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Relationships of Pelagic Seabirds with the Southern Ocean Environment Assessed by Correspondence Analysis

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Spatiotemporal changes in pelagic seabird assemblages probably reflect changes in the dispersion of prey stocks (Croxall 1984). Direct observations of seabird-prey interactions are too rare to allow modeling on that basis alone (Griffiths 1982). Construction of a deterministic model of seabird-habitat relationships, which is linked to a similar prey-habitat interaction model, seems a practical approach to determining whether or not monitoring pelagic seabirds can be useful in the management of pelagic prey stocks. Such a model requires an understanding of the multiple cues used by seabirds for purposes of long-range navigation (Baker 1978) between areas of high prey density and seabird breeding colonies.

Seabird distribution in deep-sea areas has been related qualitatively to patterns of sea temperature, salinity, and weather (Murphy 1936, Salomonsen 1965, Brown et al. 1975, Pocklington 1979). Areas of peak seabird density coincide with oceanic areas reported to contain concentrations of food (Griffiths et al. 1982, Abrams 1985a). If these areas can be recognized by simple environmental parameters, then a descriptive model of seabird-habitat-prey relationships can be developed.

Linear regression techniques applied to seabird-habitat interactions have been insufficient, suggesting that models must include nonlinear relationships between seabird abundance and, for example, sea-surface temperature (Abrams 1982, 1983, 1985b). We report on a preliminary effort to use correspondence analysis to qualify the relationships of seabird abundance with temperature, wind strength, and weather parameters. The nature of nonlinear regression equations that may fit a deterministic model can be explored in this manner.

Data on seabird distribution and environmental variables were collected aboard the M.V. 'S. A. Agul-

has' during 16 February to 10 March 1981, as part of the First International BIOMASS Experiment (FIBEX). The cruise track ran between Cape Town and a grid study area bounded by 59° and 69°S and 15° and 30°E (Fig. 1). All birds flying past and passed by the moving ship (mean speed = 23.4 km/h) in a 1-km-wide transect were recorded as described by Griffiths (1981), during 1,445 10-min seabird observations (hereafter referred to as stations).

The predictability of the abundance of seabirds in four diet classes (plankton, squid, fish, mixed; see Appendix) in relation to environmental features was assessed at oceanic and regional scales by identifying the relative strengths of seabird associations with air temperature (AIR), water temperature (WAT), barometric pressure (BAR), wind strength on Beaufort scale (WIND), and weather (WEATH) coded from 1 (clear sky) to 6 (storm with rain or snow).
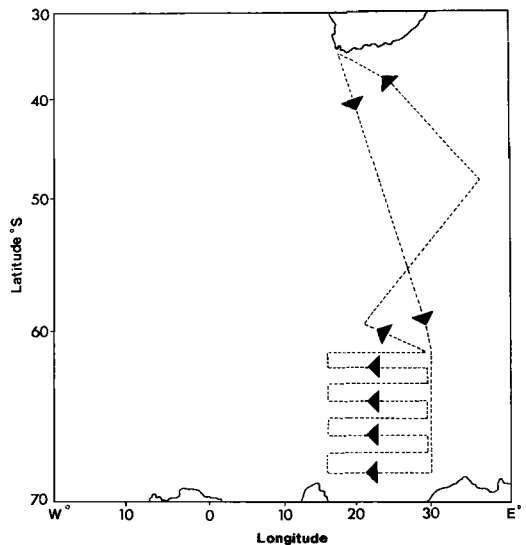

Fig. 1. African sector of the Southern Ocean showing FIBEX cruise track.

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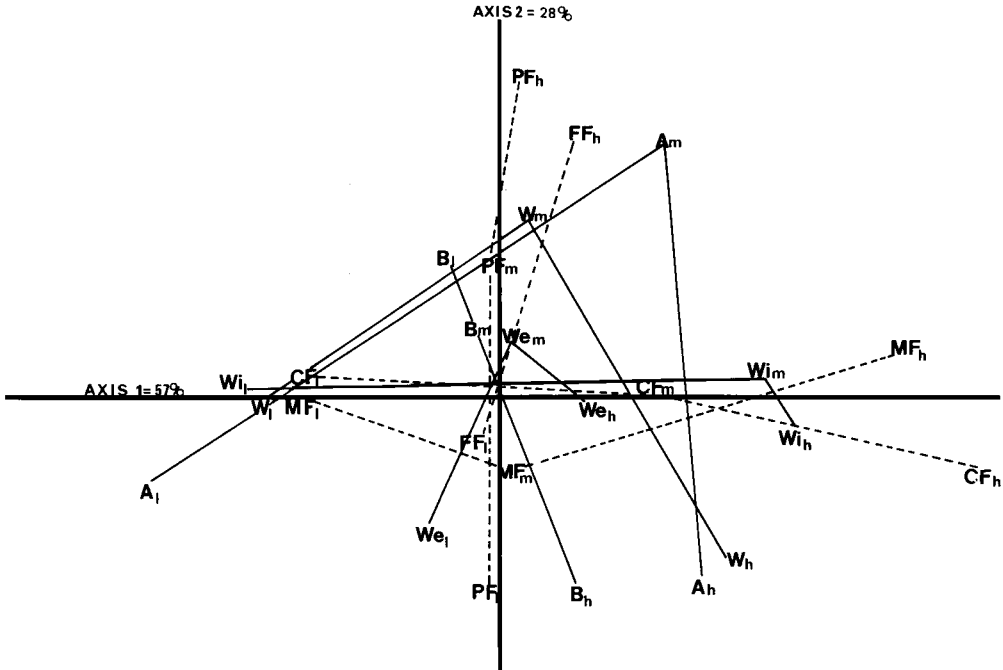
Fig. 2. Variability in seabird abundance (dashed lines; PF = plankton-eating species, CF = squid-eating species, FF = fish-eating species, MF = mixed-diet species) compared with variability in physical habitat parameters (solid lines; B = barometric pressure, A = air temperature, W = sea-surface temperature, Wi = windspeed, We = weather). The ranges for the variables are grouped as low (l), medium (m), or high (h).

Each of the variables (4 seabird and 5 environmental) was categorized on a three-point scale (high, medium, low), with cutpoints chosen so that as close as possible to ⅓ of the 1,445 data points for that variable fell into each category. The exception was the seabird diet class "fish feeders," which could be categorized only as high or low. The 9 original variables then became 15 environmental and 11 seabird variables. A 15 × 11 matrix, X, was produced, with element X_{ij} in row i and column j of X being the number of times environmental variable i and seabird group variable j co-occurred at the 1,445 stations.

The matrix X was then subjected to correspondence analysis (CA), a data analytic technique that displays the most important relationship between the rows and columns of the matrix (in this case the relationship between seabird diet classes and the environmental variables) and orders them from most to least important on a series of axes (Benzecri et al. 1973; Greenacre 1978, 1984; Greenacre and Underhill 1982). Plots can be made of pairs of axes, and the proportion of the information in the data matrix explained by each axis is determined.

Seabirds that take principally cephalopods or mixed diets occur on correspondence analysis axis 1, which accounts for 57% of the total information content of the data matrix (Fig. 2). Species that generally feed

on plankton and fish occur on CA axis 2, which accounts for a further 28% of the data matrix. Thus, the first two axes account for 85% of the information contained in the data. Species classes that sometimes occurred in large flocks, planktivores and piscivores, are independent (in terms of variables influencing their abundance) from the distribution of species that take cephalopods and mixed diets (corroborated by Griffiths et al. 1982).

Water and air temperature covary but define a nonlinear trend across CA axes 1 and 2 (Fig. 2). Temperature has a consistent association with seabird abundance based on linear analyses (Abrams and Griffiths 1981, Abrams 1985b). The CA results elaborate what have been statistically weak, but intuitively meaningful, seabird-habitat correlations. Seabird species that wander widely, and are predominant in the subtropical region (e.g. albatrosses and large petrels), coincide with the warm part of the air and water temperature curve (Abrams and Griffiths 1981, Griffiths et al. 1982, Abrams 1985b). Species that dominate the subantarctic and antarctic seas, feeding mainly on plankton and fish (e.g. prions, terns, small shearwaters, and petrels), are most abundant in association with sea-surface temperatures in the middle of the range of the areas covered by the FIBEX cruise (5–13°C). The CA suggests that the abundance of plank-

ton- and fish-eating birds may be related to temperature by a nonlinear function with a single mode (Fig. 3a, b).

Abrams and Griffiths (1981) and Griffiths et al. (1982) found relatively few of the planktivores from the Southern Ocean in the warm subtropical region. The north-south zonation of certain seabird species suggests that the Africa-Antarctica temperature gradient may be useful to the birds for navigation or orientation. Planktivores and piscivores dominated the avifauna in high latitudes (>50°S), and their abundance correlated with patches of relatively warm upwelled water in the vicinity of the "Antarctic Divergence." The curvilinear nature of seabird-temperature associations has been difficult to model (Abrams 1982, 1985b).

The contributions of weather and barometric pressure to strictly linear regression equations are weak (Abrams 1985b). Weather and wind strength show nonlinear associations with bird variables. Overcast, dry weather conditions associated with relatively high abundances of planktivores and piscivores correspond with the moderate temperatures in the CA results. This concurs with results from linear analyses that suggested that piscivores avoid bad weather and strong winds (Abrams 1983, 1985b). The results of correlations between planktivore abundance and weather in Abrams (1985b) are inconsistent, which previously suggested the curvilinear relationships elaborated by the CA (Fig. 2).

We found an association between low planktivore abundance and clear weather with high barometric pressure (Fig. 2). There may be a tendency among these species to leave an area of good weather in anticipation of incoming bad weather, as indicated by a correspondence between low barometric pressure (which accompanies a cold front) and planktivore abundance (Fig. 2). Mendelsohn (1981) found that prions (*Pachyptila*) avoided bad weather because sea-surface turbulence disperses plankton otherwise concentrated in the euphotic zone near the surface, during relative calm (Tranter 1977).

Nisbet and Drury (1968) considered that the more powerful correlates of bird migration density are parameters associated with the weather at the migrator's destination, implying that birds are adapted more to weather than to tolerance of current conditions. Unfortunately, our study does not allow discrimination between planktivore association with the leading and with the trailing edge of a weather system, but we suspect the birds can so differentiate. Further, carefully designed data collection (i.e. time-series analysis) is necessary to define the precise nature of the relationship of flocking species with the passage of weather systems.

Abrams (1983, 1985b) demonstrated that seabirds that take cephalopods and mixed diets pay only limited attention to weather, as might be expected for widely dispersed, meandering species that can go
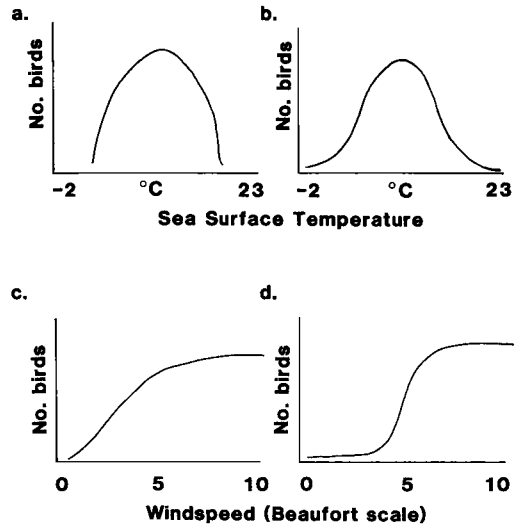

Fig. 3. Functional forms suggested by CA for modeling the relationship between temperature and abundance of (a) plankton- and (b) fish-eating seabirds and between windspeed and the abundance of (c) squid-eating and (d) mixed-diet seabirds.

relatively long periods between meals (Abrams 1985a). CA axis 1 suggests that squid-eating and mixed-diet seabirds are associated with moderate to high wind speeds (4–10 Beaufort scale, Fig. 2). Wandering Albatross (*Diomedea exulans*) in the Southern Ocean are associated with boundary areas between these wind speeds and low wind speeds (Abrams et al. 1982). The birds use wind, but do not seem constrained by it. Accordingly, the CA suggests that the abundance of seabirds that take principally squid and mixed diets is related to wind speed by a nonlinear function with an asymptote (Fig. 3c, d).

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APPENDIX.   Principal food classes, body mass (live weight), and percentage abundance (numbers of individuals) of pelagic species. Percentage abundance is presented for each species according to diet classes based on Ashmole (1971) and unpublished records from the FitzPatrick Institute, which also maintains records of bird weights.

	Mass (kg)	%
Plankton-eating		
Prions (*Pachyptila* sp.)	0.15	39.67
Blue Petrel (*Halobaena caerulea*)	0.21	11.57
Wilson's Storm-Petrel (*Oceanites oceanicus*)	0.04	0.36
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	0.05	0.01
Black-bellied Storm-Petrel (*Fregetta tropica*)	0.06	0.44
White-bellied Storm-Petrel (*Fregetta grallaria*)	0.05	0.01
European Storm-Petrel (*Hydrobates pelagicus*)	0.04	0.01
Diving petrels (*Pelecanoides* spp.)	0.12	0.18

APPENDIX. Continued.

	Mass (kg)	%
Squid-eating		
Wandering Albatross (*Diomedea exulans*)	8.60	0.27
Black-browed Albatross (*Diomedea melanophris*)	3.50	0.28
Gray-headed Albatross (*Diomedea chrysostoma*)	3.60	0.11
Yellow-nosed Albatross (*Diomedea chlororhynchos*)	2.00	0.07
Shy Albatross (*Diomedea cauta*)	4.10	0.18
Sooty Albatross (*Phoebetria fusca*)	2.50	0.22
Light-mantled Albatross (*Phoebetria palpebrata*)	2.70	0.32
Southern Fulmar (*Fulmarus glacialoides*)	1.00	0.17
Cape Petrel (*Daption capense*)	0.45	0.09
Great-winged Petrel (*Pterodroma macroptera*)	0.58	1.23
White-headed Petrel (*Pterodroma lessonii*)	0.75	0.72
Atlantic Petrel (*Pterodroma incerta*)	0.52	0.01
White-chinned Petrel (*Procellaria aequinoctialis*)	1.21	6.57
Gray Petrel (*Procellaria cinerea*)	1.03	0.11
Greater Shearwater (*Puffinus gravis*)	0.95	0.34
Fish-eating		
Cory's Shearwater (*Calonectris diomedea*)	0.96	0.15
Sooty Shearwater (*Puffinus griseus*)	0.79	18.46
Little Shearwater (*Puffinus assimilis*)	0.23	0.21
Antarctic Tern (*Sterna vittata*)	0.14	0.20
Arctic Tern (*Sterna paradisaea*)	0.13	7.07
Common Tern (*Sterna hirundo*)	0.12	0.17
Mixed-diet		
Antarctic Giant-Petrel (*Macronectes giganteus*)	4.10	0.13
Antarctic Petrel (*Thalassoica antarctica*)	0.70	0.54
Snow Petrel (*Pagodroma nivea*)	0.30	0.86
Kerguelen Petrel (*Pterodroma brevirostris*)	0.33	4.75
Soft-plumaged Petrel (*Pterodroma mollis*)	0.31	4.10
Great Skua (*Catharacta skua antarctica*)	1.63	0.01
Pomarine Jaeger (*Stercorarius pomarinus*)	0.67	0.01
Parasitic Jaeger (*Stercorarius parasiticus*)	0.53	0.01

An Alternative Method for the Analysis of Emlen Funnel Data

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The blotter paper funnel orientation cage invented by Emlen and Emlen (1966) is widely used in studies of avian migratory behavior. From the record of the birds' footprints one can determine a central tendency in the distribution of activity (e.g. a mean direction) and a measure of dispersion of the activity (e.g. a length of the mean vector, r) by using standard procedures of circular statistics (Batschelet 1981). We would also usually like to know whether the distribution of hopping differs significantly from random, i.e. whether r is significantly greater than 0. It is common practice to apply statistical inference tests (e.g. Rayleigh or V-test) to the distribution of footprint records on a single funnel and then to discrim-

inate between tests showing "significant" orientation and those in which the null hypothesis of randomness could not be rejected. Unfortunately, the use of such inference tests is not valid in this case, but the procedure continues to be used uncritically.

The basic problem is that a series of hops by an individual bird cannot be assumed to be independent. Thus, no matter how the sector densities are determined (by visual examination, counting, sampling sectors, or photo-optical methods), the sample size (n) will be based on nonindependent data. Aside from various elaborate procedures to estimate when statistical independence occurs in a sequence of hops (see Hamilton 1966, Emlen 1969), there is no certain-