

AN ECOLOGICAL COMPARISON OF OCEANIC SEABIRD COMMUNITIES OF THE SOUTH PACIFIC OCEAN

DAVID G. AINLEY AND ROBERT J. BOEKELHEIDE¹

ABSTRACT.— Five cruises in the Pacific Ocean, passing through Antarctic, subantarctic, subtropical and tropical waters, were completed during austral summers and falls, 1976 to 1980. Over equal distances, species appeared or disappeared at a rate proportional to the degree of change in the temperature and salinity (T/S) of surface waters. In oceanic waters, the most important avifaunal boundaries were the Equatorial Front, or the 23°C isotherm, separating tropical from subtropical waters, and the pack ice edge. Much less effective boundaries were the Subtropical and Antarctic Convergences. The number of species in a region was likely a function of the range in T/S.

Antarctic pack ice and tropical avifaunas were the most distinctive in several respects, compared to Antarctic open water, subantarctic and subtropical avifaunas. Several factors were used to characterize seabird communities: varying with T/S and latitude were the number of seabird species, seabird density and biomass, feeding behavior, flight behavior, the tendency to feed socially and the amount of time spent foraging. There was little pattern in the variation of species diversity. Differences in the above characteristics of seabird communities were probably functions of the abundance and patchiness of prey, the availability of wind as an energy source, and possibly the number of available habitats.

How can one answer the question, "What is a tropical (or polar, etc.) seabird?" Is it merely a seabird that lives in the tropics, or are there distinctive characteristics that make a species supremely adapted to tropical waters but not to waters in other climatic zones? The question, though having received little attention, seems to us to be rather basic to understanding seabird ecology for a fairly obvious reason. The majority of seabirds that migrate, like their terrestrial counterparts, are not tropical. Rather, they nest in polar or subpolar regions. Unlike most landbird migrants, however, the majority of migrant seabird species avoid tropical/subtropical areas, fly quickly through them in fact, and spend most of their nonbreeding period in antipodal polar/subpolar areas. Thus, seabirds that frequent polar/subpolar waters while nesting "avoid" tropical waters. Conversely, seabirds that frequent tropical waters while nesting "avoid" polar/subpolar waters. Why this is so is at present difficult to say. This basic question, which it would seem concerns the characteristics that make a tropical, subtropical, subpolar or polar seabird so special, is difficult because we have few studies that compare regional marine avifaunas, or even that compare seabird species within families or genera across broad climatic zones. Instructive are analyses such as that by Nelson (1978), who compared a small family of tropical/subtropical seabirds on the basis of breeding ecology, or those by Storer (1960), Thoresen (1969), Watson (1968), and Olson and Hasegawa (1979) who, among others, described the convergent evolution of penguins and diving petrels in the south with auks and pelecaniformes in the north polar/

subpolar zones. Not available are studies designed to compare the marine ecology of seabird groups that span disparate climatic zones. To help alleviate this situation, we undertook a series of cruises that stretched from tropical to polar waters in the South Pacific Ocean. We compared characteristics of regional avifaunas to determine whether tropical marine avifaunas actually did differ in important ways from those in the subtropics, subantarctic and Antarctic. We were also curious about what ecological/behavioral/morphological factors might underlie any differences that became apparent.

METHODS

DATA COLLECTION

We made cruises aboard small U.S. Coast Guard ice breakers, 70-90 m in length, and aboard R/V *HERO*, about 40 m long, with the following itineraries (Fig. 1): NORTHWIND 1976 = USCGC NORTHWIND from Panama City, Panama (10 Nov 1976) to Wellington, New Zealand (30 Nov) and from there (12 Dec) to the Ross Sea, and ultimately Ross Island, Antarctica (19 Jan 1977); HERO 1977 = R/V HERO from Anvers Island, Antarctica to Ushuaia, Argentina (8-10 Feb 1977); GLACIER 1977 = USCGC GLACIER from Long Beach, California (11 Nov 1977) to Papeete, Tahiti (29-30 Nov) to Wellington (9 Dec) and from there aboard USCGC BURTON ISLAND by way of Campbell Island to Ross Island (12-25 Dec 1977); GLACIER 1979 = USCGC GLACIER from Ross Island (15 Feb 1979) to Wellington (25 Feb-3 March) to Sydney, Australia (8-13 March) to Pago Pago, Samoa (22-23 March) to Long Beach (5 April); NORTHWIND 1979 = USCGC NORTHWIND from Wellington (20 Dec 1979), by way of Campbell Island to the Ross Sea, and ultimately to Ross Island (8 Jan 1980); and HERO 1980 = R/V HERO from Ushuaia (17 April 1980) to Lima, Peru (3-10 May) to Long Beach (28 May). We will not discuss here portions of cruises in subpolar waters of the northern hemisphere (a total of about six

¹ Point Reyes Bird Observatory, Stinson Beach, California 94970.

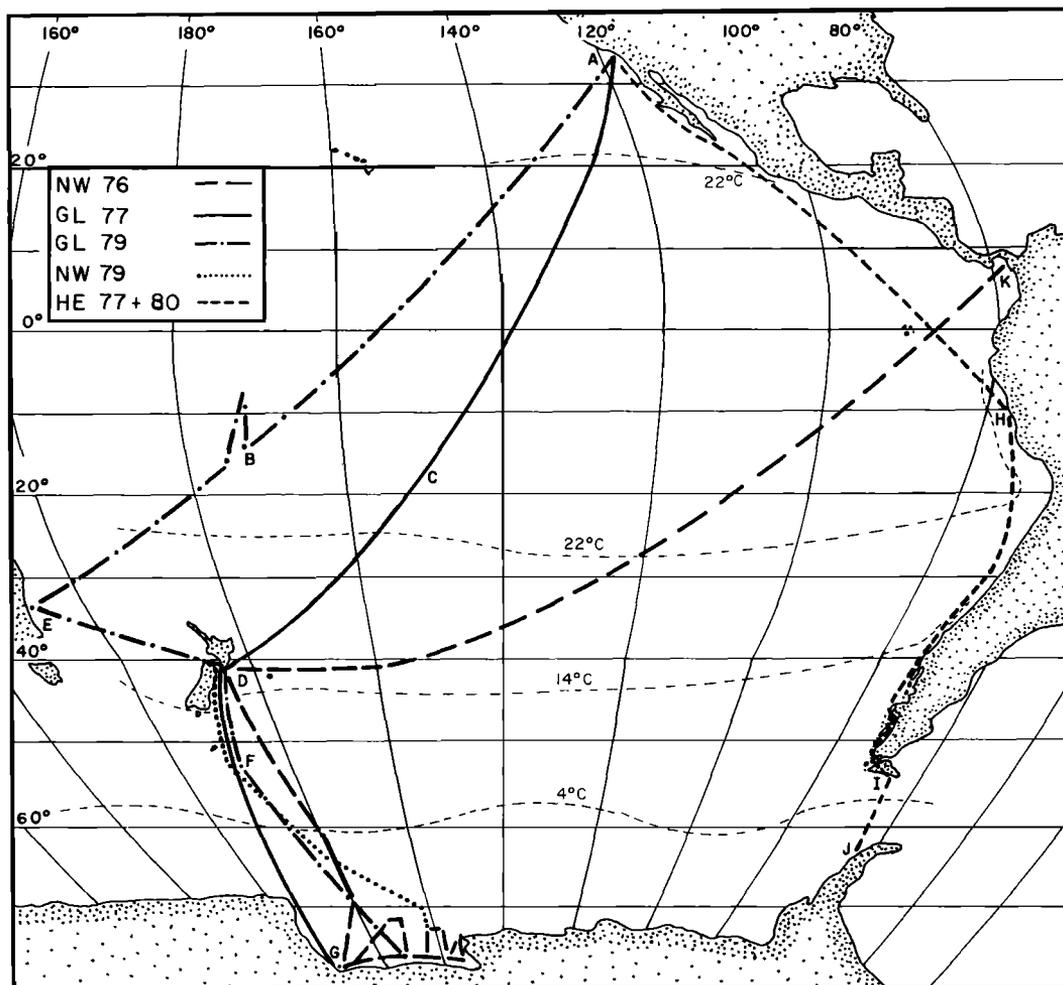


FIGURE 1. Routes of cruises; letters indicate stopping-off points: A, Long Beach, California; B, Pago Pago, Samoa; C, Tahiti; D, Wellington, New Zealand; E, Sydney, Australia; F, Campbell Island; G, Ross Island, H, Lima, Peru; I, Ushuaia, Argentina; J, Anvers Island; K, Panama City, Panama. Drawn according to Goode's homolosine equal-area projection.

days). Thus, from an austral perspective, all cruises occurred within the late spring to fall period. We generally had clear and calm weather, and on each cruise lost the equivalent of only one or two days of transects to poor visibility or impossible sea conditions. Virtually all the "lost" transects were in subantarctic waters.

On ice breakers, we made counts from the bridge wings, where eye level was about 16 m above the sea surface; on R/V HERO, we observed from the wings or front of the upper wheelhouse about 8 m above the sea surface. One 30-minute count, or "transect," was made during every hour that the ship moved at speeds of ≥ 6 kts during daylight (which increased from about 12 hours at latitude 0° to 24 hours south of latitude 60° S). In water free of pack ice, ice breakers cruised at 10–12 kts and R/V HERO at 8–9 kts. The total number

of transects (=30-min count periods) was as follows: NORTHWIND 1976 = 696, HERO 1977 = 46, GLACIER 1977 = 484, GLACIER 1979 = 544, NORTHWIND 1979 = 247, and HERO 1980 = 364. We made no counts when visibility was less than 300 m. We tallied only birds that passed within 300 m of whichever side (forequarter) of the ship we positioned ourselves to experience the least glare. Census width was determined using the sighting board technique described by Cline et al. (1969) and Zink (1981). We used binoculars (8×40) to visually sweep the outer portion of the transect zone every two to three minutes to look for small birds and for birds on the water. We firmly believe that transect widths wider than 300 m would strongly bias the data in favor of large birds, and that binoculars must be used to search for birds, instead of

using them merely as an aid to identification; otherwise, serious underestimates of bird density result (Wahl and Ainley, unpubl. data). On most transects, two observers searched for birds simultaneously. This was especially important in tropical waters where many species fly well above the sea surface. Distance traveled during each half hour transect, multiplied by census width, provides a strip of known area. This area divided into bird numbers provides an index of density. We counted birds that followed or circled the ship only if they initially flew to it out of the forequarter being censused; even so, each was allowed to contribute only 0.25 individuals assuming that they were likely attracted to the ship from up to 1 km or more away (i.e., about four times the census width away). The 300 m wide transect allowed inclusion of most birds that avoided approaching the ship closely. Density indices of a few species, however, in particular the Sooty Tern (*Sterna fuscata*) and some gadfly petrels (*Pterodroma* spp.), probably were slightly underestimated because of their tendency to avoid ships (R. L. Pitman, pers. comm.; Ainley, pers. obs.).

Immediately following each transect we measured sea surface temperature (SST) using a bucket thermometer, and on all cruises except the first halves of NORTHWIND 1976 and GLACIER 1977 we also collected a water sample to measure sea surface salinity (SSS), determined aboard ship using a portable salinometer. Following each transect, we recorded ship's position and speed, wind speed, sea conditions, depth, and distance to nearest land. All ships were equipped with satellite navigation. Every six hours, or sometimes more frequently, we recorded the thermal structure of the upper 400 m of the ocean by using an expendable bathythermograph. We entered all data into a SOLOS II microcomputer taken aboard ship on all cruises except those on R/V HERO (where data were entered after the cruise finished).

During transects, we kept a minute-by-minute tally of birds in a notebook, including information on behavior, molt or age, and later also entered these data into the computer. We recognized eleven feeding behaviors, as defined by Ashmole (1971) and modified by Ainley (1977) and Ainley et al. (1983). DIPPING: the bird picks prey from the sea surface, or just beneath it, either while remaining airborne (true *dipping*), contacting the water with the body for an instant (*contact dipping*), or contacting it with the feet (*pattering*). PURSUIT PLUNGING: the bird flies from the air into the water and then pursues prey in sub-sea surface flight. DIVING: the bird submerges from the surface to pursue prey beneath it using wings and/or feet for propulsion. SURFACE SEIZING: the bird catches prey while sitting on the surface although the bird could submerge much of its body in reaching down for prey. SCAVENGING: in which the bird eats dead prey, was included in surface seizing. SHALLOW PLUNGING: the bird hurtles head-long into the sea and submerges one to three body lengths as a result of momentum from the "fall." DEEP PLUNGING is similar but the bird "falls" from a greater height, assumes an extremely stream-lined posture, and consequently reaches much deeper depths. AERIAL PURSUIT: the bird catches prey that have leaped from the water and are airborne. PIRATING: where one bird chases another

to steal its prey, was observed too rarely to be significant relative to other methods.

DATA ANALYSIS

We assessed bird abundance by determining density (birds per km) and biomass. We used bird weights from the literature and from collected specimens in the case of several Antarctic species (Ainley et al. 1983), and multiplied density by weight to determine biomass. We calculated an index to species diversity using both density and biomass estimates. The Shannon-Weiner diversity formula is:

$$H = -\sum p \log p$$

where p is the proportion of the total density or biomass contributed by each species.

We compared feeding behavior on a zonal basis by determining the amount of avian biomass involved in various methods of prey capture. We were most interested in the relative aero- or hydrodynamic qualities of various methods which explains why we combined certain similar feeding methods (see above). For many species, the method used was determined by direct observation. If a species fed in more than one way its biomass was partitioned accordingly (Table 1). In the species for which we had no or only a few observations of feeding, we relied on data in Ashmole (1971).

We used the method of Cole (1949), which was also used by Harrison (1982), to determine the degree of species association in feeding flocks. The Coefficient of Interspecific Association, $C = (ad - bc)/(a + b)(b + d)$, and the variance, $s = (a + c)(c + d)/n(a + b)(b + d)$ where a is the number of feeding flocks (equals two or more birds feeding together) in which species A (the least abundant of the two species being compared) is present in the absence of B, b is the number of flocks where B is present in the absence of A, c is the number of flocks where both A and B occur together, d is the number of flocks where neither occur, and n equals the sum of the four variables $a, b, c,$ and d . We divided species among certain oceanographic zones before comparing their associations (see below).

MAJOR ZONES OF SURFACE WATER

We discuss here climatic zones, avifaunal barriers and species turnover relative to gradual changes in sea surface temperature (SST) and salinity (SSS). Of importance in the following discussion are Figures 2 and 3, which show the correspondence of climatic zones, as we define them, and various water masses. We define tropical waters as those having a SST of at least 22.0°C. These waters include the Tropical Surface Water

TABLE 1
PERCENTAGE OF INDIVIDUALS OBSERVED FEEDING BY VARIOUS METHODS^a

Species	n	Method					
		DIP	SEIZE	SHAL- LOW PLUNGE	DEEP PLUNGE	PUR- SUIT PLUNGE	AERIAL PUR- SUIT
<i>Diomedea melanophris</i>	3		100				
<i>Daption capense</i>	3		100				
<i>Pterodroma lessoni</i>	6		100				
Small <i>Pterodroma</i> ^b	9	33	67				
Medium <i>Pterodroma</i> ^c	12	56	9				35
Large <i>Pterodroma</i> ^d	10		100				
<i>Procellaria aequinoctialis</i>	3		100				
<i>Pr. westlandica</i>	6		100				
<i>Puffinus griseus</i>	383		11	29		60	
<i>P. pacificus</i>	71	78				17	
<i>P. bulleri</i>	28	80				20	
<i>P. nativitatus</i>	10	100					
<i>Bulweria bulwerii</i>	3	100					
<i>Pachyptilla turtur</i>	3	67	33				
Storm-Petrel ^e	26	100					
Storm-Petrel ^f	639	5	95				
<i>Oceanodroma leucorhoa</i>	49	88	12				
<i>Sula dactylatra</i>	12				100		
<i>S. sula</i>	15				60		40
<i>Phaethon rubricauda</i>	5				100		
<i>Ph. lepturus</i>	3				67	33	
<i>Fregata</i> spp. ^g	5	100					
<i>Stercorarius parasiticus</i>	5	100					
<i>Sterna fuscata</i>	210	91					9
<i>Sterna lunata</i>	12	58		42			
<i>Gygis alba</i>	14	100					
<i>Anous stolidus</i>	10	100					

^a See also Ainley et al. (1983) for similar observations on Antarctic species.

^b *Pt. longirostris*, *Pt. cookii*, and *Pt. hypoleuca/nigripennis*.

^c *Pt. e. externa*, *Pt. e. cervicalis*.

^d *Pt. phaeopygia*, *Pt. rostrata/alba*.

^e *Pelagodroma marina*, *Fregatta grallaria*.

^f *Oceanodroma markhami*, *O. tethys*, and *O. castro*.

^g *Fregata minor* and *F. ariel*.

($T \geq 25^{\circ}\text{C}$, $S < 34$ ppt) and Equatorial Surface Water ($T \geq 23^{\circ}\text{C}$, S 34–35 ppt) masses described by Wyrтки (1966), as well as “semitropical water,” i.e., warm, saline Subtropical Surface Water ($T \geq 22^{\circ}\text{C}$, $S \geq 35$ ppt). Characteristics of the thermocline also figure in defining tropical surface waters (e.g., Ashmole 1971), but we will not consider them in detail here; suffice it to say that our bathythermograph data roughly support the SST/SSS delineations of various climatic zones. The 23°C isotherm is usually considered to correspond approximately to the tropical-semitropical boundary in the South Pacific (Wyrтки 1964, Ashmole 1971). The 23°C isotherm is also at the cooler edge of the Equatorial Front. Because in our data, highly saline waters $\geq 22^{\circ}\text{C}$ shared Sooty Terns and Red-tailed Tropicbirds (*Phaethon rubricauda*) with “tropical waters,” we chose to include waters of that temperature in the tropical

zone. This in practice is not a significant departure from the usual definition. Perhaps because of our cruise tracks or when darkness happened to force our daily census efforts to end, we experienced SSTs between 22.0 and 22.9°C on only 2.5% of our transects (22 on NORTHWIND 1976, 4 on GLACIER 1977, 6 on GLACIER 1979, and 26 on HERO 1980; none on NORTHWIND 1979 or HERO 1977). Thus, in effect, our division of data between tropical and subtropical zones corresponded to Wyrтки’s definitions of the two zones. Pocklington (1979) also used the 22°C isotherm for the lowest temperature limit of tropical waters in the Indian Ocean.

At the other end of the marine temperature scale, the Antarctic Polar Front marks the transition between Antarctic and subantarctic waters. Within this frontal zone, where the really important features are subsurface (see Ainley et al.

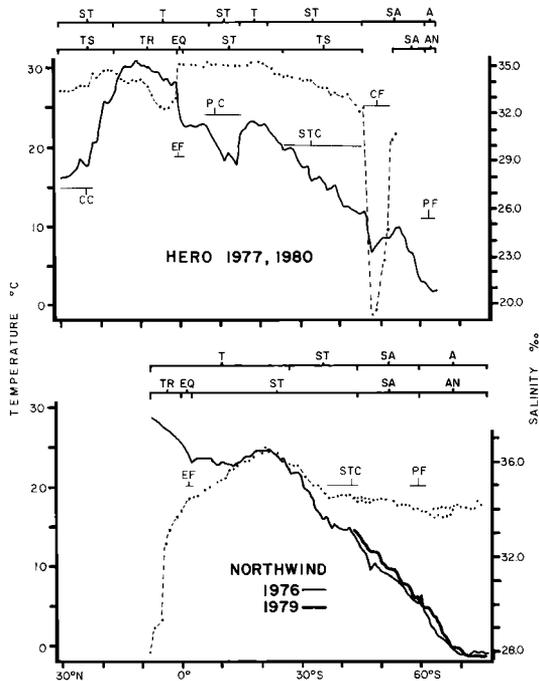


FIGURE 2. Change in sea surface temperature and salinity (T/S) with latitude along cruise tracks of NORTHWIND 1976 and 1979 and HERO 1977 and 1980. The two scales above each graph indicate the correspondence of T/S characteristics along cruise tracks with climatic zones (upper scale) and water masses (lower scale). Symbols for upper scale are: ST = subtropical zone, T = tropical zone, SA = subantarctic zone, and A = Antarctic zone; for lower scale: TS = Transitional Surface Water (SW), TR = Tropical SW, EQ = Equatorial SW, ST = Subtropical SW, SA = Subantarctic SW, and AN = Antarctic SW. Other symbols denote additional oceanographic features and translate as follows: CC = California Current, ECC = Equatorial Counter Current, EF = Equatorial Front, PC = Peru Current, CF = Chilean fjords, STC = Subtropical Convergence, and PF = Polar Front.

1983), SSTs drop rapidly from 5 to 3°C. Within this range we arbitrarily considered Antarctic waters to be those colder than 4.0°C.

The tropical and Antarctic zones were relatively easy to define. More difficult was the task of dividing those waters from 4.0 to 21.9°C between the subtropical and the subantarctic regions. The Subtropical Convergence is usually used by oceanographers and zoogeographers as the dividing "line," but using it did present some difficulties. According to Ashmole (1971), the Subtropical Convergence in the South Pacific is characterized at the surface by rapid north-south gradients in SST, the 34 ppt isopleth, and is lo-

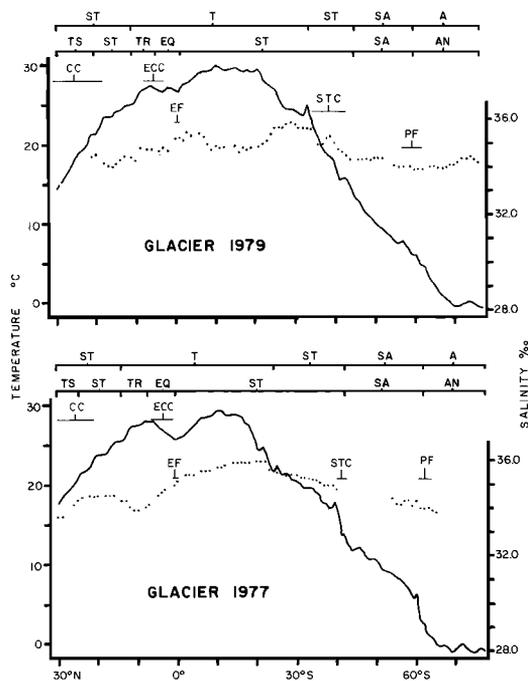


FIGURE 3. Change in sea surface temperature and salinity with latitude along cruise tracks of GLACIER 1977 and 1979. See Figure 2 for definition of symbols.

cated at about latitude 40°S. Rapid transitions from 18 to 14°C and from 35 to 34 ppt occurred between 40 and 45°S along cruise tracks in the western South Pacific and Tasman Sea (Figs. 2 and 3) and at about 26–45°S farther east. In the far eastern South Pacific the Subtropical Convergence is rather indistinct. Ashmole (1971) rather arbitrarily placed the boundary of subtropical waters at the 19°C isotherm, but in fact drew the line in his figure 3 coincident with the 14°C isotherm in the western South Pacific (compare Ashmole 1971: fig. 3 with charts in Sverdrup et al. 1942, Burling 1961, and Barkley 1968). Burling (1961) and others, in fact, place the southern edge of the Subtropical Convergence Zone approximately coincident with the 14°C isotherm in the western South Pacific and consider the zone itself to be subtropical in character. This is the definition we shall follow. Pocklington (1979) did not distinguish between subtropical and subantarctic waters in his Low Temperature Water-Type. However, in the Indian Ocean the Subtropical Convergence appears to be absent (J. A. Bartle, pers. comm.).

In summary, major zones of surface water in the South Pacific Ocean have the T/S characteristics outlined in Table 2. These zones are shown

TABLE 2
TEMPERATURE AND SALINITY CHARACTERISTICS OF WATERS IN FOUR CLIMATIC ZONES

Zone	Temperature (°C)		Salinity (‰)	
	Range	Spread	Range	Spread
Antarctic	(-1.8 to 3.9	7	33.8 to 34.6	0.8
Subantarctic	4.0 to 13.9	10	33.8 to 34.8	1.0
Subtropical	14.0 to 21.9	8	34.4 to 35.8	1.4
Tropical	≥22.0	8	29.0 to 36.2	6.2

graphically in relation to cruise tracks in Figures 2 and 3, which also show the major current systems and water masses that we crossed.

SUMMARY OF SPECIES OCCURRENCE

Considering only oceanic waters, we identified a total of 23 species in the Antarctic, 39 in the subantarctic, 52 in the subtropics, and 51 in the tropics (Table 3). Considering distinctive subspecies as being equivalent to a species (for the purposes of this analysis), no oceanic seabird was confined entirely to subantarctic waters (diving petrels, most species of which are indistinguishable at sea, might eventually prove to be exceptional), four (8%) were confined to subtropical waters, four (17%) to Antarctic waters (all but one to the pack ice), and 19 (37%) to tropical waters. Except for the Antarctic, the increase in the number of distinctive species with increasing water temperature may be a function more of salinity than temperature, or better, a combination of both. Although approximately equal ranges in temperature occurred among zones (Table 2), subantarctic waters had the narrowest range of salinities (1.0 ppt), the subtropics a broader range (1.4 ppt), and the tropics an even broader range (6.2 ppt). This broadening of the T/S regime probably increases the number of surface water-types and in effect increases the number of distinctive habitats (Pocklington 1979). In the Antarctic, with its narrow range of sea surface temperatures and salinities, species-groups separate by specific habitats defined largely by ice characteristics (Ainley et al. 1983). The extensive sharing of species between the open-water Antarctic zone and the subantarctic, and between the subantarctic and the subtropics, is evidence that the Antarctic and Subtropical Convergences are not the avifaunal barriers that we heretofore thought them to be. This conception is based largely on the zoogeographic analysis of seabird *breeding* distributions (see also Koch and Reinsch 1978, Ainley et al. 1983) and must now be re-evaluated.

Our results show tremendous overlap in species among the four major zones of marine climate.

Thus, we suggest that the major, classical oceanographic boundaries have few outstanding qualities as avifaunal barriers in the South Pacific. As we journeyed north or south on the various cruises we experienced a sometimes varying but mostly regular change in SST and SSS (Figs. 2 and 3). Coincident with this, species appeared or disappeared regularly as well (Fig. 4). Among all cruises, with each degree change in latitude, SST changed an average $0.67 \pm 0.42^\circ\text{C}$, SSS changed an average 0.13 ± 0.15 ppt and an average 1.8 species appeared and/or disappeared (Table 4). Slight but consistent peaks in species turnover did occur in conjunction with continental shelf breaks, boundary current systems (which have large numbers of endemic species), the Equatorial Front, equatorial currents, the Subtropical Convergence, and the Antarctic Convergence. This species turnover is not surprising because SST/SSS also changed more rapidly as we passed through these areas; nevertheless, three-fourths of the species remained the same across these frontal zones. Equal turnover occurred in the equatorial currents, where we did not cross any classical zoogeographic "boundaries" but remained entirely in equatorial waters. These transitional areas were thus no less or more important than such classical avifaunal barriers as the Subtropical and Antarctic Convergences. Only in the Drake Passage, where a tremendous amount of water moves rapidly through a narrow space between major land masses, and where an extremely sharp horizontal gradient in SST/SSS exists also (S. S. Jacobs, pers. comm.), did the Antarctic Convergence approximate the avifaunal barrier it has been fabled to be. Even there, however, a notable overlap in species existed between zones.

CHARACTERISTICS OF SEABIRD COMMUNITIES IN DIFFERENT ZONES

In the above analyses, it appeared that avifaunas in the Antarctic and in tropical waters may be somewhat more distinctive than those in subantarctic and subtropical waters. To examine this

TABLE 3
SUMMARY OF THE ZONAL OCCURRENCE OF SEABIRDS IN OCEANIC WATERS.

Species	Antarctic				Tropical	
	Pack ice	Open water	Subant- arctic	Sub- tropical	Salinity	
					Low	High
Emperor penguin <i>Aptenodytes forsteri</i>	*					
King Penguin <i>A. patagonicus</i>		*	*			
Adélie Penguin <i>Pygoscelis adeliae</i>	*					
Chinstrap Penguin <i>P. antarctica</i>		*				
Crested Penguin <i>Eudyptes</i> spp.		*	*			
Royal Albatross <i>Diomedea epomophora</i>			*	*		
Wandering Albatross <i>D. exulans</i>		*	*	*		*
Black-browed Mollymawk <i>D. melanophris</i>		*	*	*		
Gray-headed Mollymawk <i>D. chrysostoma</i>		*	*			
Buller's Mollymawk <i>D. bulleri</i>		*	*			
White-capped Mollymawk <i>D. cauta cauta</i>			*	*		
Salvin's Mollymawk <i>D. c. salvinii</i>			*	*		*
Chatham Is. Mollymawk <i>D. c. eremita</i>			*	*		
Light-mantled Sooty Albatross <i>Phoebastria palpebrata</i>		*	*			
Southern Giant Fulmar <i>Macronectes giganteus</i>		*	*			
Northern Giant Fulmar <i>Macronectes halli</i>			*	*		
Southern Fulmar <i>Fulmarus glacialisoides</i>		*	*			
Cape Petrel <i>Daption capense</i>		*	*	*		
Antarctic Petrel <i>Thalassoica antarctica</i>	*	*				
Snow Petrel <i>Pagodroma nivea</i>	*					
Solander's Petrel <i>Pterodroma solandri</i>						*
Tahiti/White-throated Petrel <i>Pt. rostrata/alba</i>					*	*
Hawaiian Petrel <i>Pt. phaeopygia</i>					*	*
Gray-faced Petrel <i>Pt. macroptera</i>			*	*		*
Cook's Petrel <i>Pt. cookii</i>			*	*		*
Soft-plumaged Petrel <i>Pt. mollis</i>		*	*			
Mottled Petrel <i>Pt. inexpectata</i>		*	*			
White-headed Petrel <i>Pt. lessoni</i>		*	*			
Juan Fernandez Petrel <i>Pt. e. externa</i>				*	*	*

TABLE 3
CONTINUED

Species	Antarctic				Tropical	
	Pack ice	Open water	Subant- arctic	Sub- tropical	Salinity	
					Low	High
White-necked Petrel <i>Pt. e. cervicalis</i>				*		*
Bonin/Black-winged Petrel <i>Pt. hypoleuca/nigripennis</i>				*		*
White-winged Petrel <i>Pt. l. leucoptera</i>						*
Gould's Petrel <i>Pt. l. gouldi</i>				*		*
Stejneger's Petrel <i>Pt. longirostris</i>				*		*
Herald Petrel <i>Pt. arminjoniana</i>				*		*
Kermadec Petrel <i>Pt. neglecta</i>				*		*
Shoemaker <i>Procellaria aequinoctialis</i>			*	*		
Westland Black Petrel <i>Pr. westlandica</i>			*	*		
Parkinson's Petrel <i>Pr. parkinsoni</i>				*		*
Gray Petrel <i>Pr. cinerea</i>			*	*		
Audubon's Shearwater <i>Puffinus lherminieri</i>					*	*
Wedge-tailed Shearwater <i>P. pacificus</i>					*	*
Buller's Shearwater <i>P. bulleri</i>			*	*		*
Hutton's Shearwater <i>P. gavia huttoni</i>				*		
Fluttering Shearwater <i>P. g. gavia</i>			*	*		*
Flesh-footed Shearwater <i>P. carneipes</i>				*		*
Pink-footed Shearwater <i>P. creatopus</i>			*	*		
Little Shearwater <i>P. assimilis</i>			*	*		*
Black-vented Shearwater <i>P. opisthomelas</i>				*		
Townsend's Shearwater <i>P. auricularis</i>				*	*	
Newell's Shearwater <i>P. p. newelli</i>					*	
Sooty Shearwater <i>P. griseus</i>		*	*	*		
Bulwer's Petrel <i>Bulweria bulwerii</i>						*
Antarctic Prion <i>Pachyptila desolata</i>		*	*			
Fairy Prion <i>Pa. turtur</i>			*	*		
Narrow-billed Prion <i>Pa. belcheri</i>		*	*			
Peruvian Diving Petrel <i>Pelecanoides garnoti</i>				*		
Diving Petrel spp. <i>Pe. urinatrix/georgicus/magellani</i>		*	*	*		

TABLE 3
CONTINUED

Species	Antarctic				Tropical	
	Pack ice	Open water	Subant- arctic	Sub- tropical	Salinity	
					Low	High
Black-bellied Storm-Petrel <i>Fregetta tropica</i>		*	*			
White-throated Storm-Petrel <i>F. grallaria</i>				*		*
Galápagos Storm-Petrel <i>Oceanodroma tethys</i>				*		*
Harcourt's Storm-Petrel <i>O. casto</i>				*		*
Leach's Storm-Petrel <i>O. leucorhoa</i>				*		*
Markham's Storm-Petrel <i>O. markhami</i>				*		*
Black Storm-Petrel <i>O. melania</i>				*		*
White-faced Storm-Petrel <i>Pelagodroma marina</i>			*	*		*
Wilson's Storm-Petrel <i>Oceanites oceanicus</i>	*	*	*	*		
Elliot's Storm-Petrel <i>Oc. gracilis</i>				*		*
White-throated Storm-Petrel <i>Nesofregetta albigularis</i>						*
Red-footed Booby <i>Sula sula</i>					*	*
Peruvian Booby <i>S. variegata</i>				*		
Blue-faced Booby <i>S. dactylatra</i>				*	*	*
Magnificent Frigatebird <i>Fregata magnificens</i>					*	
Lesser Frigatebird <i>Fr. ariel</i>						*
Greater Frigatebird <i>Fr. minor</i>					*	*
White-tailed Tropicbird <i>Phaethon lepturus</i>						*
Red-tailed Tropicbird <i>Ph. rubricauda</i>				*		*
Red-billed Tropicbird <i>Ph. aethereus</i>				*	*	
South Polar Skua <i>Catharacta maccormicki</i>	*	*	*	*		
Parasitic Jaeger <i>Stercorarius parasiticus</i>				*	*	*
Pomarine Jaeger <i>St. pomarinus</i>				*	*	*
Scissor-tailed Gull <i>Creagrus furcatus</i>				*	*	*
Sooty Tern <i>Sterna fuscata</i>					*	*
Gray-backed Tern <i>Sterna lunata</i>						*
Arctic Tern <i>Sterna paradisaea</i>	*	*	*	*	*	
White Tern <i>Gygis alba</i>						*
Brown Noddy <i>Anous stolidus</i>						*

TABLE 3
CONTINUED

Species	Antarctic				Tropical	
	Pack ice	Open water	Subant- arctic	Sub- tropical	Salinity	
					Low	High
Red Phalarope <i>Phalaropus fulicarius</i>			*	*	*	
Total	7	23	39	52	51	

further, we will continue the four-zone separation in the following analyses which attempt to delineate behavioral/morphological/ecological differences among the four avifaunas.

FEEDING METHODS

Ashmole (1971) emphasized the importance of feeding methods for characterizing seabird species; Ainley (1977) discussed how some oceanographic factors affect the use of various feeding methods in different regions. Ainley, however, considered only the breeding species in regional avifaunas. In some cases this was artificial because while certain feeding methods were not used by breeding species, nonbreeding species

in surrounding waters employed them to great advantage. To simplify analysis, Ainley (1977) also assumed that each species used only its principal method of feeding. This is indeed a simplification (Table 1). Our cruises afforded us the opportunity to improve Ainley's analysis by gathering data to characterize the feeding methods within entire seabird communities, including both nonbreeding and breeding individuals and species. We calculated how the total avian community biomass was apportioned among eight different methods of feeding. Where the data were available (see Table 1), we divided a species' biomass among various feeding methods if that species employed more than one.

Results confirmed Ainley's (1977) conclusions in regard to diving and plunging: moving from cold to warm, in subtropical waters diving disappeared and plunging appeared as a viable method of prey capture (Fig. 5). Trends that Ainley did not detect, however, were also evident. Dipping was a prominent method of prey capture in extremely cold water ($\leq 2^{\circ}\text{C}$) as well as in warm waters ($> 13^{\circ}\text{C}$), and especially in waters warmer than 17°C . Pursuit plunging and shallow plunging were prominent in waters where dipping was not, i.e., 2 to 17°C . Aerial pursuit was evident only in tropical waters. Surface seizing was the method least related to sea surface temperature, but it was used less in the Antarctic pack ice and tropical communities than in others. Only diving, plunging and aerial pursuit were confined to distinct ranges of SST; the remaining methods were used to some degree in all regions.

On a relative scale, cold waters have much larger standing stocks of organisms, such as zooplankton (Foxton 1956, Reid 1962), than do warm waters, and thus in cold waters birds should find it easier to locate prey (e.g., Boersma 1978). Considering this general idea, Ainley (1977) reasoned that diving was adaptive only in cold waters where prey availability was relatively reliable because diving species have limited abilities to search for prey. Results obtained in the present study confirm this pattern. On a more local level Crawford and Shelton (1978) likewise noted that

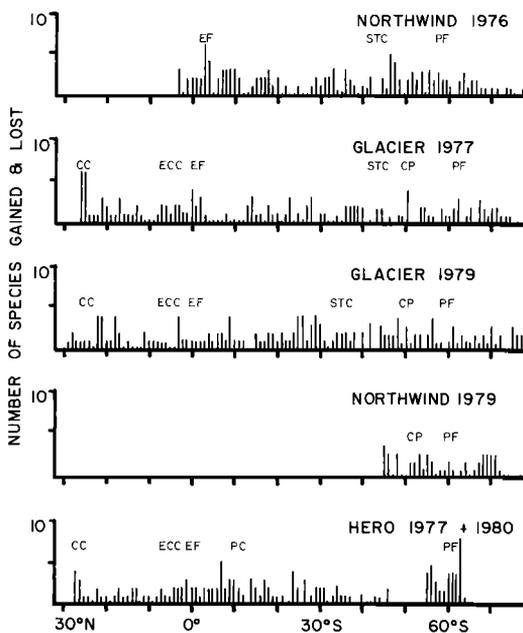


FIGURE 4. Change in species (species lost + species gained = species changed) with latitude along cruise tracks (compare with Figs. 2 and 3). See Figure 2 for definition of symbols.

TABLE 4
 APPEARANCE AND DISAPPEARANCE OF SPECIES AND CHANGE IN SEA SURFACE TEMPERATURES AND SALINITIES
 WITH ONE DEGREE CHANGES IN LATITUDE (MEAN AND SD)

Cruise	Species change ^a	Temperature °C	Salinity PPT	Number of transects
Northwind 1976	1.8 ± 1.8	0.60 ± 0.56	0.17 ± 0.19	74
Northwind 1979	2.0 ± 1.6	0.57 ± 0.45	0.10 ± 0.15	30
Glacier 1977	1.8 ± 1.8	0.65 ± 0.76	0.10 ± 0.12	93
Glacier 1979	1.7 ± 1.5	0.56 ± 0.57	0.14 ± 0.14	83
Hero 1977 & 1980	2.1 ± 1.6	0.99 ± 1.14	0.15 ± 0.15	56
Total, \bar{x}	1.8 ± 1.7	0.67 ± 0.65	0.13 ± 0.15	336

^a Species appearing plus those disappearing.

penguin (the ultimate family of divers) nesting colonies in South Africa occurred principally in conjunction with the optimal habitat for schooling fish, and not in peripheral habitat where suitable prey populations were more subject to fluctuation, and thus less reliable in availability. Continuing this line of reasoning, Ainley et al. (1983) hypothesized that Adélie Penguins (*Pygoscelis adeliae*) may feed on krill (*Euphausia* spp.) as heavily as they do perhaps not out of "specialization" but rather because such a prey

type (surface swarming crustaceans) is the most reliable and abundant food source available to a bird which, compared to all other Antarctic birds, is relatively incapable of searching large areas for food.

Another reason why it is not adaptive for diving birds to occur in warmer waters may have to do with competition from similar creatures that can exploit resources in the tropics more efficiently. Coming most to mind are the porpoises, which as a group are largely tropical and

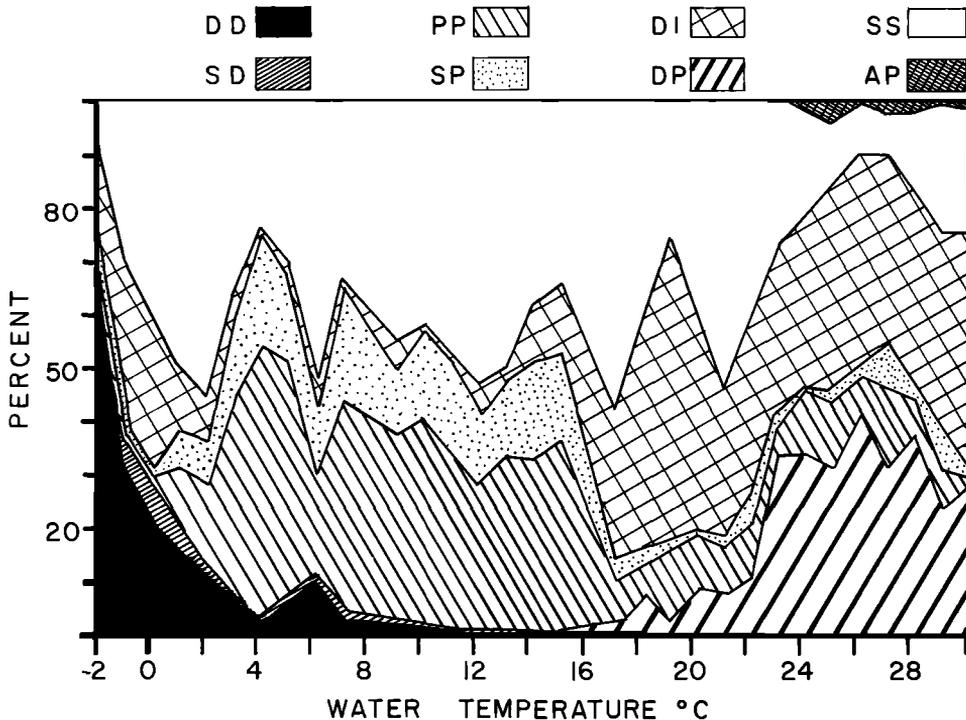


FIGURE 5. Proportion of avian biomass allocated to eight different feeding methods (see text p. 4) at different sea surface temperatures. All cruises combined; transects at similar water temperatures averaged.

subtropical in distribution (e.g., Gaskin 1982). The appearance of porpoises, from an evolutionary point of view, coincided with the disappearance of many flightless, diving birds (Simpson 1975, Olson and Hasegawa 1979), a pattern that may indicate competitive interaction between the two groups of animals.

In regard to deep plunging, which is used only among seabirds in warmer waters, Ainley (1977) reasoned that this feeding method is most effective in waters that are relatively clear. These waters have low concentrations of phytoplankton, a characteristic of subtropical and tropical waters (Forsbergh and Joseph 1964). Rather enigmatic is the Peru Current where rich blooms of phytoplankton cloud the water and where a plunging species, the Peruvian Booby (*Sula variegata*) is abundant. However, this species' usual prey, the Peruvian anchovy (*Engraulis ringens*), occurs in particularly dense schools right at the surface, a feature that may allow the Peruvian Booby, which feeds like its blue-water relatives, to occur in these waters. In addition, the aerial buoyancy of plunging species is second only to those species that feed by dipping (Ainley 1977) and thus plungers, with their efficient flight capabilities, are well adapted to search for prey under conditions where prey availability is relatively less reliable; i.e., warm waters which, as noted above, are generally considered to have more patchily distributed and lower standing stocks of prey than cold waters.

The bimodal prominence of dipping in the coldest and the warmest waters is interesting. In coldest waters, it seems that species are either capable of total immersion (penguins) or they avoid any contact with the water, and feed by dipping. Among several possible factors, this could be a function of thermal balance. Penguins can be large and have a thick insulating layer of fat because they do not have to fly in the air. Other species cannot possess these characteristics and still be able to fly, so they avoid contact with the cold water as much as possible. One way to do this is to feed by some form of dipping. Reduced contact with the sea in the tropics is manifested not only by the prominence of dipping, but also by aerial pursuit and even deep plunging (vs. actually swimming about after prey beneath the sea surface). The prominence of these methods in large part may be an artifact of a need for aerial buoyancy in waters where great mobility is advantageous (see above discussion on prey availability), but the high density of large predatory fish (e.g., sharks, tuna) in warm surface waters would also encourage adaptations for reduced contact with the sea. One has to observe only a few instances of tuna feeding at the surface to understand what advantage there is for trop-

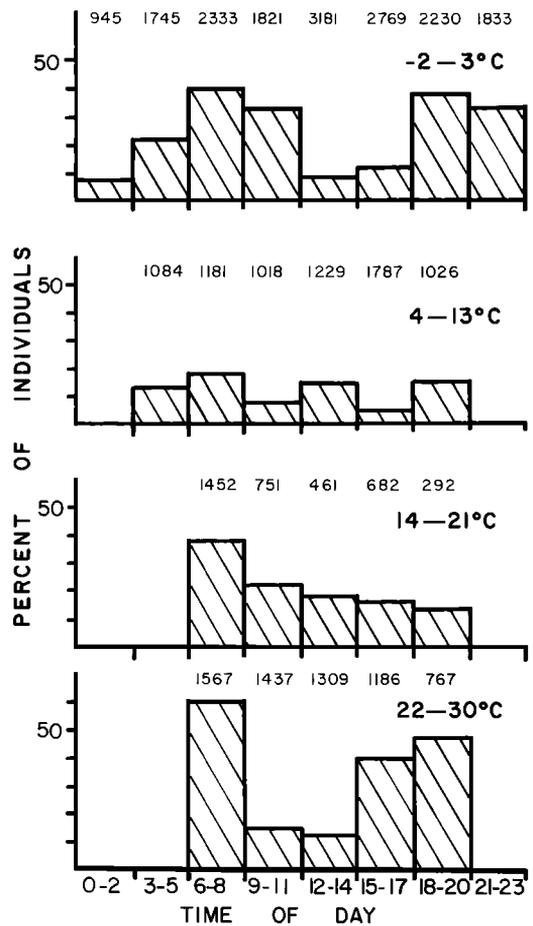


FIGURE 6. Percentage of individual birds observed feeding or in feeding flocks within three-hour periods of the day. All cruises combined; total number of birds observed in each period given at the top of each bar.

ical birds to restrict contact with the sea when feeding; if not eaten, certainly their chances of being bodily harmed would be high. Moreover, prey are often driven clear of the water by predatory fish. Being capable of catching these prey in mid-air, i.e., by aerial pursuit, would be of further advantage.

Temporal variations in feeding.—Also varying oceanographically to some degree (i.e., with SST) were the time of day when feeding occurred and the proportion of birds observed in feeding activity (Fig. 6). To study this, we grouped transects by three-hour intervals and established the following criteria for inclusion in the analysis: 1) farther than 75 km from land (to reduce the influence of shallow waters), and 2) winds less than

30 kts (because high winds increase sea surface turbulence and reduce prey visibility). Furthermore, we disregarded all penguins and diving petrels (which were difficult to distinguish as feeding or not feeding while we steamed by), and also Sooty Shearwaters (*Puffinus griseus*) and Mottled Petrels (*Pterodroma inexpectata*) (which were migrating in abundance through tropical waters but were never observed feeding there). The analysis indicates that feeding activity is dependent on time of day in all zones (G -test, $P < .01$, Sokal and Rohlf 1969; G scores as follows: Antarctic, 1513.1, $df = 7$; subantarctic, 231.0, $df = 5$; subtropics, 171.5, $df = 4$; tropics, 1074.2, $df = 4$). In essence, seabirds in oceanic waters tend to feed during the morning and evening. This was expected because as a negative response to increased light intensity, many potential prey migrate to deeper waters during the day but return to the surface when daylight fades (e.g., Imber 1973). More interesting is the fact that feeding activity was also bimodal with respect to time of day in the Antarctic where daylight is continuous during summer. At 75°S latitude, light intensity nevertheless does become reduced at "night." As a response to the change in light intensity, prey such as euphausiids migrate vertically (Marr 1962). Bimodal feeding activity has also been observed in Antarctic seals (Gilbert and Erickson 1977).

We observed a higher proportion of birds feeding in Antarctic waters compared to subantarctic and subtropical waters, which is not surprising given our opportunity in high latitudes to observe birds round the clock under conditions of continuous light (Table 5). In subantarctic and subtropical waters, the predominance of squid-feeding species (i.e., albatrosses, large petrels and gadfly petrels), which feed mainly at night, probably contributed to the low proportion of birds observed feeding. On the other hand, the high proportion of birds observed feeding in tropical areas indicates that birds may tend to feed more during the day in those waters than elsewhere. This would be consistent with the hypothesis of Ashmole and Ashmole (1967) and others that many tropical seabirds often feed in association with predatory fish which force prey into surface waters. It must certainly be easier for birds to find feeding tuna/porpoise during daylight. The higher proportion of birds observed feeding in the tropics may also indicate that tropical seabirds need to spend more time feeding than seabirds in cooler, more productive waters. In addition to prey being more patchy and generally less abundant in the tropics, tropical seabirds may also have to feed more to make up for the lower amount of energy available to them in the form of wind to help sustain flight (see below).

TABLE 5
PROPORTION OF BIRDS OBSERVED FEEDING IN
DIFFERENT OCEANOGRAPHIC ZONES^a

Zones	Birds feeding	Birds observed	Percent feeding ^b
Antarctic	3994	12,451	32.1
Subantarctic	238	1742	13.7
Subtropical	335	2134	15.7
Tropical	1969	5802	33.9

^a Includes only transects farther than 75 km from land having winds less than 30 knots; does not include penguins, diving petrels, Sooty Shearwaters or Mottled Petrels (see text).

^b Figures for Antarctic and tropical waters are not statistically different, and neither are those for subantarctic and subtropical waters; figures for Antarctic and tropical waters are statistically different from those for the subantarctic and subtropics ($P < .05$; percentage test, Sokal and Rohlf 1969).

In still another feeding-related phenomenon, the tendency of birds to occur in mixed-species feeding associations also differed by oceanographic zone. In the Antarctic, we observed mixed species feeding assemblages in 10.0% of transects ($n = 338$ total transects where depth was ≥ 1000 m and wind was < 30 knots), and the large majority of these transects where mixed flocks were observed were not in areas of pack ice. In the other three zones, the percentages of transects in which associations occurred were as follows: subantarctic 12.2% ($n = 205$), subtropics 12.4% ($n = 451$), and tropics 18.6% ($n = 693$). The percentage for the Antarctic is significantly less and that for the tropics is significantly greater than the others ($P < .05$; percentage test, Sokal and Rohlf 1969). In that prey are considered to be more patchy in occurrence in tropical waters compared to elsewhere (e.g., Boersma 1978), the above regional differences in the tendency for mixed species feeding flocks to occur may be an indirect measure of the relative degree of patchiness in seabird prey by region. More patchy prey may force seabirds to be more social in their feeding.

Regional differences in the tendency of birds to form mixed species feeding flocks are also apparent when the tendency of individual species to feed in association with others is compared (Tables 6–9). In Antarctic waters, all statistically significant "associations" were negative except those between Southern Fulmar (*Fulmarus glacialis*) and Antarctic Prion (*Pachyptila vittata*) and between Sooty Shearwater and Mottled Petrel (Table 6). Compared to other zones, a much lower proportion of Antarctic species formed positive associations and a much higher proportion formed negative associations (Table 10). The positive associations in the Antarctic occurred among species that did not occur in waters covered by pack ice. In other words, pack ice species

TABLE 6
 COLE'S COEFFICIENT OF ASSOCIATION AMONG SPECIES THAT OCCURRED IN AT LEAST THREE FEEDING FLOCKS
 WHERE SST WAS LESS THAN 4°C (UNDERLINING INDICATES SIGNIFICANCE AT $P < .01$).

Species*	Species						
	1	2	3	4	5	6	7
1. Southern Fulmar							
2. Antarctic Petrel	<u>-.40</u>						
3. Cape Petrel	<u>.14</u>						
4. Snow Petrel		<u>-.56</u>					
5. Antarctic Prion	<u>.24</u>		.23				
6. Mottled Petrel							
7. South Polar Skua				<u>-.36</u>			
8. Adélie Penguin	-.26						
9. Sooty Shearwater						<u>.50</u>	
10. Wilson's St-Petrel	<u>-.62</u>	.15	<u>-.46</u>				-.15
11. Arctic Tern	<u>-.12</u>	.31					

* Numbers in this column correspond to those across top of table; species are in taxonomic order more or less except 8-11, placed at the end to reduce table width.

“avoided” one another, probably as an artifact of their marked preferences for different habitats which were defined largely by ice characteristics. In the case of the Snow Petrel (*Pagodroma nivea*) and skua (*Catharacta maccormicki*), it may well have been an active avoidance of the skua on the part of the petrel (Ainley et al. 1983). In spite of their different habitat preferences, Antarctic species have similar diets when they do feed in the same vicinity (Ainley et al. 1983).

In the subantarctic, none of the statistically significant feeding associations was negative (Table 7). Although nine different species were observed in feeding flocks with the Sooty Shearwater, only one of these associations, a positive one with the White-headed Petrel (*Pterodroma lessona*), was significant. Compared to the Antarctic, a slightly higher proportion of species formed positive feeding associations. In the subtropics and tropics (Tables 8 and 9), there were also very few negative associations but the proportion of species forming significant positive associations was much higher than in the two cooler zones (Table 10). In the subtropics, 11 species associated positively with the Pink-footed Shearwater (*Puffinus creatopus*), 13 species with the Sooty Shearwater and 14 species with the Shoemaker (*Procellaria aequinoctialis*). Nine other species had negative associations with the Sooty. In the tropics, 11 species had positive associations with the Wedge-tailed Shearwater (*P. pacificus*), Sooty Tern, and Brown Noddy (*Anous stolidus*), and 13 with the Red-footed Booby (*Sula sula*). Three of the five significant negative associations in the subtropics and tropics involved the Juan Fernandez Petrel (*Pterodroma e. externa*); two of its negative associations were with species which, like it, use aerial

pursuit as a means of capturing prey (Buller's Shearwater *Puffinus bulleri* and Sooty Tern). In general, from the Antarctic to the subantarctic and subtropics, shearwaters, and especially the Sooty Shearwater, were important components in mixed-species feeding flocks. In the tropics, species showing a high tendency to associate were more diverse taxonomically, but a shearwater was among these species as well. The numerous associations of shearwaters with other species argues for their role as “catalysts” to be much more significant than any role they may play as “suppressors” in seabird feeding flocks (see Hoffman et al. 1981).

FLIGHT CHARACTERISTICS

A factor to which marine ornithologists have not given much attention is the use by seabirds of wind as an energy source, and particularly the efficiency with which different species use it to their advantage. On the basis of morphology, Kuroda (1954) suggested that aquatic and aerial abilities among the shearwaters were inversely related, some species being more aquatic and less aerial than others. This idea was suggested also, and extended to all seabirds, by Ainley (1977) who demonstrated that feeding methods and aerial buoyancy (Hartman 1961) were interrelated. Harrington et al. (1972) showed that wind regimes interacting with the aerial buoyancy of the Magnificent Frigatebird (*Fregata magnificens*) affected the species behavior, occurrence and distribution. Considering these facts and that regional differences in wind patterns exist (see below), we thought it worthwhile to explore the possibility that wind conditions also may have an effect on structuring entire seabird communities.

TABLE 7
 COLE'S COEFFICIENT OF ASSOCIATION AMONG SPECIES THAT OCCURRED IN AT LEAST THREE FEEDING FLOCKS
 WHERE SST WAS 3.0 TO 13.9°C (UNDERLINING INDICATES SIGNIFICANCE AT $P < .01$)

Species ^a	Species										
	1	2	3	4	5	6	7	8	9	10	11
1. Royal Albatross											
2. Black-browed Mollymawk	.16										
3. No. Giant Fulmar											
4. Cape Petrel	<u>.30</u>	<u>.58</u>									
5. Antarctic Prion		.16									
6. Mottled Petrel		.05									
7. Stejneger's Petrel											
8. White-headed Petrel		.05		<u>.31</u>	<u>.41</u>						
9. Shoemaker	.16	.24									
10. Sooty Shearwater		.05	-.08	.19	.02	.19	.19	<u>.70</u>			
11. Wilson's St-Petrel		-.12					<u>.64</u>			-.08	
12. Magellanic Penguin		-.05							.12		.03
13. Chatham I. Mollymawk	<u>.79</u>								.17		
14. White-capped Mollymawk	<u>.37</u>								.17	-.03	
15. Southern Fulmar			.10								
16. Fairy Prion						.29				-.04	
17. Black-bellied St-Petrel			-.06		-.08					-.05	

^a Numbers in this column correspond to those across top of table; species are in taxonomic order, except 12-17 placed at the end to reduce table width.

The Antarctic and subantarctic are generally considered to be windier than the subtropics and tropics. This is supported by a comparison of average wind speeds relative to 1.0°C intervals of sea surface temperature along our cruise tracks (Fig. 7). Wind speeds were indeed lowest in the tropics: beginning at 14°C, winds averaged 6-12 kts after averaging approximately 10-20 kts where waters were colder. The standard deviations of the average wind speeds, however, were consistently similar from 0 to 30°C, indicating similar variation. Compared to their respective averages, this meant that the usual amount of negative deviation from the mean in Antarctic and subantarctic areas still allowed 8-15 kts of wind, but in the subtropics and tropics, the lower level of usual conditions meant that only two to six knots of wind were available. Thus it seems that flight could potentially be more energetically costly in the tropics than elsewhere.

We compared the proportion of birds employing various kinds of flight with wind speed. Transects were grouped in 1.0°C intervals of SST. The proportion of birds gliding was directly related ($r = .5111$, $n = 33$, $P < .01$) and the proportion in flapping flight was inversely related ($r = -.5687$, $n = 33$, $P < .01$) to average wind speed. Obviously we saw more birds in flapping flight in the tropics than elsewhere. In addition, only in tropical waters did we observe soaring birds, including not just frigatebirds but boobies and Sooty Terns as well. The most commonly observed method of flight, flapping interspersed

with gliding, showed no relationship to wind speed ($r = .0674$).

Seabirds, and other species with long, thin wings, must fly faster to remain aloft in calm conditions than birds with short, broad wings (Greenewalt 1962). If wind is available, seabirds are able to fly more slowly and use relatively less energy in maintaining speed than they would when winds are calm. However, having more of a choice between fast and slow flight is an obvious advantage to seabirds, particularly when feeding and looking for food. In the tropics and subtropical zones, with less wind available, seabirds should have to be more efficient at using wind energy than in the cooler, windier regions. One type of evidence for this is the prevalence in the tropics of species with high degrees of aerial buoyancy, a characteristic typical of birds that feed by dipping, plunging and aerial pursuit (Table 1 in Ainley 1977). About 80% of birds (in terms of biomass) fed by these methods in the tropics, compared to about 50% in the subtropics and 30% or less in the subantarctic and Antarctic (Fig. 5). Another type of evidence is information on wing shapes and wing loadings. Such data are inadequate at present, but those presented by Warham (1977) certainly show that collecting more would prove to be fruitful. Warham (1977) collected and summarized information on 48 species of procellariiformes but unfortunately only a few were tropical. Among species of intermediate size, the three species having lower wing loading than average were gadfly petrels,

TABLE 9
 COLE'S COEFFICIENT OF ASSOCIATION AMONG SPECIES THAT OCCURRED IN AT LEAST THREE FEEDING FLOCKS WHERE SST WAS $>22.0^{\circ}\text{C}$ (UNDERLINING INDICATES SIGNIFICANCE AT $P < .01$)

Species*	Species																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. Bk-wing'd Petrel																						
2. Great-wing'd Petrel																						
3. Tahiti Petrel																						
4. Wh-neck'd Petrel				.31																		
5. Parkinson's Petrel	.66																					
6. Wedge-t'd Shearwater	.07	.36	-.03																			
7. Fl-foot'd Shearwater	.30	.22		.30	.30																	
8. Elliott's St-Petrel																						
9. Galapagos St-Petrel							.70	.49														
10. Harcourt's St-Petrel							.71	.19	-.08													
11. Leach's St-Petrel			.12				.46	.65	.58	-.04												
12. Markham's St-Petrel							.46	.65	.22		.28											
13. Wh.-bell'd St-Petrel							.46	.12	.19		.08	.28										
14. Wh.-faced St-Petrel									-.05		.03	.30	.14									
15. Masked Booby			.21			-.03																
16. Red-foot'd Booby	.12		.21			.23									.05							
17. Frigatebird, G & L			.24			.57									.51	.30						
18. White Tern	.07					.43									.22	.22	.26					
19. Gray-backed Tern						.57									.30	.30						
20. Sooty Tern			.35			.51					-.24				.09	.22	1.0	-.11	1.0			
21. Black Noddy	.13					.26									.40	.40		.11				
22. Brown Noddy	.07					.46									-.04	.22	.26	.04	.26	.25	.68	
23. Hawaiian Petrel			.21						.15	.18	.18	.13			.05	.05				-.04		
24. Juan Fernan. Petrel						-.19			-.08	-.02	-.05	.22	.10		.06		-.04	-.04	-.20			
25. Gould's Petrel	.31										.32											.26
26. Christmas Shearwater						.49			.23	.39	.13	.12			.15	.15			.31	.74		
27. Black St-Petrel			-.23												.30							
28. Bulwer's Petrel			.32			.57														.57	.74	
29. Wh.-t'd Tropicbird	.17	.22				.23									.30		.49		.56	.22	.17	.33
30. Parasitic Jaeger	.13	.22				.45	.25								.37			.26		.35	.37	.50

* Numbers in this column correspond to those at top of table; species are in alphabetic order within taxonomic groups which are in taxonomic order more or less, except 23-30 placed at the end to reduce table width.

TABLE 10
TENDENCIES OF SPECIES IN DIFFERENT ZONES TO FORM MIXED SPECIES FEEDING FLOCKS;
DATA SUMMARIZED FROM TABLES 6-9

Zone	A	B	C	D	E	F	G
	No. species ^a	No. species in mixed flocks	B ÷ A	No. species in positive association ^b	D ÷ A	No. species in negative association ^b	F ÷ A
Antarctic	23	11	0.478	4	0.174	5	0.227
Subantarctic	39	17	0.436	9	0.231	0	0.000
Subtropical	52	31	0.596	29	0.558	3	0.055
Tropical	51	30	0.588	27	0.529	2	0.038

^a From Table 2.

^b Statistically significant associations in Tables 6-9.

and two of these were tropical and subtropical in occurrence, the Bonin Petrel (*Pterodroma hypoleuca*) and the Juan Fernandez Petrel. The latter often feeds by aerial pursuit. The one gadfly petrel that had atypically high wing loading was the Mottled Petrel, the main Antarctic representative of this group and the only gadfly petrel observed to dive into the sea somewhat like a

shearwater. The unpublished data of Eric Knudtson (pers. comm.) are also encouraging. He calculated buoyancy indices for two tropical shearwaters, the Wedge-tailed and the Christmas Shearwater (*P. nativitatus*), to be 3.3 and 3.8, respectively, which indicates much more aerial efficiency than does the value of 2.7 for their cold-water relative, the Sooty Shearwater (cal-

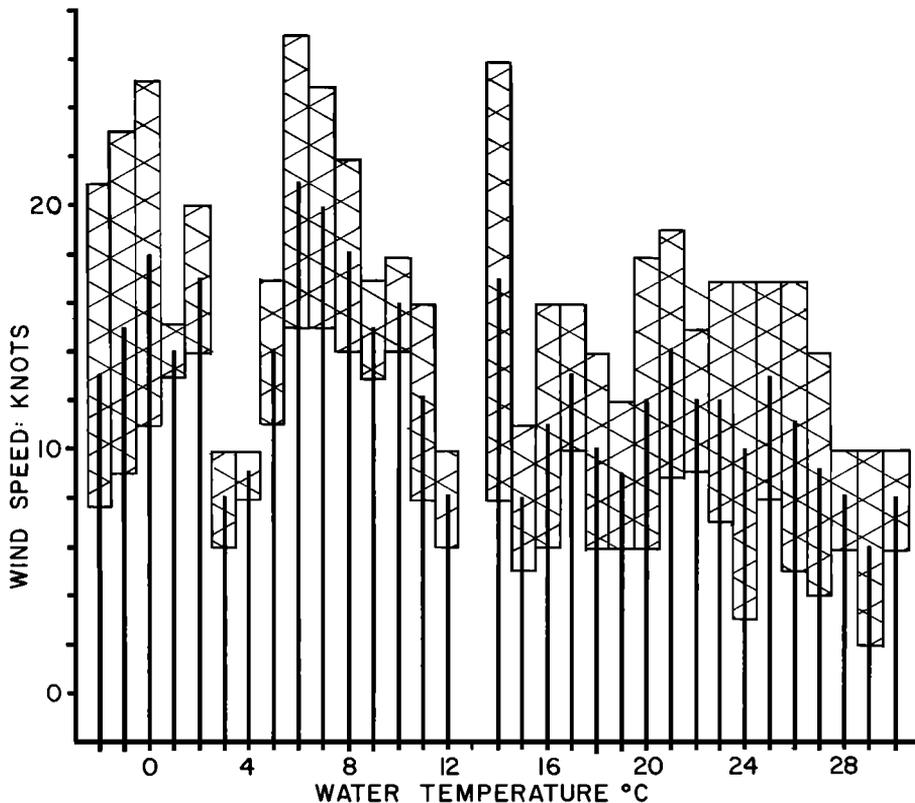


FIGURE 7. Mean wind speed (\pm SD, cross hatching) recorded on transects at 1.0 C° intervals of sea surface temperature; all cruises combined.

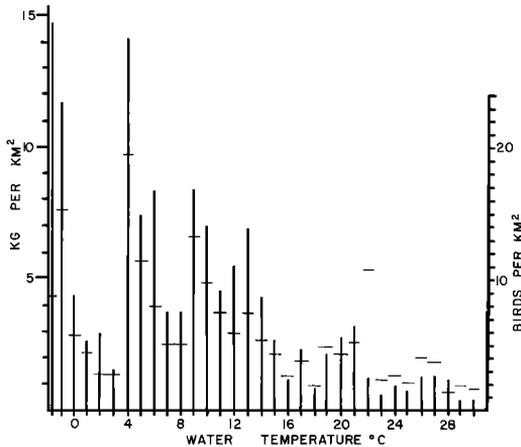


FIGURE 8. Mean density (vertical bars) and biomass (horizontal lines) of seabirds at 1.0°C intervals of sea surface temperature; all cruises combined.

culated by using Warham's 1977 data). Kuroda (1954), based on morphology, also suggested that the flight capabilities of the Wedge-tailed and Christmas Shearwater differed from the Sooty, but he did not really consider that climatic differences could be an underlying factor; rather, he ascribed the differences mainly to the more aquatic abilities of the Sooty. Much more comparative work is needed on the flight morphology of seabirds.

COMMUNITY BIOMASS AND SPECIES DIVERSITY

Density and biomass varied as one would expect in relation to the productivity of surface waters: they were highest in the Antarctic, declined with increasing temperatures, and were lowest in the tropics (Fig. 8, Table 11). Densities in the Antarctic and subantarctic were not sig-

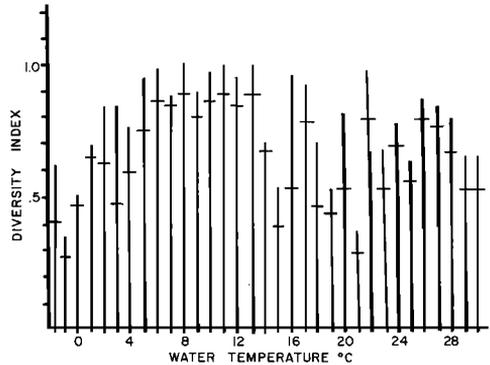


FIGURE 9. Mean indices of species diversity based on density (vertical bars) and biomass (horizontal lines) at 1.0°C intervals of sea surface temperature; all cruises combined.

nificantly different. Penguins comprise a relatively high proportion of individuals in Antarctic communities and storm-petrels comprise a relatively high proportion of individuals in the tropics. This, and the fact that penguins are large and storm-petrels are small, would explain in part the greater discrepancy between Antarctic and tropical avifaunas in biomass (11-fold difference) compared to density (three-fold difference).

Trends in species diversity were not clearly evident (Fig. 9, Table 11). The mean diversity index for each of the four climatic zones was statistically significant from figures for each of the other zones. The lack of trend in species diversity is in contrast to the number of species in each zone: 23 in the Antarctic, 39 in the subantarctic, and 52 and 51 in the subtropics and tropics, respectively (Table 3). This tends to support our earlier suggestion that the number of species may prove to be a function of the range

TABLE 11
DENSITY, BIOMASS AND SPECIES DIVERSITY OF SEABIRDS IN FOUR BROAD ECOLOGICAL ZONES: MEAN (\pm SD)
VALUES FOR TRANSECTS FARTHER THAN 50 KM FROM LAND

	Number of Transects	Density ^a Birds/km ²	Biomass ^b kg/km ²	Species Diversity ^c			
				Density		Biomass	
Antarctic	573	9.5 \pm 7.4	10.2 \pm 5.4	-.5386	.1826	-.3362	.1642
Subantarctic	276	9.0 \pm 4.5	6.7 \pm 3.0	-.8788	.0940	-.7258	.1686
Subtropical	392	4.2 \pm 1.2	2.7 \pm 1.1	-.6642	.2038	-.4698	.1725
Tropical	654	3.4 \pm 2.9	0.9 \pm 0.4	-.7534	.1204	-.5926	.1217
Total	1895	6.2 \pm 4.1	4.9 \pm 2.4	-.6891	.1526	-.5091	.1519

^a Figures for Antarctic and subantarctic are not significantly different, but all other figures in the column are (*t*-test, $P < .01$).

^b All figures are statistically significant (*t*-test, $P < .01$).

^c All figures within each column, not including "Total," are significantly different from each other (*t*-test, $P < .01$).

in the temperatures and especially salinities in a region; a wider range means more habitats or water-types which in turn allows the presence of more species.

DISCUSSION

In general, the steepness of horizontal temperature and salinity gradients in surface waters seemed to determine the amount of avifaunal change that we encountered as we steamed across the ocean. Like Pocklington (1979) we found that the transition between subtropical and semitropical/tropical waters (i.e., approximately the 23°C isotherm) was a major avifaunal "barrier" in warmer oceanic waters. In the South Pacific, this isotherm is at the cooler edge of the Equatorial Front, which with its strong gradient in SST, may prove to be the actual barrier. Another major avifaunal barrier in oceanic waters was the pack ice edge. The Antarctic and Subtropical Convergences were relatively less effective as avian zoogeographic boundaries.

The tropical marine avifauna was rather distinctive in several ways.

(1) Tropical waters shared first place with subtropical waters in having the highest number of species.

(2) The proportion of species confined to tropical waters, however, was much higher than the proportion of subtropical species confined to subtropical and subantarctic species confined to subantarctic waters.

(3) In the tropical avifauna there existed the strongest tendency for species to associate in multispecies feeding flocks.

(4) Tropical species fed more by dipping, plunging and aerial pursuit than did species in other avifaunas, and correspondingly, they apparently had much higher degrees of aerial buoyancy (and in general, probably lower wing loading). Greater aerial buoyancy was adaptive because wind speeds were generally lowest in the tropics.

(5) The density and biomass of the tropical avifauna was much lower than elsewhere.

The other distinctive avifauna was that of the Antarctic pack ice. Many of this avifauna's characteristics were similar in nature to those of the tropical avifaunas but were different in extreme (usually opposite).

(1) Antarctic pack ice had the lowest number of species, but

(2) had the second highest proportion of species confined only to it. Ice-free waters of the Antarctic, and waters of the subantarctic and subtropics, had very few species confined to any one of the three zones.

(3) The low number of species in the Antarctic corresponded to that zone's narrow range in sea

surface salinities; that narrow range plus the uniqueness of pack ice, corresponded to a distinct group of species associated with the pack ice (Ainley et al. 1983).

(4) Species in the pack ice showed a markedly strong negative tendency to associate in mixed species foraging flocks, i.e., they avoided one another.

(5) Antarctic pack ice species, more than other avifaunas, fed by deep diving; like birds in the tropics, they fed to a great extent by dipping.

(6) The density and biomass of birds in Antarctic waters were the highest.

Based on inferences from data on breeding biology, marine ornithologists generally agree on the hypothesis that tropical seabirds experience food that is relatively less abundant and, mainly, more patchy in occurrence than avifaunas of other regions, and that the opposite is true of Antarctic seabirds. Many of the characteristics listed above could be explained by that hypothesis, but would also be consistent with the hypothesis that seabirds are strongly tied by morphological/behavioral adaptations to specific water-types or marine habitats (habitats which move about somewhat seasonally and interannually) and that in the tropics more habitats are available for exploitation. This is a complicated hypothesis which seems to be supported by Pocklington's (1979) study of avifaunal association to water-types in the Indian Ocean, and an hypothesis about which we will soon have more to say when we analyze the T/S regimes of individual species and species groups in our own data for the Pacific.

The differences in species diversity among tropical, subtropical, subantarctic and Antarctic avifaunas indicated that it may have been the number of habitats or T/S water-types that determined the number of species in an area, assuming that the number of water-types is a function of the range in temperature and salinity. If the Indian Ocean system studied by Pocklington is typical of the Pacific, this assumption should be a safe one. The widest and narrowest ranges in the salinity of oceanic waters of the Pacific occurred in the tropical and Antarctic zones, respectively. These zones had similar species diversity but, also respectively, had the highest and lowest number of species. Such patterns also point to the need to understand better the association of species to water-types and to the number of water-types per region.

The species diversity estimates we present here are comparable to those calculated for grassland avifaunas by Willson (1974), and also for seabirds near Hawaii by Gould (1971). Since species diversity is a function of habitat complexity in terrestrial ecosystems, we conclude that oceanic marine habitats rank among the least complex

for birds. Bird habitats in oceanic waters are largely two dimensional, although depth does add a third dimension. Compared to waters of the continental shelf, however, depth is less important in oceanic waters. If a greater degree of variation in depth penetration were possible by birds in oceanic waters, depth might be more important and we might expect higher estimates of bird species diversity. At first glance, it would appear that depth is a more significant factor in Antarctic and subantarctic avifaunas because they contain diving species. Tropical and subtropical avifaunas are compensated, however, because prey that would otherwise remain deep are forced to the surface by porpoise, tuna, and other predatory fish. While the importance of tuna to tropical seabirds has often been intimated, and is agreed upon by seabird biologists, we lack direct observations on the interaction of seabird flocks with tuna schools. The mobility of tuna may be another factor, along with wind conditions and prey availability, that places a premium on flight efficiency for tropical seabirds. A detailed study of the interaction between seabirds and tuna schools is long overdue (see Au et al. 1979).

Rather low species diversity also argues against there being many different foraging guilds (see Willson 1974) in oceanic habitats. The guilds would be definable in oceanic waters mainly by feeding behavior. Unlike terrestrial habitats and even shallow water habitats (see Ainley et al. 1981), foraging substrate is everywhere rather similar, and, because seabirds are rather opportunistic in their feeding, little diet specialization exists (e.g., Ashmole and Ashmole 1967, Ainley and Sanger 1979, Croxall and Prince 1980, Ainley et al. 1983, Harrison et al., 1983; also, compare Brown et al. 1981, Ogi, In press, and Chu, In press). Increasing our knowledge about the habitats and water-types preferred by seabirds may eventually help to integrate our rather checkerboard concept of seabird diet. For instance, we may be better able to explain the dramatic differences in diet between species nesting in both the Northwestern Hawaiian Islands (Harrison et al., 1983) and at Christmas Island (Ashmole and Ashmole 1967; Schreiber and Hensley 1976), which geographically are relatively close together, or between species frequenting both the Ross Sea (Ainley et al. 1983) and Scotia Sea (Croxall and Prince 1980), which are geographically far apart. More research on the biology of seabirds at sea is obviously needed.

ACKNOWLEDGMENTS

We are grateful for the usually enthusiastic logistic support given by the officers and crew of R/V HERO (cruise 80/5) and USCG Cutters BURTON ISLAND, GLACIER and NORTHWIND. Indispensable was the

help in data collection given by G. J. Divoky, R. P. Henderson and E. F. O'Connor; and the help in data analysis given by P. Geis and L. Karl. S. S. Jacobs of Lamont-Doherty Geological Observatory loaned us a portable salinometer for some cruises, and supplied us with salinity data on others. We also appreciated his and A. W. Amos' comradeship aboard ship, their insights into oceanography, and their interest in our studies. Quite useful was the preview that E. Knudtson provided of his data on the aerial buoyancy of tropical seabirds, and the comments that R. G. B. Brown, G. L. Hunt, S. Reilly and R. W. Schreiber provided on an earlier draft of the manuscript. M. Sanders and O'B. Young assisted in preparing the manuscript. The National Science Foundation, Division of Polar Programs provided financial support (Grants DPP 76-15358, 76-15358 A01, 78-20755 and 78-20755 01). This is contribution no. 252 of the Point Reyes Bird Observatory.

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