

SPECIES-HABITAT RELATIONSHIPS AMONG ANTARCTIC SEABIRDS: A FUNCTION OF PHYSICAL OR BIOLOGICAL FACTORS?¹

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Abstract. We employed a "natural experiment" to evaluate the hypothesis that a major physical feature of high-latitude marine habitat, the percentage of the sea covered by pack ice, affects species composition among Antarctic seabirds. Our experiment entailed replicate transects through markedly altered physical habitat in the Scotia-Weddell Confluence: a series of storms caused the pack ice to advance and retreat rapidly and repeatedly over a 200-km-wide area. Regardless of where their habitat moved, pack-ice and open-water species occurred at significantly higher densities in the ice and open-water habitats, respectively. There were no time lags in the response of species to habitat alteration. In addition, pack-ice and open-water species had identical diets regardless of where their preferred habitat was located. These results supported the hypothesis and showed that physical rather than biological variables affect species composition among pelagic assemblages of Antarctic seabirds. Results supported the conclusion that a lack of appropriate adaptations constrain open-water species to reside away from the pack ice and that unremarkable prey availability fails to attract pack-ice species to open waters.

Key words: Southern Ocean; pack ice; pelagic seabirds; habitat selection; habitat alteration.

INTRODUCTION

The Antarctic avifauna, from a marine perspective, is divisible into two major groups: one associated with pack-ice covered waters and the other associated with ice-free, open waters (Murphy 1936; Cline et al. 1969; Ainley et al. 1984; Ainley et al., in press). Composition of the pack-ice assemblage changes little seasonally, although its at-sea range tracks the extensive seasonal expansion and contraction of the ocean area covered by pack-ice (Ainley et al. 1984; Ainley et al., in press). Indeed, composition of the Antarctic pack-ice assemblage appears to be among the least variable of all seabird assemblages (Ribic and Ainley 1988/89). The open-water assemblage is more variable than that of the pack-ice because it also contains species that are seasonal visitants. Within the pack ice, species occurrence is affected by physical habitat characteristics, such as the concentration of ice over and the size of

ice floes (Cline et al. 1969, Ainley et al. 1984). This pattern and the lack of much spatial overlap between the two Antarctic assemblages led us to question whether these species select their at-sea habitat on the basis of physical factors (e.g., ice cover) or biological ones (e.g., prey type).

Wiens (1989) pointed out that physical factors have been emphasized among those thought to determine the structure of bird assemblages, in part because physical factors are much easier to measure than are biological ones. Physical factors suggested to affect composition of marine avifaunas include ocean depth, water temperature and salinity, wind regimes, water transparency, presence of pack ice and distance from breeding or roosting sites (Abrams et al. 1981, Ainley 1977, Ainley and Boekelheide 1983, Ainley et al. 1984, Ashmole 1971, Briggs et al. 1987, Brown et al. 1975, Griffiths 1983, Haney 1986a, Hunt and Schneider 1987, Pennycuick et al. 1984, Pocklington 1979, Wahl et al. 1989). Biological factors suggested to affect seabird distribution include the general productivity of surface waters

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and the distribution of prey (Ashmole 1971, Haney 1986a, Hunt et al. 1981, Ribic and Ainley 1988/89), but these relationships are not well understood. There is also a consensus among seabird biologists that prey specialization strongly affects the occurrence and distribution of individual seabird species and, therefore, assemblage composition (see Ashmole 1971, Hunt and Schneider 1987, Hunt and Harrison 1990). The importance of prey specialization, however, has not been well investigated.

Many studies (see Wiens 1989 for discussion of some pertaining to birds), have evaluated the importance of physical features in habitat selection by various organisms, including invertebrates and vertebrates, by artificially altering the habitat. Alterations have been made using clearcuts, defoliants, plowing, burning or scraping. Virtually all have been directed at sedentary (or seasonally fixed) organisms. We offer here an experiment, albeit a "natural" one, to observe the response of non-territorial organisms to dramatic habitat alteration. We also evaluate trophic factors possibly involved in habitat selection, an aspect of habitat rarely treated in habitat-manipulation studies. Taking advantage of a remarkable opportunity, we changed our research design in the field to document three rapid advances and retreats of the pack ice within a 200-m wide band in the Southern Ocean. We determined species composition and diet of the seabirds when pack ice was or was not present, while our colleagues determined availability of potential prey. Our spatial scale encompassed several thousand square kilometers and thus overcame the patchy distribution perceived at smaller scales; our temporal scale was defined by hours. On the basis of seasonal studies (Ainley et al., in press), our null hypothesis was that species composition in the study area would not be affected by a change in physical habitat (i.e., a switch from ice-covered to ice-free seas). We further hypothesized that if this first hypothesis was rejected, a change in species composition would not occur concomitant with a change in diet.

METHODS

DATA COLLECTION

This study was part of an integrated oceanographic project, called AMERIEZ (Antarctic Marine Ecosystem Research in the Ice Edge Zone), in which a scientific group studied all major el-

ements of the marine ecosystem, including both the physics and biology. On board the R/V *Polar Duke*, we investigated ecological interactions during August 1988, the first major investigation of marine ecology in the Antarctic during winter. The study area consisted of a section of the Scotia-Weddell Confluence (Husby et al. 1989). The southern boundary of the Scotia Sea occurred in the extreme northward edge of the area and the northern boundary of the Weddell Sea coincided with the southern boundary of the study area (Fig. 1). Waters of this confluence were continually very near freezing (at -1.7°C), compared with Scotia Sea Water which was cold, but too warm to freeze (around 0°C), and Weddell Sea Water, which was always frozen.

The cruise was initially designed to conduct a series of oceanographic stations along lines 36° , 40° , 44° and 48° W longitude, between about 57° and 60° S latitude (each line being about 200 km in length; see Ainley and Sullivan [1989] for cruise details). Upon seeing the dramatic freeze and thaw cycle, and its effect on seabird distribution along the first line (36° W), we altered the cruise track slightly to set up an experiment. Subsequently, the ship traveled the entire length of the next lines both into and out of the pack ice, rather than cutting over to the next line as soon as open water was reached (Fig. 1). Cruising the entire line both ways provided a means of replicating the weather/ice cycle three times. It took about two days to make each pass, one way.

We censused seabirds between oceanographic stations; we do not include the data from 36° W because we ran the track prior to our experiment. Otherwise, whenever the ship was underway during daylight hours (about 6 hr of light/day), we sequentially conducted 30-min strip-censuses. A total of 102 censuses were made along the three track lines. Only birds seen within 300 m of one glare-free forequarter of the ship were counted; ship-followers were excluded (see Tasker et al. 1984). Two observers counted simultaneously, because searching for and finding aerial species and swimming penguins is not otherwise possible with any degree of reliability. A total of 2,691 individuals were seen during the 102 censuses. Densities were calculated using a strip transect estimate (Burnham et al. 1980) and were adjusted for average flight speed and direction of the birds relative to speed and direction of the ship (Spear et al. 1992; Spear and Ainley, unpubl. data). We did not census in open water when

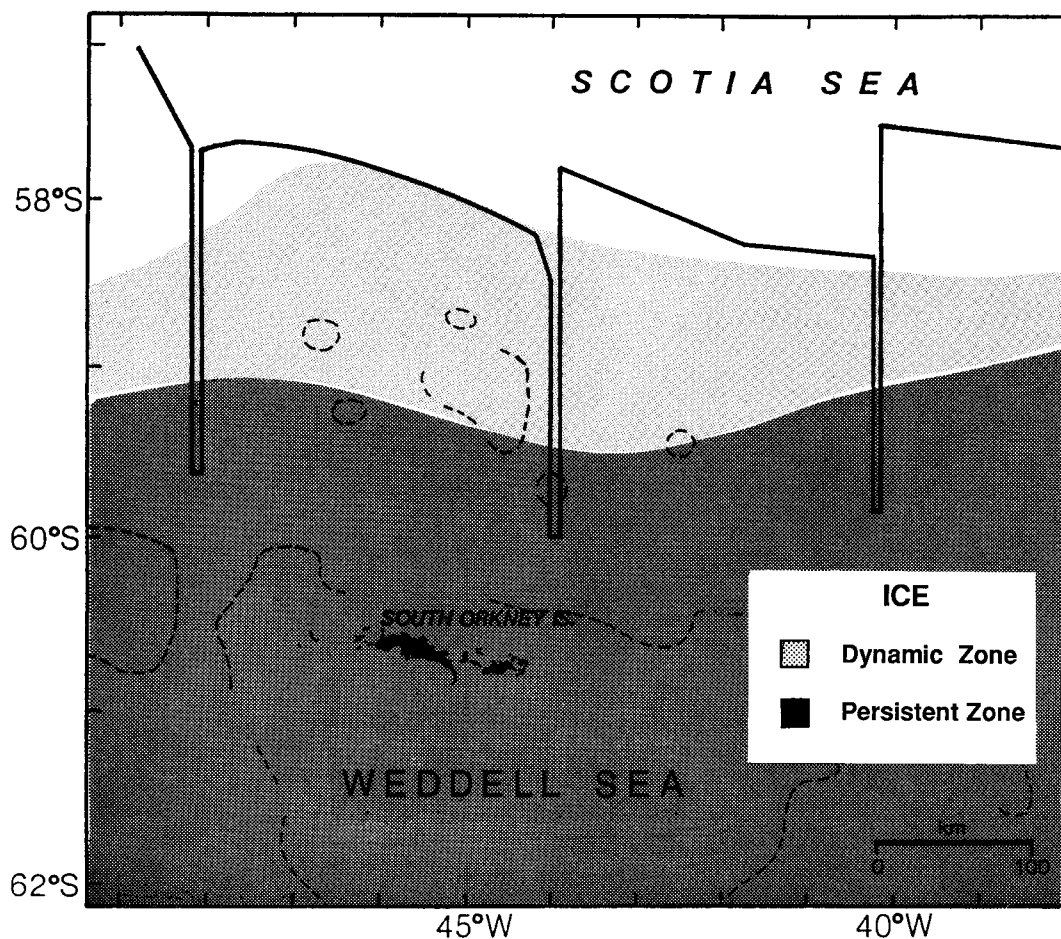


FIGURE 1. The study area in the Scotia-Weddell Confluence showing the location of the longitudinal meridians along which seabird censuses were made into and out of the pack ice, August 1988. The dynamic zone refers to the area in which the pack ice advanced or retreated as a result of storm fronts (see text).

winds exceeded 20 m/sec nor when visibility was less than 300 m. Because the ship moved into the pack ice when strong winds blew, however, we rarely experienced these restrictions; fog impeded observations during only 3 hr on one day.

Physical habitat variables were measured at the start of every 30-min transect. If conditions changed appreciably before 30 min passed, the transect was terminated and a new one was begun. Physical variables recorded were: distance-to-the-pack-ice-edge in kilometers (a negative distance indicates distance from the edge into the ice pack), coded ice characteristics (a nominal ice variable that includes percentage ice cover, floe size and ice type), sea-surface temperature (SST; °C), salinity (ppt), ocean depth (m), and

distance-to-nearest-land (km; i.e., the South Orkney Islands, an important seabird breeding locality; see Fig. 1). We did not expect distance-to-land to be a factor during winter, but we included this variable in our studies during other seasons and even during the non-breeding seasons it had an effect (Ainley et al., in press).

We collected up to five specimens of each species present at seven stations, three in water with minimal ice cover (0–0.5 cover) and four within heavier pack ice. A total of 109 specimens were collected of the species considered herein; see Ainley et al. (1992) for further details. Our collecting protocol was designed to minimize the possibility of biasing our results towards dietary overlap between species. First, oceanographic

stations at which birds would be collected were chosen 24 hr in advance as part of the daily science plan. Then, once on station and if sea conditions allowed, our small boat was launched. Second, we did not collect birds from feeding flocks, often a common practice among seabird researchers, nor did we collect in the vicinity of the few feeding flocks that we saw. Feeding flocks, in fact, are rare in Antarctic pelagic waters (Ainley and Boekelheide 1983). Stomach contents were sorted immediately upon return to the ship, and each prey item eventually was identified at least to genus and was measured. Weights of individual items were determined directly (when the ship was in the ice and did not roll) or by regression calculated from the size of hard parts. Of these, only fresh exoskeletons, otoliths and squid beaks were included (see Ainley et al. 1992 for further details).

During this cruise, Lancraft et al. (1989, 1991) used a series of discrete-depth net trawls at oceanographic stations to determine the density, degree of patchiness, depth distribution and species composition of zooplankton and micronekton (i.e., potential seabird prey). Throughout Confluence Water, the zooplankton and micronekton differed in these four characteristics from analogous organisms caught by trawl in Scotia Sea Water. As a result of this differing pattern, seabird data (including those for diet) taken from Scotia Sea Water were not included in our analyses.

DATA ANALYSIS

We tested the hypothesis that ice did not affect the density of either the open-water or pack-ice species group along each transect replicate (40°, 44° and 48° W, with each northward and southward excursion analyzed separately). We used the Mann-Whitney test (Conover 1980), because, for one transect, one data set had a zero variance within the ice portion. To be consistent, the same test was used for all transect lines. The Mann-Whitney test statistic was adjusted for ties. We tested correspondence between the two species groups and the presence or absence of ice in the entire data set using a two-way analysis of variance (ANOVA) on $\ln(\text{density} + 1)$ and tested for interaction at $\alpha = 0.10$.

To investigate relationships between species and habitat variables in a multivariate framework, we used canonical correlation analysis (COR; Gittins 1985) and canonical correspon-

dence analysis (CCA; Ter Braak and Prentice 1988). For COR, typically used in a linear framework, we added squared terms for the environmental variables (F. Ramsey, Dept. of Statistics, Oregon State University, pers. comm.). CCA is a technique developed for situations where an entire gradient is sampled resulting in nonlinear, nonmonotonic relationships among environmental variables. CCA is a direct gradient analysis technique and can be considered an extension of correspondence analysis, an indirect gradient technique, but can also be related to other parametric multivariate techniques (Ter Braak 1988, Ter Braak and Prentice 1988). For both multivariate techniques, several measures were used to assess the success of the analyses (e.g., percentage variance of species data explained by the species composite and by the environmental composite). We used these measures to identify the important environmental variables and the species explained by the analyses. Specifically, for the environmental and species variables, respectively, those with >25% and >15% of their variance explained by the environmental and species composites were considered to be important and explained by the analyses. These breakpoints were based on the observed patterns in the measures. In addition, for the CCA, overall tests of significance and of the first canonical axis were made with a permutation test at $\alpha = 0.01$. COR was done using BMDP (Dixon et al. 1988); CCA was done using CANOCO, version 3.1 (Ter Braak 1988, 1990). Biplots of species and environmental scores from CCA were used to illustrate the gradient relationships between species and the environmental variables.

We used diet composition (based on mass contribution) and Morisita's index (Horn 1966) to compare diet overlap; an overlap value >0.80 denoted diet similarity (Ainley et al. 1984, 1991, 1992; Diamond 1984).

RESULTS

SPECIES-HABITAT RELATIONSHIPS

Species in the pack-ice assemblage included the Antarctic Petrel *Thalassoica antarctica*, Snow Petrel *Pagodroma nivea*, Southern Fulmar *Fulmarus glacialis* and Southern Giant Petrel *Macronectes giganteus*; the open water assemblage included the Cape Petrel *Daption capense*, Blue Petrel *Halobaena caerulea*, Kerguelen Pe-

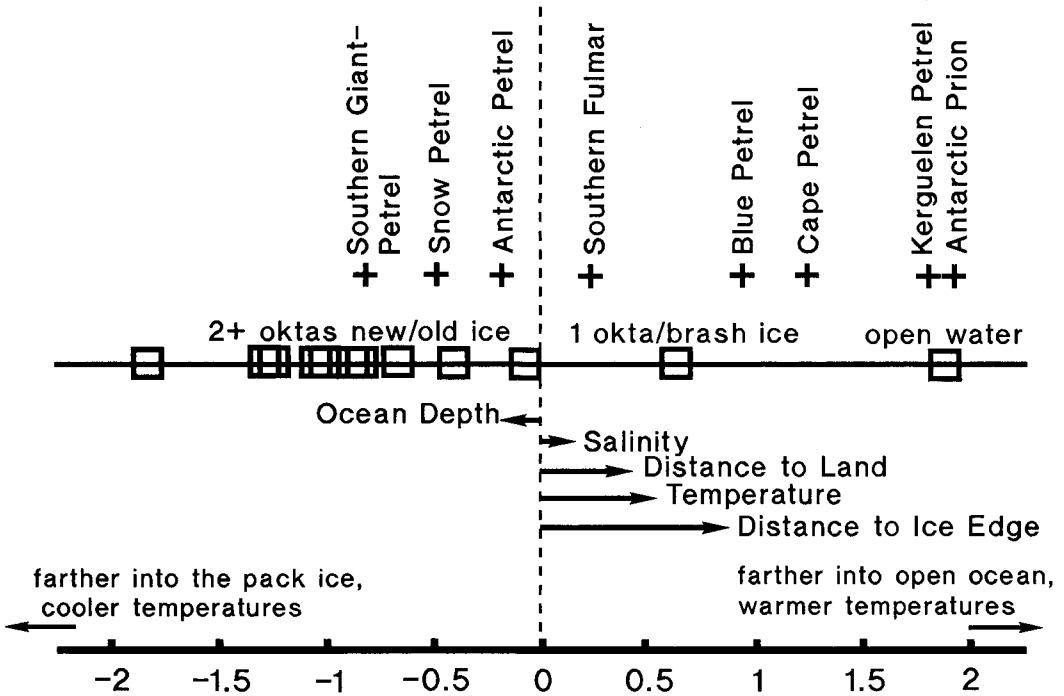


FIGURE 2. Biplot of first species/environmental axis from canonical correspondence analysis. The vertical line denotes the ice edge and the mid-point of the temperature gradient (relative scale at the bottom of the figure). Biplot scores for continuous environmental variables are presented as arrows; the longer the arrow, the more important the variable. Nominal ice variables are represented by squares with placement depending on centroid scores standardized along the top axis. The species' scores (with relative placement represented by species' names) are the weighted average of the projection points of the samples on the environmental arrows.

retel *Lugensa* (*Pterodroma*) *brevirostris* and Antarctic Prion *Pachyptila desolata* (interaction $F = 14.089$; $df = 1, 52$; $P < 0.001$; Fig. 2). Hereafter, we did not include Southern Giant Petrels in further analyses because of their infrequent occurrence in our study area and our difficulty in separating them in the field from their close congener, the Northern Giant Petrel *M. halli* (Ainley et al., in press), due to time constraints of our census method. Only one species-environmental axis was necessary to explain the relationship between the species and the physical variables (percentage variance explained by the first axis: 74% (COR) ($P < 0.001$), 69% (CCA) ($P < 0.001$); percentage of remaining variance explained by the second axis: 47% (COR) ($P > 0.10$), 23% (CCA). The important environmental variables (found in both analyses) were the presence or absence of ice and the distance-to-the-ice-edge, followed by SST (which itself is inversely related to distance-to-the-ice-edge, particularly in the open water direction from the edge) and dis-

tance-to-land. Two of the three species in the pack-ice group were explained by the analysis (percentage of the variance explained by the species composite: 20% [Antarctic Petrel], 85% [Snow Petrel]), as were three of the open-water group (percentage variance explained by the species composite: 16–53% [Antarctic Prion, Blue, and Kerguelen petrels]). The pack-ice group and the open-water group were clearly separated by ice and distance-to-the-ice-edge (Fig. 2).

NATURAL EXPERIMENT

Low-pressure centers passed along the northern edge of the Confluence at an interval of about one every week. While each storm front was approaching from the west, winds blew from the north over the warm Scotia Sea. The winds were warm enough to melt the pack and cause the ice edge to retreat about 200 km in fewer than two days. When the front passed, the winds switched to southerly and thus became colder; the sea surface froze overnight to shift the ice edge to its

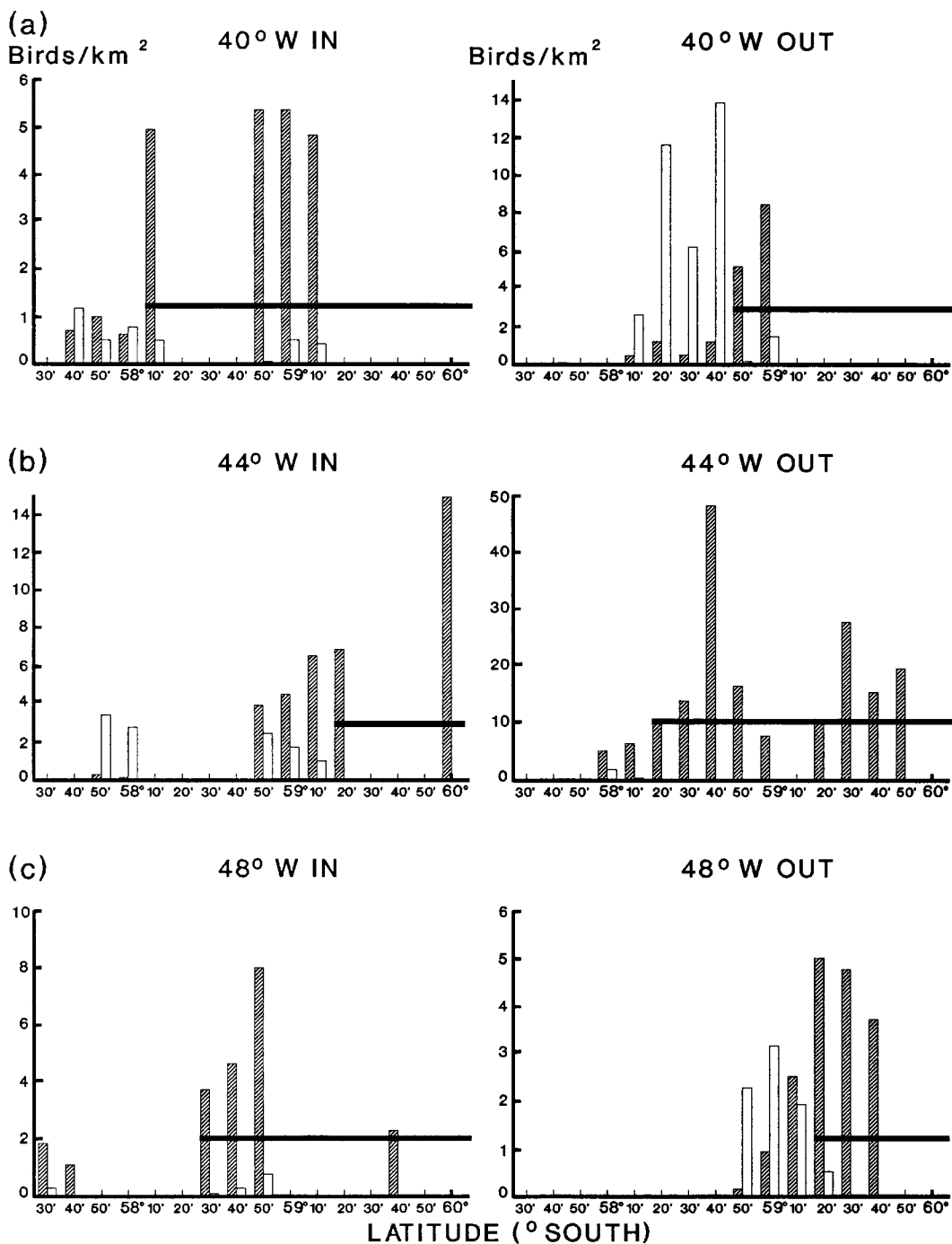


FIGURE 3. Densities of seabird species groups determined by 0.5 longitudinal-degree increments along three meridians, each one transited into and out of the ice pack: (a) 40°W, (b) 44° W, and (c) 48° W (see Fig. 1). The horizontal line depicts presence of pack ice; shaded bars represent the pack-ice species group and open bars the open-water species group.

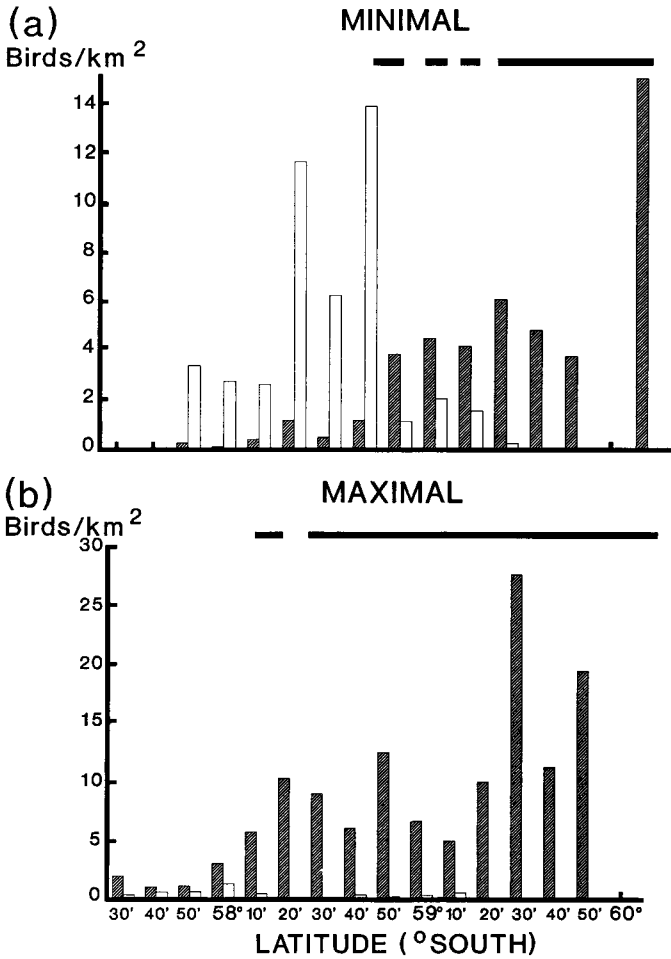


FIGURE 4. Species-group densities, ice-versus open-water assemblage, relative to ice extent, summarized for all north-south transects. The horizontal line depicts presence of (a) minimal and (b) maximal pack ice.

former, northernmost position. The refreeze produced ice 30–50 cm or more thick that almost entirely covered the sea surface (70% or heavier coverage) except at the outer edge of the pack ice (<25% coverage). This cycle produced a zone of dynamic pack ice about 200 km wide to the north of a zone of persistent ice (Fig. 1). For each longitudinal oceanographic line, at 40°, 44° and 48° W, the northward extent of the pack ice differed appreciably during our southward and northward excursions (Fig. 3).

The distribution along the transects of the two species groups changed according to the extent of pack ice. The group—Antarctic Petrel, Snow Petrel, Antarctic Fulmar—had significantly higher densities in the ice for each ship track ($P <$

0.05, all tests). Conversely, the group—Cape Petrel, Blue Petrel, Antarctic Prion—had significantly higher densities in open water for five of the six tracks ($P < 0.05$ for each track, except for the southward track on 40° W, where $P = 0.19$; Figs. 3, 4).

SEABIRD DIET

The myctophid fish, *Electrona antarctica*, comprised >61% of the diet for all seabirds except the Southern Giant Petrel, which fed entirely on carrion. Except for Antarctic Petrel (62%) and Cape Petrel (71%), *E. antarctica* contributed >91% of the diet for the other species. Additional prey included one species of squid, three of crustaceans, and three other mesopelagic fish

TABLE 1. Indices of overlap in the diets of seabirds in the Scotia-Weddell Confluence, winter 1988; diet composition is determined by weight (n = number of samples).

	n	FUSO	PEAN	PEBL	PETC	PETS	PTKG
Southern Giant Petrel	1	0.000	0.000	0.000	0.000	0.000	0.000
Southern Fulmar	11	—	0.874	0.995	0.952	0.999	0.995
Antarctic Petrel	30	—	—	0.849	0.945	0.867	0.917
Blue Petrel	8	—	—	—	0.929	0.997	1.000
Cape Petrel	12	—	—	—	—	0.948	0.929
Snow Petrel	46	—	—	—	—	—	0.997
Kerguelen Petrel	1	—	—	—	—	—	—

(which like *E. antarctica*, migrate to the surface at night; see Ainley et al. 1991 and 1992 for further details.). Sample sizes for Southern Giant Petrel and Kerguelen Petrel were small but diet composition did not differ from individuals of these species collected in other seasons in the study area (Ainley et al. 1992) nor from those collected at sea elsewhere in the Antarctic (Ainley et al. 1984, 1992).

Diet overlap exceeded 0.848 in comparisons among all species, except for those with Southern Giant Petrel, where the overlap index was 0.000 (Table 1). Size of prey did not differ significantly either (Ainley et al. 1992). Obviously, diets were highly similar.

Other than the selection of myctophids over the more abundant euphausiids in both habitats, the composition of seabird diets reflected the relative abundance of the various prey species in the water column (Ainley et al. 1992). In both the pack ice and the open water, the composition and relative abundance of potential prey in the micronektonic fauna was similar; the only major difference in prey availability was the shallower occurrence of organisms in waters covered by ice (Lancraft et al. 1989, 1991; see also Ainley et al. 1986).

DISCUSSION

The open-water and pack-ice assemblages overlapped in space but not time, depending on whether or not pack ice covered the "common" water. As noted above, species composition of the pack-ice assemblage was the most persistent in space and time among seabird fauna thus far studied anywhere in the world ocean (Ribic and Ainley 1988/89). The pack-ice assemblage observed in this study also contained some additional species that did not appear in our experimental results. Emperor Penguins *Aptenodytes forsteri* and Adélie Penguins *Pygoscelis adeliae*

were not present in the dynamic pack-ice zone but were present farther into the pack (as determined on other legs of the cruise; Ainley et al., in press). Because of their reduced mobility, penguins likely found it difficult to cope with rapid changes in habitat and, thus, avoided the zone of variable ice cover. Similarly, the Chinstrap Penguin *P. antarctica* also resided just out of the dynamic pack ice zone, in this case in open water.

Results thus show *experimentally* that the boundary between the open-water and the pack-ice seabird assemblages in the Antarctic is determined by a physical environmental factor, the location of the pack ice edge, and not by differences in prey species' occurrence patterns. Such a conclusion had been deduced by inference from seasonal correlations (Ainley et al. 1992, in press). In the experiment there were no differences in either prey density or in prey type (Lancraft et al. 1989, 1991) to confound the separation of factors that were responsible for seabird species' residency. In that regard, results supported the contention that, when not constrained by breeding, seabirds forage opportunistically depending on the availability of prey in their preferred habitat (reviewed by Hunt and Schneider 1987; see also Ainley et al. 1991, 1992).

Can conclusions from our experiment be generalized to other avifaunas? Compared with pack ice, few other physical features anywhere in the world ocean form such a stark environmental boundary in surface waters. The most closely comparable situation is in the tropical Atlantic, where extensive mats of pelagic *Sargassum* provide a habitat physically distinct from the open water (Haney 1986a, 1986b). In the ice system, sea-surface temperature, an important seabird habitat variable elsewhere (e.g., Briggs et al. 1987, Hunt and Schneider 1987, Wahl et al. 1989), is also important, but this factor, too, is strongly driven by the presence or absence of ice, which

in this experiment was determined by air temperature.

Our results provide a clear example of a situation in which physical factors strongly affect species composition, although the way in which these factors exert their control and the reason that year-round resident, pack-ice species avoid open water require additional study (see below). Ainley et al. (in press) show that open-water species become much less abundant during winter, and Ainley et al. (1991) show that food availability at the surface decreases as well in open-water (but not in pack ice) at that time. Thus, there appears to be little reason for the pack-ice species to expand their habitat to include that left vacant by seasonal species. In general, the phenomenon appears analogous to that involving year-round, resident tropical landbird species, which remain in their respective niches even when adjacent habitats and niches are vacated seasonally by migrants (see Keast [1980] for a summary). The polar Southern Ocean and seabird habitats in general, however, are much less stable and less predictable as avian habitat than are tropical forests; an enormous seasonal contrast in productivity exists and biological resources are patchy when they are available (see Smith and Sakshaug 1990). In such a situation, one might expect physical features to determine species composition. The converse situation appears to be the tropical, terrestrial habitats, which are stable over a broad temporal scale and in which patchiness of resources is expressed at a much finer spatial scale (see review in Wiens [1989]).

We hypothesize that the pack-ice species, as a result of alteration in behavior, morphology and physiology, are able to exploit the opportunities present in the pack ice. Lacking these adaptations (some of which we discuss below), open-water species remain clear of the ice. Some of the possible adaptations involved are as follows:

First, the behavior of prey might be altered by the presence of pack ice, a situation that would require specialization in foraging behavior to allow successful exploitation. Several potential prey organisms rise closer to the surface under the ice than they do in the open water (Ainley et al. 1986), especially during winter (Ainley et al. 1991). Among the aerial pack-ice species, Snow and Antarctic petrels exhibit feeding techniques to surprise organisms who reside under ice floes and who at times stray close to floe edges (Ainley

et al. 1984). Snow Petrels, especially, have a wing shape that allows the high degree of maneuverability needed to fly along the irregular floe edges, as these petrels characteristically do (Griffiths 1983; Ainley et al. 1984; Spear, Ainley and Ribic, unpubl. data). Snow Petrels can also capture prey by ambush feeding, in which their cryptic plumage allows them to rest unobserved on the ice at floe edges. Among other pack-ice species, the Antarctic Petrel feeds by pursuit plunging, a behavior that allows it to fly rapidly and plunge head-long into the water of the ephemeral leads between floes, sometimes to appreciable depths. Whether or not any specialized feeding behaviors exist for species such as Antarctic Fulmars is unknown.

Second, pack-ice and open-water species could be adapted to different temperature regimes. This possibility requires much additional research but is suggested by the fact that all pack-ice species frequently rest and huddle on ice surfaces (floes and bergs). Such behavior is rare among the open-water species, even though ice bergs can exist well away from the pack ice. Finally, the wind patterns and swells that seabirds use to their advantage in flight on the open sea (Pennycuik 1987) are not available over the pack ice (Griffiths 1983). Thus, for this reason, too, aerial pack-ice species may possess different flight morphology than do aerial open-water birds, a subject we are currently investigating (Spear, Ainley and Ribic, unpubl. data).

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LITERATURE CITED

- ABRAMS, R. W., A. M. GRIFFITHS, Y. HAJEE, AND E. SCHOEPE. 1981. A computer-assisted plotting program for analyzing the dispersion of pelagic seabirds and environmental features. P.S.Z.N.I. Mar. Ecol. 2:363-368.

- AINLEY, D. G. 1977. Feeding methods of seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean, p. 669-685. *In* G. A. Llano [ed.], Adaptations within Antarctic ecosystems. Gulf Publ., Houston, TX.
- AINLEY, D. G., AND R. J. BOEKELHEIDE. 1983. An ecological comparison of oceanic seabird communities of the South Pacific Ocean. *Stud. Avian Biol.* 8:2-23.
- AINLEY, D. G., W. R. FRASER, AND C. A. RIBIC. 1987. AMERIEZ 1986: oceanic factors affecting the occurrence of seabirds in the Scotia and Weddell seas. *Antarc. J. U.S.* 22(5):172-173.
- AINLEY, D. G., W. R. FRASER, W. O. SMITH, T. L. HOPKINS, AND J. J. TORRES. 1991. The structure of upper level pelagic food webs in the Antarctic: effect of phytoplankton distribution. *J. Mar. Syst.* 2:111-122.
- AINLEY, D. G., W. R. FRASER, C. W. SULLIVAN, J. J. TORRES, T. L. HOPKINS, AND W. O. SMITH. 1986. Antarctic mesopelagic micronekton: evidence from seabirds that pack ice affects community structure. *Science* 232:847-849.
- AINLEY, D. G., E. F. O'CONNOR, AND R. J. BOEKELHEIDE. 1984. The marine ecology of birds in the Ross Sea, Antarctica. *Amer. Ornithol. Union, Monogr. No. 32.*
- AINLEY, D. G., C. A. RIBIC, AND W. R. FRASER. 1992. Does prey preference affect habitat choice in Antarctic seabirds? *Mar. Ecol. Progr. Ser.* 90:207-221.
- AINLEY, D. G., C. A. RIBIC, AND W. R. FRASER. *In press.* Ecological structure among migrant and resident seabirds of the Scotia-Weddell Confluence Region. *J. Anim. Ecol.* 63(2).
- AINLEY, D. G., AND C. W. SULLIVAN. 1989. AMERIEZ 1988: a summary of activities on board M/V *Polar Duke*. *Antarc. J. U.S.* 24(5):144-147.
- ASHMOLE, N. P. 1971. Seabird ecology and the marine environment, p. 223-287. *In* D. S. Farner and J. R. King [eds.], *Avian biology*, vol. 1. Academic Press, New York, NY.
- BRIGGS, K. T., W. B. TYLER, D. B. LEWIS, AND D. R. CARLSON. 1987. Bird communities at sea off California: 1975 to 1983. *Stud. Avian Biol.*, No. 11.
- BROWN, R.G.B., F. COOKE, P. K. KINNEAR, AND E. L. MILLS. 1975. Summer seabird distributions in Drake Passage, the Chilean fjords and off southern South America. *Ibis* 117:339-356.
- BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr. No. 72.*
- CLINE, D. R., D. B. SINIFF, AND A. W. ERICKSON. 1969. Summer birds of the pack ice in the Weddell Sea, Antarctica. *Auk* 86:701-716.
- CODY, M. L. [ED.]. 1985. *Habitat selection in birds*. Academic Press, New York.
- CONOVER, W. J. 1980. *Practical nonparametric statistics*, 2nd ed. Wiley and Sons, New York.
- DIAMOND, A. W. 1984. Feeding overlap in some tropical and temperate seabird communities. *Studies in Avian Biol.* 8:24-46.
- DIXON, W. J., M. B. BROWN, L. ENGELMAN, M. A. HILL, AND R. I. JENNRICH. 1988. *BMDP Statistical Software*. Univer. of California Press, Berkeley, CA.
- GITTINS, R. 1985. *Canonical analysis*. Springer-Verlag, New York.
- GRIFFITHS, A. M. 1983. Factors affecting the distribution of the Snow Petrel (*Pagodroma nivea*) and the Antarctic Petrel (*Thalassoica antarctica*). *Ardea* 71:145-150.
- HANEY, J. C. 1986a. Seabird segregation at Gulf Stream frontal eddies. *Mar. Ecol. Progr. Ser.* 28: 279-285.
- HANEY, J. C. 1986b. Seabird patchiness in tropical oceanic waters: the influence of *Sargassum* "reefs." *Auk* 103:141-151.
- HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *Amer. Nat.* 100: 419-424.
- HUNT, G. L., JR., P. J. GOULD, D. J. FORSELL, AND H. PETERSON, JR. 1981. Pelagic distribution of marine birds in the eastern Bering Sea, p. 689-718. *In* D. W. Hood and J. A. Calder [eds.], *The eastern Bering Sea shelf: oceanography and resources*, vol. 2. Univ. Wash. Press, Seattle, WA.
- HUNT, G. L., JR., AND N. M. HARRISON. 1990. Foraging habitat and prey selection by Least Auklets at King Island, Alaska. *Mar. Ecol. Progr. Ser.* 65: 141-150.
- HUNT, G. L., JR., AND D. C. SCHNEIDER. 1987. Scale-dependent processes in the physical and biological environment of marine birds, p. 7-42. *In* J. P. Croxall [ed.], *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge Univ. Press, Cambridge, England.
- HUSBY, D. M., R. D. MEUNCH, AND J. T. GUNN. 1989. Oceanographic observations in the Scotia Sea marginal ice zone June-August 1988. U.S. Natl. Ocean. Atmos. Admin., Tech. Memo. No. NOAA-TM-NMFS-SWFC-127, La Jolla, CA.
- KEAST, A. 1980. Synthesis: the ecological basis and evolution of the nearctic-neotropical bird migration system, p. 561-576. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Instit., Washington, DC.
- LANCRAFT, T. M., J. J. TORRES, AND T. L. HOPKINS. 1989. Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). *Polar Biol.* 9:225-233.
- LANCRAFT, T. M., T. L. HOPKINS, J. J. TORRES, AND J. DONNELLY. 1991. Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during winter. *Polar Biol.* 11:157-167.
- MURPHY, R. C. 1936. *Oceanic birds of South America*. Macmillan, New York, NY.
- PENNYCUICK, C. J. 1987. Flight of seabirds, p. 43-62. *In* J. P. Croxall [ed.], *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge Univ. Press, Cambridge, England.
- PENNYCUICK, C. J., J. P. CROXALL, AND P. A. PRINCE. 1984. Scaling of foraging radius and growth rates in petrels and albatrosses. *Ornis. Scand.* 15:145-154.
- POCKLINGTON, R. 1979. *An oceanographic interpre-*

- tation of seabird distributions in the Indian Ocean. *Mar. Biol.* 51:9-21.
- RIBIC, C. A., AND D. G. AINLEY. 1988/89. Constancy of seabird species assemblages: an exploratory look. *Biol. Oceanogr.* 6:175-202.
- SMITH, W. O., AND E. SAKSHAUG. 1990. Polar phytoplankton, p. 477-526. *In* W. O. Smith [ed.], *Polar oceanography*. Academic Press, Orlando, FL.
- SPEAR, L., N. NUR, AND D. G. AINLEY. 1992. Estimating absolute densities of flying seabirds using analysis of relative movement. *Auk* 109:385-389.
- TASKER, M. L., P. HOPE JONES, T. DIXON, AND 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.
- TER BRAAK, C.J.F. 1988. CANOCO—a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (Version 2.1). Tech. Rept. LWA-88-02. Agricul. Math. Group, Wageningen, The Netherlands.
- TER BRAAK, C.J.F. 1990. Update notes: CANOCO Version 3.10. Agricul. Math. Group, Wageningen, The Netherlands.
- TER BRAAK, C.J.F., AND I. C. PRENTICE. 1988. A theory of gradient analysis. *Advances Ecol. Res.* 18:271-317.
- WAHL, T. R., D. G. AINLEY, A. H. BENEDICT, AND A. R. DEGANGE. 1989. Associations between seabirds and water masses in the northern Pacific Ocean in summer. *Mar. Biol.* 103:1-11.
- WIENS, J. 1989. *The ecology of bird communities*. Cambridge Univ. Press, Cambridge, England.