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SEABIRD INTERACTIONS WITH DOLPHINS AND TUNA IN THE EASTERN TROPICAL PACIFIC[1]

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Abstract. Bird flocks associated with dolphins in the eastern tropical Pacific are described from observations obtained during eight cruises that took place from January to March of 1976, 1977, 1979, and 1980. In the northern tropical waters between latitudes 5°N and 30°N, 43% to 53% of bird flocks co-occurred with dolphins. In equatorial and southern subtropical waters between latitudes 5°N to 12°S and in the central Pacific less than 8% of the flocks were associated with dolphins. In northern tropical waters about 70% of dolphin schools associated with flocks were composed of spotted or spotted plus spinner dolphins; conversely, 59% of spotted dolphin and 96% of spotted plus spinner dolphin schools co-occurred with bird flocks. Most large schools of these dolphins were associated with birds, and the number and diversity of bird species increased with dolphin school size. The average species composition of birds in dolphin-associated flocks of northern tropical waters was: boobies 41.7%, Wedge-tailed Shearwaters (*Puffinus pacificus*) 31.4%, jaegers 12.8%, Sooty Terns (*Sterna fuscata*) 6%, frigatebirds 3.6%, and others 4.5%. Positive statistical associations were found among these bird species, which are explained by common attraction to food made available by feeding yellowfin tuna. In the southern latitudes and in the central Pacific, flocks were dominated by Sooty Terns, and few flocks were associated with dolphins. These flocks appeared to be associated with skipjack rather than yellowfin tuna.

Key words: *Foraging interactions; tropical seabirds; tuna; dolphins; Pacific Ocean.*

INTRODUCTION

Flocks of seabirds accompanying dolphin schools (order Cetacea) are a conspicuous sight in the eastern tropical Pacific (ETP). Tuna fishermen search for these flocks to locate dolphin schools and the yellowfin tuna (*Thunnus albacares*) that swim with them. These flocks are usually associated with only a few of the many species of dolphins found in the ETP. It is only those few dolphin species, in turn, that are commonly associated with tuna. The dolphin-associated tuna are primarily yellowfin and, less frequently, skipjack *Katsuwonus pelamis* (Hammond 1981). In this paper, we describe the characteristics of seabird flocks that associate with dolphins and also describe the nature of the joint aggregations of birds, dolphins, and tuna. We present evidence for a major discontinuity in the pelagic community—between multispecies flocks associated with dolphins and yellowfin tuna, on the one hand, and single species flocks associated with small tuna, on the other.

METHODS

Our seabird observations began in 1976 during cetacean surveys carried out by the Southwest Fisheries Center. The main surveys jointly used NOAA ships *David Starr Jordan* and *Townsend Cromwell* during each January through early March of 1976, 1977, 1979, and 1980; the combined eight cruises broadly sampled the main yellowfin tuna fishing grounds in the eastern Pacific (Fig. 1). These grounds, described by Calkins (1975), lie roughly within the triangular area whose base is formed by the American coasts between latitudes 25°N and 15°S and whose apex is offshore at latitude 10°N, longitude 150°W.

Though the main purpose of the surveys was to determine the distribution and relative abundance of the different cetacean species, especially the dolphins that interact with the tuna fishery (Au and Perryman 1985), sightings of birds were also recorded. During daylight hours the sea surface was searched continuously while ships were underway, using two pairs of 20 or 25 power binoculars mounted port and starboard on or above each ship's bridge. We watched for bird flocks because of their association with cetaceans and also for independent avian studies. All observed species and numbers of birds were recorded. Because large flocks were difficult to enumerate, the counts are our best estimates. Although individual species of both birds and cetaceans differ in conspicuousness, possible biases in species counts are mitigated in this study by focus on the more carefully observed dolphin-associated flocks. When a cetacean school and/or bird flock was sighted, the ship approached it and usually passed through the aggregation. In this way we obtained close-up observations of species composition and behavior of the bird flocks and of the cetaceans. The distance to the horizon was 10.2 to 13.0 km, depending

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upon the height of the observer's eye above the sea surface.

In this paper we discuss bird observations from the research cruises in 1977, 1979, and 1980 (13 cruise months). This data set was obtained with better areal coverage and species identifications than in 1976. Information from other, shorter research cruises (11 between 1976 and 1981) was also used.

We divided the data into two latitude intervals: 5°N to 30°N and <5°N to 12°S. The northern interval enclosed northern tropical (NT) waters and the southern interval the equatorial and southern tropical and subtropical (ESTS) waters surveyed. These oceanographic water types were defined by Wyrtki (1967); Ashmole (1971) discussed the seabirds, and Au and Perryman (1985) discussed the dolphins associated with these water types. Briefly, NT waters are the warm (>25°C), low salinity (<34‰) waters of the Equatorial Counter Current and the southern portion of the North Equatorial Current. Seasonal changes in NT characteristics are relatively small. The ESTS waters lie along the equator (equatorial water) and extend southward into the southern ocean (southern subtropical water). ESTS waters are seasonally variable, affected by upwelling, extensions of the Peru Current, and large seasonal changes in weather. The data are presented here with respect to the two latitude intervals to show the broad patterns of bird-dolphin interactions that are related but not restricted to the specific water types in each interval.

Characteristics of bird flocks, the composition of species in the flocks, and their degree of association with species of cetacea are described from the counts of individuals of each species. Aggregations of more than 10 birds were considered to be flocks; fewer birds were often too scattered to be described as a flock. The species composition of flocks associated with dolphins is described from the counts of all birds found with the dolphins. Association among these bird species was ascertained using Chi-square tests of 2 × 2 presence-absence tables of species in the flocks (e.g., Pielou 1969).

RESULTS

FLOCK CHARACTERISTICS AND CO-OCCURRENCE WITH DOLPHINS

The species composition of flocks, as well as the proportion of flocks associated with cetaceans, varies by area. Table 1 gives the aggregate data for the main species that make up these flocks, regardless of whether the flocks were associated with cetaceans. In addition to the NT and ESTS latitude intervals, the data are also classified according to two main longitude (zonal) intervals that we call the eastern Pacific (Central America to longitude 125°W) and the central Pacific (longitude 125°W to 155°W). Most avian species or groups were proportionately less abundant in flocks from central Pacific and ESTS waters than in flocks from NT waters of the eastern Pacific. The terns were a notable exception to this trend; in particular, Sooty Terns (*Sterna fuscata*) increased in the eastern Pacific from 15.1% of total birds in NT waters to 62.2% in ESTS waters, while in the central Pacific they increased from 63.5% in NT waters to 79.4% in ESTS waters.

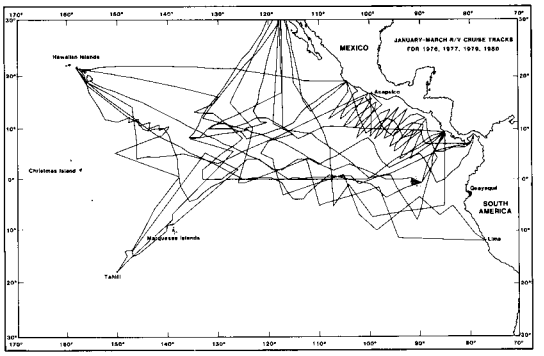

FIGURE 1. Research cruise tracks along which bird observations were taken.

Bird flocks that co-occurred with cetaceans were associated primarily with delphinids, in particular certain dolphins. But whereas less than 8% of flocks were with these dolpins in central Pacific and ESTS waters, the percentage of flocks with dolphins averaged 43% to 53% in NT waters of the eastern Pacific (Table 2). The 53% pertains to a coastal belt about 1,100 km wide off Central America, which was surveyed intensively in 1979 (see Fig. 1). Flocks were rarely seen with whales, even off Central America.

Dolphin-associated flocks were significantly larger than those not associated with dolphins. In NT waters the geometric mean of flock size (appropriate because flock size distribution tends to be skewed) increased from 27.3 birds (95% confidence interval 24.4–30.5) in flocks without dolphins to 57.0 (95% CI 47.7–68.1) in flocks with dolphins. In ESTS waters mean flock size increased from 29.1 in flocks without dolphins (95% CI 26.3–32.2) to 43.4 in flocks with dolphins (95% CI 36.3–51.9).

SPECIES OF DOLPHINS ASSOCIATED WITH BIRD FLOCKS

Seabird flocks regularly associated with only 5 dolphin species out of at least 23 species of cetaceans, including whales, found in the ETP. The degree of association varied greatly among these 5 species of dolphins. In both NT and

TABLE 1. Major species in flocks with ≥10 birds, eastern vs. central Pacific.[1]

Bird species	Eastern Pacific coast–125°W				Central Pacific[2] 125°–155°W			
	5°N–30°N		<5°N–12°S		5°N–30°N		<5°N–12°S	
	n	%	*n*	%	*n*	%	*n*	%
Booby spp.								
Sula sula, etc.	9,774	34.27	2,490	15.26	161	0.40	751	0.47
Wedge-tailed Shearwater								
Puffinus pacificus	7,146	25.03	293	1.80	447	11.27	249	1.57
Sooty Tern								
Sterna fuscata	4,300	15.06	10,153	62.21	2,519	63.50	12,567	79.37
Jaeger spp.								
Stercorarius spp.	2,686	9.41	88	0.54	116	2.92	28	0.18
Noddy/other Terns								
Anous, Chlidonius, Gygis spp.	1,984	6.95	2,618	16.04	6	0.15	2,254	14.24
Frigatebird								
Fregata spp.	1,050	3.68	303	1.86	9	0.23	146	0.92
Other shearwaters								
Puffinus lherminieri, P. auricularis, P. nativitatus, etc.	1,179	4.13	28	0.17	104	2.62	11	0.06
White-necked/Juan Fernandez/Dark-Rumped petrels								
Pterodroma externa, P. phaeopygia	309	1.08	319	1.95	692	17.44	259	1.64
Other gadfly petrels								
Pterodroma spp.	118	0.41	29	0.18	58	1.46	245	1.54
Totals	28,546	100	16,321	100	3,967	100	15,834	100

[1] From January–March cruises, 1977, 1978, 1980.
[2] From total counts taken aboard R/V *Townsend Cromwell*. Data from near Marquesas, Tuamotu, and Society islands excluded.

ESTS waters, spotted (*Stenella attenuata*) and spinner (*S. longirostris*) dolphins co-occurred most frequently with flocks; 58.9% and 52.9% respectively of these dolphins' schools were associated with flocks in NT waters (Fig. 2, top). These two dolphin species often occur together (approximately one third of spotted dolphin schools are found mixed with spinner dolphins [Au and Perryman 1985]); 96.4% of such mixed schools were with bird flocks in NT waters. In those same waters 30.6% of common dolphin (*Delphinus delphis*) schools were with flocks, and only 12.5% of rough-toothed dolphin (*Steno bredanensis*) and 1.6% of striped dolphin (*Stenella coeruleoalba*) schools were with flocks. Notice that the percentage of schools of the above dolphin species that were associated with birds decreased markedly in ESTS waters compared with NT waters.

We measured the relative likelihood of a particular dolphin species being found in any given bird-dolphin aggregation as the percent of all dolphin-associated bird flocks that co-occurred with each dolphin species or group (Fig. 2, bottom). Of the above five dolphin species, spotted and mixed spotted plus spinner dolphin schools were the most likely (35.9%

TABLE 2. Percent of flocks (≥10 birds/flock) with cetaceans.

Area	Latitude	Flocks	w. Delphinids[a]			w. Whales		
			n	%	Range[b]	*n*	%	Range[b]
1. Eastern Pacific								
Entire	5°N–30°N	363	155	42.7	36.4–52.1	5	1.4	1.1–1.6
Off Cent. Amer.	5°N–30°N	256	135	52.7	48.0–75.9	4	1.6	0–2.6
Off Cent. Amer.	<5°N	344	26	7.6	4.3–33.3	3	0.9	0–2.0
2. Central Pacific	5°N–30°N	76[c]	3	3.9[d]	—	0	0	—
	<5°N	305[c]	1	0.3[d]	—	0	0	—

[a] Includes dolphins and certain small "whales," e.g. pilot whale.
[b] Range among cruises.
[c] Data based on *Townsend Cromwell* cruise 77–1; flocks based upon flock counts of *Sterna fuscata* only.
[d] Maximal estimates.

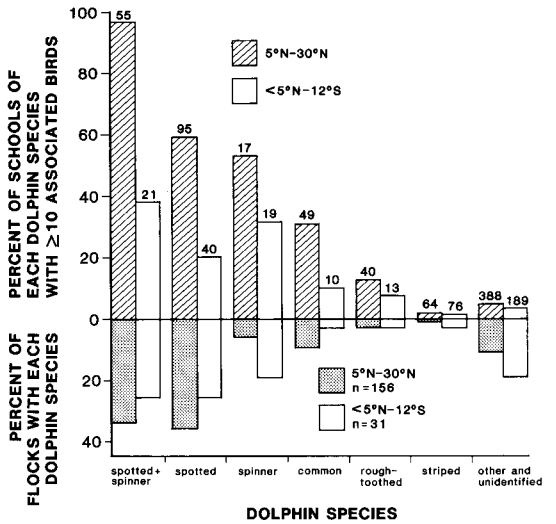

FIGURE 2. The percent of dolphin schools of each species or species group with bird flocks (upper) and the percent of all dolphin-associated flocks with each species or species group of dolphins (lower). Numbers over the bars are the schools examined. "Other and unidentified" category probably includes many spotted and spinner dolphin schools.

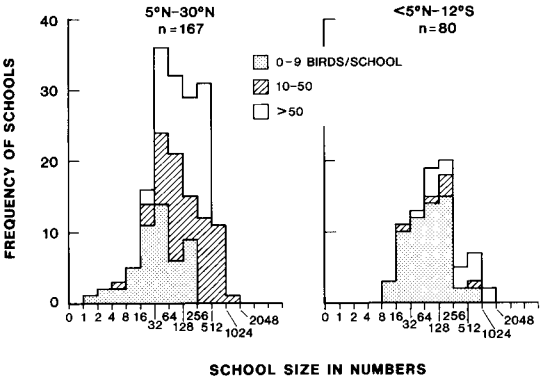

FIGURE 3. Effects of school size (spotted and/or spinner dolphins only) on the frequency of schools with bird flocks.

and 34.0%, respectively) and the striped dolphin least likely (0.6%) to be present in bird-dolphin aggregations. The spinner dolphin, in unmixed schools, was relatively more likely to be found in such aggregations in ESTS waters than in NT waters. In part because most spinner schools with birds in NT waters were also with spotted dolphins. Common dolphins were more likely to occur in bird-dolphin aggregations in the northern latitudes.

EFFECTS OF SIZE OF BIRD FLOCKS AND OF DOLPHIN SCHOOLS

The size of bird flocks associated with dolphins tended to increase with the size of the dolphin schools. In both NT and ESTS waters the correlation between school size and flock size was positive (NT waters: $r = 0.308$, $n = 133$, $P < 0.01$; ESTS waters: $r = 0.317$, $n = 42$, $P < 0.05$).

There was a marked difference in this relationship, however, between the northern and southern waters, most apparent among the spotted and spinner dolphins either in single or mixed species schools (Fig. 3). In NT waters these schools increasingly co-occurred with flocks of 10 to 50, or with 50 or more birds as school size increased. All schools larger than 256 animals were associated with flocks of at least 10 birds (school size interval is plotted on a logarithmic scale). In contrast, most of such schools in ESTS waters were without flocks, and the frequency of schools co-occurring with flocks increased only gradually as school size increased.

The average size of bird flocks varied with the species of dolphin. The largest flocks co-occurred with spotted and mixed spotted plus spinner schools (Table 3). As flocks associated with these dolphins increased in size, the number of birds of each species also increased. This was especially evident for boobies (*Sula* spp.), Wedge-tailed Shearwaters (*Puffinus pacificus*) and jaegers (*Stercorarius* spp.) in NT waters and for Sooty Terns and boobies in ESTS waters (Table 4). At the same time, the average number of bird species per flock increased from 3.4 to 5.9 as flock size increased from less than 50 to greater than 150 birds (Table 4).

THE SPECIES OF BIRDS IN DOLPHIN-ASSOCIATED FLOCKS

In NT waters, flocks associated with spotted and/or spinner dolphins consisted of 41.7% boobies, 31.4% Wedge-tailed Shearwaters, 12.8% jaegers, 6% Sooty Terns, 3.6% frigatebirds (*Fregata* spp.), and 4.5% other species (Fig. 4). The boobies were primarily Red-footed (*S. sula*) and Masked (*S. dactylatra*), but also included Brown (*S. leucogaster*) and a few Blue-footed (*S. nebouxii*). Frigatebirds included both Great (*F. minor*) and Magnificent (*F. magnificens*); jaegers were primarily Pomarine (*Stercorarius pomarinus*), and to a lesser extent, Parasitic (*S. parasiticus*). In ESTS waters only boobies (50.2%) and Sooty Terns (32.1%) were significantly associated with spotted and/or spinner dolphins, although they did not usually occur in the same flocks. Most Sooty Tern flocks there were not associated with any species of dolphin (see Tables 1 and 2).

Among the 20 bird flocks that co-occurred with unmixed spinner dolphin schools, Wedge-tailed Shearwaters, Sooty Terns, and White-necked(WN)/Juan Fernandez(JF)/Dark-rumped(DR) Petrels (*Pterodroma externa cervicalis/P. e. externa/P. phaeopygia*), and boobies were most numerous, in that order, in

TABLE 3. Seabird species associated with five dolphin species. n = total birds; % n = % bird sp. composition; f = total flocks; n/f = mean size of sp. flocks; F = flocks associated with a dolphin sp.; % f/F = % of flocks containing a bird sp.

1. 5°N–30°N

Dolphin spp.:

Flocks (F): / Schools:	Spotted or spot. + spin. 134 / 150		Spinner alone 11 / 17		Common 23 / 49		Striped 6 / 64		Rough-toothed 17 / 40		All dolphins 190 / 320				
Bird spp.	n	f	n	f	n	f	n	f	n	f	n	% n	f	n/f	% f/F
Sooty Tern	955	57	77	7	110	5	4	2			1,146	6.3	71	16.1	37.4
Noddy Tern	175	7			15	1	4	1			194	1.1	9	21.6	4.7
Other terns	161	18			57	4	12	2			230	1.3	24	9.6	12.6
RFB + booby[a]	5,583	101	53	3	122	12	7	2	62	8	5,827	32.0	126	46.2	66.3
Brown Booby	1,130	26	7	2	2	2			13	3	1,152	6.3	33	34.9	17.4
Msk/Bf booby	371	46	3	2	17	7	1	1	9	5	401	2.2	61	6.6	32.1
Frigatebird	617	90	3	2	90	8	1	1	22	13	733	4.0	114	6.4	60.0
WTSW	5,184	82	202	7	114	10			32	6	5,532	30.4	105	52.7	55.3
Other shearwaters	237	41			194	3	7	2	26	4	464	2.5	50	9.3	26.3
WN/JF/DR petrels	87	18	60	7	103[b]	2	1	1			251	1.4	28	9.0	14.7
Other pterodromas	12	7			3	1			10	1	25	0.1	9	2.8	4.7
Storm-petrels	29	6			3	2			6	1	38	0.2	9	4.2	4.7
Jaeger spp.	2,168	78	29	4	6	5			9	6	2,212	12.1	93	23.8	49.0
Gull spp.					2	2					2	0.01	2	1.0	1.0
Tropicbird	1	1	3	2			1	1			5	0.02	4	1.2	2.1
Other			1	1							1	0.01	1	1.0	0.5
Total	16,710		437		838		37		189		18,213				
Mean flock size[c]	41.6		19.9		13.5		2.7		6.0						
0.95 CI	31.6–54.8		8.7–45.8		6.7–27.2		0.8–10.3		3.2–11.4						

TABLE 3. Continued.

2. <5°N–12°S
Dolphin spp.:

Flocks (F): / Schools:	Spotted or spot. + spin. 33 / 61		Spinner alone 9 / 19		Common 1 / 10		Striped 6 / 76		Rough-toothed 2 / 13		All dolphins 51 / 179				
Bird spp.	*n*	f	*n*	f	*n*	f	*n*	f	*n*	f	*n*	% *n*	f	*n*/f	% f/F
Sooty Tern	592	8	530	5			81	2			1,203	32.9	15	80.2	29.4
Noddy Tern															
Other terns	321[d]	3	20	2			8	1			349	9.6	6	58.2	11.8
RFB + booby[a]	1,743	13	10	2			8	1	13	2	1,774	48.6	18	98.6	35.3
Brown Booby															
Msk/Bf booby	5	1			30	1					35	1.0	2	17.5	3.9
Frigatebird	116	15	32	6			1	1			149	4.1	22	6.8	43.1
WTSW	7	3	19	2							26	0.7	5	5.2	9.8
Other shearwaters	10	1					1	1			11	0.3	2	5.5	3.9
WN/JF/DR petrels	8	4	28	2							36	1.0	6	6.0	11.8
Other pterodromas	3	2	16	2							19	0.5	4	4.8	7.8
Storm-petrels	28	4							10	1	38	1.0	5	7.6	9.8
Jaeger spp.	1	1	10	2							11	0.3	3	3.7	5.9
Gull spp.															
Tropicbird	1	1									1	0.0	1	1.0	2.0
Other			1	1			1	1			2	0.0	2	1.0	3.9
Total	2,835		665		30		100		23		3,654				
Mean flock size	16.3		35.9		30		8.0		4.7						
0.95 CI	7.8–33.7		25.5–48.6				1.4–47.0								

[a] Red-footed + Unidentified Booby; many of latter were probably RFB; Msk/Bf = Masked/Blue-footed booby; WTSW = Wedge-tailed Shearwater; WN/JF/DR Petrels = White-necked/Juan Fernandez/Dark-rumped petrels.
[b] Includes 100 *P. externa* from 1 flock in Central Pacific.
[c] Geometric mean of individual flock size.
[d] Includes unidentified terns, some likely being Sooty Terns.

TABLE 4. Number of birds (n) and mean flock size ($\bar{x}$) of species components of flocks according to three levels of total flock size. Flocks were associated with spotted and/or spinner dolphins.

Bird spp.	Total flock size							
	<50		50–150		>150		All	
	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
1. 5°N–30°N								
Sooty Tern	217	6.78	468	22.29	347	31.55	1,032	16.12
Other terns	58	7.25	209	26.13	69	13.80	336	16.00
Booby spp.	459	9.00	1,312	37.49	5,366	178.87	7,137	61.53
Frigatebird	135	3.65	133	4.16	352	15.30	620	6.74
WN/JF/DR petrels	125	5.95	22	5.50			147	5.88
Other petrels	30	3.33	10	5.00			40	3.64
Wedge-tailed Shearwater	199	5.53	574	22.96	4,613	164.75	5,386	60.52
Other shearwaters	18	1.50	22	2.20	197	10.37	237	5.78
Jaeger spp.	151	5.21	280	11.20	1,766	60.90	2,197	26.47
Other	4	2.00			11	11.00	15	5.00
							17,147	
Mean no. spp./flock	3.45		5.32		5.87		4.45	
SD	1.56		1.92		1.70		2.02	
2. <5°N–12°S								
Sooty Tern	47	7.83	250	83.33	825	206.25	1,122	86.31
Other terns			10	10.00	331	82.75	341	68.20
Booby spp.	42	6.00	140	70.00	1,576	262.67	1,758	117.20
Frigatebird	28	2.55	20	5.00	100	16.67	148	7.05
WN/JF/DR petrels	8	2.00	8	8.00	20	20.00	36	6.00
Other petrels	31	6.00	16	8.00	1	1.00	48	6.00
Wedge-tailed Shearwater	26	5.20					26	5.20
Other shearwaters					10	10.00	10	10.00
Jaeger spp.			5	5.00	6	3.00	11	3.67
Other	1	1.00			1	1.00	2	1.00
							3,502	
Mean no. spp./flock	1.58		3.00		2.27		1.93	
SD	1.03		1.22		1.10		1.16	

NT waters. Only Sooty Terns were abundant in the flocks associated with this dolphin in ESTS waters (Table 3). However, frigatebirds occurred in six of nine flocks there.

There were few bird flocks associated with the remaining dolphin species. In those flocks, boobies, Wedge-tailed Shearwaters, frigatebirds, and Sooty Terns were often associated with the common dolphin, which frequently occurs near upwelling areas (Au and Perryman 1985). However, most numerous with this dolphin were the small, rapid-flying shearwaters, primarily Audubon's (*Puffinus lherminieri*) and Townsend's shearwaters (*P. auricularis*), which also seem attracted to upwelling and coastal areas. The few flocks associated with striped dolphins were notable in that none contained Wedge-tailed Shearwaters or jaegers. Flocks associated with rough-toothed dolphins did not include terns.

In ESTS waters flocks were less heterogeneous in species composition than in NT waters. Whereas boobies, frigatebirds, Wedge-tailed Shearwaters, and jaegers all occurred in at least 50% of the flocks (i.e., >72 of 145 flocks) associated with spotted, spinner, and spotted plus spinner dolphin schools in NT waters, only frigatebirds occurred with such frequency (21 of 42 flocks) among these dolphins in ESTS waters (Table 3).

In these same flocks, the occurrence of Sooty Terns decreased from 44.1% in NT waters to 31.0% of the flocks in ESTS waters. However their numbers, as a percent of total birds in the flocks, rose from 6.0% in NT waters to 32.1% in ESTS waters. The overall mean flock size of Sooty Terns also increased greatly from 16.1 to 80.2 birds per flock in the ESTS waters (Table 3).

Although the percent occurrence of frigatebirds decreased in ESTS waters, it was never less than 50% of flocks among all spotted and/or spinner dolphin schools in either the northern or southern water type. Thus frigatebirds are good indicators of the presence of these dolphins (and also of yellowfin tuna), as fishermen well know, even though their average flock size was only six or seven individuals.

Finally, all individual avian species co-occurred most frequently with spotted and spotted plus spinner schools, as was shown above for flocks in general (Table 3). In 11 of the 16 different bird species or species groups from NT waters, 75% or more of their dolphin-as-

sociated flocks were associated with spotted or spotted plus spinner dolphins. In contrast, the percent of dolphin-associated flocks seen with schools of unmixed spinner schools was relatively low; among the different birds, the highest proportion of flocks with this dolphin was 25%, due to WN/JF/DR petrels. These observations all indicate that seabirds are primarily associated with the spotted dolphin, though the relationship is probably not direct.

BIRD-SPECIES ASSOCIATIONS IN FLOCKS

Because boobies, Wedge-tailed Shearwaters, jaegers, Sooty Terns, frigatebirds, and WN/JF/DR petrels were most prevalent in bird flocks, we looked at the possibility of interactions among these species. Initially, a comparison of the frequency distribution of flocks with 1, 2, . . ., n species with the distribution expected if the species had joined the flocks independently of each other (Pielou 1974) revealed significant nonindependence among the more abundant bird species in the flocks associated with spotted and spotted plus spinner schools and with common dolphin schools. We therefore looked for specific interactions among the above six principal species or species groups of birds in the flocks co-occurring with these two groups of dolphins, using Chi-square association tests. Significant species associations were found among the flocks co-occurring with spotted and spotted plus spinner dolphins, but not among flocks co-occurring with common dolphins, possibly because there were only 22 flocks with the common dolphin usable for such a test in our sample. The numbers of flocks with spotted and spinner dolphins in which various combinations of species pairs co-occurred are summarized in Table 5. The Chi-square tests were applied to these data, after rearrangement, and the results are also given in the table.

There were statistically significant, positive associations in these flocks from NT waters between boobies and frigatebirds, boobies and jaegers, boobies and Wedge-tailed Shearwaters, frigatebirds and Sooty Terns, and jaegers and Wedge-tailed Shearwaters. These positive associations suggest an interaction complex composed of boobies, Wedge-tailed Shearwaters, and jaegers, on the one hand, and a Sooty Tern-frigatebird interaction on the other, both linked by the booby-frigatebird association. Our observations indicate that the former complex is characteristic of dolphin-associated flocks from the eastern portion of NT waters, and the latter is characteristic of such flocks from the western and southern boundaries of the ETP.

Significant negative associations were found

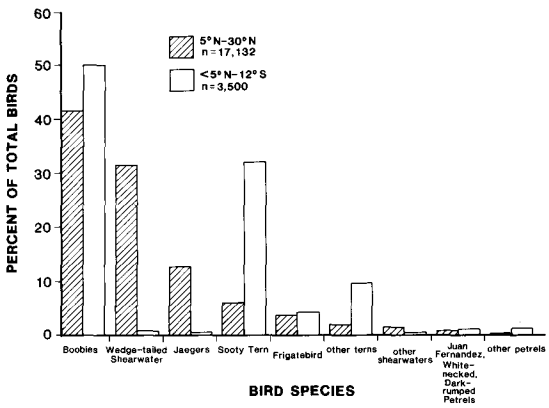

FIGURE 4. Percent of each bird species or species group in all flocks associated with spotted, spinner, and spotted-plus-spinner dolphin schools.

between boobies and WN/JF/DR petrels in NT waters and between boobies and Sooty Terns in ESTS waters, where the latter were the only two abundant bird species in dolphin-associated flocks. The negative associations are probably best explained by geographic differences: in NT waters WN/JF/DR petrels occur primarily west of Clipperton Island (10.2°N, 109.3°W) where boobies are relatively uncommon and, when they do occur, are mainly the Masked Booby; in ESTS waters boobies are found near islands and continental coasts, while Sooty Tern flocks occur in the more oceanic habitats.

The significance of these associations should be viewed with some caution, because all possible combinations of these bird species were tested, a procedure that increased the chance for a Type 1 statistical error. If a "supercritical" level of significance were adopted to adjust for this possibility (Pielou 1974), only the Sooty Tern-frigatebird association would be significant. Nevertheless the correspondence of these associations with the species characteristics of dolphin-associated flocks from different areas and also the involvement of the sometimes kleptoparasitic frigatebirds and jaegers in the positive associations suggest real interactions. Furthermore, positive correlations between subflock sizes of certain species pairs can be demonstrated. Where pairs of species co-occurred in flocks over spotted and spotted plus spinner dolphins in NT waters, the Spearman rank correlation was significant ($P < 0.001$) and positive between the sizes of subflocks of Red-footed Boobies and Wedge-tailed Shearwaters ($r_s = 0.414$, $n = 65$), between Red-footed Boobies and jaegers ($r_s = 0.415$, $n = 66$), and between Wedge-tailed Shearwaters and jaegers ($r_s = 0.532$, $n = 59$). The correlation between subflocks of boobies

TABLE 5. Frequency of flocks (f) containing each bird species pair and the Chi-square association statistics from flocks with spotted + spinner dolphins.

Spp.		Co-occurring with: Sooty	Booby	Frigate	WTSW	WN/JF/DR petrels	Jaeger
1. 5°N–30°N (131 flocks)							
Sooty Tern	f	57	50	48	40	10	37
	χ^2	—	0.35	10.05**	1.94	0.73	0.37
Booby spp.	f		111	81	74	8	74
	χ^2		—	4.93*	4.07*	−22.70**	8.10**
Frigatebird	f			90	59	9	60
	χ^2			—	0.71	−2.46	3.08
WTSW	f				82	9	59
	χ^2				—	−0.86	9.73*
WN/JF/DR petrels	f					18	9
	χ^2					—	−0.60
Jaegers	f						80
	χ^2						—
2. <5°N–12°S (33 flocks)							
Sooty Tern	f	8	0	2	1	2	1
	χ^2	—	−4.86*	−0.86	—	0.44	0.37
Booby spp.	f		13	6	0		
	χ^2		—	—	−0.71	−1.38	−0.05
Frigatebird	f			15	2	0	0
	χ^2			—	0.03	−1.99	—
WTSW	f				3	1	0
	χ^2				—	0.06	—
WN/JF/DR petrels	f					4	0
	χ^2					—	—
Jaegers	f						1
	χ^2						—

Note: χ^2 = Chi-square statistic of interaction table, df = 1. * and ** indicate $P < 0.05$ and <0.01 respectively. Examples of association test statistic for Sooty Tern and Boobies (5°N–30°N):
Both spp. occur together in 50 flocks.
Sooty Terns only occur in 57 − 50 = 7 flocks.
Boobies only occur in 111 − 50 = 61 flocks.
Neither spp. occur in 131 − 50 − 7 − 61 = 13 flocks.
A blank indicates χ^2 is very small or test is inappropriate; a minus sign indicates association is negative.
The value of χ^2 does not measure the magnitude of association, but can be converted to measure correlation in presence-absence data, equivalent to Yule's coefficient (Pielou, 1969:166).

and Sooty Terns was negative, but not significantly so.

DISCUSSION

Studies of seabirds can lead to insights into the ecology of pelagic communities, an idea perhaps best expounded by Murphy (1936). In the eastern tropical Pacific (ETP) the interactions of seabirds with dolphins and tuna reveal different species-specific behaviors and requirements for exploiting what must be sparse and patchily distributed prey. Tropical seabirds appear to have developed flight characteristics for efficient searching over large areas that have relatively light winds and for maneuvering rapidly over fleeting prey. Probably because prey is unpredictably concentrated and not abundant over large areas, pursuit diving by tropical seabirds has almost been eliminated (Ainley 1977); the birds feed near the surface instead. Many species show a strong tendency to form multispecies feeding flocks (Ainley and Boekelheide 1983) that are strongly dependent upon prey driven to the surface by predatory fish, mainly tuna (see Ashmole and Ashmole 1967).

THE RELATIONSHIP TO YELLOWFIN TUNA

We think that seabirds in bird-dolphin associations are primarily associated with the yellowfin tuna that co-occur with the dolphins, and that both birds and dolphins feed mainly on prey made available by the tuna. Yellowfin range primarily between the surface and the 20°C isotherm that typically lies in the upper thermocline (Blackburn 1965). Where the thermocline is shallow and its gradient strong, surface-feeding schools of medium to large tuna are often abundant (Sund et al. 1981). In contrast to most of the central and western Pacific, the thermocline depth in the ETP is frequently less than 30 m (Wyrtki 1964), and this seems to bring the yellowfin and their prey near the surface. Particularly in offshore waters of the ETP, these surface schools are composed of large yellowfin (Cole 1980) that feed and in-

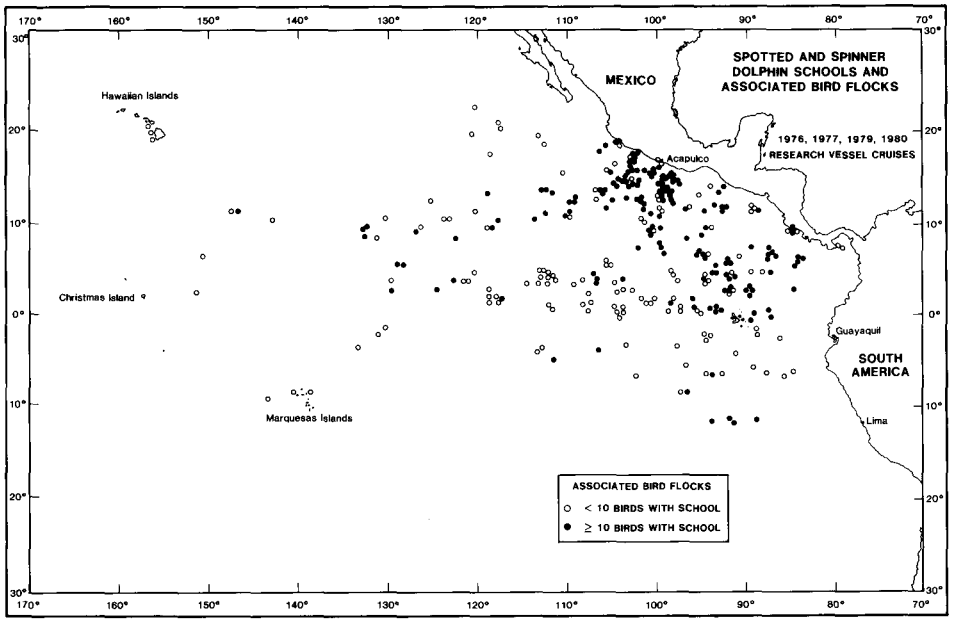

FIGURE 5. January–March distribution of spotted and/or spinner dolphin schools, with those schools accompanied by flocks indicated.

teract with dolphins and birds. It is only in the ETP that surface schools of yellowfin commonly occur (Cole 1980; R. Kearney, pers. comm.), and it is only there that birds are known to commonly co-occur with dolphins, and the dolphins with tuna, though all species involved in such associations are also found in the central and western Pacific.

Because seabirds in the ETP associate mainly with the spotted dolphin, the species primarily involved in the "tuna-porpoise" fishery for yellowfin, the birds appear to be ultimately linked to this fish. In this fishery, purse-seiners catch yellowfin by capturing (and later releasing) the dolphins that swim with this tuna (Perrin 1969). Although these tuna clearly follow the dolphins when the latter are chased by fishermen, we think such behavior is not typical of a feeding school (see below). Skipjack are also sometimes caught with the dolphins, but usually as a mixed catch with the yellowfin (Hammond 1981). Thus the areal pattern of bird flocks associated with spotted and/or spinner dolphins (Fig. 5) is essentially that of surface-schooling yellowfin (cf. Calkins 1975, Sund et al. 1981). Important fishing areas for this tuna extend westward along latitude 10°N from areas off Central America and southern Mexico; equatorial waters, where relatively few bird-associated dolphin schools occur, are not important in this fishery.

Both the yellowfin and the spotted dolphin are diurnally active species that probably feed together when associated (Perrin et al. 1973). Yellowfin are known to be diurnal feeders (Reintjes and King 1953, Cole 1980), and both spotted dolphins and these tuna frequently form large schools, especially on the ETP yellowfin fishing grounds (for these dolphins in northern tropical (NT) waters: $\bar{x} = 221.7$, $s = 217.2$, $n = 124$).

Seabirds co-occur less frequently with other species of dolphins (Fig. 2), and these other dolphins are correspondingly less often associated with yellowfin, consistent with our view that the birds follow the fish. Spinner dolphins in unmixed schools are relatively unproductive in tuna-porpoise fishing in comparison with spotted or mixed spotted plus spinner schools (Smith 1979, Hammond 1981), and spinner dolphins also rank third in degree of association with birds (Fig. 2). The spinner dolphin is also active diurnally and often forms large schools, but its food differs enough from spotted dolphins (Perrin et al. 1973) to indicate a less direct interaction with tuna. The common dolphin is much less productive for catching yellowfin in this same fishery, and birds correspondingly flock much less often with this species. The common dolphin also occurs in large, active schools but, unlike the spotted dolphin, it prefers habitats affected by upwelling (Au and Perryman 1985), and likely feeds at night (Evans 1971). The striped dolphin is a relatively large and diurnally active species, but it occurs in small schools ($\bar{x} = 60.8$, $s = 69.8$, $n = 187$) that are seldom seen with birds or fish (Au and Perryman 1985). It is seldom purposely caught by tuna fishermen. The few birds seen with this species were prob-

ably feeding on prey flushed unintentionally by the swimming dolphins rather than driven by associated tuna (this appears to happen with other dolphin species as well). The rough-toothed dolphin occurs in even smaller schools ($\bar{x} = 12.4$, $s = 9.9$, $n = 53$), and is a sluggish, inactive swimmer during the day (pers. obs.); it is only accidentally caught by purse-seiners. However this dolphin was more frequently associated with birds than was the striped dolphin. The reason may be that rough-toothed dolphins often occur near flotsam (pers. obs.), which attract fish, including tuna (Greenblatt 1979), and birds. This dolphin will feed upon small flotsam-associated fish (Pitman, pers. obs.; W. A. Walker, pers. comm.), but it probably does not associate directly with tuna.

The spatial arrangement of birds, dolphins, and tuna within feeding aggregations also suggests that the birds are primarily associated with the feeding tuna. It appeared from our shipboard observations that the birds worked mainly on the forward edge of the relatively scattered dolphin schools, sometimes among leaping tuna. Observations from helicopters provided better views: Au and Perryman (1982) saw feeding aggregations in which the bird flocks were often separated from the dolphins; R. P. Hewitt and G. L. Friedrichsen (unpubl.) described phalanx-like schools of tuna, attended by bird flocks, that swam at the front of the associated oval-shaped dolphin schools. These and the above observations suggest that birds and dolphins both take advantage of the feeding activities of tuna. It must be mentioned, however, that there are other interpretations; e.g., Norris et al. (1985) think it is the dolphins that are "nuclear."

THE RELATIONSHIP TO BIOLOGICAL PRODUCTIVITY

The development of seabird-dolphin-tuna associations appears to be promoted by increased biological production. It is significant that in the Pacific these associations are common only in the relatively rich ETP, especially within the "inner" areas (see fig. 75 in Wyrtki 1964) where the thermocline is especially shallow and where feeding situations are likely to develop close to the surface. These areas include the principal purse-seine fishing grounds, where in recent years (1972 to 1981) an average of 164,000 metric tons of yellowfin have been harvested annually (IATTC 1984), more than from any other surface fishery for this tuna. Because large schools of both spotted and spinner dolphins and surface-feeding yellowfin accompanied by birds occur in these waters, formation of opportunistic, multispecies feeding aggregations is to be expected (Evans 1982). Such feeding aggregations might start by convergence onto productive food patches by species adapted to finding and exploiting those patches. The aggregations may be long-lasting on the more productive patches, and interspecific competition there may be low (Schoener 1982). Commensal relationships may also develop, which may induce the species to stay together for some time.

Surprisingly, tuna are seldom associated with dolphins in the productive eastern tropical Atlantic (Levenetz et al. 1980; Stretta and Slepoukha, in press), where an important purse-seine fishery for yellowfin also exists. Fishing conditions there are similar in many respects to those in the eastern Pacific, including the frequent association of birds with tuna. The reason for this nonassociation is obscure. Is it because the dolphin fauna of the eastern Atlantic is different, or does it have to do with the abundance and structure of the prey population?

NATURE OF THE FEEDING INTERACTION

In the feeding aggregations observed in NT waters, prey driven to the surface, probably mainly by large yellowfin, is evidently abundant and diverse enough to allow dolphins and many bird species to feed at the same time. Differentiation of feeding behavior among the seabird species is quite apparent, although overlap in species or size of prey may be high (Diamond 1983). Boobies plunge-dive from above or snatch their prey from the air during aerial pursuit. Wedge-tailed Shearwaters feed on the water or, with the boobies, race at mid-height laterally along the front of advancing activity attempting to intercept unpredictably surfacing prey. Sooty Terns watch from vantages high overhead, then make swooping dives en masse wherever their component of prey surfaces. The second author has, on several occasions, observed groups of Sooty Terns ignoring the larger prey (especially flying fish) pursued by the other birds, then dropping to the surface seconds later to pick at smaller organisms. Evidently a wide spectrum of size, behavior, and perhaps species of prey is available, of which flying fish and juvenile ommastrephid squids are important both to the birds (Ashmole and Ashmole 1967, Diamond 1983, Harrison et al. 1983) and to the tuna and dolphins (Perrin et al. 1973). Prey driven to the surface may sometimes be superabundant. We have seen groups of apparently satiated boobies, Wedge-tailed Shearwaters, and jaegers resting on the water while others continued to feed. The associated dolphins meanwhile also appeared to be feeding. Small pods within the body of the school changed swim-

ming direction often. Individuals could be seen "milling around," and what seemed to be diving behavior was observed. Sometimes both dolphin and tuna appeared to leap after the same fish or squid prey.

The positive associations found among the different species of birds is sufficiently explained by common attraction to these localized feeding situations, where food is made available by feeding tuna. The association of frigatebirds with boobies in NT waters and frigatebirds with Sooty Terns in equatorial/southern tropical/subtropical (ESTS) waters may be the most characteristic of the associations. Ainley and Boekelheide (1983) also found such associations in tropical seabird flocks, although their sample from the eastern Pacific was sparse, and dolphin-associated flocks were not treated specifically.

A DICHOTOMY IN THE PELAGIC COMMUNITY

Multispecies bird flocks associated with spotted and/or spinner dolphins and yellowfin tuna are characteristic of NT waters of the ETP. The contrast between these flocks and those dominated by Sooty Tern flocks without dolphins in ESTS waters is one of the striking biological features of the eastern Pacific. Boobies and frigatebirds are typical associated species in the multispecies flocks of NT waters, stemming from their similar, ready attraction to feeding tuna or tuna-dolphin schools. Boobies range far beyond their breeding colonies and are widespread with schools of surface yellowfin over the entire eastern Pacific fishing grounds. These colonies (mainly on Clipperton, Malpelo, Cocos, and the Galápagos islands) are probably the world's largest (Nelson 1978), an indication of the great advantage boobies gain from feeding with surface yellowfin.

Beyond the main fishing grounds for surface yellowfin, i.e., southwest of the Galápagos Islands and in the central Pacific, especially in ESTS waters, is a second community in which Sooty Terns predominate and associate with small fast-moving tuna that seldom co-occur with dolphins. The tuna are probably skipjack (Murphy and Ikehara 1955, Waldron 1964, Hida 1970), though small yellowfin and bigeye (*Thunnus obesus*) are sometimes seen, and frigate mackerel (*Auxis* sp.) may be involved. Dolphins, especially the spotted and spinner species, are much less abundant in these waters (Au and Perryman 1985) and evidently feed largely independently of tuna and birds there. Presumably, because large yellowfin there feed well below the surface, the link between dolphins and seabirds is broken.

As noted above, Sooty Tern flocks are notably abundant and characteristic of the region southwest of the Galápagos Islands and west of the Peru Current (Table 1; fig. 18 in Gould 1974; Pitman, unpubl.). (Although we have described Sooty Terns as being abundant in ESTS waters, they, as well as most other squid/fish-eating birds, are actually infrequent along the equator, at least east of about 130°W [Au et al. 1980].) Because there are only a few, relatively small, Sooty Tern colonies in the eastern Pacific (mainly on Clipperton and the Galápagos islands), most of the terns in this southeastern region must originate from the central Pacific, where large breeding colonies occur (see Table 1 in Gould 1974).

We have no information to the contrary regarding the qualitative features of the dichotomy discussed, although our samples during the northern summer were relatively sparse. In NT waters the tuna fishery "on porpoise" occurs year-round. This fishery expands far to the west of Clipperton Island during the summer, where Juan Fernandez Petrels predominate with tuna schools associated with dolphins. In ESTS waters, especially in the eastern Pacific, Sooty Terns may or may not be year-round residents, but they do not appear to be replaced by other birds from NT waters at any time.

SOOTY TERNS AND SMALL TUNA—THE FAR OFFSHORE LINK

Sooty Terns appear to be highly adapted for feeding with skipjack or skipjack-like tuna in less productive, far offshore waters beyond the surface yellowfin habitat, where they clearly dominate the avifauna. In contrast many other bird species of the eastern and central Pacific achieve their highest abundance in the more productive "inner" areas of the ETP, e.g., boobies, frigatebirds, Pomarine Jaeger, and light morph Wedge-tailed Shearwater (Pitman, pers. obs.). While this may result from greater interspecific competition faced by Sooty Terns closer toward shore (Diamond 1978), it is more likely a direct consequence of strong association with the tuna we think are skipjack (which occur throughout the tropical Pacific [Love 1971]). Just as boobies are widespread with surface yellowfin on the purse-seine fishing grounds, so too do Sooty Terns appear widespread with surface-schooling skipjack in far offshore waters. In the central Pacific small yellowfin are in surface schools close to islands, but skipjack schools predominate far offshore (Murphy and Shomura 1972). Since Sooty Terns also forage far from islands (Ashmole and Ashmole 1967, Diamond 1978, pers. obs.), this apparent avoidance of yellowfin habitat again indicates a strong proclivity to feed with

skipjack. Admittedly these Sooty Terns may be associated with other small tunas, e.g., frigate mackerel, whose larvae have been found widely distributed in the southeastern Pacific (Love 1971); however adults of that species are caught primarily in coastal seas (Uchida 1981).

Sooty Terns seem to be near-obligate commensals with the small tuna they follow. They seem always to be either feeding with tuna schools or searching for such schools. Although occasionally reported to feed independently of tuna (Gould 1967, 1974), such feeding is rare, for Sooty Terns are unable to capture prey more than a few cm below the surface. This behavior is in contrast with most other birds that commonly feed with tuna. Only Sooty Terns seem to have achieved large success in exploiting that habitat where prey is made available largely by small tunas, and where prey independent of feeding tunas may be too infrequent for most birds. Still, the tuna-driven prey must be unsuitable or the energetic cost of following these tuna too high for most other birds; otherwise they would simply follow the Sooty Terns to feed. Sooty Terns cannot take large food (see Harrison et al. 1983), and this suggests that the prey made available to them is small. Nor can they rest long on the water (Gould 1974), as would be necessary if they were to feed heavily or on large prey, suggesting that the food patches are small and quickly dispersing. Sooty Tern adaptations for efficiently finding feeding tuna must include their continuous, agile flight, their high-flying habit that likely enables distant recognition of feeding behavior in other flocks or detection of surfacing fish (see Gould 1974), their strong flight for fast convergence on such feeding opportunities, and their seemingly constant vocalizations. The latter suggests cooperative foraging, perhaps expected in animals that exploit highly patchy and ephemeral prey (Horn 1968).

The Sooty Tern is evidently very successful in exploiting the far offshore habitat, being by far the most abundant bird in the southeastern and central tropical Pacific (Table 1; Gould 1974; Pitman, unpubl.). The small tuna are also very abundant (especially skipjack), and the two species seem to employ similar foraging tactics. As these far offshore waters are generally considered impoverished, the abundance of Sooty Terns there suggests very efficient foraging and also the possibility of underestimated biological production.

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LITERATURE CITED

AINLEY, D. G. 1977. Feeding methods of seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean, p. 669–686. *In* G. H. Llano [ed.], Adaptations within Antarctic ecosystems. Gulf Publ. Co., Houston, TX.

AINLEY, D. G., AND R. J. BOEKELHEIDE. 1983. An ecological comparison of oceanic seabird communities of the South Pacific. Studies in Avian Biology No. 8.

ASHMOLE, N. P. 1971. Seabird ecology and the marine environment, p. 223–286. *In* D. S. Farner, D. R. King, and K. C. Parkes [eds.], Avian biology. Vol. 1. Academic Press, New York.

ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. Peabody Mus. Nat. Hist. Yale Univ. Bull. 24: 1–131.

AU, D., AND W. PERRYMAN. 1982. Movement and speed of dolphin schools responding to an approaching ship. Fish. Bull. U.S. 80:371–379.

AU, D. W., AND W. L. PERRYMAN. 1985. Dolphin habitats in the eastern tropical Pacific. Fish. Bull. U. S. 83:623–643.

AU, D. W., W. L. PERRYMAN, R. L. PITMAN, AND M. S. SINCLAIR. 1980. Cetacean populations and equatorial oceanography. Univ. Wash. Trop. Ocean Atmos. Newsletter 4:6, 10.

BLACKBURN, M. 1965. Oceanography and ecology of tunas. Oceanogr. Mar. Biol. Annu. Rev. 3:299–322.

CALKINS, T. P. 1975. Geographical distribution of yellowfin and skipjack tuna catches in the eastern Pacific Ocean, and fleet and total catch statistics, 1971–1974. Inter-Am. Trop. Tuna Comm. Bull. 17:1–116.

COLE, J. S. 1980. Synopsis of biological data on the yellowfin tuna, *Thunnus albacares* (Bonnaterre, 1788), in the Pacific Ocean. Inter-Am. Trop. Tuna Comm. Spec. Rep. 2:71–150.

DIAMOND, A. W. 1978. Feeding strategies and population size in tropical seabirds. Am. Nat. 112:215–233.

DIAMOND, A. W. 1983. Feeding overlap in some tropical and temperate seabird communities. Studies in Avian Biology No. 8.

EVANS, P.G.H. 1982. Associations between seabirds and cetaceans: a review. Mammal Rev. 12:187–206.

EVANS, W. C. 1971. Orientation behavior of delphinids: radio telemetric studies. Ann. N.Y. Acad. Sci. 188: 142–160.

GOULD, P. J. 1967. Nocturnal feeding of *Sterna fuscata* and *Puffinus pacificus*. Condor 69:529.

GOULD, P. J. 1974. Sooty Tern (*Sterna fuscata*), p. 6–52. *In* W. B. King [ed.], Pelagic studies of seabirds in the central and eastern Pacific Ocean. Smithsonian Contrib. Zool. No. 158.

GREENBLATT, P. R. 1979. Associations of tuna with flotsam in the eastern tropical Pacific. Fish. Bull. U.S. 77:147–155.

HAMMOND, P. S. [ED.] 1981. Report on the workshop on tuna dolphin interactions, Managua, Nicaragua. Inter-Am. Trop. Tuna Comm. Spec. Rep. No 4.

HARRISON, C. S., T. S. HIDA, AND M. P. SEKI. 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. No. 85.

HIDA, T. S. 1970. Surface tuna schools located and fished in equatorial eastern Pacific. Commer. Fish. Rev. 32: 34–37.

HORN, H. S. 1968. The adaptive significance of colonial

nesting in Brewer's Blackbird (*Euphagus cyanocephalus*). Ecology 49:682–694.

IATTC. 1984. Annual Report of the Inter-American Tropical Tuna Commission (IATTC). La Jolla, CA.

LEVENETZ, J., A. FONTENEAU, AND R. REGALADO. 1980. Resultats d'une enquete sur l'importance des dauphins dans la pecherie thoniere FISM. Int. Comm. Conserv. Atlant. Tunas Coll. Vol. Sci. Papers 9:176–179.

LOVE, C. M. [ED]. 1971. Biological and nutrient chemistry data from principle participating ships, first survey cruise, February–March 1967. Eastropac atlas, Vol. 2. U.S. Dep. Commer. Nat. Mar. Fish. Serv. Circ. 330.

MURPHY, G. I., AND I. I. IKEHARA. 1955. A summary of sightings of fish schools and bird flocks and of trolling in the central Pacific. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 154.

MURPHY, G. I., AND R. S. SHOMURA. 1972. Pre-exploitation abundance of tunas in the equatorial central Pacific. Fish. Bull. U.S. 70:875–913.

MURPHY, R. C. 1936. Oceanic birds of South America, Vol. 1. American Museum of Natural History, New York.

NELSON, J. B. 1978. The Sulidae: gannets and boobies. Oxford Univ. Press, Oxford, England.

NORRIS, K. S., B. WURSIG, R. S. WELLS, M. WURSIG, S. M. BROWNLEE, C. JOHNSON, AND J. SOLOW. 1985. The behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. NOAA (Nat. Ocean. Atmos. Adm.) NMFS (Nat. Mar. Fish. Serv.) Rep. LJ–85–06C.

PERRIN, W. F. 1969. Using porpoise to catch tuna. World Fishing 18:42–45.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS. 1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed species aggregations. Fish. Bull. U.S. 71:1077–1092.

PIELOU, E. C. 1969. An introduction to mathematical ecology. Wiley Interscience, New York.

PIELOU, E. C. 1974. Population and community ecology. Gordon and Breach, New York.

REINTJES, J. W., AND J. E. KING. 1953. Food of the yellowfin tuna in the central Pacific. Fish. Bull. U.S. 54:91–110.

SCHOENER, T. W. 1982. The controversy over interspecific competition. Amer. Sci. 70:516–595.

SMITH, T. D. [ED.]. 1979. Report of the workshop on status of porpoise stocks; La Jolla, Calif. 27–31 August 1979. NOAA (Nat. Ocean. Atmos. Adm.) NMFS (Nat. Mar. Fish. Serv.) Rep. LJ–70–41.

STRETTA, J. M., AND M. SLEPOUKHA. In press. Analyse des facteurs biotiques et abiotiques associes aux bancs de thons. *In* P.E.K. Symons [ed.], Proceedings, Int. Skipjack Year Program Conf., ICCAT.

SUND, P. N., M. BLACKBURN, AND F. WILLIAMS. 1981. Tunas and their environment in the Pacific Ocean: a review. Oceanogr. Mar. Biol. Annu. Rev. 19:443–512.

UCHIDA, R. N. 1981. Synopsis of biological data on frigate tuna, *Auxis thazard*, and bullet tuna, *A. roche*: FAO Fish. Synop. No. 124. NOAA (Nat. Ocean. Atmos. Adm.) Tech. Rep. NMFS (Nat. Mar. Fish. Serv.) Circ. 436.

WALDRON, K. D. 1964. Fish schools and bird flocks in the central Pacific Ocean, 1950–1961. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 464.

WYRTKI, K. 1964. The thermal structure of the eastern Pacific Ocean. Erganzunsh. Dtsch. Hydrogr. Z. Reiche A 8(6).

WYRTKI, K. 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1:117–147.