

SEABIRD COMMUNITY STRUCTURE ALONG A PRODUCTIVITY GRADIENT: IMPORTANCE OF COMPETITION AND ENERGETIC CONSTRAINT

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Abstract. The oceanic eastern tropical Pacific supports a speciose seabird community that feeds in flocks and depends for food on schools of tunas and dolphins, which force prey to the surface. We analyzed data collected throughout an area of 40×10^6 km² of open ocean over 10 years (1979–1988) during 1136 at-sea days, from 1750 feeding flocks comprising 51 688 birds of 49 species. A PCA identified three distinct flock types based on species composition: “Sooty Tern Flocks” ($n = 941$ flocks) with a large number of Sooty Terns (*Sterna fuscata*), “Juan-Wedge Flocks” ($n = 402$ flocks) with a large number of Juan Fernandez Petrels (*Pterodroma externa*) and Wedge-tailed Shearwaters (*Puffinus pacificus*), and “Booby Flocks” ($n = 407$ flocks) with a large number of Red-footed and Masked Boobies (*Sula sula* and *S. dactylatra*, respectively). Flock types exhibited largely disjunct distributions that mirrored patterns in thermocline depth and surface water chlorophyll content. Sooty Tern Flocks occurred in areas with deepest thermocline (77.6 m) and lowest chlorophyll (0.14 mg/m³), Juan-Wedge Flocks in areas of intermediate thermocline (68.8 m) and chlorophyll (0.16 mg/m³), and Booby Flocks in areas of shallowest thermocline (62.5 m) and highest chlorophyll (0.17 mg/m³). These differences were statistically significant. As thermocline depth and surface water chlorophyll are reliable indicators of surface water productivity, we conclude that Sooty Tern Flocks foraged in waters of low productivity, Juan-Wedge Flocks in waters of intermediate productivity, and Booby Flocks in waters of highest productivity.

Differences in published cost-of-flight values support the hypothesis that energetic constraint determines flock structure at the low-productivity end of the system. Sooty Terns have the lowest flight costs (4.8 W) and feed in waters of lowest productivity. Flight costs are progressively higher for those species feeding in more productive waters (9.9 W for Wedge-tailed Shearwaters, 19.0 W for Red-footed Boobies). Differences in body size support the hypothesis that interference competition determines flock structure at the high-productivity end of the system. The largest species, Masked Boobies (1987 g) and Red-footed Boobies (1003 g), feed in areas of highest productivity; progressively smaller species, Juan Fernandez Petrels (430 g) and Wedge-tailed Shearwaters (388 g), and Sooty Terns (180 g), feed in areas of decreasing productivity. We hypothesize that this community is largely structured by two factors, competition and energetic constraint, that operate at opposite ends of a productivity gradient. As productivity decreases (low prey abundance), flight proficiency is increasingly important because only species with relatively low flight costs will be able to transit between prey patches. As productivity increases (high prey abundance), competitive ability is increasingly important because competitive dominants will exclude other species from feeding flocks. Our hypothesis is in accordance with empirical data and theoretical models designed to explain factors structuring communities for a wide variety of habitats and taxa.

Key words: body size; community ecology; competition; energetic constraint; energetic cost of flight; feeding flocks; flight proficiency; productivity gradient; seabird communities; seabird distribution; species composition; tropical Pacific.

INTRODUCTION

Community ecologists have been studying species assemblages for decades. The factors that structure

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these communities and how they interact have been the subject of much empirical and theoretical research (Cody and Diamond 1975, Strong et al. 1984, Wiens 1989, Ricklefs and Schluter 1993). Yet, the vast majority of this work has been conducted in terrestrial or marine intertidal habitats. Few studies have been conducted in open ocean systems (Venrick 1990), so we know relatively little about how oceanic communities are structured.

Seabirds have long been the focus of open ocean research (Murphy 1936). They are unique among marine vertebrates in that they are completely dependent upon the ocean for food, yet are restricted to the air for breathing and, largely, for locomotion (for all but the Spheniscidae). Thus, they can be observed above the water surface, a situation that is rare, if possible at all, for other oceanic organisms. As a result, distribution patterns for the world's seabirds are relatively well known (Harrison 1987). These distributions have often been correlated with habitat features, e.g., sea surface temperature, salinity, or productivity (Pocklington 1979, Schneider and Brown 1986, Schneider 1990, Elphick and Hunt 1993). Various communities have been described and correlated with these same types of habitat parameters (Ainley et al. 1984, 1993, Briggs et al. 1987, Ribic and Ainley 1988/1989, Ribic et al. 1992).

That seabird communities change with their marine habitat is well documented. However, relatively little progress has been made with respect to understanding why. How are features of an oceanic environment important in structuring seabird communities, and by what mechanisms does this structuring take place? Historically, marine ornithologists have found that changes in water mass characteristics can affect the prey base such that prey species and, therefore, predator species will change (reviews by Brown 1980, Hunt 1990). In this paper, we will demonstrate how changes in prey *abundance*, even in the absence of changes in prey type, can explain structure in a community of predators (see Piatt 1990). We will describe composition and distribution of seabird feeding flocks in the tropical Pacific, showing predictable changes that correlate with surface water productivity. We also will hypothesize that this structure is manifested through two factors: competition and energetic constraint, which operate at opposite ends of a prey abundance gradient.

Our study will focus on a distinct and prevalent community in the oceanic eastern tropical Pacific that we will refer to as the "subsurface predator-dependent" seabird community. These seabirds feed in flocks, in association with subsurface predators (Au and Perryman 1985, Au and Pitman 1986, 1988). The predators are primarily spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*, respectively) and yellowfin and skipjack tuna (*Thunnus albacares* and *Katsuwonus pelamis*, respectively), which force prey to the surface (Au and Pitman 1986). Seabirds depend upon these predators to make prey available (Ashmole and Ashmole 1967), and they form flocks as a consequence of feeding over these distinct patches (Ballance 1993).

Many features of this system are unique, either to oceanic systems in general, or to tropical seabirds, and it is instructive to highlight them here.

1) The spatial scale of open ocean systems is large relative to terrestrial systems (Steele 1991, McGowan and Walker 1993). When searching for food, many sea-

birds regularly traverse hundreds or thousands of kilometers in a period of days (Harrington 1977, Stahl et al. 1985, Jouventin and Weimerskirch 1990, Flint 1991). This occurs both during reproductive periods, when birds are more closely tied to a relatively localized area around a breeding colony, and during non-reproductive times.

2) The structural complexity of oceanic habitats is extremely low relative to even the most homogeneous of terrestrial systems. Gradients in environmental properties exist in the vertical dimension at scales of tens to hundreds of meters (McGowan and Walker 1993). With the exception of oceanographic fronts, which can provide localized areas of sudden changes in temperature, salinity, and biomass along a horizontal plane (Wolanski and Hamner 1988), changes in environmental properties along a horizontal dimension occur on a scale of hundreds to thousands of kilometers (Owen 1981), and large-scale structural heterogeneity is absent. Tropical seabirds are restricted to the water surface or just a few meters below (Ashmole 1968, Ashmole and Ashmole 1968, Diamond 1978); some species are not known to enter the water at all (Ashmole 1963, Serventy et al. 1971). Although they can indirectly exploit the vertical dimension by associating with subsurface predators, oceanic tropical seabirds operate essentially in a two-dimensional, highly homogeneous habitat.

3) Predation, a dominant force in many terrestrial communities, is rare, if present at all, for volant seabirds at sea (Hoffman et al. 1981). Some species must cope with significant predation pressure on breeding colonies (Warham 1990), and some suffer kleptoparasitic attacks at sea (Furness 1987). Sharks may occasionally take those few species that rest on the water surface (Nelson 1978, Schreiber and Chovan 1986, Pitman 1993). However, for the vast majority of species, seabirds are free of predation when at sea.

Therefore, despite its large spatial scale, this system is a highly simplified one, affording an opportunity to interpret community patterns in the absence of significant habitat heterogeneity and predation. A final unique feature has to do with our particular data set. Seabirds easily can be observed at sea; however, many are simply in transit, either migrating through a particular area or dispersing from a breeding colony. This makes it difficult to know whether or not these individuals are actually foraging in a given habitat. By studying feeding assemblages and the species that comprise them, we can be certain that our data represent a direct link between a particular seabird and the habitat on which it depends.

METHODS

Study area and data collection

Our study area encompassed the ocean between 30° N and 20° S latitude, from the coast of Central and

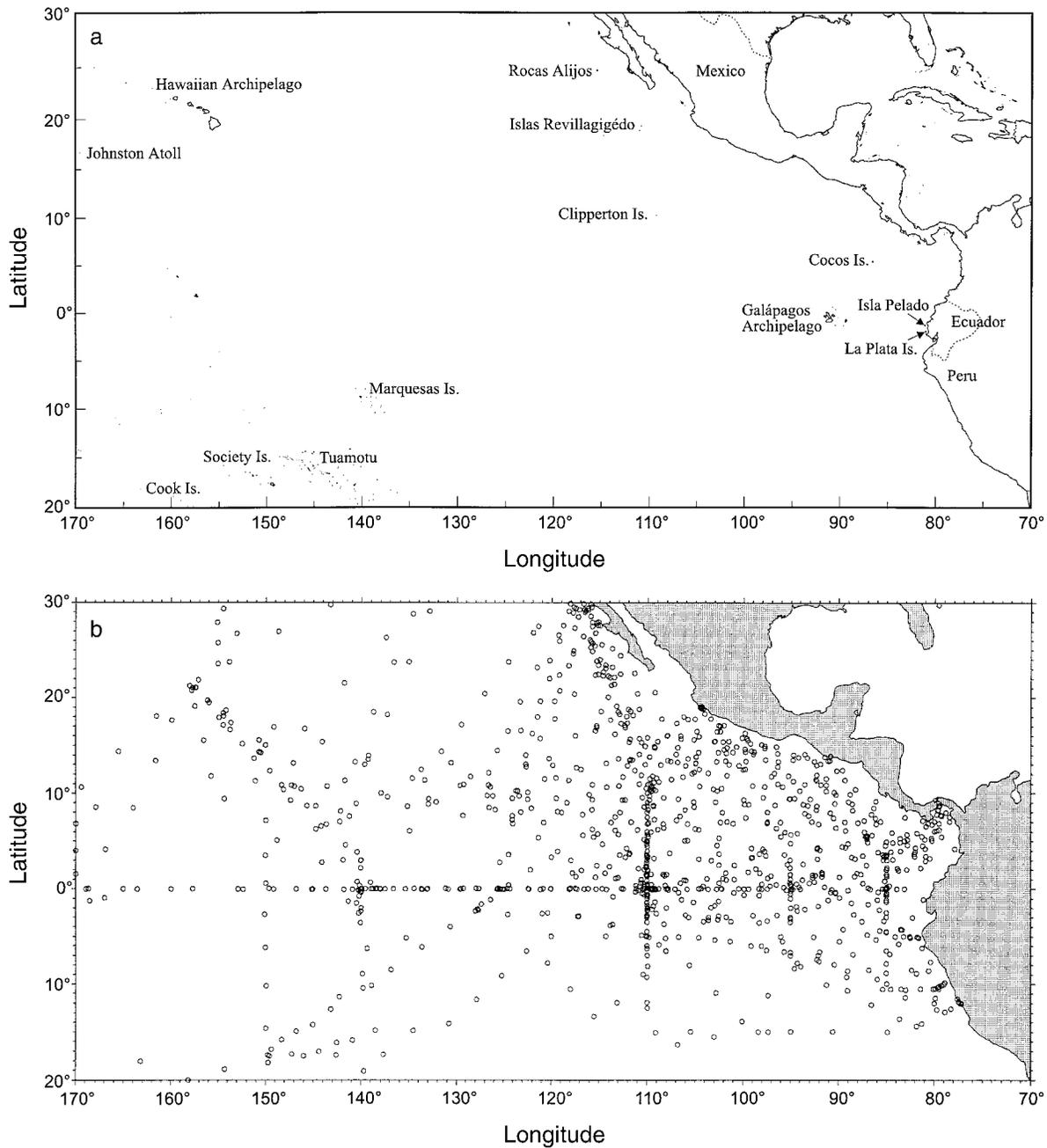


FIG. 1. (a) Map of the study area, the eastern tropical Pacific. (b) Distribution of the survey effort over a 10-yr period. Each point represents the research vessel's noon position on a survey day ($n = 1316$ d).

South America to 170° W longitude, $\approx 40 \times 10^6$ km² of water (Fig. 1a). Three major currents dominate the surface oceanography of this area: the westward-flowing North and South Equatorial currents, and the eastward-flowing North Equatorial Countercurrent (Wyrtki 1966, 1967, Fiedler et al. 1992). Data were collected from National Oceanic and Atmospheric Administration research vessels during a 10-yr period, from 1979 to 1988. This survey effort represented a total of 1136

d at sea, distributed primarily in the "oceanic" realm: seaward of the continental shelf (Fig. 1b). Yearly (113.6 ± 9.1 d/yr, mean ± 1 SE) and monthly (94.7 ± 8.9 total d/mo) distribution of the survey effort is depicted in Fig. 2.

Research trips were of two types: oceanographic cruises and marine mammal surveys. Oceanographic cruises followed predetermined cruise tracks and stopped periodically to collect oceanographic data at

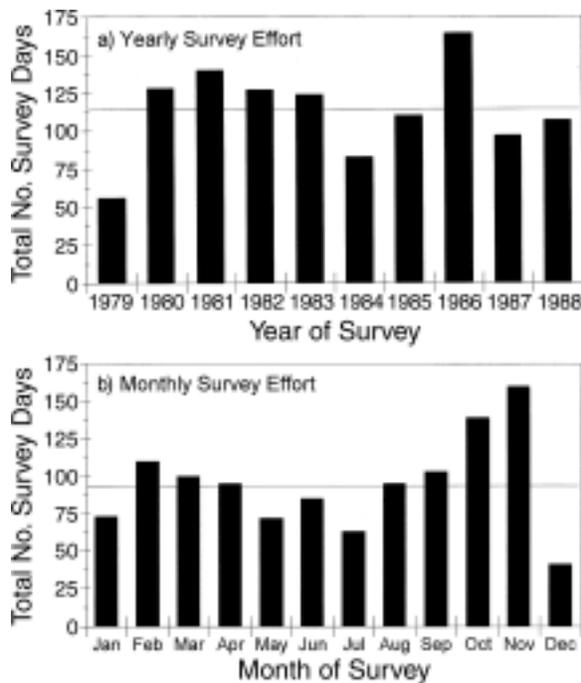


FIG. 2. Survey effort by (a) year, and (b) month. The horizontal lines represent mean values.

predetermined sites. Mammal surveys also followed predetermined tracks, but the vessel was diverted briefly when cetaceans were sighted, in order to identify species and count individuals (see Holt and Sexton 1989 for detailed methodology). On all vessels, seabird observations were made when the ship was in transit, for 2–10h/d, depending upon weather conditions and ship activity. We used mounted 20×120 or 25×150 binoculars to scan the ocean area in front of the ship from beam to beam and out to the horizon. Depending upon the vessel, the height of the binoculars above the water ranged from 10 to 15 m, and the sighting distance to the horizon from 13 to 16.5 km.

We recorded information for all flocks that were sighted. A flock was defined as any group of five or more birds. For each flock, the identity of all species to the lowest possible taxon and the number of individuals of each species were recorded. (We use common names for seabirds in the text, figures, and tables; scientific names are given in Appendix A.) We also recorded the identity of any associated cetaceans or fish, and the behavior of seabirds and other associated species.

Detailed oceanographic data were collected on some cruises from 1986 to 1988 as part of another project. For these years, we used surface water chlorophyll content in milligrams per cubic meter and thermocline depth (depth of the 20°C isotherm; Fiedler et al. 1992) as indices of surface water productivity, because these are reliable indicators of the relative levels of phytoplankton standing stocks, biomass of zooplankton, and

in some regions, abundance of tuna in surface waters (Brandhorst 1958, Nielsen 1959, Blackburn et al. 1970, Fiedler and Philbrick 1991, Fiedler et al. 1992). The term “productivity” in this paper will, therefore, denote the relative abundance of organisms in surface waters, and not the rate of carbon fixed through primary production. “High surface water productivity” (or simply “high productivity”), defined by a relatively shallow thermocline and high chlorophyll, will be assumed to indicate a high abundance of organisms. “Low surface water productivity” (also referred to as “low productivity”), defined by a relatively deep thermocline and low chlorophyll, will be assumed to indicate a low abundance of organisms.

The values of these parameters recorded at noon on each day were used to represent oceanographic conditions for all flocks sighted during that day. We believe this spatial scale of analysis to be appropriate, because daily variation in surface chlorophyll and thermocline depth (measured over a linear distance of 150–200 km) averaged an order of magnitude less than the variation in these parameters over the entire study area (Fig. 3).

Data analysis

Our first objective was to determine whether certain species associated regularly in feeding flocks, or whether flocks were better described as multispecies assemblages with more random composition. To investigate this, we used a principal component analysis (PCA). To ensure that data represented complete information on feeding associations, we analyzed only flocks for which we were able to identify all seabirds to the generic level and to count all individuals. This included 3888 seabird flocks, comprising 138 300 birds. We restricted our analysis to the oceanic sub-surface predator-dependent community by including only nektonic-feeding seabirds as species variables (excluding planktonic-feeding species, i.e., storm-petrels and phalaropes), and by excluding rare or highly localized species (only species that were recorded in ≥ 100 flocks during the 10-yr survey period were included). We performed the PCA on the 13 seabird species or species groups that met these criteria (Table 1), using log-transformed data and a covariance matrix. We used the broken stick model (Legendre and Legendre 1983, Jackson 1993) to determine the number of components to use in data interpretation. In the results that follow, “component loading” will refer to that value relating each of the 13 species variables to each principal component, and “component score” will refer to that value relating each of the 3888 flocks to each principal component.

Our next objective was to categorize each flock based on results of the PCA. Because the first three principal components identified three distinct feeding assemblages or “flock types” (see *Results*), we plotted a frequency histogram of flock component scores for each of these three components to visually identify

TABLE 1. Component loadings of each of 13 species variables on the first three principal components. Loadings have been standardized to have a maximum value = 1.0.

Species variable	Component loadings		
	PC I	PC II	PC III
Brown Booby	-0.029	0.072	0.336
Red-footed Booby †	-0.016	0.167	1.000
Pomarine Jaeger	0.010	0.070	0.132
Brown Noddy	-0.003	-0.002	0.164
Christmas Shearwater	0.027	0.049	0.050
Pink-footed Shearwater	0.009	0.083	0.100
Sooty Tern †	1.000	-0.324	0.026
White Tern	0.096	-0.112	0.138
Juan Fernandez Petrel †	0.085	0.788	-0.641
Masked Booby †	-0.062	0.157	0.585
Townsend's/Newell's Shearwater	0.021	0.082	0.162
Wedge-tailed Shearwater †	0.277	1.000	0.203
Great/Magnificent Frigatebird	0.041	0.031	0.341

† Species accounting for most of the variation in each principal component are shown in boldface. Scientific names are in Appendix A.

those flocks that represented each type (see *Results*). Some flocks ($n = 527$ flocks, 13.6% of all flocks) met the component score criterion for more than one flock type. We excluded these from further analyses. An additional 1611 flocks (41.4% of all flocks) did not meet any of the three criteria. These were flocks comprising planktonic-feeding species or flocks restricted to continental shelf waters, including the Humboldt or California currents. We also excluded these from further analysis.

Our data then consisted of 1750 flocks that fell into one of three flock types representing the oceanic community of subsurface predator-dependent seabirds. These were used to characterize each flock type in terms of composition, association with subsurface predators, distribution (plotted as the noon position of the vessel on the day the flock was sighted), and productivity of surface waters over which these flocks foraged.

Most feeding flocks in the eastern tropical Pacific are associated with tuna (Au and Pitman 1988). However, it was often not possible to identify, or even to detect, these predators because fish may remain below the surface. Because mammals must surface to breathe, they were presumably always detected, and usually identified. In the analyses that follow, we therefore present quantitative data only for cetacean associations, but assume that feeding flocks were also associated with fish.

We used multivariate Analysis of Variance (MANOVA) to test for differences between flock types. All results are reported as mean \pm 1 SE.

RESULTS

Flock types

The PCA reduced the original 13 species variables to three new principal components (PCS) that accounted for 68% of the variance in the data (PC I, 34%; PC II, 21%; PC III, 13%). The first PC was primarily as-

sociated with Sooty Terns, the second with Juan Fernandez Petrels and Wedge-tailed Shearwaters, and the third with Red-footed Boobies and Masked Boobies and the absence of Juan Fernandez Petrels (Table 1 and Fig. 4). Therefore, the PCA identified three flock types: "Sooty Tern Flocks" with a large number of Sooty Terns; "Juan-Wedge Flocks" with a large number of Juan Fernandez Petrels and Wedge-tailed Shearwaters; and "Booby Flocks" with a large number of Red-footed and Masked Boobies and an absence of Juan Fernandez Petrels.

Frequency histograms of flock component scores allowed us to graphically identify those flocks representing each type (Fig. 5). From inspection of the histogram of PC I component scores, we chose 0.5 as a conservative value to represent the lower limit of the Sooty Tern Flock mode (Fig. 5a); therefore, flocks with a PC I component score ≥ 0.5 were considered to be Sooty Tern Flocks ($n = 941$ flocks). Similarly, flocks with a PC II component score > 0.5 were considered to be Juan-Wedge Flocks (Fig. 5b, $n = 402$ flocks), and flocks with a PC III component score > 0.4 were considered to be Booby Flocks (Fig. 5c, $n = 407$ flocks).

Composition

Each flock type contained a total of 35 different species, although the identity of these 35 varied between flock types (Table 2). As expected from results of the PCA, the most common species in each flock type were those with high component loadings on each of the first three PCS (Tables 2a-c).

Most species were observed in more than one flock type. Of 49 total species recorded in all three flock types, 23 (47%) were members of all three, and 10 (20%) were members of two flock types. Those species recorded only in one flock type (five species in Sooty Tern, six in Juan-Wedge, and five in Booby flocks) were invariably rare.

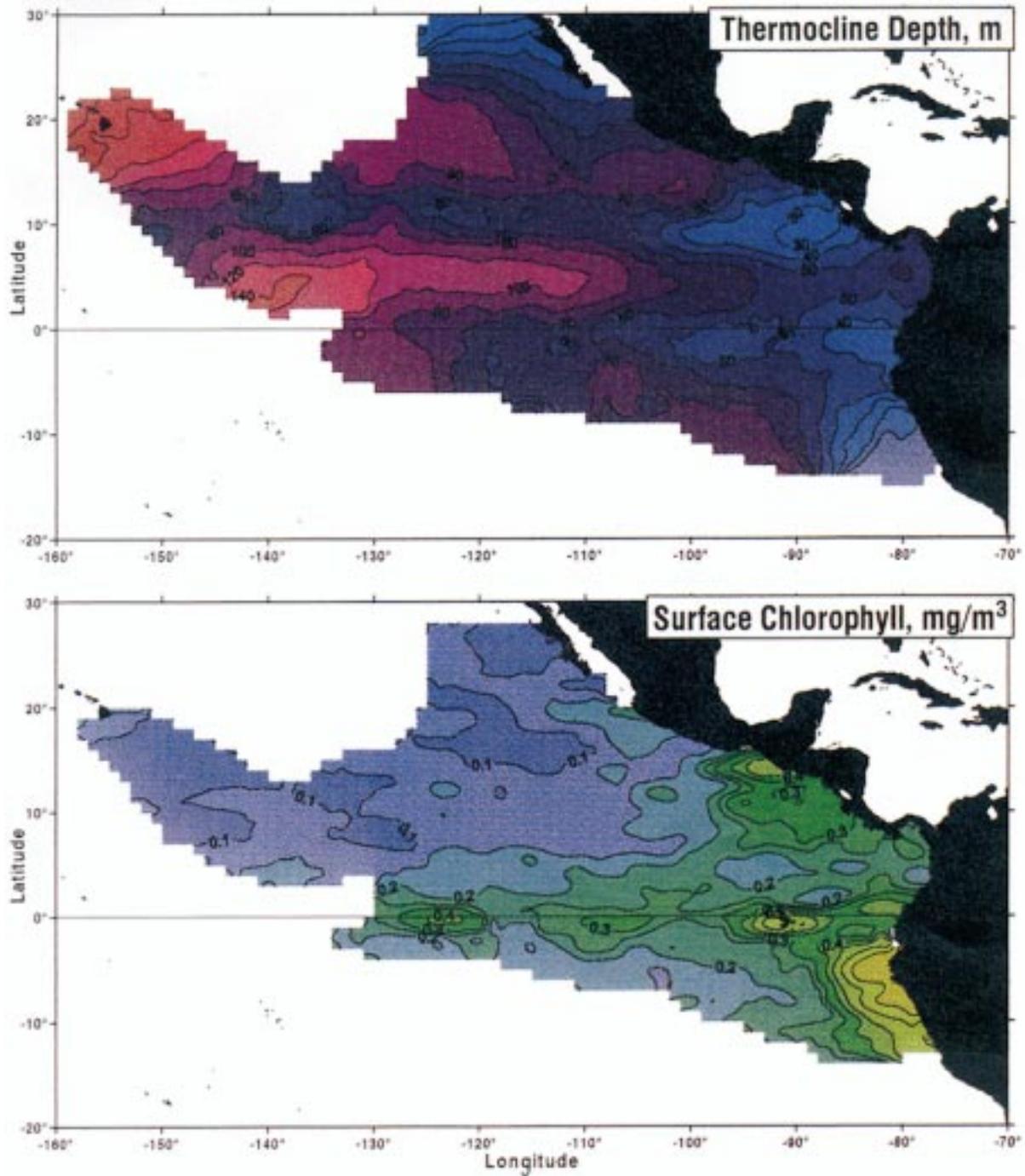


FIG. 3. (a) Thermocline depth (depth of 20°C isotherm) and (b) surface water chlorophyll content in the eastern tropical Pacific during August–November, 1986–1988. Thermocline depth data were gridded by kriging with search radii of 7.9° longitude and 5.1° latitude; surface water chlorophyll data were log-transformed and gridded by kriging (a method for spatial smoothing and interpolation) with search radii of 6.2° longitude and 2.5° latitude. Both data sets were contoured using Surfer volume 6 (Keckler 1995).

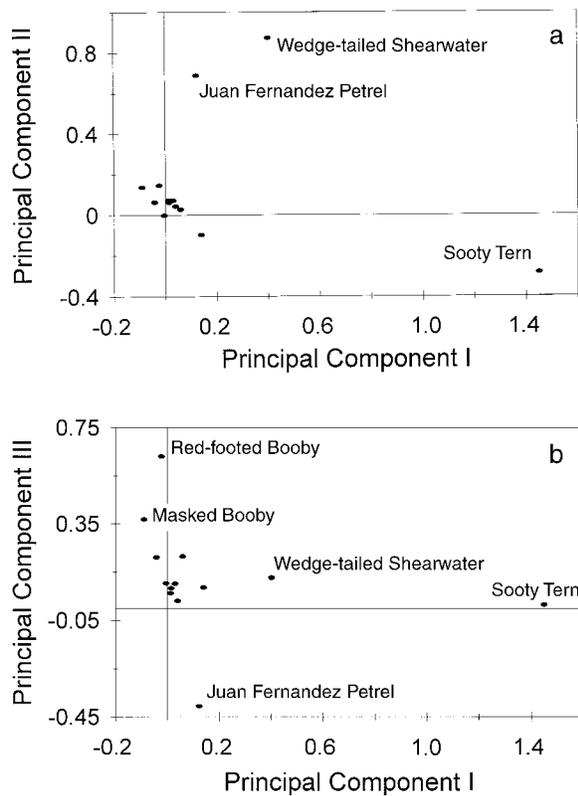


FIG. 4. Component loadings of 13 species variables on the first three principal components (PCs; see Table 1). (a) Loadings on the first two PCs. PC I is almost entirely accounted for by the presence of Sooty Terns in flocks, PC II by the presence of Wedge-tailed Shearwaters and Juan Fernandez Petrels. (b) Loadings on PCs I and III. PC III is almost entirely accounted for by the presence of Red-footed and Masked Boobies in flocks, and by the absence of Juan Fernandez Petrels.

Whereas flock types were defined primarily by the predominance of one or two species, many flocks were multispecies aggregations. Although 46% of Sooty Tern Flocks were monospecific aggregations of Sooty Terns, 35% were flocks of two species, and the remaining 19% consisted of 3–8 species. Similarly, 65% of Juan-Wedge Flocks consisted of one or two species (primarily Juan Fernandez Petrels and/or Wedge-tailed Shearwaters), but the remaining 35% consisted of 3–8 species. Among Booby Flocks, 66% consisted of one or two species (primarily Red-footed and/or Masked Boobies), but 44% consisted of 3–8 species. The identity of those species comprising the second (in the case of Sooty Tern Flocks) or third and subsequent species was variable (Table 2).

Associations with cetaceans

Flocks were associated with ≥ 11 species of cetaceans (Table 3). These were almost always dolphins, and most commonly, spotted and spinner dolphins, for

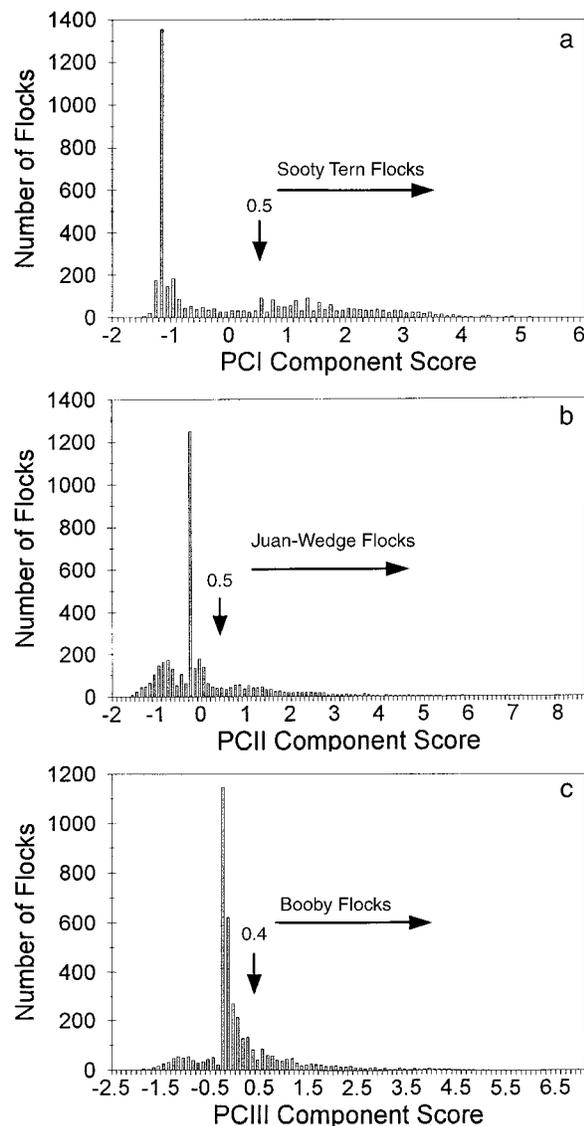


FIG. 5. Frequency histograms of component scores for each of 3888 flocks for the first three PCs. (a) Sooty Tern Flocks have a PC I component score ≥ 0.5 ; (b) Juan-Wedge Flocks have a PC II component score > 0.5 ; (c) Booby Flocks have a PC III component score > 0.4 .

all three flock types. Flocks also occasionally associated with whales.

The frequency of association with schools of cetaceans differed according to flock type (Table 4). Approximately one-fourth of all Juan-Wedge and Booby flocks were associated with cetaceans, whereas this was the case for $< 3\%$ of Sooty Tern Flocks.

Distribution

Flock types exhibited largely disjunct distributions (Fig. 6). Sooty Tern Flocks were most abundant along a broad band running southeast to northwest, from 95° to 160° W longitude, crossing the equator west of 125°

TABLE 2. Descriptive statistics for species recorded in Sooty Tern Flocks ($n = 941$), Juan-Wedge Flocks ($n = 402$), and Booby Flocks ($n = 407$): total number of individuals, mean number of birds per flock (mean ± 1 SE), and total number of flocks in which each species was recorded. Only those species with a mean value of ≥ 0.1 birds per flock are listed.

Species	No. of individuals	No. birds per flock	No. flocks
a) Sooty Tern Flocks			
Sooty Tern†	26 357	28.0 \pm 1.1	941
White Tern†	1048	1.1 \pm 0.1	238
Wedge-tailed Shearwater†	503	0.5 \pm 0.1	172
Juan Fernandez Petrel†	213	0.2 \pm 0.04	74
Great/Magnificent Frigatebird†	169	0.2 \pm 0.03	83
Townsend's/Newell's Shearwater†	143	0.2 \pm 0.05	23
b) Juan-Wedge Flocks			
Juan Fernandez Petrel†	5328	13.3 \pm 1.2	324
Wedge-tailed Shearwater†	3567	8.9 \pm 0.9	274
Masked Booby†	90	0.2 \pm 0.05	41
Sooty Tern†	48	0.1 \pm 0.02	38
Black Tern†	47	0.1 \pm 0.1	4
Black Storm-Petrel	40	0.1 \pm 0.1	2
Townsend's/Newell's Shearwater†	37	0.1 \pm 0.02	21
Arctic Tern†	37	0.1 \pm 0.03	13
Tahiti Petrel†	36	0.1 \pm 0.05	10
Pink-footed Shearwater†	36	0.1 \pm 0.02	22
Great/Magnificent Frigatebird†	28	0.1 \pm 0.01	22
Herald Petrel	26	0.1 \pm 0.03	7
Cook's Petrel†	26	0.1 \pm 0.04	4
Black-winged Petrel	21	0.1 \pm 0.01	15
Leach's Storm Petrel†	21	0.1 \pm 0.03	6
c) Booby Flocks			
Masked Booby†	2643	6.5 \pm 1.0	251
Red-footed Booby†	2452	6.0 \pm 0.8	213
Brown Noddy†	2161	5.3 \pm 1.7	35
Black Noddy	1434	3.5 \pm 1.6	18
Brown Booby†	1114	2.7 \pm 0.6	118
Blue-footed Booby	805	2.0 \pm 1.3	9
Great/Magnificent Frigatebird†	788	1.9 \pm 0.6	93
White Tern†	428	1.1 \pm 0.2	37
Arctic Tern†	103	0.3 \pm 0.1	13
Townsend's/Newell's Shearwater†	100	0.2 \pm 0.1	23
Sooty Tern†	93	0.2 \pm 0.04	34
Pomarine Jaeger†	66	0.2 \pm 0.1	15
Audubon's Shearwater†	65	0.2 \pm 0.1	6
Black Tern†	40	0.1 \pm 0.1	5
Pink-footed Shearwater†	30	0.1 \pm 0.02	16

† Species recorded in all three flock types.

W. In contrast, Juan-Wedge Flocks were distributed primarily along the 10° N latitude line from 115° to 155° W longitude. Booby Flocks were most abundant around breeding islands: Clipperton, Galápagos, Cocos, Tuamotu, and Societies.

On a large spatial scale, this distribution pattern mirrored surface water productivity (Fig. 3). In general, productivity declined from east to west, with westward extensions of shallow thermocline along the equator and at 10° N latitude, and a westward extension of high chlorophyll along the equator. In fact, there were significant differences in the surface water productivity over which each flock type foraged (MANOVA: Wilks' lambda $F = 8.847$; $df = 4$ 660; $P < 0.001$). Sooty Tern Flocks occurred in areas with the deepest thermocline and lowest chlorophyll, Booby Flocks in areas of the shallowest thermocline and highest chlorophyll, and

Juan-Wedge Flocks in intermediate areas with respect to both parameters (Table 4).

DISCUSSION

Our analyses revealed a distinct structure within this oceanic community of subsurface predator-dependent seabirds. Flocks were not simply random assemblages of seabirds dispersed throughout the eastern tropical Pacific. Instead, there were patterns with respect to which species associated in feeding flocks; these flock types had disjunct distributions; and these distributions were correlated with a gradient in surface water productivity. We will consider four factors that may contribute to producing or maintaining this structure: (1) energetic constraint, (2) competition, (3) proximity to breeding colonies, and (4) prey partitioning. Because flock types were identified primarily on the basis of numerical abun-

TABLE 3. Marine mammals recorded in association with each seabird flock type. Values represent the total number of flocks associated with each mammal and the percentage of mammal-associated flocks represented by each association (in parentheses).

Marine mammals	Sooty Tern Flocks	Juan-Wedge Flocks	Booby Flocks
Balaenopteridae			
<i>Balaenoptera edeni</i>	1 (3.7%)	1 (1.0%)	0
<i>Balaenoptera</i> sp.	3 (11.1%)	0	1 (1.0%)
Delphinidae			
<i>Pseudorca crassidens</i>	0	3 (2.9%)	1 (1.0%)
<i>Orcinus orca</i>	1 (3.7%)	0	0
<i>Globicephala</i> sp.	1 (3.7%)	0	0
<i>Steno bredanensis</i>	0	1 (1.0%)	6 (6.2%)
<i>Lagenodelphis hosei</i>	0	1 (1.0%)	0
<i>Delphinus delphis</i>	1 (3.7%)	4 (3.9%)	7 (7.3%)
<i>Tursiops truncatus</i>	1 (3.7%)	4 (3.9%)	4 (4.2%)
<i>Stenella attenuata</i>	11 (40.7%)	41 (39.8%)	37 (38.5%)
<i>Stenella coeruleoalba</i>	1 (3.7%)	5 (4.8%)	6 (6.2%)
<i>Stenella longirostris</i>	4 (14.8%)	32 (31.1%)	22 (22.9%)
Unidentified dolphin	3 (11.1%)	11 (10.7%)	12 (12.5%)

dance of one or two species, the following discussion will focus on attributes of these key species: Sooty Tern, Wedge-tailed Shearwater, Juan Fernandez Petrel, Red-footed Boobies, and Masked Boobies.

Energetic constraint

Flocks found in areas of lowest productivity were dominated by Sooty Terns. Why was this species so abundant here, whereas other species were much less so? Theoretically, a seabird with proficient flight will be able to travel farther between prey patches than a seabird with less proficient flight. Therefore, seabird distribution and, thus, species associations in feeding flocks, may reflect a prey abundance gradient that corresponds to the relative cost of flight for each species. This leads to a testable prediction: species found in Sooty Tern Flocks should have a lower cost of flight than species in Juan-Wedge Flocks, which, in turn, should have a lower cost of flight than species in Booby Flocks. Inherent in this prediction is the assumption that surface water productivity generally correlates

with prey *availability* over the spatial scales at which foraging flocks operate, and that, as productivity decreases, the distance between prey patches will increase and feeding opportunities will be fewer.

Flint and Nagy (1984) measured the energetic cost of flight for Sooty Terns using the doubly labeled water method, and Ballance (1995; L. T. Ballance, *unpublished data*) used similar methods to measure flight cost for Red-footed Boobies and Wedge-tailed Shearwaters. Data from these studies support the prediction. The cost of flight was lowest for Sooty Terns, two times higher for Wedge-tailed Shearwaters, and highest for Red-footed Boobies, again by a factor of approximately two (Table 5).

The hypothesis that seabird communities may be structured by flight costs operating along a productivity gradient is not new. Ainley (1977) documented essentially this same pattern on a global scale for seabirds in the Pacific. That is, there were predictable changes in species composition with changes in latitude and productivity, and these relationships were reflected in the flight abilities of the birds. Others have noted the correlation between the relatively low productivity of tropical oceans and the proficient flight of the seabirds that exploit them (Brown 1980, Hulsman 1980, Ainley and Boekelheide 1983, Au and Pitman 1986).

Such a relationship between productivity and flight proficiency should not be surprising. Although a variety of hydrographic features can serve to concentrate seabird prey (Hunt and Schneider 1987, Hunt 1990), prey are patchy in space and time in the vast expanses of the open ocean. As productivity drops, seabirds should be increasingly selected for their ability to efficiently locate these patches. Although there are different strategies (Pitman and Ballance 1990, 1992), one way to locate a patch is simply to cover large areas; seabirds using this strategy should exhibit adaptations for proficient flight. They might be adapted to use the wind as an energy source when flying (Ballance 1995), or they might exhibit morphological adaptations particularly suited for proficient flight (Warham 1977). At the low-productivity end of the system, seabirds in general, and this community in particular, may be structured by energetic constraint.

TABLE 4. Summary information for each flock type. Standard errors are presented with means.

	Sooty Tern Flocks	Juan-Wedge Flocks	Booby Flocks
Total no. flocks	941	402	407
No. flocks with oceanographic data	112	120	102
Total no. species	35	35	35
No. (and %) flocks associated with marine mammals	27 (2.9%)	103 (25.6%)	96 (23.6%)
Mean thermocline depth (m)*	77.6 ± 2.0	68.8 ± 1.9	62.5 ± 1.4
Mean surface chlorophyll (mg/m ³)*	0.14 ± 0.01	0.16 ± 0.01	0.17 ± 0.01

* Significant difference among flock types at the $\alpha = 0.05$ level.

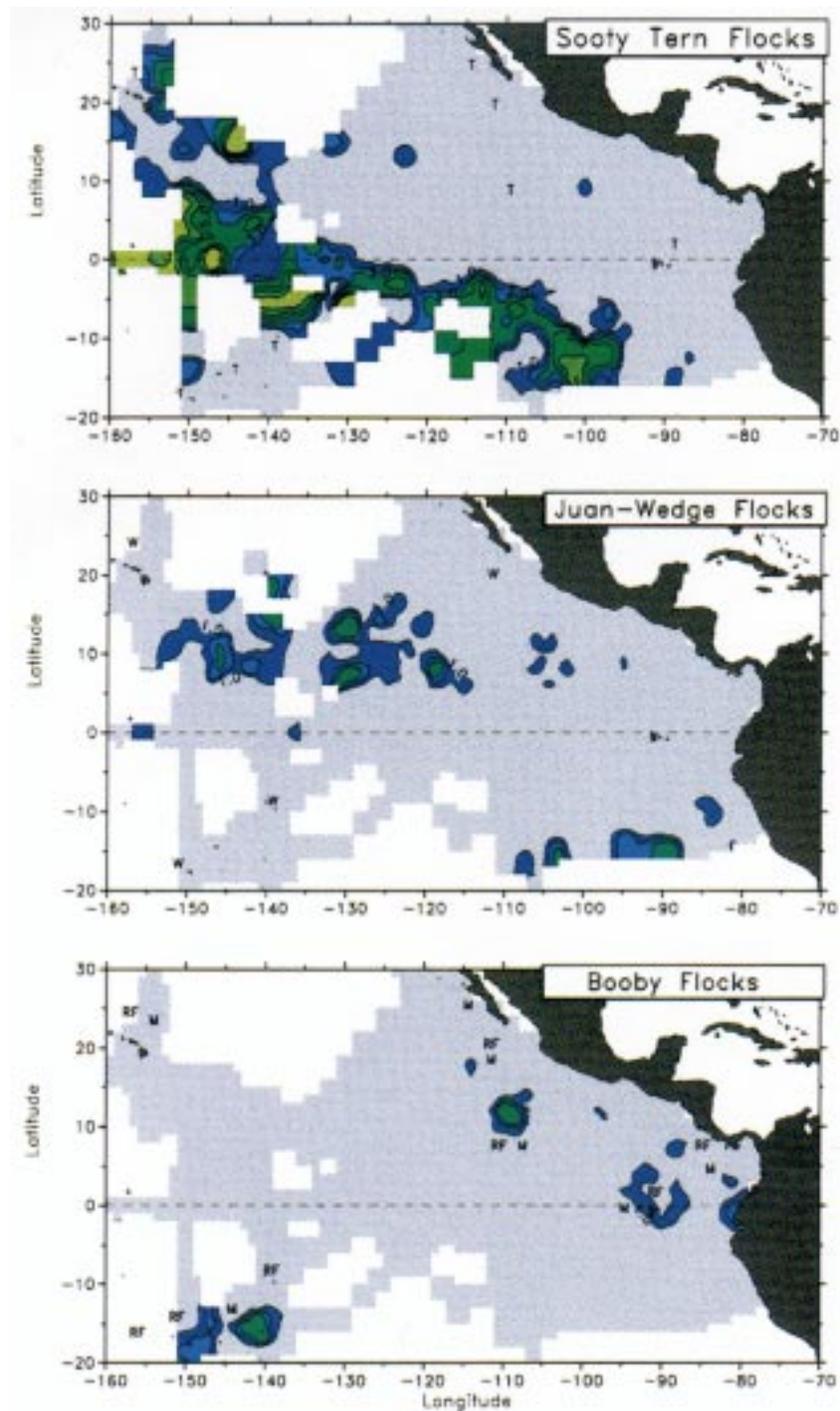


FIG. 6. Distribution of each of three flock types. The areas not surveyed are white; areas surveyed are light blue. The horizontal axis is degrees west longitude; the vertical axis is degrees north (positive) and south (negative) latitude. Colors and contours represent the total number of flocks sighted in that area during the entire survey: for Sooty Terns, dark blue = 1, royal blue = 2, first dark green contour = 3, second dark green contour = 5, stippled green contour = 6, and stippled yellow = 7 flocks; for Juan-Wedge Flocks and Booby Flocks, dark blue = 1, royal blue = 2, and dark green = 3 flocks. Data were gridded by inverse distance with a search radius of 2° latitude by 2° longitude, then contoured using Surfer volume 6. Letters represent approximate locations of breeding colonies (Fig. 1a and Appendix B) for Sooty Terns (T), Wedge-tailed Shearwaters (W), Red-footed Boobies (RF), and Masked Boobies (M).

TABLE 5. Energetic cost of flight, body mass, feeding methods, and the relative depth to which each allows a bird to feed, presented for the numerically abundant flocking species.

Characteristic	Sooty Tern	Wedge-tailed Shearwater	Juan Fernandez Petrel	Red-footed Booby	Masked Booby
Cost of flight (W) [†]	4.8	9.9	unknown	19.0	unknown
Mass (g) [‡]	180	388	430	1003	1987
(Range)	(147–220)	(320–510)	(389–471)	(850–1210)	(1503–2353)
Sample size (<i>n</i>)	95	124	45	40	53
Feeding methods§ (Relative depth)	aerial pursuit (none) dipping (surface) surface plunging (surface)	surface seizing (surface) pursuit plunging? (below surface) pursuit diving? (below surface)	aerial pursuit (none) surface seizing (surface)	aerial pursuit (none) surface seizing? (surface) surface plunging? (surface)	deep plunging (below surface)

[†] For Sooty Tern, *n* = 14, mean mass = 187 g (Flint and Nagy 1984); for Red-footed Booby, *n* = 6, mean mass = 1014 g (Ballance 1995); for Wedge-tailed Shearwater, *n* = 5, mean mass = 418 g (L.T. Ballance, *unpublished data*).

[‡] Mean mass, range, and *n* from Dunning (1993), with the exception of Juan Fernandez Petrel: mean \pm 1 SD body mass and *n* from Warham (1977).

[§] From Ashmole (1971), Ballance (1993); R. L. Pitman, *unpublished data*.

^{||} Depth description in parentheses: None = no contact with the water; surface = penetration < 1 m; below surface = penetration > 1 m; from R. L. Pitman, *unpublished data*.

Competition

Energetic constraint cannot explain community structure at the high-productivity end of the system, as species with low flight costs are easily able to fly into areas of high prey abundance. Why, then, are flocks in productive waters numerically dominated by boobies, and why are Juan Fernandez Petrels, Wedge-tailed Shearwaters, and Sooty Terns not more abundant here? One possibility is interspecific competition. In the case of highly mobile seabirds, we might expect that an individual would attempt to feed in areas of highest resource availability. Therefore, interspecific competition, or its effects, would be most intense in areas of highest productivity. This leads to the prediction that species found in Booby Flocks should be competitively superior to species in Juan-Wedge Flocks, which, in turn, should be competitively superior to species in Sooty Tern Flocks. Again, this prediction assumes that surface water productivity correlates with prey availability.

Direct competitive interactions between feeding seabirds do occur (Feare 1981, Hoffman et al. 1981, Duffy 1986), and birds in feeding flocks in the eastern tropical Pacific are no exception (Ballance 1993). Typically, prey are forced to the surface by tunas, and escape by leaping or flying out of the water in densely packed groups. Seabirds descend on these boils in a concentration of furious activity, jostling for position, vocalizing and jabbing at other birds, and attempting to capture prey while simultaneously avoiding mid-air collisions with birds or with tunas that catapult out of the water at high speed. Such a situation prompts at least two predictions about competitive abilities of species in these flocks.

First, larger species may be expected to outcompete smaller species via interference competition, simply because the probability of injury from aggressive in-

teractions or collisions with other members of the feeding assemblage increases with decreasing body size (Schoener 1983, Persson 1985, Dickman 1988, Smith 1990). In fact, there is a body size gradient among the five numerically abundant flocking species (Table 5), and this gradient holds true for flock types. The largest species occurred predominantly in Booby Flocks and fed in areas of highest productivity. Progressively smaller species occurred predominantly in the other two flock types (where larger species were less common or absent) and fed in areas of decreasing productivity. Similar patterns of non-overlapping body size for species that share general food requirements are common (Schoener 1970, Hespeneide 1971, McNab 1971, Brown 1975, Hertel 1994), and are generally interpreted as implying that competition has been a factor in structuring these communities (Brown 1975).

A second prediction is that species able to penetrate farther beneath the surface may outcompete those restricted to the surface via exploitative competition (see also Hoffman et al. 1981). This is because diving seabirds may drive prey down into the water column, indirectly preventing seabirds restricted to shallower depths from feeding successfully. Predators are theoretically always present below the prey, but prey may be found at differing depths, depending upon the relative pressures from the seabirds above. Feeding methods and categorical estimates of foraging depths for the five key flocking species show no clear pattern (Table 5); each of the Booby and Juan-Wedge flocks is defined by both a species that is restricted to the surface, and one that can dive below. However, we have no data to describe the proportion of total feeding attempts that each method comprises for a given species, nor do we know the exact depths to which a bird reaches when using each method. From our field experience, it is obvious that Masked Boobies can dive at least several

meters below the water surface, whereas Sooty Terns reach depths of a few centimeters at most. Clearly, we need more data to determine whether or not exploitative competition between seabird species occurs along this axis.

The idea that competition becomes more important with an increase in productivity should also be no surprise. As productivity increases, selection should shift from favoring a seabird's ability to locate prey patches to favoring its ability to capture prey within a patch. Indeed, it is in the most productive waters that we find those seabirds with superior abilities to forage within the water column: the alcid, diving petrels, and penguins (Brown 1980). The latter group has completely lost the ability to fly, trading flight proficiency for proficiency in swimming.

Proximity to breeding colonies

Because seabirds are restricted to islands for reproduction, it is reasonable to expect that species distribution patterns at sea, and thus availability of a species for participation in feeding flocks, may simply reflect the location of breeding colonies.

Breeding colonies for each of the key flocking species (Appendix B) are shown in Figs. 1a and 6. The visual pattern illustrated in Fig. 6c clearly shows that this prediction is supported for Red-footed and Masked Boobies. Major colonies are found in the eastern tropical Pacific, including the largest in the world for both of these pantropical species (Tower Island of the Galápagos Archipelago for Red-footed Booby, Nelson 1978; Clipperton Island for Masked Booby, R. L. Pitman, *unpublished data*). Not surprisingly, the ocean areas around both islands are centers of distribution for Booby Flocks.

Yet, location of breeding colonies may not be solely responsible for the at-sea distribution of Booby Flocks. Although colonies influence patterns at sea, oceanographic factors obviously influence patterns of colony size and location, since a bird can breed on an island only if it can forage successfully in surrounding waters. We believe that it is the high productivity of surface waters adjacent to the Galápagos Archipelago and Clipperton Island that allows these colonies to reach such huge sizes. Thus, productivity, by supporting high numbers of boobies on these colonies, may be indirectly responsible for the prevalence of Booby Flocks around them.

Figure 6a and b illustrates that locations of breeding colonies do not explain Juan-Wedge or Sooty Tern flock distributions. None of the Wedge-tailed Shearwater breeding colonies was a site of high Juan-Wedge Flock distribution, nor were Sooty Tern colonies the sites of high Sooty Tern Flock distribution. There are no Juan Fernandez Petrel colonies in the eastern tropical Pacific at all. Our data were collected throughout the year. During the nonbreeding season when birds migrate away from colonies, patterns in flock distribution rep-

resent the importance of factors other than colony location. In sum, the location of breeding colonies can, at best, only partially explain flock patterns; in fact, it is the flock patterns themselves that reveal distribution of foraging areas, which in turn may influence colony size and location.

Prey partitioning

If seabirds specialize on prey species or size classes, and if these prey have disjunct distributions, seabird distribution and, consequently, species associations in feeding flocks, may simply reflect this distribution of prey.

Available information suggests, however, that diet diversity of the seabirds in this community is low. Although studies of tropical seabirds often reveal partitioning with respect to prey species and prey size (Ashmole and Ashmole 1967, Ashmole 1968, Schreiber and Hensley 1976, Hulsman 1980, 1987, Diamond 1983, Harrison et al. 1983), much of this partitioning occurs with respect to fishes that originated in reefs. For tropical seabirds that feed far from islands and reefs (the case for the vast majority of our feeding flocks), diet diversity is much lower (Diamond 1983, Harrison et al. 1983), and is comprised almost exclusively of only two prey types, flying fish (Exocoetidae) and ommastrephid squid (Ashmole and Ashmole 1967, 1968, Ashmole 1968, Schreiber and Hensley 1976, Harrison et al. 1983, 1984a, Seki and Harrison 1989). Consequently, diet overlap between these species is high (Ashmole and Ashmole 1967), exceeding 90% in one study (Diamond 1983).

Much less is known about prey distribution. In the oceanic Pacific in general, phytoplankton, macrozooplankton, and nekton show distinct spatial patterns of distribution and species co-occurrence, patterns that occur on a very large scale, are few in number, and are clearly related to the large, general features of surface circulation (McGowan 1974, McGowan and Walker 1993). However, details for particular species of exocoetid flying fish and ommastrephid squid have yet to be documented.

There is evidence that feeding *opportunities* may change geographically; Booby and Juan-Wedge flocks associated with dolphins to a much greater degree than did Sooty Tern Flocks. Similarly, Au and Pitman (1986) found that flocks in the southern and central Pacific were dominated by Sooty Terns, and few were associated with dolphins. The fish in these aggregations were mostly skipjack, smaller yellowfin, and bigeye (*Thunnus obesus*) tuna, as compared with large yellowfin tuna of the eastern and northern portions of the eastern tropical Pacific. Because of the importance of subsurface predators to seabirds in this community, this change may be significant. How such a change might affect flock structure is yet to be discovered.

Summary and perspectives

We propose that this oceanic community of subsurface predator-dependent seabirds is largely structured by two factors that operate at opposite ends of a productivity gradient. As productivity decreases (low prey abundance), flight proficiency becomes increasingly important, because only species with relatively low flight costs will be able to transit between prey patches. As productivity increases (high prey abundance), competitive ability becomes increasingly important, because competitive dominants will exclude other species from feeding flocks.

This general idea was articulated long ago: "Not until we reach the extreme confines of life, in the arctic regions or on the borders of an utter desert, will competition cease" (Darwin 1859: 78); "When we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements" (Darwin 1859: 69). More recently, Menge and Sutherland (1987) proposed a model similar to ours to explain community structure for marine benthic and terrestrial habitats. For the top trophic level, the model predicts that tolerance of physical factors will regulate community structure when environmental stress is high, and as the environment moderates, competition will become more important. Arnott and Vanni (1993) proposed a similar model to explain zooplankton assemblages in freshwater lakes in North America. Similar relationships, with one species being the competitive dominant and another having a higher tolerance to physical stress, have been documented for a wide variety of organisms along environmental gradients (Dunham 1980, Brown and Gibson 1983, Connell 1983). Our system, strikingly different with respect to habitat structure and complexity, spatial scale, taxa, and number of species affected, provides another specific example of what seems to be a general pattern for the selective forces that structure communities.

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APPENDIX A

Scientific names of seabird species in this study, listed in taxonomic order.

Common name	Scientific name
Order Procellariiformes	
Family Procellariidae	
Tahiti Petrel	<i>Pterodroma rostrata</i>
Herald Petrel	<i>Pterodroma heraldica</i>
Juan Fernandez Petrel	<i>Pterodroma externa</i>
Cook's Petrel	<i>Pterodroma cookii</i>
Black-winged Petrel	<i>Pterodroma nigripennis</i>
Pink-footed Shearwater	<i>Puffinus creatopus</i>
Wedge-tailed Shearwater	<i>Puffinus pacificus</i>
Christmas Shearwater	<i>Puffinus nativitatis</i>
Townsend's/Newell's Shearwater	<i>Puffinus auricularis</i>
Audubon's Shearwater	<i>Puffinus lherminieri</i>
Family Hydrobatidae	
Leach's Storm-Petrel	<i>Oceanodroma leucorhoa</i>
Black Storm-Petrel	<i>Oceanodroma melania</i>
Order Pelecaniformes	
Family Sulidae	
Blue-footed Booby	<i>Sula nebouxii</i>
Masked Booby	<i>Sula dactylatra</i>
Red-footed Booby	<i>Sula sula</i>
Brown Booby	<i>Sula leucogaster</i>
Family Fregatidae	
Magnificent Frigatebird	<i>Fregata magnificens</i>
Great Frigatebird	<i>Fregata minor</i>
Order Charadriiformes	
Family Stercorariidae	
Pomarine Jaeger	<i>Stercorarius pomarinus</i>
Family Laridae	
Black Tern	<i>Chlidonias niger</i>
Arctic Tern	<i>Sterna paradisaea</i>
Sooty Tern	<i>Sterna fuscata</i>
Brown Noddy	<i>Anous stolidus</i>
Black Noddy	<i>Anous tenuirostris</i>
White Tern	<i>Gygis alba</i>

APPENDIX B

Breeding colonies in the eastern tropical Pacific for each of the five numerically abundant flocking species. Locations of colonies are given in Figs. 1a and 6.

Species	Breeding colonies	References
Sooty Tern	Cocos Island (?)	Stiles 1984
	Isla Pelado (?)	Duffy and Hurtado 1984
	Galápagos Archipelago	Coulter 1984
	Hawaiian Archipelago, Johnston Atoll	Harrison et al. 1984 <i>b</i>
	Tuamotu, Marquesas, Societies, Cooks (?)	Garnett 1984
	Islas Revillagigedo, Rocas Alijos	Everett and Anderson 1991
Wedge-tailed Shearwater	Clipperton Island	R. L. Pitman, <i>unpublished data</i>
	Hawaiian Archipelago, Johnston Atoll	Harrison et al. 1984 <i>b</i>
	Tuamotu (?), Marquesas, Societies	Garnett 1984
Juan Fernandez Petrel	Islas Revillagigedo	Everett and Anderson 1991
	None	Stiles 1984
Red-footed Booby		Duffy and Hurtado 1984
		Coulter 1984
		Harrison et al. 1984 <i>b</i>
		Garnett 1984
		Everett and Anderson 1991
		Stiles 1984
Masked Booby	Cocos Island	Coulter 1984
	Galápagos Archipelago	Harrison et al. 1984 <i>b</i>
	Hawaiian Archipelago, Johnston Atoll	Garnett 1984
	Marquesas, Societies, Cooks	Everett and Anderson 1991
	Islas Revillagigedo	R. L. Pitman, <i>unpublished data</i>
Masked Booby	Clipperton Island	Duffy and Hurtado 1984
	La Plata Island, Isla Pelado	Coulter 1984
	Galápagos Archipelago	Harrison et al. 1984 <i>b</i>
	Hawaiian Archipelago, Johnston Atoll	Garnett 1984
	Tuamotu	Everett and Anderson 1991
Masked Booby	Islas Revillagigedo, Rocas Alijos	R. L. Pitman, <i>unpublished data</i>
	Clipperton Island	