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Constancy of Seabird Species Assemblages: An Exploratory Look

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Abstract *The temporal and spatial persistence of seabird species assemblages is described from investigations using strip-censuses conducted on 10 cruises that traversed the South Pacific Ocean from tropical to antarctic regions as well as east to west. Several groups of pelagic seabird species persisted over time and between widely spaced localities. Another group, that of the Peruvian upwelling region, was restricted spatially. Sea-surface temperature was the primary factor explaining variability in species group composition; secondary factors differed among regions, but included salinity, distance to land, water depth, and the presence of pack ice. The temperature-salinity relationship may not directly influence species occurrence, but rather may indicate a relationship to relative productivity of different water masses. Within species groups, ecological structure may be a function of prey size and type as mediated by predator body size and feeding behavior, respectively. These results from exploratory analyses of an existing data set indicate that more formal study of seabird species groups and their relationship to environmental variables should prove fruitful.*

Keywords Seabirds, community structure, weight ratios, species assemblages, habitat structure.

Introduction

According to the well-known maxim of community ecology, the physical heterogeneity of habitats affects the number of species present (e.g., Cody, 1974, 1985). This phenomenon, however, brings great complexity to the distributional patterns of species, a complexity that in turn affects our perceptions of species associations. If species associations appear to be in a state of spatial or temporal flux, questions arise as to the degree to which associations and interactions among species are important in affecting community structure and the evolution of individual adaptations (James & Boecklen, 1984). Such complexity led MacArthur (1972), for instance, to propose the possibility

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that distributions of terrestrial species in North America were the result of interactions with climate at their northern boundary and competitive interactions at their southern boundary. Unlike the less structurally complex terrestrial habitats such as grasslands, tundra, or desert, which are products of specific climatic regimes, the habitats of pelagic seabirds, though equally simple, stretch over the entire climatic spectrum, warm to cold and wet to dry (i.e., low to high salinity). Regardless of locality, seabird species diversity is low and is equivalent to that of birds in the simplest grassland habitats (Gould, 1971; Abrams & Griffiths, 1981; Ainley and Boekelheide, 1983). The apparent structural homogeneity of the ocean as bird habitat, regardless of climate, offers an opportunity to investigate constancy in species associations with minimum influence from changes in structural complexity at different boundaries of species or community distributions.

Our data set consists of information collected on several cruises that stretched from equatorial to antarctic waters in the Pacific Ocean. When the data were collected, we were aware of the studies by Brown et al. (1975) and Pocklington (1979) who had described the association of individual seabird species with particular types of surface water identifiable by temperature and salinity characteristics. The associations of species assemblages with particular water types, however, could not be detected in those studies, perhaps because of the limited geographic scope or the a posteriori merging of seabird and oceanographic data in the two studies, respectively. Alternatively, there may have been no constancy to species assemblages. A recent attempt by Wahl et al. (1989) to relate species assemblages to water types in the subarctic Pacific, and a review by Hunt and Schneider (1986), which emphasized how different spatial scales might affect the perception of seabird avifaunas, motivated us to attempt the analysis presented here.

Much work has been done on the constancy of species assemblages in marine plankton (e.g., see reviews in Longhurst, 1981; Dayton, 1984; Longhurst & Pauly, 1987). In general, distinct plankton communities, which persist in time and space, have been identified, and the spatial patterns of these communities have been found to resemble the major circulation-recirculation systems of the Pacific (McGowan, 1986). The mechanisms for maintenance of the groups within the communities, though, have not been identified (McGowan & Walker, 1985). We thought that seabirds would offer a good chance to investigate the phenomenon higher in the marine food web.

This article reports analyses of the densities of apex predators, seabirds, collected over several years in different parts of the South Pacific. We explore the degree to which assemblages of seabird species may constitute associations that persist through space and time. We also investigate some of the environmental and biological factors that may affect associations among seabirds of the pelagic habitat.

Methods

The cruises and methods of data collection are detailed in Ainley and Boekelheide (1983) and Ainley et al. (1984). Because of the latitudinal spread of three cruises (from the tropics to the Antarctic), resulting data sets were divided into tropical-to-subtropical and subantarctic-to-antarctic segments. Overall we had 10 cruise segments with which to work (Fig. 1). Hereafter, we refer to each segment as a "cruise." The definitions of broad climatic zones, e.g., tropics, are also shown in Figure 1.

Bird densities were estimated using standardized strip transect methods as described by Tasker et al. (1984) and modified slightly by Ainley and Boekelheide (1983). Number of transects per cruise can be found in Appendix 1. Density estimates for each species

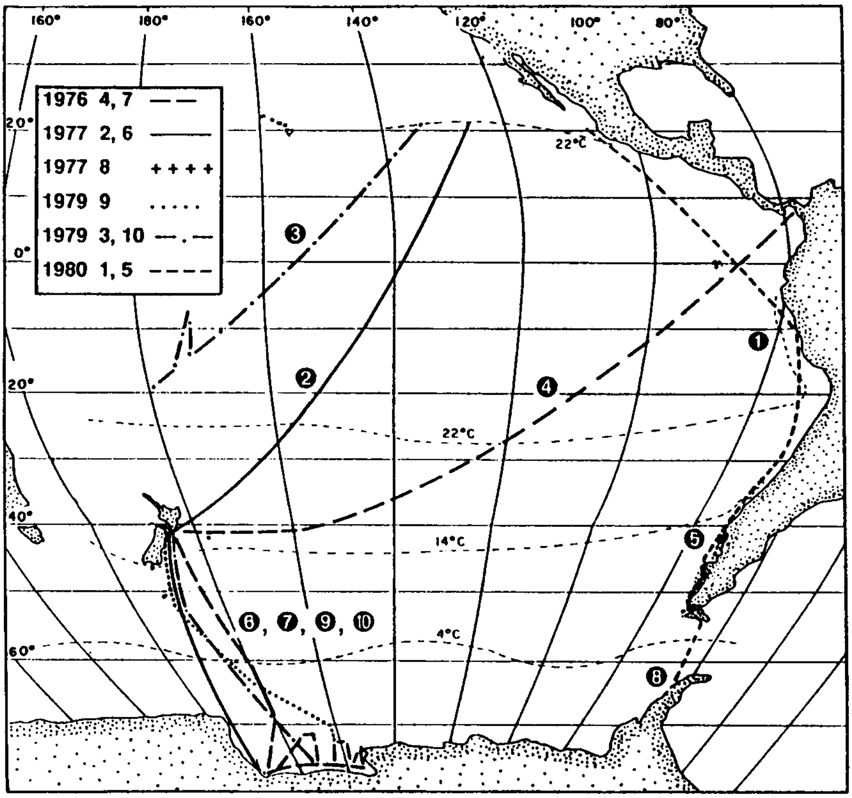

Figure 1. Ship tracks across the South Pacific, and the temperature-determined boundaries of climatic zones used in the analyses (4 °C = antarctic/subantarctic boundary; 14 °C = subantarctic/subtropical boundary; 22 °C = subtropical/tropical boundary). Numbers and temperature boundaries identify the cruises described in Appendix 1.

were based on half-hour transects 0.3 km in width and about 8 km in length, depending on the ship's speed during the census interval. Only censuses made when the ship was moving at least 10.6 km/hr were included. Consecutive transects, then, were an average of 8.8 km apart. We reduced complications that might arise because of breeding aggregations by considering only transects farther than 80 km from land. Only the common species, those seen on more than 5% of the transects, were analyzed. All densities were analyzed as ln (density + 1). The scientific and common names of the species are contained in Appendix 1.

The following environmental variables were collected for each transect on all but one cruise: sea-surface temperature (°C) and salinity, ocean depth (m), distance from land (km), and presence of pack ice; on the one cruise temperature and salinity data were not available. At one time or another, each of these factors, separately and in various combinations, has been considered an important determinant of the observed spatial stratification of seabirds (Murphy, 1936; Brown et al., 1975; Pocklington, 1979; Pennycuick et al., 1984; Haney, 1986; Briggs et al., 1987). In addition, *sigma*-t, a measure of water density (kg m^{-3}) using temperature and salinity, was used as an alternative to temperature and salinity in a separate analysis. Water density is important because of its effects on the circulation and dynamics of water masses.

We employed cluster analysis in the spirit of hypothesis generation (Cormack, 1971) and used three different methods to measure the similarity or dissimilarity of species pairs. The first was correlation, used when variables are of the same scale (Cormack, 1971; Seber, 1984), a quality that holds for bird densities. The second was Jaccard's Index, based on presence/absence of a species (Everitt, 1980) and used to investigate the groupings on a large scale as well as to help deflate any extreme densities. The last measure was a metric, Euclidean distance on standardized densities. Clustering algorithms included average and complete linkage and Ward's method (for distance only; see Seber, 1984). Average linkage does not dilate or shrink the variable space and is the most commonly used algorithm; complete linkage, which dilates the space, can sharpen cluster boundaries and is useful for exploratory analysis; and Ward's method is based on a minimization of sums of squares within a group and maximization between groups (Seber, 1984). We generated icicle plots and dendrograms, using SPSS-PC+ (Norusis, 1988) and BMDP7M (Dixon et al., 1983), in order to judge the number of clusters present. Because different measures and algorithms produce different clusters, common clusters were taken from a comparison of results in tabular format (Afifi & Clark, 1984). Common clusters were taken from the table when over half of the dendrograms were in agreement.

Although a number of species pairs repeated themselves in various clusters, for further analysis we considered only recurring groups of three or more species for comparison between cruises. Consideration of multispecies groups (three species or more) would more effectively lead us to conclusions about assemblage persistence. Within groups, we ranked species by body weight and calculated weight ratios between adjacent species. If weight is an indicator of size (and, ultimately, prey size), some information on size distribution within groups and potential resource-use overlap is gained (Isaacs, 1973; Diamond, 1986).

We used canonical correlation to investigate relationships between species groups and environmental variables. Measures used to assess the success of the canonical correlation included: intraset communalities (proportion of variance of individual species groups and environmental variables associated with their respective canonical variates), interset communalities (proportion of variance of individual species groups predictable from the environmental canonical variate), variance extracted (measure of how much variance was explained for all the species groups and all the environmental variables by their respective canonical variates), and redundancy (measure of how well the environmental canonical variates explained the overall variance of the species groups) (Gittins, 1985). Plots of the canonical variates were employed to assess the success of the canonical correlations and to identify possible nonlinearities (Gittins, 1985). We also investigated possible nonlinear relationships with univariate regressions (Draper & Smith, 1981), but none were found to significantly affect the analyses. We recognize the dangers of using canonical correlation over too long a gradient (Gittins, 1985), but we are applying the analysis in an exploratory way to identify common environmental variables and species-group relationships between cruises.

Results

Species Associations

We considered species to belong to separate groups if they were clustered together at level 2 or 3 of an icicle plot, depending on number of species; for an example, see

Figure 2. Because clustering depends on the entire variable set, comparisons between cruises in different latitudinal divisions was restricted. A review of groups in Appendix 1 shows immediately the overlapping associations of species that so confuses our perceptions of animal communities. For example, in high-latitude antarctic cruises 6 and 9 (both during summer; Appendix 1), sooty shearwater was not associated with white-chinned petrel. But the association existed in subantarctic cruise 5 during late fall.

Within latitudinal divisions, five species groupings persisted over time and change of place; a sixth appeared to be spatially confined (Table 1). The first set of cruises, tropical-to-subtropical, occurred at various times and in various locations; all crossed the central gyre of the South Pacific (Fig. 1). The first common group in the division (A1; Table 1) consists of species found in tropical waters; the second consists of species found in subtropical to tropical regions. The third group consists of species found in the subantarctic and subtropical regions. Thus the groupings in the tropical segment of the cruises appear to be related to latitudinal differences. There was only one cruise in the subtropical-to-subantarctic division (cruise 5, Appendix 1). It traversed the west coast to South America, and the first species group (B1) (Table 1) consisted of those unique to the upwelling zone of the Peru Current (see Murphy, 1936). Few of the B1 species were encountered elsewhere. The other two groups represented overlap between the tropical-to-subtropical division (B2) and the subantarctic-to-antarctic division (B3) (Table 1).

The most persistent associations occurred in the subantarctic-to-antarctic division. Group C1 (Table 1) was the strongest, consisting of six open-water species. All six grouped together in cruise 7 and all but one (white-chinned petrel) grouped in cruises 6, 9, and 10 (Appendix 1). Group C2 consists of pack-ice species (Table 1). All five species were grouped together in cruise 7 (Appendix 1). Three clustered together in cruise 6 (Adélie penguin, snow petrel, Wilson's storm-petrel), with antarctic petrel grouping with cape petrel (the fifth species, emperor penguin, was not seen). For cruise 9, the penguins were separated from the other three species (Appendix 1). The lower latitude antarctic cruise (cruise 8) had few species in common with the other cruises (Appendix 1). Cruise 8 occurred in the eastern (i.e., Drake Passage) rather than western Pacific, and no pack ice was encountered. Thus the weak overlap with groupings on other cruises was, in retrospect, not surprising. In addition some elements of South Atlantic faunas were evident in the Drake Passage, and these likely also affected the clusterings.

Hutchinsonian Weight Ratios

When we ordered species within groups by body weight and looked at between-species ratios for each latitudinal division, the median weight ratio for the tropical-to-subtropical division was 1.8, for the subtropical-to-subantarctic division, 1.5, and for the subantarctic-to-antarctic, 2.0. Many of the ratios were less than 2.1 (Fig. 3). On the basis of theoretical considerations, it has been hypothesized that pairs having weight ratios less than 2.1 may experience much niche overlap (Diamond, 1986, but see MacNally, 1988). Such species might compete for the same prey. However, if another niche dimension is considered, that represented by feeding method, when ratios less than 2.1 occur, species forage differently in 87.5% of the cases (n = 64 ratios) (Appendix 1). For instance, species that feed by seizing would take live prey. Feeding methods such as surface plunging, dipping, and aerial pursuit capture increasingly more lively prey. Plunging, pursuit plunging, and diving allow capture at increasingly deeper depths. For

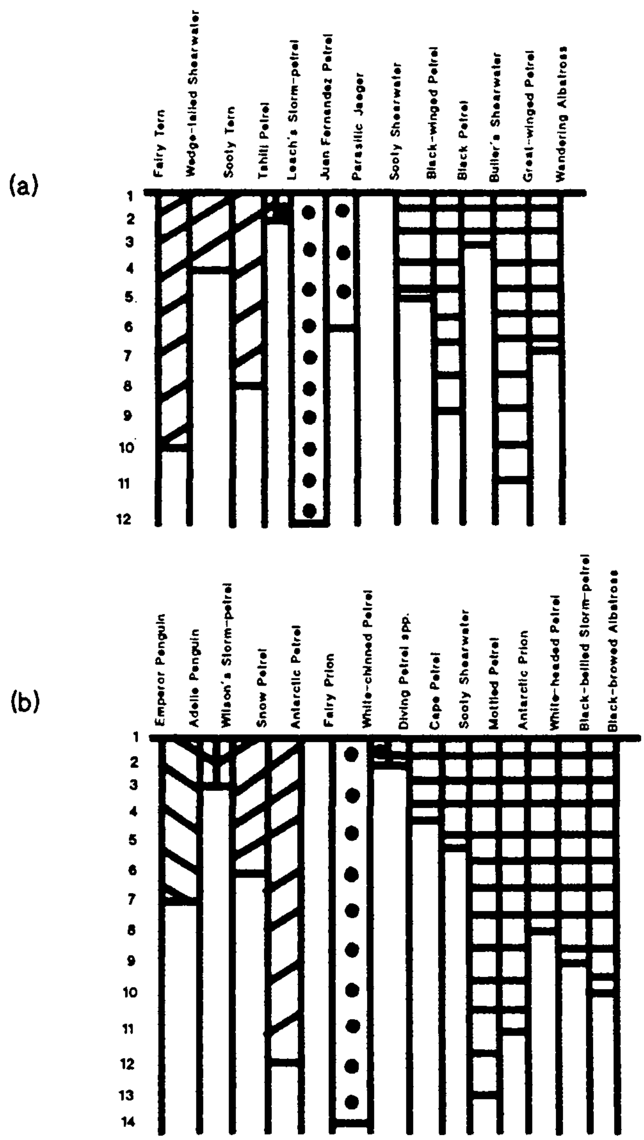

Figure 2. Examples of icicle plots resulting from (*a*) correlation/average linkage for cruise 2 and (*b*) Jaccard Index/complete linkage for cruise 8. Separate species groups using level 3 (*a*) and level 4 (*b*) are denoted by different crosshatching patterns.

species with the same feeding methods, ratios ranged between 1.0 and 1.5 ($n = 8$ ratios) (Appendix 1). Most of the species were from Group B1 (Table 1), the Peruvian Current, and are some of the least known of all seabirds.

Environmental Correlates of Species Associations

In general, the proportion of variance of the first species-group canonical variate explained by the first environmental canonical variant (using temperature and salinity) was large (>50%) (Table 2). The typical linear relationship between the variates is presented in Figure 4. The results using *sigma*-t instead of temperature and salinity were similar to those presented in Table 2 and are not presented here. See Appendix 2 for the mean and other summary statistics of the environmental parameters for each species group. We could account for over 50% of the variance in the species groups and the environmental variables for each cruise with the first two canonical variates (variance extracted, Table 2). However, how well the species groups were predicted by the first two environmental canonical variates was relatively low; total variance explained ranged from 19% to 48% (redundancy, Table 3).

Table 1

Latitudinal Summary of Repetitive Groups of Seabird Species Common to Cruises Done 1976–1980

A. Latitudinal division: tropical-to-subtropical
Data: 4 cruises—eastern Pacific, May 1980; eastern to western Pacific, November 1976 and 1977, March 1979

Group	Species
1	Sooty tern
	Wedge-tailed shearwater
	Tahiti petrel
2	Masked booby
	Wedge-rumped storm-petrel
	Leach's storm-petrel
3	Wandering albatross
	Black-winged petrel
	Great-winged petrel
	Sooty shearwater

B. Latitudinal division: subtropical-to-subantarctic
Data: 1 cruise—eastern Pacific, April–May 1980

Group	Species
1	Salvin's albatross
	Waved albatross
	Peruvian booby
	Elliot's storm-petrel
	Wedge-rumped storm-petrel
	Harcourt's storm-petrel
	Hornby's storm-petrel
	Markham's storm-petrel
2	Masked booby
	Leach's storm-petrel
3	Black-browed albatross
	Sooty shearwater

(Table continues on next page)

Table 1 (*continued*)

C. Latitudinal division: subantarctic-to-antarctic
Data: 4 cruises (high latitude): western Pacific, December 1976–January 1977, December 1977, December 1979–January 1980, February 1979; 1 cruise (low latitude): eastern Pacific (Drake Passage), February 1977

Group	Species
1	Black-browed albatross
	White-chinned petrel
	Antarctic prion
	White-headed petrel
	Sooty shearwater
	Black-bellied storm-petrel
2	Emperor penguin
	Antarctic petrel
	Adélie penguin
	Snow petrel
	Wilson's storm-petrel

Note. Latitudinal divisions follow Ainley and Boekelheide (1983) and are depicted in Figure 1.

Considering those environmental variables that had over 50% of their variance associated with the first two environmental canonical variates (Table 3), we see that temperature is important for all the cruises. Typically, temperature was associated with the first canonical variate for each cruise. For the other variables, the pattern is not as strong. For three of the four tropical-to-subtropical cruises, salinity and distance from land were important (Table 3). Typically, these variables were associated with the second canonical variate. For subantarctic-to-subtropical cruise 5, all environmental variables had more than 50% of their variance associated with the first two canonical variates (Table 3). Among antarctic-to-subantarctic cruises, salinity and depth to the ocean floor were important in two of the four cruises (Table 3).

Two to three species groups dominated the first two species-group canonical variates, with greater than 50% of the variance explained (intraset communality, Table 4). Over half of the individual species groups were explained moderately well by the environmental canonical variates (25–50% of variances explained) (interset communalities, Table 4). In general, the species groups not explained well by the analyses (Table 4) were those seen on the fewest transects (Appendix 2).

Discussion

Pelagic communities are especially interesting from the community perspective because organization seems to be different from substrate-associated communities (Dayton, 1984). The analytical explorations of the large data set in this study were useful as a way to generate ideas and tentative conclusions from which specific studies can be designed.

The species groups revealed through our analysis made biological sense. One species group represented a specialized community associated with pack ice or pack-ice-influenced ocean. Pack ice adds an element of habitat heterogeneity having no analog in lower latitudes (Murphy, 1936; Ainley et al., 1984). The pack ice assemblage may be one of the most spatially and temporally coherent at the megascale (> 1000 km) as well as at smaller scales; the same assemblage is also evident in the South Atlantic sector of the Antarctic, and at all seasons of the year (Ainley et al., unpublished data). The influence of the pack ice on the structure of seabird assemblages is a current area of research (Fraser & Ainley, 1986). A major hypothesis being tested is that physical habitat features (e.g., ice) are not as important as biological features (e.g., food web) in determining assemblages of apex predators.

Another species group, perhaps representing another specialized community, was associated with the Peruvian upwelling region. Environmental elements that set Peruvian

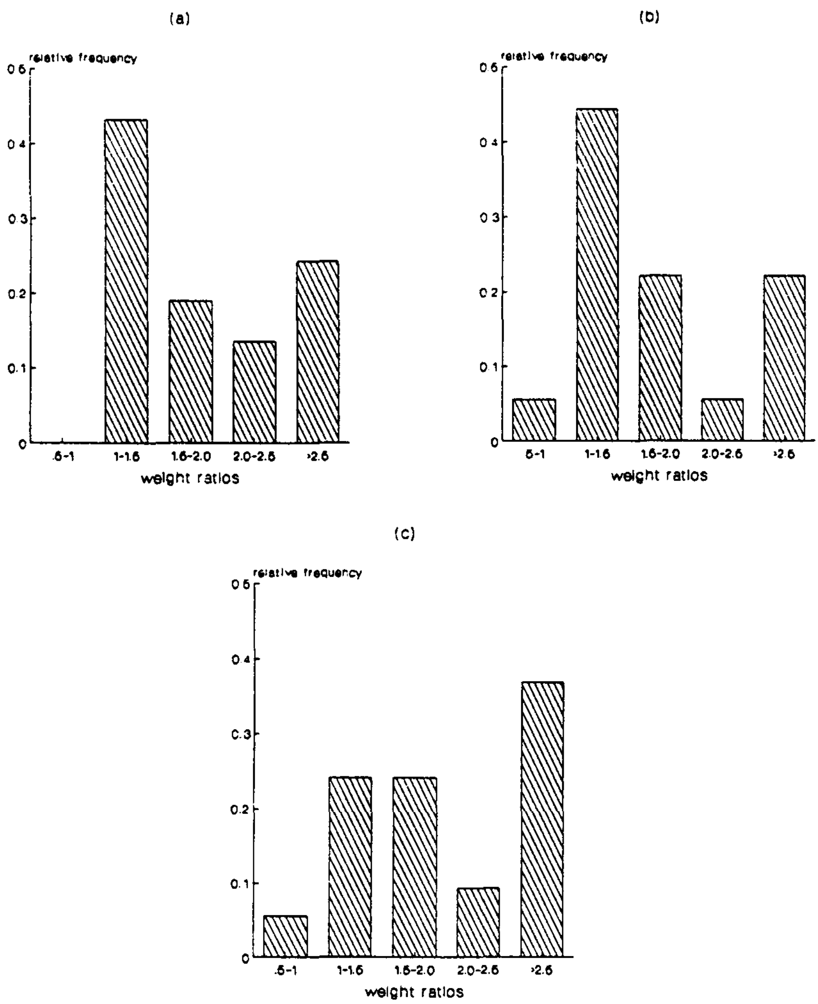

Figure 3. Histograms of weight ratios between adjacent pairs of seabirds ranked by weight for all species groups in the (*a*) tropical-to-subtropical division, (*b*) subtropical-to-subantarctic division, and (*c*) subantarctic-to-antarctic division.

Table 2
Correlations for the First Canonical Variates, as Well as Redundancy (for the species groups) and Variance Extracted for the First Two Canonical Variates

			Variance extracted	
Cruise[a]	First canonical correlation[b]	Redundancy	Species groups	Environmental variables
1	0.74 (.54)	0.24	0.53	0.66
2	0.73 (.53)	0.36	0.74	0.69
3	0.66 (.43)	0.19	0.65	0.69
4	0.83 (.69)	0.35	0.73	0.54
5	0.91 (.83)	0.39	0.52	0.82
6	0.89 (.79)	0.48	0.67	0.68
7	0.82 (.67)	0.30	0.59	0.49
9	0.88 (.77)	0.37	0.60	0.69
10	0.87 (.75)	0.41	0.62	0.51

[a]Cruise numbers refer to the cruises listed in Appendix 1.
[b]In parentheses is the proportion of variance explained by the first canonical variate.

waters apart from other regions surveyed, though not measured in the present study, might be shallow thermocline (a physical element that, like pack ice, might increase habitat heterogeneity; Briggs et al., 1987), decreased water clarity (Ainley, 1977), and enhanced productivity (Hayward & McGowan, 1979; Haney, 1986; Wahl et al., 1989). Further work on the Peruvian avifauna is also underway (Spear et al., unpubl. data). The work here is more descriptive, as we are attempting to quantify species assemblages and learn more about basic natural history.

The degree to which other species associations appeared to persist over space and time varied among the latitudinal regions. This could have been due to the nature of the data sets and particularly their grossly uneven coverage of different water masses, or to the confounding effects of abundant migratory species (note the inclusion of sooty shearwater and mottled petrel in a variety of antarctic to tropical groups; Appendix 1). There could also be real patterns involved, but with this data set there is no way to make a judgment. If it is possible to extrapolate from plankton studies (McGowan & Walker, 1979), we would hypothesize greater persistence among assemblages of the central gyre of the South Pacific.

Persistence of groupings from the cruise done in the eastern Pacific in April-May (cruise 1 of Appendix 1) to the others that crossed from east to west (cruises 2–4, done in November-March) does argue for some degree of constancy in these assemblages. The most persistent assemblages in the tropical-to-subtropical division could be assigned to limited temperature/salinity regimes. Oceanographers use temperature and salinity to characterize and distinguish water masses, but how direct the associations are between these factors and the limits of seabird ranges is not known. Water masses differ to some degree in productivity and this may well be an important link (Pocklington, 1979; Haney, 1986; Wahl et al., 1989). We would hypothesize that differences in ocean productivity, indexed by primary production but constrained by physical features, explains assemblage variation to an appreciable degree.

One additional factor adds support to the apparent reality of seabird species assemblages at the megascale. Even though the 1976 cruises (4 and 7) were done during El Nino-Southern Oscillation (ENSO), which would likely alter the position and quality of water mass boundaries, species associations appearing in that cruise were found in cruises done in other years and seasons. This is also the subject of current research in the eastern equatorial Pacific (Ainley et al., unpubl. data). We hypothesize, among other things, that when ENSO changes or obliterates water mass characteristics, that species associations do not change.

Among the various environmental factors correlated with the distribution of seabird

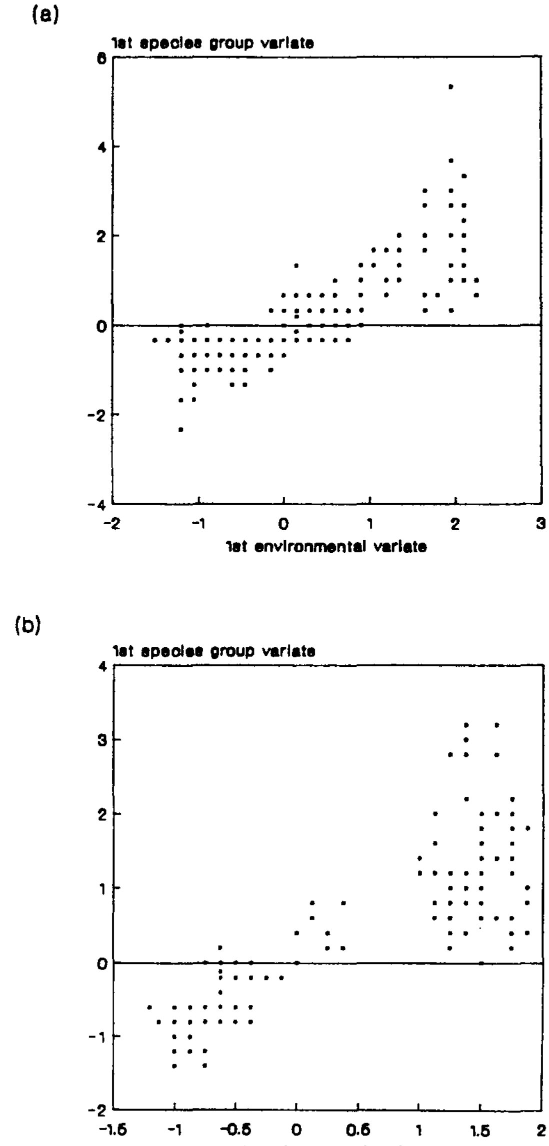

Figure 4. The linear relationship between the first set of canonical variates for (*a*) cruise 4 and (*b*) cruise 9.

groups, sea surface temperature explained the largest amount of variation in the groups. The secondary factors depended on latitudinal division. For the tropical-to-subtropical division, salinity and distance from land were of secondary importance. Ainley and Boekelheide (1983) suggested that salinity would be important due to the wider range of values in tropical waters resulting in more water types. The importance of distance-from-land may be due to the breeding season and may indicate that tropical/subtropical seabirds travel farther from breeding sites in search of food than do seabirds of cooler waters. There was no similar effect in cooler waters, apparently because our limitation of the data to transects done farther than 80 km from land effectively removed this effect. For the subantarctic-to-antarctic division, ocean depth was of secondary importance, a prediction made by Ainley and Boekelheide (1983) on the basis of the wide continental shelf of the region traversed and on the large proportion of diving species present.

What the factors are that bring structure within the species groupings requires much additional work. We hypothesize that one important factor is body size. Pelagic food webs are considered to be unstructured, compared to benthic and terrestrial ones, because size is a major factor that determines who eats whom (Isaacs, 1973). Our results indicate that size ratios among coexisting, marine apex predators might well prove illuminating Within each species group, except perhaps cruise 5 (subtropical-to-subantarctic segment) Group 1, which involved some of the least known of all seabirds, body sizes (and thus prey sizes) overlapped little and where they did, foraging behavior (and thus prey type) differed. Another behavioral dimension that cannot now be resolved is the degree to which species are diurnal or nocturnal foragers. This, for example, might resolve the apparent coexistence and niche overlap between certain albatross species. In any case, size and, secondarily, behavior also appear to organize communities of birds in the New Guinea rain forest

Table 3
Intraset Communalities for the First Two Canonical Variates for Environmental Factors

Cruise	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Presence of pack ice
		Tropical-to-subtropical			
1	0.87	0.32	0.75	0.72	
2	0.99	0.95	0.01	0.82	
3	0.65	0.55	0.80	0.78	
4	0.90	0.73	0.22	0.30	
		Subantarctic-to-subtropical			
5	0.95	0.85	0.88	0.59	
		Antarctic-to-subantarctic			
6	0.91	0.64	0.61	0.55	
7	0.93	0.47	0.27	0.30	0.46
9	0.94	0.37	0.97	0.45	
10	0.99	0.94	0.02	0.10	

Note. Cruise numbers refer to the cruises listed in Appendix 1.

Table 4
Intraset and Interset Communalities for the First Two Canonical Variates for the Species Groups

	Intraset communality species group					Interset communality species group				
Cruise	1	2	3	4	5	1	2	3	4	5
					Tropical-to-subtropical					
1	.21	.08	.94	.89		.08	.03	.50	.25	
2	.72	.99	.49			.37	.47	.24		
3	.42	.98	.55			.18	.20	.23		
4	.35	.90	.94			.15	.24	.64		
					Subtropical-to-subantarctic					
5	.97	.23	.12	.66	.65	.81	.15	.08	.43	.48
					Subantarctic-to-antarctic					
6	.70	.47	.90	.61		.48	.32	.64	.48	
7	.02	.89	.92	.50		.01	.27	.61	.32	
9	.73	.13	.91	.62		.38	.08	.69	.36	
10	.20	.58	.97	.70		.16	.20	.25		

Note. Cruise and species group numbers refer to the cruises and groups listed in Appendix 1, respectively.

(Diamond, 1986). The frequency distribution of the size ratios we observed, however, indicates that Hutchinsonian ratios may not apply (see also MacNally, 1988).

Hunt and Schneider (1987) speculated that physical environmental features should be of ultimate importance in defining seabird habitat at the megascale, and biological factors should be important at or below the mesoscale (100–1000 km). Haney (1986) argued that both are important at the mesoscale. On the basis of the present analysis, we hypothesize that at the scale of water masses (megascale), physical environmental features define seabird assemblages between water masses, and biological features may well define or structure them within water masses.

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Appendix 1

Results of Cluster Analysis Showing Species Groups on Each Cruise Segment, and a Listing of Latin Names, Body Weights (kg), and Feeding Methods

Latitudinal division: tropical-to-subtropical; cruise 1.
Eastern Pacific, May (fall) 1980 (n = 132)

Group	Species	Weight	Feeding method
1	Sooty tern *Sterna fuscata*	0.18	7,9
	Newell's shearwater *Puffinus newelli*	0.42	10,12
	Tahiti petrel *Pterodroma rostrata*	0.43	1
2	Townsend's shearwater *Puffinus townsendi*	0.40	10,12
3	Elliot's storm-petrel *Oceanites gracilis*	0.03	?1,2,6,7
	White-faced storm-petrel *Pelagodroma marina*	0.05	6,13
	Markham's storm-petrel *Oceanodroma markhami*	0.06	?1,2,6,7
4	Wedge-rumped storm-petrel *Oceanodroma tethys*	0.02	1,2,6,7
	Leach's storm-petrel *Oceanodroma leucorhoa*	0.04	1,2,6,7
	Dark-rumped petrel *Pterodroma phaeopygia*	0.41	8
	Red-billed tropicbird *Phaethon aethereus*	0.75	11
	Red-footed booby *Sula sula*	0.99	8,11
	Masked booby *Sula dactylatra*	2.07	11

Latitudinal division: tropical-to-subtropical; cruise 2.
Eastern to western Pacific, November (spring) 1977 (n = 234)

Group	Species	Weight	Feeding method
1	Black-winged petrel *Pterodroma nigripennis*	0.19	1,2,9
	Buller's shearwater *Puffinus bulleri*	0.38	2,7
	Great-winged petrel *Peterodroma macroptera*	0.52	1,2
	Sooty shearwater *Puffinus griseus*	0.79	10,12
	Westland petrel *Procellaria westlandica*	1.08	1,2,9,12
	Wandering albatross *Diomedea exulans*	8.0	1,2
2	Leach's storm-petrel	0.04	1,2,6,7
	Juan Fernandez petrel *Pterodroma externa*	0.43	8
	Parasitic jaeger *Stercorarius parasiticus*	0.46	14
3	Fairy tern *Gygis alba*	0.13	7
	Sooty tern	0.18	7,9
	Wedge-tailed shearwater *Puffinus pacificus*	0.39	8,9
	Tahiti petrel	0.43	1

Appendix 1 (*continued*)

Cruise 3. Eastern to western Pacific, March (spring) 1979 (n = 159)

Group	Species	Weight	Feeding method
1	Newell's shearwater	0.42	10,12
	Juan Fernandez petrel	0.43	8
	Parasitic jaeger	0.46	14
2	White-tailed tropicbird *Phaethon lepturus*	0.30	11
	Fairy tern	0.13	7
3	Sooty tern	0.18	7,9
	Wedge-tailed shearwater	0.39	8,9
	Leach's storm-petrel	0.04	1,2,6,7
	Sooty shearwater	0.79	10,12
	Mottled petrel *Peterodroma inexpectata*	0.32	1,2,9
	Bulwer's petrel *Bulweria bulwerii*	0.15	1,2,7
	Tahiti petrel	0.43	1
	Masked booby	2.07	11

Cruise 4. Eastern to western Pacific, November (spring) 1976 (n = 265)

Group	Species	Weight	Feeding method
1	Juan Fernandez petrel	0.43	8
	Red-tailed tropicbird *Phaethon rubicauda*	0.61	11
2	Wedge-rumped storm-petrel	0.02	1,2,6,7
	Leach's storm-petrel	0.04	1,2,6,7
	Masked booby	2.07	11
3	Gray-backed storm-petrel *Garrodia nereis*	0.03	6,7,9
	Fairy prion *Pachyptila turtur*	0.12	2,7
	Black-winged petrel	0.19	1,2,9
	Great-winged petrel	0.52	1,2
	Sooty shearwater	0.79	10,12
	Buller's albatross *Diomedea bulleri*	3.0	1,2
	Northern giant fulmar *Macronectes halli*	4.4	1
	Wandering albatross	8.0	1,2

(Table continues on next page)

Appendix 1 (*continued*)

Latitudinal division: subtropical-to-subantarctic; cruise 5.
Eastern Pacific, April–May (fall) 1980 (n = 81)

Group	Species	Weight	Feeding method
1	Wedge-rumped storm-petrel	0.02	1,2,6,7
	Elliot's storm-petrel	0.03	?1,2,6,7
	Harcourt's storm-petrel *Oceanodroma castro*	0.04	?1,2,6,7
	Hornby's storm-petrel *Oceanodroma hornbyi*	0.05	?1,2,6,7
	Markham's storm-petrel	0.06	?1,2,6,7
	Peruvian booby *Sula variegata*	1.25	11
	Waved albatross *Diomedea irrorata*	2.3	1,2
	Salvin's albatross *Diomedea cauta salvini*	3.3	1,2
2	Leach's storm-petrel	0.05	1,2,6,7
	Masked booby	2.07	11
3	Pomarine jaeger *Stercorarius pomarinus*	0.68	14
4	Wilson's storm-petrel *Oceanites oceanicus*	0.03	1,2,6,7
	Stejneger's petrel *Pterodroma longirostris*	0.20	1,2,9
	Swallow-tailed gull *Larus furcatus*	0.70	?7,9
	Pink-footed shearwater *Puffinus creatopus*	0.72	2,9,12
	Sooty shearwater	0.79	10,12
	White-chinned petrel *Procellaria aequinoctialis*	1.27	1,2,9,12
	Chilean skua *Catharacta chilensis*	1.35	2,9
	Black-browed albatross *Diomedea melanophris*	3.02	1,2
5	White-throated storm-petrel *Nesofregetta albigularis*	0.05	?1,2,6,7
	White-bellied storm-petrel *Fregetta grallaria*	0.06	6,7
	Cook's petrel *Pterodroma cooki*	0.20	1,2,9
	Buller's shearwater	0.38	2,7
	Juan Fernandez petrel	0.43	8
	Red-billed tropicbird	0.75	11

Latitudinal division: subantarctic-to-antarctic; cruise 6. (high latitude)
Western Pacific, December (spring) 1977 (n = 155)

Group	Species	Weight	Feeding method
1	Fairy prion	0.12	2,7
	Great-winged petrel	0.52	1,2
	White-chinned petrel	1.27	1,2,9,12
	White-capped albatross *Diomedea cauta cauta*	3.3	1,2
	Royal albatross *Diomedea epomophora*	6.6	1,2

Appendix 1 (*continued*)

Latitudinal division: subantarctic-to-antarctic; cruise 6. (high latitude)
Western Pacific, December (spring) 1977 (n = 155) (continued)

Group	Species	Weight	Feeding method
2	Cape petrel *Daption capense*	0.45	1,2,5,6
	Antarctic petrel *Thalassoica antarctica*	0.68	2,9,10
	Antarctic fulmar *Fulmarus glacialoides*	0.78	1,2
3	Wilson's storm-petrel	0.03	1,2,6,7
	Snow petrel *Pagodroma nivea*	0.37	2,9
	Adélie penguin *Pygoscelis adeliae*	4.2	8
4	Black-bellied storm-petrel *Fregetta tropica*	0.06	6,7
	Antarctic prion *Pachyptila desolata*	0.16	2,7,9
	Mottled petrel	0.32	1,2,9
	White-headed petrel *Pterodroma lessoni*	0.75	1,2
	Sooty shearwater	0.79	9,10,12
	Light-mantled sooty albatross *Phoebetria palpebrata*	3.0	?1,2
	Black-browed albatross	3.02	1,2
	Southern giant fulmar *Macronectes giganteus*	4.4	1

Latitudinal division: subantarctic-to-antarctic; cruise 7. (high latitude)
Western Pacific, December 1976–January (summer) 1977 (n = 311)

Group	Species	Weight	Feeding method
1	South polar skua *Catharacta maccormicki*	1.26	2,9
2	Mottled petrel	0.32	1,2,9
	Cape petrel	0.45	1,2,5,6
3	Black-bellied storm-petrel	0.03	6,7
	Antarctic prion	0.16	2,7,9
	White-headed petrel	0.75	1,2
	Sooty shearwater	0.79	9,10,12
	White-chinned petrel	1.27	1,2,9,12
	Black-browed albatross	3.01	1,2
4	Wilson's storm-petrel	0.03	1,2,6,7
	Snow petrel	0.37	2,9
	Antarctic petrel	0.68	2,9,10
	Adélie penguin	4.2	8
	Emperor penguin *Aptenodytes forsteri*	25.0	8

(Table continues on next page)

Appendix 1 (*continued*)

Cruise 8. (low latitude) Eastern Pacific, February (summer) 1977 (n = 26)

Group	Species	Weight	Feeding method
1	Light-mantled sooty albatross	3.0	?1,2
	Black-browed albatross	3.02	1,2
	Gray-headed albatross *Diomedea chrysostoma*	3.6	1,2
	Northern giant fulmar	4.4	1
	Wandering albatross	8.0	1,2
2	Wilson's storm-petrel	0.03	1,2,6,7
	Black-bellied storm-petrel	0.06	6,7
	Cape petrel	0.45	1,2,5,6
	Chinstrap penguin *Pygoscelis antarctica*	4.2	8
3	Diving petrel spp. *Pelecanoides ?urinatrix*	0.09	8
	Antarctic prion	0.16	2,7,9
	Rockhopper penguin *Eudyptes chrysocome*	2.5	8
4	Soft-plumaged petrel *Pterodroma mollis*	0.30	1,2,9

Latitudinal division: subantarctic-to-antarctic; cruise 9. (high latitude) Western Pacific, December 1979–January (summer) 1980 (n = 215)

Group	Species	Weight	Feeding method
1	Fairy prion	0.12	2,7
	White-chinned petrel	1.27	1,2,9,12
2	Adélie penguin	4.2	8
	Emperor penguin	25.0	8
3	Black-bellied storm-petrel	0.06	6,7
	Diving petrel spp.	0.09	8
	Antarctic prion	0.16	2,7,9
	Mottled petrel	0.32	1,2,9
	Cape petrel	0.45	1,2,5,6
	White-headed petrel	0.75	1,2
	Sooty shearwater	0.79	9,10,12
	Black-browed albatross	3.02	1,2
4	Wilson's storm-petrel	0.03	1,2,6,7
	Snow petrel	0.37	2,9
	Antarctic petrel	0.68	2,9,10

Appendix 1 (*continued*)

Cruise 10. (high latitude) Western Pacific, February (summer) 1979 (n = 146)

Group	Species	Weight	Feeding method
1	Wilson's storm-petrel	0.03	1,2,6,7
	Snow petrel	0.37	2,9
	South polar skua	1.26	2,9
	Light-mantled sooty albatross	3.0	?1,2
2	Black-bellied storm-petrel	0.06	6,7
	Fairy prion	0.12	2,7
	White-chinned petrel	1.27	1,2,9,12
3	Antarctic prion	0.16	2,7,9
	Mottled petrel	0.32	1,2,9
	Cape petrel	0.45	1,2,5,6
	White-headed petrel	0.75	1,2
	Sooty shearwater	0.79	9,10,12
	Southern giant fulmar	4.4	1
	Black-browed albatross	3.02	1,2

Note. In parentheses, n = the number of transects done. Weights and feeding methods from Ashmole (1971), Abrams and Griffiths (1981), Ainley and Boekelheide (1983), Harper et al. (1985), and our unpublished data. Feeding methods are as follows (see Harper et al., 1985): 1, scavenge; 2, surface seize; 3, surface filtering; 4, hydro-planing; 5, foot paddling; 6, pattering; 7, dipping; 8, aerial pursuit; 9, surface plunging; 10, pursuit plunging; 11, plunging; 12, surface diving; 13, pursuit diving; 14, piracy.

Appendix 2

Statistics for Environmental Variables for Groups of Species Per Cruise Segment as Found from Cluster Analysis (see Methods for details)

Cruise 1

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1 (sooty tern, Newell's shearwater, Tahiti petrel)					
mean	28.7	33.88	3687.9	226.6	21.315
s.d.	2.5	.84	580.3	83.5	1.18
median	29.8	34.1	3700	218	21.032
n	33				
2 (Townsend's shearwater)					
mean	27.6	34.17	2833.3	138.7	21.876
s.d.	3.3	1.00	859.4	69.7	1.648
median	29.3	34.15	2800	147	21.058
n	6				
3 (Elliot's storm-petrel, white-faced storm-petrel, Markham's storm-petrel)					
mean	23.6	34.83	3753.3	168.1	23.622
s.d.	2.3	.84	758.3	71.7	1.302
median	22.8	35.10	3700	179	24.116
n	30				
4 (wedge-rumped storm-petrel, Leach's storm-petrel, dark-rumped petrel, red-billed tropicbird, red-footed booby, masked booby)					
mean	26.5	34.17	3379.0	183.5	22.262
s.d.	3.0	1.01	928.7	105.3	1.600
median	27.2	34.17	3600	130	22.450
n	105				

Cruise 2

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1 (black-winged petrel, Buller's shearwater, great-winged petrel, sooty shearwater, black petrel, wandering albatross)					
mean	21.8	35.08	4997.6	444.1	24.288
s.d.	4.1	.42	954.3	286.1	1.247
median	20.1	35.15	5000	415	24.998
n	106				

Appendix 2 (*continued*)

Cruise 2 (continued)

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
2 (Leach's storm-petrel, Juan Fernandez petrel, parasitic jaeger)					
mean	25.3	34.71	4970.0	669.0	23.030
s.d.	2.9	.52	419.8	317.2	.878
median	25.9	34.60	5000	755	22.988
n	90				
3 (fairy tern, sooty tern, wedge-tailed shearwater, Tahiti petrel)					
mean	27.3	35.03	4989.2	560.3	22.643
s.d.	1.4	.70	355.4	405.0	.626
median	27.4	35.30	5000	478	22.636
n	65				

Cruise 3

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1 (Newell's shearwater, Juan Fernandez petrel, parasitic jaeger)					
mean	25.9	34.56	4658.4	612.3	22.737
s.d.	1.7	.31	215.3	238.5	0.401
median	25.7	34.50	4600	718	22.676
n	38				
2 (white-tailed tropicbird, fairy tern)					
mean	29.3	34.88	3689.3	120.5	21.907
s.d.	0.7	.32	1042.9	94.3	.380
median	29.2	34.80	4000	79	21.784
n	28				
3 (sooty tern, wedge-tailed shearwater, Leach's storm-petrel, sooty shearwater, Bulwer's petrel, Tahiti petrel, masked booby)					
mean	27.0	34.76	4230.5	396.6	22.537
s.d.	2.5	.39	873.1	348.2	.664
median	27.3	34.80	4600	229	22.589
n	155				

(Table continues on next page)

Appendix 2 (*continued*)

Cruise 4

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1 (Juan Fernandez petrel, red-tailed tropicbird)					
mean	23.3	35.85	4091.5	583.8	24.496
s.d.	1.0	.50	530.1	207.9	.320
median	23.4	36.00	4060	571	24.515
n	40				
2 (wedge-rumped storm-petrel, Leach's storm-petrel, masked booby)					
mean	24.0	34.35	3885.1	388.4	23.163
s.d.	1.4	1.45	762.7	289.2	1.451
median	23.5	34.55	4080	232	23.614
n	66				
3 (gray-backed storm-petrel, fairy prion, black-winged petrel, great-winged petrel, sooty shearwater, Buller's albatross, northern giant fulmar, wandering albatross)					
mean	16.0	34.73	4750.4	710.3	25.524
s.d.	2.8	3.30	1052.8	563.4	.503
median	14.7	34.60	5200	485	25.721
n	122				

Cruise 5

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1 (wedge-rumped storm-petrel, Elliot's storm-petrel, Harcourt's storm-petrel, Hornby's storm-petrel, Markham's storm-petrel, peruvian booby, waved albatross, Salvin's albatross)					
mean	21.9	35.16	3371.4	141.6	24.380
s.d.	1.1	.21	1931.3	76.6	.265
median	22.2	35.20	4400	170	24.286
n	35				
2 (Leach's storm-petrel, masked booby)					
mean	22.4	35.09	4666.7	208.7	24.201
s.d.	1.1	.31	302.5	43.5	.087
median	22.9	35.20	4500	197.5	24.170
n	12				

Appendix 2 (*continued*)

Cruise 5 (continued)

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
3	(pomarine jaeger)				
mean	17.0	34.15	4000	128.5	24.886
s.d.	.6	.06	0	4.5	.090
median	16.9	34.15	4000	127	24.904
n	4				
4	(Wilson's storm-petrel, Stejneger's petrel, swallow-tailed gull, pink-footed shearwater, sooty shearwater, white-chinned petrel, chilean skua, black-browed albatross)				
mean	19.7	34.61	3445.3	137.0	24.553
s.d.	2.5	.57	1505.6	68.3	.302
median	20.2	34.40	4000	129	24.502
n	64				
5	(white-throated storm-petrel, white-bellied storm-petrel, Cookilaria spp., Buller's shearwater, Juan-Fernandez petrel, red-billed tropicbird)				
mean	20.2	34.65	3995.2	158.3	24.463
s.d.	2.6	.56	1118.5	67.6	.311
median	20.3	34.50	4400	145	24.378
n	73				

Cruise 6

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1	(fairy prion, great-winged petrel, white-chinned petrel, white-capped albatross, royal albatross)				
mean	10.4	34.30	1555.0	130.4	26.348
s.d.	1.4	.04	1469.9	64.3	.240
median	10.5	34.30	1030	129.5	26.339
n	34				
2	(cape petrel, antarctic petrel, antarctic fulmar)				
mean	1.2	34.02	3012.1	173.0	27.185
s.d.	3.5	.17	939.2	65.5	.352
median	−.1	34.00	3200	159	27.237
n	42				

(Table continues on next page)

Appendix 2 (*continued*)

Cruise 6 (continued)

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
3 (Wilson's storm-petrel, snow petrel, Adélie penguin)					
mean	−.9	34.15	2056.2	103.0	27.479
s.d.	.4	.11	1213.9	42.1	.119
median	−1.0	34.20	2550	88.5	27.525
n	40				
4 (black-bellied storm-petrel, antarctic prion, mottled petrel, white-headed petrel, sooty shearwater, light-mantled sooty alabtross, black-browed albatross, southern giant fulmar)					
mean	5.9	34.05	2606.1	164.7	26.703
s.d.	4.7	.33	1494.3	67.7	.348
median	7.8	34.10	2400	159	26.682
n	33				

Cruise 7

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1 (south polar skua)					
mean	−.7	34.21	790.9	139.0	27.511
s.d.	1.2	.18	1015.5	96.7	.194
median	−1.2	34.30	600	118	27.602
n	25				
2 (mottled petrel, cape petrel)					
mean	5.9	34.05	2606.1	164.7	26.703
s.d.	4.7	.33	1494.3	67.7	.348
median	7.8	34.10	2400	159	26.682
n	33				
3 (black-bellied storm-petrel, antarctic prion, white-headed petrel, sooty shearwater, white-chinned petrel, black-browed albatross)					
mean	6.9	34.14	3366.4	266.0	26.708
s.d.	3.3	.25	1887.9	128.1	.291
median	7.0	34.20	4100	216	26.791
n	70				

Appendix 2 (*continued*)

Cruise 7 (continued)

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
4 (Wilson's storm-petrel, snow petrel, antarctic petrel, Adélie penguin, emperor penguin)					
mean	−1.0	34.13	1590.7	165.9	27.461
s.d.	.7	.19	1192.4	71.7	.166
median	−1.3	34.10	873.5	165	27.471
n	212				

Cruise 9

Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1 (fairy prion, white-chinned petrel)					
mean	10.5	34.30	1601.3	118.9	26.325
s.d.	1.9	.10	1658.2	89.7	.296
median	11.3	34.30	1200	92.5	26.196
n	30				
2 (Adélie penguin, emperor penguin)					
mean	−1.3	33.94	3082.0	251.1	27.320
s.d.	.4	.13	1562.3	98.3	.088
median	−1.5	33.90	3900	290	27.298
n	35				
3 (black-bellied storm-petrel, diving petrel spp., antarctic prion, mottled petrel, cape petrel, white-headed petrel, sooty shearwater black-browed albatross)					
mean	5.9	34.18	3422.8	227.4	26.8365
s.d.	4.2	.21	1830.5	161.3	.509
median	5.5	34.20	3400	165.5	26.816
n	98				
4 (Wilson's storm-petrel, snow petrel, antarctic petrel)					
mean	−.5	34.03	2754.3	220.1	27.345
s.d.	1.7	.19	1709.3	104.7	.224
median	−1.1	33.90	3200	212.5	27.298
n	120				

(Table continues on next page)

Appendix 2 (*continued*)

Cruise 10					
Group	Sea surface temperature	Sea surface salinity	Ocean depth	Distance from land	Sigma-t
1 (south polar skua, snow petrel, Wilson's storm-petrel, light-mantled sooty albatross)					
mean	.2	34.17	1882.2	188.7	27.418
s.d.	2.2	.14	1679.2	103.0	.279
median	−.4	34.20	800	195	27.518
n	70				
2 (fairy prion, black-bellied storm-petrel, white-chinned petrel)					
mean	9.2	34.25	1833.9	147.9	26.446
s.d.	3.9	.14	1537.0	122.5	.465
median	10.4	34.30	1400	110	26.344
n	28				
3 (wedge-tailed shearwater, black-winged petrel & Cookilaria spp.)					
mean	20.3	35.12	2124.2	116.5	24.631
s.d.	6.3	.65	823.2	25.5	1.1
median	24.2	35.50	1900	118	24.132
n	19				
4 (antarctic prion, cape petrel, southern giant fulmar, sooty shearwater, white-headed petrel, mottled petrel, black-browed albatross)					
mean	5.7	34.12	3312.6	228.7	26.802
s.d.	4.4	.17	1871.3	176.8	.490
median	5.7	34.10	4000	142.5	26.757
n	82				

Note. Cruise numbers are from Appendix 1; n = number of transects on which group was seen.

References

Abrams, R. W. and A. M. Griffiths, 1981. Ecological structure of the pelagic seabird community in the Benguela Current region. *Marine Ecology Progress Series* 5:269–277.

Afifi, A. A. and V. Clark, 1984. *Computer-aided Multivariate Analysis.* Lifetime Learning Publications, Belmont, California, 458 pp.

Ainley, D. G. and R. J. Boekelheide, 1983. An ecological comparison of seabird communities in the South Pacific Ocean. *Studies in Avian Biology* 8:2–32.

Ainley, D. G., E. F. O'Connor, and R. J. Boekelheide, 1984. The Marine Ecology of Birds in the Ross Sea, Antarctica. *American Ornithologist Union Monograph* No 32, 97 pp.

Ashmole, N. P., 1971. Seabird Ecology and the Marine Environment. In: D. S. Farner, J. K. King, and K. C. Parkes (eds.) *Avian Biology,* vol. 1. Academic Press, New York, 223–286.

Briggs, K. T., W. B. Tyler, D. B. Lewis, and D. R. Carlson, 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology* 11:1–74.

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.

Cody, M. L., 1974. *Competition and the Structure of Bird Communities.* Princeton University Press, Princeton, New Jersey, 318 pp.

Cody, M. L. (ed.), 1985. *Habitat Selection in Birds,* Academic Press, Orlando, Florida, 558 pp.

Cormack, R. M., 1971. A review of classification. *Journal of the Royal Statistical Society,* Series A 134:231-367.

Dayton, P. K., 1984. Processes Structuring Some Marine Communities: Are They General? In: D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle (eds.) *Ecological Communities: Conceptual Issues and the Evidence.* Princeton University Press, Princeton, New Jersey, 180-197.

Diamond, J., 1986. Evolution of Ecological Segregation in the New Guinea Montane Avifauna. In: J. Diamond and T. J. Case (eds.) *Community Ecology.* Harper and Row, New York: 98-125.

Dixon, W. J. (ed.), 1985. *BMDP Statistical Software.* University of California Press, Berkeley, 734 pp.

Draper, N. and H. Smith, 1981. *Applied Regression Analysis,* 2nd ed., John Wiley & Sons, New York, 709 pp.

Everitt, B., 1980. *Cluster Analysis,* 2nd ed., John Wiley, New York, 136 pp.

Fraser, W. R. and D. G. Ainley, 1986. Ice edges and seabird occurrence in Antarctica. *Bioscience* 36:258-263.

Gittins, R., 1985. *Canonical Analysis.* Springer-Verlag, New York, 351 pp.

Gould, P. J., 1971. Interactions of seabirds over the open ocean, PhD dissertation, University of Arizona, Tucson, 110 pp.

Haney, J. C., 1986. Seabird segregation at Gulf Stream frontal eddies. *Marine Ecology Progress Series* 28:279-285.

Harper, P. C., M. P. Croxall, and J. Cooper, 1985. A Guide to Foraging Methods Used by Marine Birds in Antarctic and Subantarctic Seas. *Scientific Committee for Antarctic Research BIOMASS Handbook* No. 24, 22 pp.

Hayward, T. L. and J. A. McGowan, 1979. Pattern and structure in an oceanic zooplankton community. *American Zoologist* 19:1045-1055.

Hunt, G. L. and D. D. Schneider, 1987. Scale-dependent Processes in the Physical and Biological Environment of Marine Birds. In: J. P. Croxall (ed.) *Seabirds: Feeding Ecology and Role in Marine Ecosystems.* Cambridge University Press, Cambridge, 7-42.

Isaacs, J. D., 1973. Potential trophic biomass and trace-substance concentration in unstructured marine food webs. *Marine Biology* 22:97-104.

James, F. C. and W. J. Boeklen, 1984. Interspecific Morphological Relationships and the Densities of Birds. In: D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle (eds.) *Ecological Communities: Conceptual Issues and the Evidence.* Princeton University Press, Princeton, New Jersey, 458-477.

Longhurst, A. R. (ed.), 1981. *Analysis of Marine Ecosystems,* Academic Press, New York, 741 pp.

Longhurst, A. R. and D. Pauly, 1987. *Ecology of Tropical Oceans.* Academic Press, New York, 407 pp.

MacArthur, R. H., 1972. *Geographical Ecology.* Princeton University Press, Princeton, New Jersey, 269 pp.

MacNally, R. C., 1988. On the statistical significance of the Hutchinsonian size-ratio parameter. *Ecology* 69:1974-1982.

McGowan, J. A., 1986. The biogeography of pelagic ecosystems. *UNESCO Technical Papers in Marine Science* 49:191-200.

McGowan, J. A. and P. W. Walker, 1985. Dominance and diversity maintenance in an oceanic ecosystem. *Ecological Monographs* 55:103-118.

Murphy, R. C., 1936. *The Oceanic Birds of South America*, American Museum of Natural History, New York, 1245 pp.

Norusis, M. J., 1988. *SPSS/PC+ Advanced Statistics V2.0.* SPSS Inc., Chicago, 343 pp.

Pennycuick, C. J., J. P. Croxall, and P. A. Prince, 1984. Scaling of foraging radius in petrels and albatrosses. *Ornis Scandinavia* 15:145–154.

Pocklington, R., 1979. An oceanographic interpretation of seabird distributions in the Indian Ocean. *Marine Biology* 51:9-21.

Seber, G. A., 1984. *Multivariate Observations*, John Wiley, New York, 686 pp.

Tasker, M. L., P. H. 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.

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. *Marine Biology* 103:1–11.