological structure of the pelagic seabird community in the Benguela Current region. *Marine Ecol. Prog. Ser.* 5: 269-277.
- AINLEY, D. G., & R. J. BOEKELHEIDE. 1983. An ecological comparison of oceanic seabird communities of the south Pacific Ocean. Pp. 2-23 in *Tropical seabird biology* (R. W. Shreiber, Ed.). *Studies Avian Biol.* No. 8.
- , E. F. O'CONNOR, & R. J. BOEKELHEIDE. 1983. The marine ecology of the birds in the Ross Sea, Antarctica. *Ornithol. Monogr.* 32.
- BECK, J. R. 1969. Food, moult and age of first breeding in the Cape Pigeon, *Daption capensis* Linnaeus. *Brit. Antarctic Surv. Bull.* 21: 33-44.
- , & D. W. BROWN. 1972. The biology of Wilson's Storm-Petrel *Oceanites oceanicus* (Kuhl), at Signy Island, South Orkney Islands. *Brit. Antarctic Surv. Sci. Rept.* 69: 1-54.
- BIERMAN, W. H., & K. H. VOOUS. 1950. Birds observed and collected during the whaling expeditions of the *Wilhelm Barendsz* in the Antarctic, 1946-1947 and 1947-1948. *Ardea*, extra no.: 1-123.
- BROWN, R. G. B. 1980. Seabirds as marine animals. Pp. 1-39 in *Behavior of marine animals*, vol. 4 (J. Burger, B. Olla, and H. E. Winn, Eds.). New York, Plenum Press.
- , F. COOKE, P. K. KINNEAS, & E. L. MILLS. 1975. Summer seabird distributions in the Drake Passage, the Chilean fjords and off southern South America. *Ibis* 117: 339-366.
- CLARKE, A. 1980. The biochemical composition of krill *Euphausia superba* from South Georgia. *J. Exp. Marine Biol. Ecol.* 43: 221-236.
- CROXALL, J. P., & P. A. PRINCE. 1980. Food, feeding ecology, and ecological segregation of seabirds at South Georgia. *Biol. J. Linnean Soc. London* 14: 103-131.
- , & ———. 1981. A preliminary assessment of the impact of seabirds on marine resources at South Georgia. *Colloq. Ecosystemes Subantarctiques* 51: 501-509.
- DEWITT, H. H., & T. L. HOPKINS. 1977. Aspects of the diet of the antarctic silverfish, *Pleuragramma antarcticum*. Pp. 557-567 in *Adaptations within antarctic ecosystems* (G. A. Llano, Ed.). *Proc. 3rd SCAR Symp. on Antarctic Biol.* Washington, D.C., Smithsonian Inst.
- GOULD, P. J. 1983. Seabirds between Alaska and Hawaii. *Condor* 85: 286-291.

- GRIFFITHS, A. M., W. R. SIEGFRIED, & R. W. ABRAMS. 1982. Ecological structure of a pelagic seabird community in the southern ocean. *Polar Biol.* 1: 39-46.
- HAMNER, W. H. 1975. Underwater observations of blue-water plankton: logistics, techniques, and safety procedures for divers at sea. *Limnol. Oceanogr.* 20: 1045-1051.
- , P. HAMNER, S. STRAND, & R. GILMER. 1983. Behavior of antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting. *Science* 220: 433-435.
- HAURY, L. R., J. A. MCGOWEN, & P. H. WIEBE. 1978. Patterns and processes in the time-space scales of plankton distributions. Pp. 277-327 in *Spatial pattern in plankton communities* (J. H. Steele, Ed.). New York, Plenum Press.
- HUNT, G. L., JR., & D. SCHNEIDER. In press. Scale dependent processes in the physical and biological environment of marine birds. In *Seabird feeding ecology: the role of seabirds in marine ecosystems* (J. P. Croxall, Ed.). Cambridge, England, Cambridge Univ. Press.
- HUNTER, S. 1983. The food and feeding ecology of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. *Emu* 82: 92-100.
- IMBER, M. J. 1973. The food of Grey-faced Petrels [*Pterodroma macroptera gouldi* (Hutton)], with special reference to diurnal vertical migration of their prey. *J. Anim. Ecol.* 42: 645-662.
- . 1976. Comparison of prey of the black *Procellaria* petrels of New Zealand. *New Zealand J. Marine Freshwater Res.* 10: 119-130.
- JEHL, J. R. 1973. The distribution of marine birds in Chilean waters in winter. *Auk* 90: 114-135.
- . 1974. The distribution and ecology of marine birds over the continental shelf of Argentina in winter. *Trans. San Diego Soc. Nat. Hist.* 17: 217-234.
- KALINOWSKI, J., & Z. WITEK. 1980. Diurnal vertical distribution of krill aggregations in the western Antarctic. *Polish Polar Res.* 1: 127-147.
- KANDA, K., K. TAKAGI, & Y. SEKI. 1982. Movement of the larger swarms of the antarctic krill, *Euphausia superba*, populations off Enderby Land during the 1976-1977 season. *J. Tokyo Univ. Fish.* 68: 25.
- KENDEIGH, S. C., V. R. DOL'NIK, & V. M. GAVRILOV. 1977. Avian energetics. Pp. 127-204 in *Granivorous birds in ecosystems* (J. Pinowski and S. C. Kendeigh, Eds.). Cambridge, England, Cambridge Univ. Press.
- LISHMAN, G. S., & J. P. CROXALL. 1983. Diving depths of the Chinstrap Penguin *Pygoscelis antarctica*. *Brit. Antarctic Surv. Bull.* 61: 21-25.
- MARR, J. W. S. 1962. The natural history and geography of the antarctic krill (*Euphausia superba* Dana). *Discovery Repts.* 32: 33-464.
- MAUCLINE, J. 1980. The biology of mysids and euphausiids. *Advances in Marine Biol.* 18: 527-542.
- PENNYCUICK, C. J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Phil. Trans. Royal Soc. London B* 300: 75-106.
- PINDER, R. 1966. The Cape Pigeon, *Daption capensis* Linnaeus, at Signy Island, South Orkney Islands. *Brit. Antarctic Surv. Bull.* 8: 19-47.
- POCKLINGTON, R. 1979. An oceanographic interpretation of seabird distributions in the Indian Ocean. *Marine Biol.* 51: 9-21.
- PRINCE, P. A. 1980a. The food and feeding ecology of Blue Petrel (*Halobaena caerulea*) and Dove Prion (*Pachyptila desolata*). *J. Zool.* 190: 59-76.
- . 1980b. The food and feeding ecology of Grey-headed Albatross *Diomedea chrysostoma* and Black-browed Albatross *D. melanophris*. *Ibis* 122: 476-488.
- SCHLATTER, R. P., & C. A. MORENO. 1976. Habitos alimentarios del cormoran antartico *Phalacrocorax atriceps bransfieldensis* (Murphy) en Isla Green, Antartica. *Ser. Cient. Inst. Antart. Chileno* 4(1): 69-88.
- SCHNEIDER, D. 1982. Fronts and seabird aggregations in the southeastern Bering Sea. *Marine Ecol. Prog. Ser.* 10: 101-103.
- SHUNTOV, V. P. 1974. Seabirds and the biological structure of the ocean. Washington, D.C., U.S. Dept. Interior, transl. TT 74-55032.
- THOMAS, G. 1982. The food and feeding ecology of the Light-mantled Sooty Albatross at South Georgia. *Emu* 82: 92-100.
- TICKELL, W. L. N., & R. PINDER. 1975. Breeding biology of the Black-browed Albatross *Diomedea melanophris* and Grey-headed Albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 117: 433-450.
- TRIVELPIECE, W., & N. J. VOLKMAN. 1982. Feeding strategies of sympatric South Polar (*Catharacta maccormicki*) and Brown skuas (*C. lombergi*). *Ibis* 124: 50-54.
- VOLKMAN, N. J., P. PRESLER, & W. TRIVELPIECE. 1980. Diets of pygoscelid penguins at King George Island, Antarctica. *Condor* 82: 373-378.
- , W. TRIVELPIECE, & S. TRIVELPIECE. 1983. Pygoscelid penguins in the Antarctic Peninsula region: their role as predators of euphausiids. *Abstr., 101st stated meeting of the Amer. Ornithol. Union*: 123.
- WALSBERG, G. E. 1983. Avian ecological energetics. Pp. 161-220 in *Avian biology*, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- WATSON, G. E., J. P. ANGLE, P. C. HARPER, M. A. BRIDGE, R. P. SCHLATTER, W. L. N. TICKELL, J. C. BOYD, & M. M. BOYD. 1971. Birds of the Antarctic and Subantarctic. *Antarctic Map Folio Ser.* 14: 1-18.
- YOUNG, E. C. 1963. Feeding habits of the South Polar Skua. *Ibis* 105: 301-318.