

BROADSCALE DENSITY AND AGGREGATION OF PELAGIC BIRDS FROM A CIRCUMNAVIGATIONAL SURVEY OF THE ANTARCTIC OCEAN

RICHARD R. VEIT¹ AND GEORGE L. HUNT JR.

*Department of Ecology and Evolutionary Biology, University of California,
Irvine, California 92717 USA*

ABSTRACT.—We analyzed the spatial distribution and habitat relationships of pelagic birds on a circumnavigational cruise of Antarctica. Our analysis focused on two issues. First, we present a quantitative description of the structure of Antarctic seabird assemblages. This descriptive information benefits from a much more longitudinally extensive data set than previously available. Second, we used 18 crossings of the edge of the pack ice and 15 crossings of the continental slope to clarify the spatial relationship between aggregations of pelagic birds and these physical features. Our analysis corroborates the uniformity of bird species composition over the longitudinal range we covered. We found that the habitats with light ($\frac{2}{10}$ to $\frac{5}{10}$ coverage) pack-ice cover had the lowest density and biomass of birds of the four ice habitats (open water, icebergs only, light pack ice, heavy pack ice) surveyed. Even though overall bird abundance was not concentrated at the ice edge, aggregations of individual species were statistically likely to appear there. We found only a slight (34%) elevation in bird biomass over the continental slope, despite repeated previous findings of bird aggregations associated with the Antarctic slope front. Finally, 45% of the seabirds we observed were in three large aggregations. We suggest this concentration demonstrates the importance of localized patches of prey to foraging seabirds in the Antarctic. Received 3 October 1990, accepted 2 March 1991.

THE WORLD'S oceans are divided into many habitats or zones with different physical and biological characteristics. Each zone or habitat is populated by a particular assortment of seabirds (Ainley and Boekelheide 1984, Brown 1980, Murphy 1936, Pocklington 1979, Veit 1988). For example, the subtropical zone of the Pacific Ocean is inhabited by an assemblage of pelagic bird species different from that in the Pacific Subarctic Zone (Wahl et al. 1989). Such species segregation between habitats is evident also at a much smaller spatial scale (Hunt et al. 1990). Despite this relationship between bird species composition and oceanographic habitats, correspondence among the distributions of individual species is often weak or absent (Veit 1988). The ocean surrounding Antarctica is distinguished by its uniformity over an enormous longitudinal range (Deacon 1982), and this uniformity is reflected in the circumpolar ranges of many planktonic organisms (Bushnell and Hedgepeth 1969). We wanted to determine if the Antarctic Ocean is populated by a uniform

"community" of pelagic birds. The distribution of breeding colonies of birds in the Antarctic suggests that this is probably the case (Hunt and Nettleship 1988), as do compilations of incidental sightings of seabirds (Watson et al. 1971).

A number of physical structures within the Antarctic Ocean have often been described as foci for aggregations of pelagic birds. Two emerge as the most consistently attractive: the seaward edge of the pack ice and a hydrographic front overlying the Antarctic continental slope (Ainley and Jacobs 1981, Veit and Braun 1984, Fraser and Ainley 1986). There is ample biological reason to suspect that birds should aggregate near these structures. For example, phytoplankton and zooplankton are often concentrated at the edge of the pack ice (Ainley et al. 1988) and Antarctic krill (*Euphausia superba*) often aggregate over continental or insular slopes (e.g. Makarov et al. 1988). However, statistically significant associations between aggregations of birds and physical features have been elusive. The main problem seems to be that, even if birds aggregate at edges or slopes, the aggregations are not distributed uniformly along these features. Also, sufficiently large samples have proven difficult to obtain. On our

¹ Present address: Department of Zoology NJ-15, University of Washington, Seattle, Washington 98195 USA.

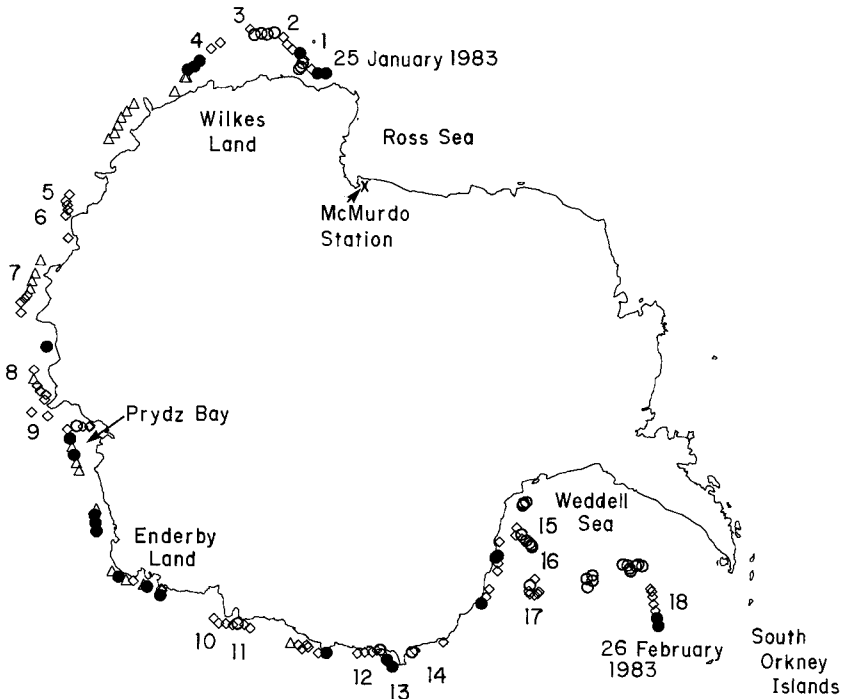


Fig. 1. Cruise track and distribution of ice habitats 25 January to 26 February, 1983. The habitats are as follows: pack ice (O), ice edge (◇), icebergs only (△), and open water (●). Numbers indicate the positions of the 18 ice-edge crossings.

circumnavigational cruise, we crossed the edge of the pack ice 18 times, and the continental slope 15 times. These samples of slope and edge crossings are sufficiently large for statistical analysis. To clarify the relationship between the locations of aggregations of seabirds and edges and slopes, we introduce statistical techniques that we believe will be useful in future analyses of pelagic bird distribution.

During the austral summer of 1982–1983, we measured the longitudinal variation in abundance and species diversity of pelagic birds on a circumnavigational cruise of Antarctica (Holm-Hansen and Chapman 1983). This lengthy cruise provided data representing a broader longitudinal coverage than has ever been reported for Antarctic birds during a single year. We use these data to examine hypotheses about associations between bird aggregations and physical oceanographic features generated from other studies (Abrams 1985, Ainley et al. 1984, Bierman and Voous 1950, Brown et al. 1975, Johnstone and Kerry 1974, Kock and Reinsch 1978, Montague 1988, Thurston 1982, van Oordt and Kruijt 1953, Zink 1981).

METHODS AND STUDY AREA

The USCGC 'Polar Star' left McMurdo Station (73°S, 180°) on 23 January 1983, traveled westward, and arrived at Palmer Station (64°S, 64°W) on 6 March 1983 (Fig. 1). The main purpose of the cruise was to inspect research bases in Antarctica, and our control of the cruise track was limited. Periods of steaming were punctuated by brief visits ashore. As we approached each research base, we requested that the ship cross both the ice edge and the continental slope at as nearly perpendicular an orientation as possible. For this paper, we analyzed only those data collected between the Ross and Weddell seas. To complete the journey quickly, the Polar Star followed the outer edge of the pack ice closely.

We surveyed two major water masses, the East Wind Drift and the West Wind Drift. The boundary between these two masses is the Antarctic Divergence, where Circumpolar Deep Water upwells to the surface (Foster 1984). The East Wind Drift, which borders the continent, flows to the west. The West Wind Drift flows eastward farther offshore. During summer the surface waters of the East Wind Drift are somewhat colder (<0°C) and less saline (<33.8 ppt) than those of the West Wind Drift (Foster 1984). The East Wind Drift is usually covered with pack ice, so that large

portions are exposed to the sun only during late summer.

We made strip transects that were divided into different length intervals depending on the question being addressed. In each interval, we observed both birds and physical features. We used a variety of statistical analyses to ask what patterns (if any) emerge from the data. We counted birds from the flying bridge (17 m above the sea surface) or in the pilot house (15 m above the sea surface) with methods described by Tasker et al. (1984). We calculated bird densities by dividing the number of birds counted in the strip by the strip's area. To estimate the strip's area, we used a radar-based estimation of the ship's speed. We calibrated these estimates of speed against "fixes" of the ship's position, which came at irregular intervals from a satellite. Ship-following birds were recorded when first seen within the counting area, and ignored subsequently. Most of the data on birds were collected by a single observer, but in a few places where birds were extremely numerous, one observed while the other recorded. We collected observations continuously while underway during daylight hours. Day length varied between 24 h (in January 1983) and 18 h (by the end of the study on 27 February 1983).

The ship's technicians collected surface water samples by bucket in every hour during which we were counting birds. They measured temperature to the nearest 0.1°C with a thermometer and salinity to the nearest 0.001 ppt with an inductive salinometer. Bottom depth was recorded continuously with a precision depth recorder. We visually estimated the percentage of ice coverage every 10 min, and also obtained large-scale maps of ice coverage from helicopter reconnaissance.

For analysis of interspecific association, we divided the continuous transect data into 2-h segments. In contrast, for analyses of single-species patterns we divided our data into 10-min intervals. We chose to divide our data into intervals of time rather than distance because we received position fixes at irregular intervals. Therefore, most of the positions we recorded were interpolations. We chose different scales for the different analyses because associations between species are likely to be evident at a larger scale than are associations between single species and physical features within the environment (Hunt and Schneider 1987).

We used two methods to assess the degree to which species associated with one another. The first was "recurrent group analysis" (Fager 1957). Fager's method determines which species form "very frequent" parts of each other's environment, where the term "very frequent" has a precise statistical definition. In Fager's method, one measures concordance or correlation among species, *after* it has been determined that the species have largely overlapping distributions.

We also used cluster analysis of Pearson product-

moment correlation coefficients (Aldenderfer and Blashfeld 1984). Unlike Fager's method, cluster analysis addresses whether or not oceanographic zones differ with respect to bird species composition. We used discriminant analysis (Klecka 1980) to test the statistical distinctiveness of the clusters.

To determine whether birds aggregated at the edge of the pack ice, we selected our most nearly perpendicular *ice-edge crossings* (i.e. we picked crossings in which 2 h of continuous travel in open water was followed by 2 h of continuous travel on the same heading in ice, or vice versa). We excluded crossings of poorly defined ice edges (i.e. places where we encountered gradually increasing ice coverage over an extended distance). On each of these ice-edge crossings, the ship was traveling towards or away from land. We excluded oblique crossings such as might have resulted from the ship's attempt to shortcut across a tongue of pack ice. On average, we traveled somewhat slower in ice (18.5–20.4 km/h) than in open water (25.9–26.6 km/h). For each such crossing, we integrated bird numbers over 10-min intervals.

We had to develop a criterion for identifying aggregations. We defined an *aggregation* of birds as a number of birds per 10-min interval that exceeded the mean for the entire 4-h transect by > 1.96 SD units. For each 4-h transect, we determined if any of four 10-min segments (two to either side of the ice edge) contained an aggregation.

To establish whether or not the distribution of aggregations was related to ice edges, we integrated bird numbers over 40-min segments (because we had first searched for aggregations occurring 20 min to either side of the edge). We then randomized the spatial distribution of the resulting 106 forty-minute segments 100 times. Out of the total of 100, we counted the number of trials for which the number of edge segments containing aggregations equaled or exceeded the number that we actually observed.

We constructed the distributional maps using DIS-SPLA graphics software on a VMS VAX computer at the University of California-Irvine. We used a Lambert Azimuthal Equal Area projection, with the pole on the geographic south pole. This projection preserves proportional areas at the expense of distorting bearings at the edges of the map. All the statistical computations were performed with SYSTAT (Wilkinson 1986).

RESULTS

Communities.—Our observations are consistent with the notion that the Antarctic Ocean supports a geographically uniform assemblage of seabirds. The most numerous species we recorded—Antarctic Petrel (*Thalassoica antarctica*), Adélie Penguin (*Pygoscelis adeliae*), Snow Petrel (*Pagodroma nivea*), and Arctic Tern (*Sterna par-*

adisaea)—accounted for >90% of the total. These four species maintained their numerical dominance over the entire area surveyed. The persistence of this assemblage is supported by comparisons to surveys in the Bellingshausen and Amundsen seas during 1976 (Zink 1981), in the Ross Sea during 1976–1980 (Ainley et al. 1984), and in Prydz Bay during 1982 (Montague 1988). In all four surveys, spread over 7 yr, the same three species of birds dominated the avian community.

We found a wide geographical similarity in species composition, but we found no “recurrent groups” of species among the 22 that we analyzed. This means that the distribution of each species does not for the most part depend on the distributions of others. Therefore, we perceive the assemblage of pelagic birds in the Antarctic Ocean to be a collection of species distributed according to their individual needs and not an organic entity or integrated structure. Our view of the Antarctic seabird community thus resembles the concept of plant communities propounded by Gleason rather than the more integrated or cohesive view of Clements (see Moore 1990).

At a pairwise level, we detected some non-random associations. In particular, 8 pairs of species showed significant association. Of 171 possible comparisons, 8–9 such pairs are expected due to chance. However, the pairings that emerged from our analysis seemed intuitively reasonable. For example, species most often associated with pack ice (Adélie Penguin, Snow Petrel, Antarctic Petrel, Arctic Tern) were grouped together, as were the “open water” species [Light-mantled Sooty-Albatross (*Phoebastria palpebrata*), White-chinned Petrel (*Procellaria aequinoctialis*), Antarctic Prion (*Pachyptila desolata*)]. Montague (1988) detected these same interspecific associations at Prydz Bay.

Adélie Penguins, Antarctic Petrels, Snow Petrels, and Arctic Terns were numerically dominant and tended to co-occur in space, even though they did not form a recurrent group. Therefore, we further examined the relationship in abundance among these four species with measures of correlation and concordance. The four species tended to reach maximum abundance within the same 2-h segments (Kendall's coefficient of concordance = 0.301, $P = 0.050$, $df = 145$). However, there were many 2-h segments in which one species was aggregated but the others were not (Fig. 2). Thus, the over-

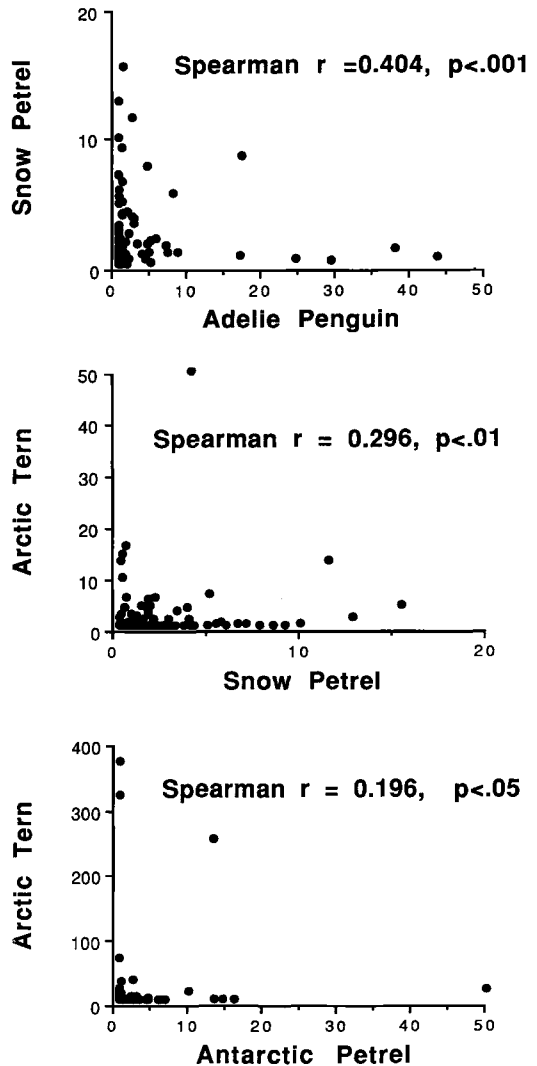


Fig. 2. Rank correlation of abundance between pairs of species revealed by recurrent group analysis. The species are also among the numerically dominant within the area studied. The units (density) are individuals per square kilometer.

all pattern is one of weak interdependence of distribution.

Despite the lack of groupings of *species* within the area we surveyed, groupings of *habitats* did emerge. We found distinctive groupings (clusters) of species associated with the East Wind Drift and West Wind Drift zones, and also with different ice habitats (Fig. 3). We partitioned our data into three geographical sectors (Ross Sea to 90°E, 90° to 15°E, and 15° to the Weddell Sea) and found that the groupings were consistently

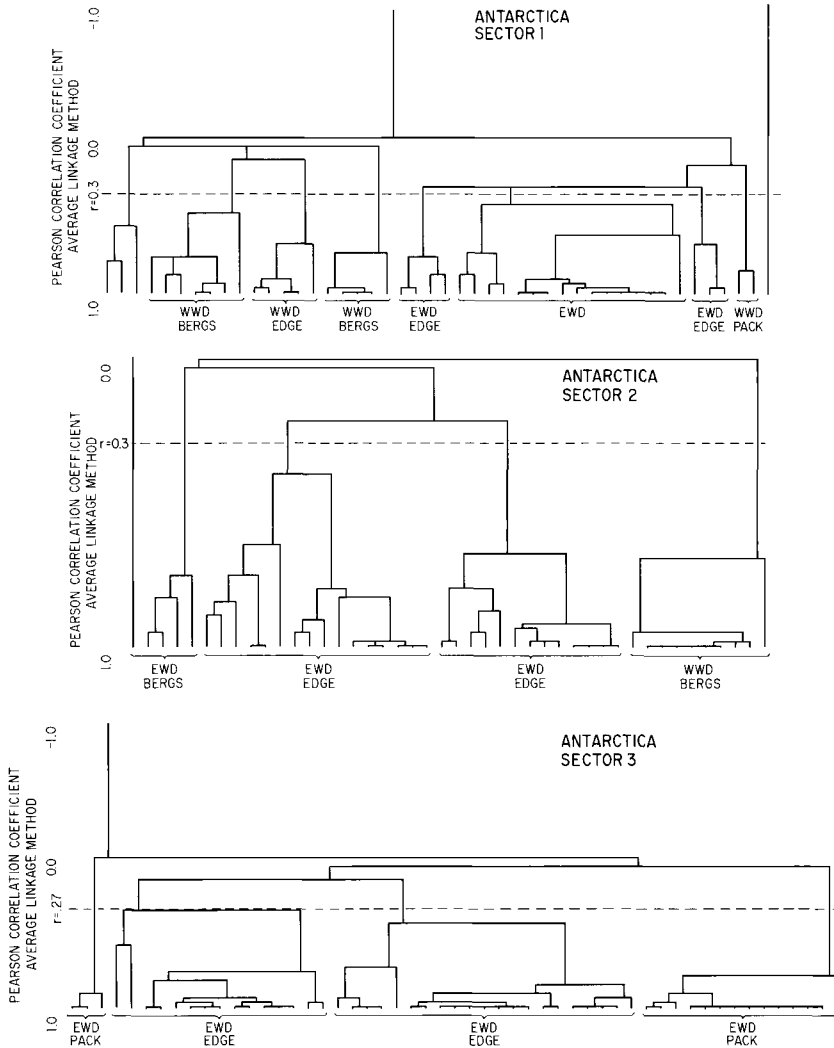


Fig. 3. Cluster dendrograms of samples (2-h segments) based on similarity of species composition. (Sector 1) Ross Sea to 90°E; (sector 2) 90° to 15°E; and (sector 3) 15°E to the Weddell Sea.

apparent in all three sectors. The species assemblages that we identified were strongly influenced by the type and amount of ice that was present. For example, in the East Wind Drift, the birds of the ice-edge zone were different from those not associated with ice. Within the West Wind Drift, there were three assemblages of birds: one associated with icebergs, a second with the ice edge, and a third with open water. These divisions persisted in each of the three sectors. The statistical significance of the distinctiveness of the ice clusters was supported by discriminant analysis (Wilks' Lambda = 0.515, $P < 0.001$), but 38% of the samples were sub-

sequently misclassified by the discriminant functions. The division between East Wind Drift and West Wind Drift clusters was somewhat more clear (Wilks' Lambda = 0.758, $P < 0.001$, only 15% of samples misclassified). This clear pattern emerged despite possible misclassification of some samples due to intrusion of pack ice into the saltier waters of the West Wind Drift.

Aggregations.—We encountered three very large aggregations of birds, which together contained >45% of the birds seen on the entire survey. One of these was near a place previously thought to support elevated abundance of krill

(Marr 1962). On 28 January off Wilkes Land (66°6'S, 110°50'E), we saw a feeding aggregation of approximately 100,000 Short-tailed Shearwaters, 500 White-headed Petrels, 500 Light-mantled Sooty-Albatrosses, and 500 Mottled Petrels, plus smaller numbers of Antarctic Prions and White-chinned Petrels. We assumed previously (Hunt and Veit 1983) that the dark shearwaters were *Puffinus griseus*, but recent evidence suggests that all dark shearwaters visiting that area are *P. tenuirostris* (Kerry et al. 1983). Veit's field notes mentioned that approximately 30% of the shearwaters appeared to have dark underwings, a feature characteristic of *P. tenuirostris*.

Previous distributional summaries (Palmer 1962, Watson 1975) indicate a puzzling inconsistency in the distribution of *P. griseus* at high latitudes. In the Arctic, *P. griseus* barely enters the Bering Sea, while in the Antarctic it supposedly occurs over much colder water near the coast of Antarctica. Our data and that of Kerry et al. (1983) strongly suggest that the southern limit of the distribution of *P. griseus* has been exaggerated. *P. tenuirostris* is the Polar species in both the northern and southern hemispheres.

Off Enderby Land (65°41'S, 25°51'E), we encountered on 8 February an enormous feeding flock of Antarctic Petrels, which we estimated to contain one million individuals. The petrels appeared to be catching euphausiids. The third major aggregation we encountered comprised several thousand Emperor (*Aptenodytes forsteri*) and Adélie penguins roosting on the ice in the central Weddell Sea (68°42'S, 23°33'W; 25 February). The aggregation of Antarctic Petrels off Enderby Land was near a place Marr (1962: 61) described as containing a "principal concentration" of krill. The multispecies aggregation off Wilkes' Land was near two "principal concentrations," whereas the aggregation of penguins in the Weddell Sea was in a region not sampled by Marr.

FACTORS INFLUENCING ABUNDANCE AND SPECIES COMPOSITION

Ice.—We categorized our samples into four arbitrarily chosen ice habitats. We used a non-parametric analysis of variance to detect differences in abundance between habitats (Fig. 4). Of these four habitats, the one we called light pack ice ($\frac{2}{10}$ to $\frac{5}{10}$ ice cover) had the lowest den-

sity and biomass of birds. Only two species, Snow Petrel and Arctic Tern, were numerous there. Of the 22 species, 10 were most numerous in places where there were many icebergs but no pack ice. Both Emperor and Adélie penguins were most numerous in pack ice, and only the Cape Petrel (*Daption capense*) was most numerous over open water.

We made 18 nearly perpendicular crossings of the edge of the pack ice. On four crossings, aggregations of seabirds (all species lumped together) occurred within 20 min (ca. 5 km) to either side of the ice edge. Spatial randomization of the aggregations showed that peaks of avian biomass occurred at the ice edge no more often than would be expected due to chance (Fig. 5). A similar analysis on individual species provided evidence for nonrandom association. Aggregations of Snow Petrels, for example, occurred at 44% of all crossings. This is appreciably more often than would be expected from a random distribution and is consistent with our—and numerous others' (e.g. Fraser and Ainley 1986)—observations that Snow Petrels often forage along the edge of the pack ice. We often saw Arctic Terns sitting on brash ice and on small cakes of pack ice near the ice edge, and sometimes we saw flocks feeding over polynyas. We saw significant aggregations of Arctic Terns at the ice edge on 22% of all crossings, and on 44% of crossings during transects on which >10 Arctic Terns occurred. In summary, aggregations of at least one species occurred much more often than would be expected due to chance. Thus, our intuition that aggregations of birds are to be anticipated at the ice edge was borne out.

Frequency distributions of the spatial distribution of bird aggregations with respect to the position of the ice edge (Fig. 5) clarify this point. On any single crossing of the ice edge one is statistically likely to encounter an aggregation of some species of seabird, although total bird abundance is no higher at the ice edge than it is over either open water or heavy pack ice.

Slopes.—We were not able to determine whether a hydrographic front was present on most of our crossings of the continental slope. Therefore, we searched for an elevation in bird density over the continental slope, on the premise that the presence of such a front in the Ross Sea is important to foraging seabirds (Ainley and Jacobs 1981). On our cruise, avian biomass was only 34% higher in waters over the conti-

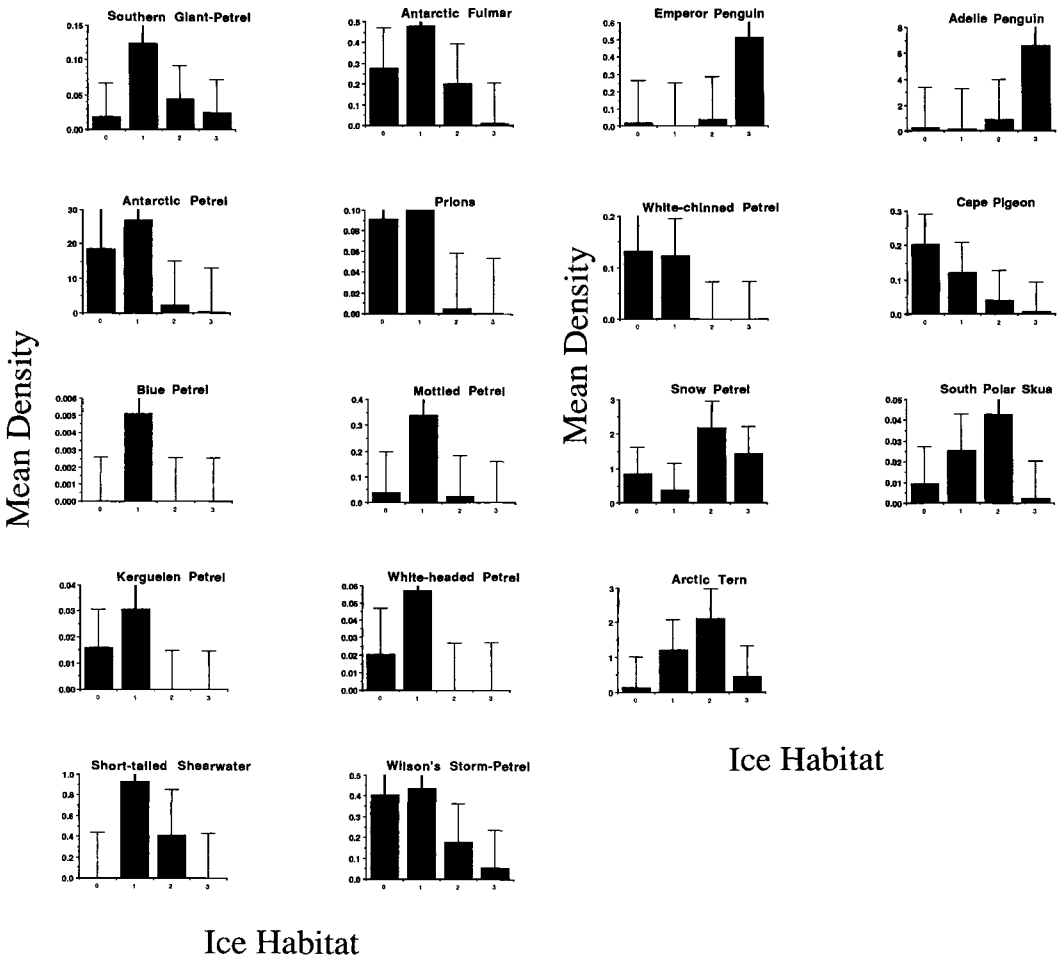


Fig. 4. Comparative bird abundance in four ice habitats ($\bar{x} \pm 1.96$ SD units). The four habitats are open water (0), icebergs but no pack ice (1), pack-ice edge (2), and heavy pack ice (3).

mental slope than over either shelf or deep waters (Mann-Whitney U -statistic = 3,089, $P = 0.022$). The only species whose abundance was significantly higher over slope waters was the Snow Petrel ($U = 3,166.5$, $P = 0.019$). Because we found no strong relationship between bird abundance and the location of the Antarctic continental slope, we did not conduct more detailed statistical analyses of the slope/seabird spatial association, as we did for the edge of the pack ice.

Temperature/salinity relationships.—Differences in bird species composition between the East Wind Drift and the West Wind Drift depended mainly on ice cover. Both Emperor and Adélie penguins were more abundant in the East Wind Drift, as were Snow Petrels and Arc-

tic Terns. These species' preference for waters adjacent to the ice edge likely accounts for their distribution. The most numerous species in the West Wind Drift were Short-tailed Shearwater, White-chinned and White-headed petrels, and prions. However, the majority of individuals of all these species were concentrated in one restricted area, off Wilkes' Land.

DISCUSSION

The uniform composition of bird species assemblages over a broad longitudinal range in the Antarctic Ocean was supported by our data. There was, however, little cohesion among the distributions of individual species. Each species exploits the environment in a fashion that is

independent of the actions of other species. Despite the independence of species distributions, we identified discrete habitats in the Antarctic on the basis of the mix of pelagic bird species that inhabits them. The division between habitats persists through the entire longitudinal range surveyed, and also corresponds to divisions described by Ainley et al. (1984) and by Montague (1988). For example, the "pack ice" community of Ainley et al. (1984) is very similar to the assemblage of species that we found over pack ice (ice habitats: light and heavy pack ice). There were only minor differences in species composition between the three surveys. The "iceberg" habitats in the three studies were also very similar. Antarctic Petrel was consistently the most numerous species. Ainley et al. saw more Snow Petrels whereas we saw more Short-tailed Shearwaters. The open-water habitats of the three studies differed considerably; ours was dominated by Antarctic Petrels, Montague's (1988) by Southern Fulmars (*Fulmarus glacialis*) and Ainley et al.'s (1984) by Sooty Shearwaters. These differences probably reflect differences in ice coverage or geographical location of the respective surveys. During our time in East Antarctica, most of the pack ice had melted, so Antarctic Petrels had no ice over which to forage. We only saw Sooty/Short-tailed Shearwaters in a small portion of the longitudinal range we covered, and Montague may have been too far south to record either shearwater species.

Antarctic breeding species had distributions that were continuous within the area surveyed, as did wintering Arctic Terns. The main geographical differences in species composition seemed to be a consequence of the location of nesting colonies. For example, Short-tailed Shearwaters (*Puffinus tenuirostris*) were most common in the sector south of Tasmania, Mottled and White-headed petrels (*Pterodroma inexpectata* and *Pterodroma lessoni*) were most common south of New Zealand, and White-chinned Petrels and Antarctic Prions were most numerous to the south of the Kerguelen Islands (Fig. 6).

The elevated abundance of birds we recorded to the north of the pack-ice edge, in open water interspersed with icebergs, is consistent with previous observations of intense biological activity in that general area. Fraser and Ainley (1986) have hypothesized that seabirds aggregate to the north of the retreating ice edge in

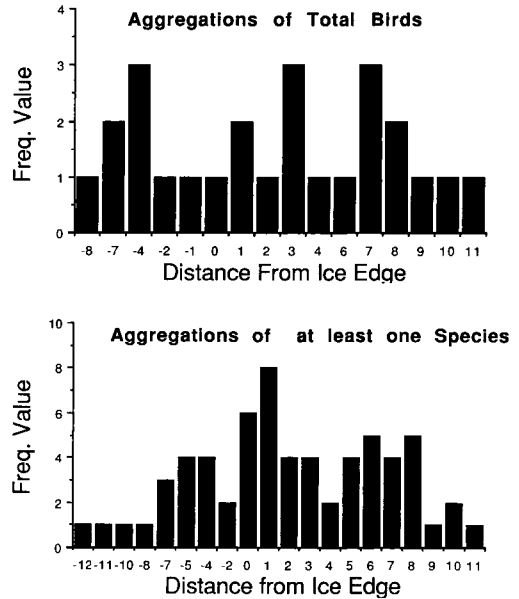


Fig. 5. Distance of bird aggregations from the edge of the pack ice. The units are 10-min segments, and positive values indicate distance *towards* land from the ice edge. Thus, a distance of -4 indicates 40 min of steaming time *offshore* from the ice edge.

late summer. In that part of the Antarctic Ocean that has been recently exposed to sunlight, algal populations grow very quickly because fresh water left by the melting ice maintains a shallow and stable mixed layer (Smith et al. 1988). This area of rapidly growing algal blooms (the Marginal Ice Zone) subsequently attracts populations of krill and other grazers, which serve as prey for seabirds. An alternative explanation for the elevated abundance of birds observed north of the pack ice involves the icebergs. Antarctic icebergs generate upwelling in their immediate vicinity as they melt (Neshyba 1977), so they may support algal blooms, which then serve as foci for foraging krill. Our analysis shows clearly that seabirds tend to aggregate over iceberg-laden waters north of the pack ice. We suggest that future research should determine the mechanism that results in bird prey becoming especially abundant or available in that area.

Our analysis of the occurrence of bird aggregations at the ice edge helps to clarify the spatial association between birds and this physical boundary. We have shown that on any given crossing of the ice edge, an encounter with an aggregation of birds is statistically likely. Yet,

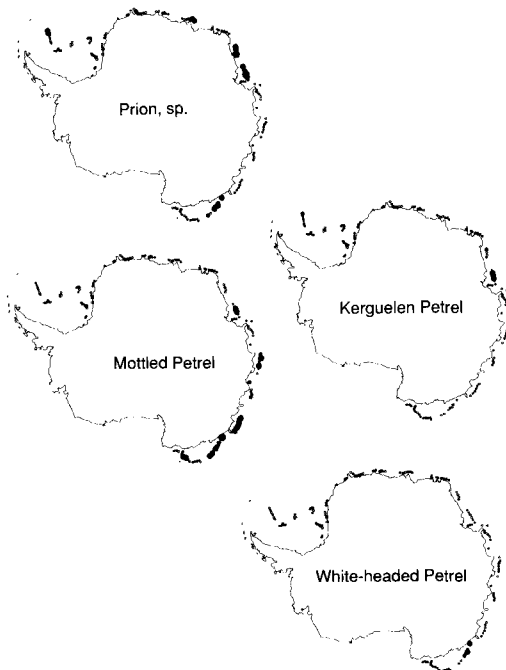


Fig. 6. Distribution of Antarctic Prion, Mottled Petrel, White-headed Petrel, and Kerguelen Petrel. Each point represents a 2-h segment; open circles = zero density; filled circles of increasing size represent densities of 0.1–10.0 birds/km².

neither abundance nor biomass of birds is higher than average at the ice edge, compared with other habitats that we surveyed. Perhaps foraging birds are attracted to the ice edge because it presents a strong visual clue, but prey are not consistently abundant there. Our findings pertain to the actual ice edge rather than the Marginal Ice Zone. The latter is an extensive (200–400 km wide) band of relatively fresh water that derives from the melting sea ice and that seems to strongly influence trophic interactions (Fraser and Ainley 1986). Our finding may be more broadly applicable to a variety of physical features hypothesized to be of importance to birds and other predators. Although aggregations of single species may occur, these aggregations do not always affect the overall distribution of abundance.

Our analysis of bird aggregations near the continental slope only weakly corroborate the findings of Ainley and Jacobs (1981). Possibly the Antarctic slope front in the Ross Sea is more conducive to attracting seabirds than the slope front elsewhere in the Antarctic. It is also possible that at some places where we crossed the

continental slope, there was no front. We suggest that the hydrography overlying the slope, rather than the slope itself, is the feature of importance to foraging birds.

Apart from results that pertain to specific species or biological associations, we present an observation, based on our analyses, which may be broadly applicable to analysis of spatial patterns. We suggest that increased variance of abundance, rather than increased mean abundance, might be a better statistical measure of aggregation. We hypothesize that biologically productive zones should be characterized by significantly higher variance in seabird abundance than less productive areas. This statistical difference arises from the tendency of foraging birds to form aggregations in response to elevated prey density. To test this, we measured the mean abundance, variance, and Green's coefficient of dispersion (G_x ; Andrew and Mapstone 1987) for each day of sampling. Of the three major aggregations we found, one (Antarctic Petrels off Enderby Land) had both the highest mean abundance and highest variance of all our days of sampling, and one (mixed species off Wilkes' Land) had the highest "patchiness" as indicated by G_x . The highest total number of birds we saw within our counting zone on any one day was within the aggregation of penguins in the Weddell Sea, but that aggregation was not characterized by either high variance or high G_x . It is perhaps significant that the penguins within that aggregation were not feeding, but were roosting and molting. Thus, we cannot suggest a "best" way to describe bird aggregations based on the data available. However, comparisons of mean abundance are certainly inadequate for portraying the dramatic changes in pattern that emerge from distributions of pelagic birds at sea.

ACKNOWLEDGMENTS

We thank the officers and crew of the USCGS 'Polar Star' for their skillful assistance, and for their hospitality while we were on board. Lisa Ferm and Sheldon Fisher helped us in the field. We thank Peter Kareiva, Richard G. B. Brown, and an anonymous reviewer for helpful criticisms of the manuscript. This research was supported by NSF grant DPP 82-06052 to G. L. Hunt Jr.

LITERATURE CITED

ABRAMS, R. W. 1985. Energy and food requirements of pelagic aerial seabirds in different regions of

- the African sector of the southern ocean. Pp. 466-472 in *Antarctic nutrient cycles and food webs* (W. R. Siegfried, P. R. Condy, & R. M. Laws, Eds.). New York, Springer-Verlag.
- AINLEY, D. G., & R. J. BOEKELHEIDE. 1984. An ecological comparison of oceanic seabird communities of the South Pacific Ocean. *Stud. Avian Biol.* 8: 2-23.
- , W. R. FRASER, & K. L. DALY. 1988. Effects of pack ice on the composition of mikronekton communities in the Weddell Sea. Pp. 140-146 in *Antarctic ocean and resources variability* (D. Sahrhage, Ed.). Berlin, Springer-Verlag.
- , & S. S. JACOBS. 1981. Sea-bird affinities for ocean and ice boundaries in the Antarctic. *Deep-Sea Res.* 28A: 1173-1185.
- , E. F. O'CONNOR, & R. J. BOEKELHEIDE. 1984. The marine ecology of birds in the Ross Sea, Antarctica. *Ornithol. Monogr.* No. 32.
- ALDENDERFER, M. S., & R. K. BLASHFELD. 1984. Cluster analysis. Beverly Hills, California, Sage Publ.
- ANDREW, N. L., & B. D. MAPSTONE. 1987. Sampling and the description of spatial pattern in marine ecology. *Annu. Rev. Oceanogr. Mar. Biol.* 25: 39-90.
- BIERMAN, W. H., & K. H. VOOUS. 1950. Birds observed and collected during the whaling expeditions of the 'William Barendsz' in the Antarctic, 1946-1947 and 1947-1948. *Ardea Suppl.*: 1-124.
- BROWN, R. G. B. 1980. Seabirds as marine animals. Pp. 1-39 in *Behavior of marine animals: current perspectives in research*, vol. 4 (J. Burger, B. L. Olla, H. E. Winn, Eds.). New York, Plenum Press.
- , F. COOKE, P. K. KINNEAR, & E. L. MILLS. 1975. Summer seabird distribution in Drake Passage, the Chilean fjords and off southern South America. *Ibis* 117: 339-356.
- BUSHNELL, V. C., & J. W. HEDGEFETH (EDS.). 1969. Distribution of selected groups of marine invertebrates in waters south of 35° S latitude. *Antarctic Map Folio Ser. No. 11*. Washington, D.C., Am. Geogr. Soc.
- COLE, L. C. 1949. The measurement of interspecific association. *Ecology* 30: 411-424.
- DEACON, G. E. R. 1982. Physical and biological zonation in the southern ocean. *Deep-Sea Res.* 29A: 1-15.
- FAGER, E. W. 1957. Determination and analysis of recurrent groups. *Ecology* 38: 586-595.
- FOSTER, T. D. 1984. The marine environment. Chapter 6 in *Antarctic ecology* (R. M. Laws, Ed.). London, Academic Press.
- FRASER, W. B., & D. G. AINLEY. 1986. Ice edges and seabird occurrence in Antarctica. *Bioscience* 36: 258-263.
- HANEY, J. C. 1986. Seabird patchiness in tropical oceanic waters: the influence of *Sargassum* "reefs." *Auk* 103: 141-151.
- HOLM-HANSEN, O., & A. S. CHAPMAN. 1983. Antarctic circumnavigation cruise, 1983. *Antarctic J. U.S.* 1983 Rev. Issue: 162-163.
- HUNT, G. L., JR., D. HEINEMANN, R. R. VEIT, R. B. HEYWOOD, & I. EVERSON. 1990. The distribution, abundance and community structure of marine birds in southern Drake Passage and Bransfield Strait, Antarctica. *Cont. Shelf Res.* 10: 243-257.
- , AND D. N. NETTLESHIP. 1988. Seabirds of high-latitude northern and southern environments. Pp. 1143-1155 in *Acta XIX Congr. Int. Ornithol.*, vol. 1 (H. Ouellet, Ed.). Ottawa, Univ. Ottawa Press.
- , & D. C. SCHNEIDER. 1987. Scale-dependent processes in the physical and biological environment of marine birds. Pp. 7-42 in *Seabirds: feeding ecology and role in marine ecosystems* (J. P. Croxall, Ed.). Cambridge, U.K., Cambridge University Press.
- , & R. R. VEIT. 1983. Marine bird distribution in Antarctic waters. *Antarctic J. U.S.* 18: 167-169.
- JOHNSTONE, G. W., & K. R. KERRY. 1974. Ornithological observations in the Australian sector of the southern ocean. Pp. 725-738 in *Proc. 16th Int. Ornithol. Congr.* (H. J. Frith and J. H. Calaby, Eds.). Canberra, Australia, Australian Acad. Sci.
- KERRY, K. R., R. S. C. HORNE, & D. F. DORWARD. 1983. Records of the Short-tailed Shearwater *Puffinus tenuirostris* in Antarctic waters. *Emu* 83: 35-37.
- KLECKA, W. R. 1980. Discriminant analysis. Beverly Hills, California, Sage Publ.
- KOCK, K. H., & H. H. REINSCH. 1978. Ornithological observations during the German Antarctic expedition 1975/1976. *Beitr. Vogelkd.* 24: 305-328.
- MAKAROV, R. R., V. V. MASLENNIKOV, E. V. SOLYANKIN, V. A. SPIRIDONOV, & V. N. YAKOLEN. 1988. Variability in population density of Antarctic krill in the western Scotia Sea in relation to hydrological conditions. Pp. 231-236 in *Antarctic ocean and resources variability* (D. Sahrhage, Ed.). Berlin, Springer-Verlag.
- MARR, J. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba*, Dana). *Discovery Rep.* 32: 33-364.
- MONTAGUE, T. L. 1988. Birds of Prydz Bay, Antarctica: distribution and abundance. *Hydrobiologia* 165: 227-237.
- MOORE, P. D. 1990. Vegetation's place in history. *Nature* 347: 710.
- MURPHY, R. C. 1936. *Oceanic birds of South America*. New York, Am. Mus. Nat. Hist.
- NESHYBA, S. 1977. Upwelling by icebergs. *Nature (London)* 267: 507-508.
- PALMER, R. S. 1962. *Handbook of North American birds*, vol. 1. New Haven, Connecticut, Yale Univ. Press.
- POCKLINGTON, R. 1979. An oceanographic interpretation of seabird distributions in the Indian Ocean. *Mar. Biol.* 51: 9-21.
- SMITH, W. O., N. K. KEENE, & J. C. COMISO. 1988. Interannual variability in estimated primary pro-

- ductivity of the Antarctic Marginal Ice Zone. Pp. 131-139 in *Antarctic ocean and resources variability* (D. Sahrage, Ed.). Berlin, Springer-Verlag.
- TASKER, M. L., P. H. JONES, T. DIXON, & B. F. BLAKE. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101: 567-577.
- THURSTON, M. H. 1982. Ornithological observations in the South Atlantic Ocean and Weddell Sea, 1959-1964. *Bull. Br. Antarctic Surv.* 55: 77-103.
- VAN OORDT, G. J., & J. P. KRUIJT. 1953. On the pelagic distribution of some Procellariiformes in the Atlantic and southern ocean. *Ibis* 95: 615-637.
- VEIT, R. R. 1988. Spatial dispersion patterns of Antarctic seabirds. Ph.D. dissertation, Irvine, Univ. California.
- & R. M. BRAUN 1984. Hydrographic fronts and marine bird distribution in Antarctic and Subantarctic waters. *Antarctic J. U.S.* 1984 Rev. Issue: 165-167.
- WAHL, T. R., D. G. AINLEY, A. H. BENEDICT, & A. R. DEGANGE. 1989. Associations between seabirds and water-masses in the northern Pacific Ocean in summer. *Mar. Biol.* 103: 1-11.
- WATSON, G. E. 1975. *Birds of the Antarctic and Subantarctic*. Washington, D.C., Am. Geophys. Union.
- , 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., Folio 14. New York, Am. Geogr. Union.
- WILKINSON, L. 1986. SYSTAT: the system for statistics. Evanston, Illinois.
- ZINK, R. M. 1981. Observations of seabirds during a cruise from Ross Island to Anvers Island, Antarctica. *Wilson Bull.* 93: 1-20.

100 Years Ago in The Auk



Excerpt from "Recent Literature" (1891, *Auk* 8: 379-381)

"Sharpe's 'Review of Recent Attempts to Classify Birds.'*—Dr. Sharpe prefaces his own scheme with some well-considered remarks on the slow process of building up a natural classification of birds, which he compares to the construction of a building to which each labourer in the field contributes his quota. 'Sometimes the structure has to be altered and amended but it is seldom that a labourer, whose soul is in his work, retires without having added something in the shape of useful materials. It takes a long time—it may be years of study—before a sound brick is baked. . . . It is certain, however, that by this 'brick'-making materials for the structure of the Classification of Birds will be slowly gathered.' He has also a word for the critic who pulls down but never builds up. This is followed by some practical and very sensible remarks upon the exhibition of bird material in museums, and on the general subject of the study of birds. He says: 'If the system of teaching by artistic groups be adapted, then only the principal forms would require illustration, and a representation of the leading type of each order or sub-order would suffice. A supplementary gallery might be provided, in which types of each family, subfamily, and genus of birds would be exhibited, but lower than genera I would never descend in a public exhibition. The student of species should find his material in the 'study' series, . . . and there each species should be amply illustrated by actual specimens showing the plumage of both sexes at all times of the year, young birds in all stages, moulting individuals, and a full series exhibiting geographical distribution and variation in the species, even if it requires a series of specimens. The days have gone by where the description of new species was the be-all and end-all of an ornithologist's hopes. The warfare over priority of nomenclature is fast showing signs of waning. . . . It is time, however, that by some such means as an International Congress of Ornithologists the names of the species of birds were settled once and for all, in order that we may turn our attention to the far more important facts of geographical distribution and life history of species. We are approaching a time when the study of rainfall and climate, of altitude and locality, and even the conditions of weather under which a specimen was procured, will be considered indispensable for the minute study which is to be our portion in the not very distant future.'" (Doubtless Dr. Sharpe is not unaware that these important factors have already received much attention in some quarters, having been uppermost in the minds of many American students for the last two decades at least.)"—J. A. Allen.

*A Review of Recent Attempts to Classify Birds; an Address delivered before the Second International Ornithological Congress on the 18th of May, 1891. By R. Bowdler Sharpe, LL.D., F.L.S., etc. (Zoological Department British Museum.) Budapest, 1891. (Published at the Office of the Congress.) Roy. 8vo. pp. 90, pll. xii.