

AN ANNUAL CYCLE OF PELAGIC BIRDS IN THE GULF OF PANAMA

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Abstract. Ten cruises were made in the Gulf of Panamá at roughly equal intervals between August 1968 and August 1969, to observe, identify and count seabirds found there over a year's cycle. A total of 24 species were identified. Several first specimens for Panama Pacific waters were collected, and knowledge of seasons of occurrence and relative abundance was altered or clarified. Relatively little difference in frequency of birds seen was noted from cruise to cruise despite seasonal nutrient enrichment by Gulf upwelling. Locally-breeding seabirds (4 spp.) and boreal-breeding migrants (12 spp.) together comprised 96.4% of all birds seen; austral migrants (3 spp.) and tropical visitors (5 spp.) made up the balance. Seasonally, however, the latter two groups each comprised 10% or more of birds seen on some cruises. Viewed broadly, the seabirds encountered presented more the aspect of temporally varying assemblages of migrant and local species than of integrated bird communities. *Accepted 27 August 1991.*

Key words: Pelagic birds, seabirds, Gulf of Panama, Panama, eastern Pacific.

INTRODUCTION

Jehl (1974) remarked that seabird data from the nearshore Pacific Ocean off Middle America pertain for the most part to large, conspicuous colonial-breeding species of coastal waters, while „data on the distribution, abundance, ecology, and migration of more pelagic species are either fragmentary, inferred, or non-existent”. Jehl concluded that detailed year-round studies are needed in that area to resolve such problems.

The Gulf of Panamá has been "explored" for seabirds as well or better than most equivalent eastern Pacific tropical areas, and the species occurring there are relatively well documented (Wetmore 1965; Ridgely & Gwynne 1989). But observations of seabirds in the Gulf have been opportunistic for the most part, carried out incidentally to other purposes for being at sea. In this region where most birds (kinds and numbers) enter from distant area and in differing seasons, the situation is much as described by Jehl (1974) concerning seabird seasonal abundance, times of arrival and departure, activities and interactions at sea, through an annual cycle or longer.

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This paper reports the findings of 10 cruises carried out between August 1968 and August 1969 in the Gulf of Panamá specifically for seabird study, comprising 290 hours of observation made over 3,458 km. Done in collaboration with the Smithsonian Institution Pacific Ocean Biological Survey Program (POBSP), this survey had three principal goals: (1) to determine the components of the oceanic avifauna and their seasonal changes in the Gulf; (2) to relate seasonal changes observed to wider patterns of seabird movement and distribution along the eastern Pacific; and (3) to determine if seabirds from central Pacific areas (where POBSP was most active) moved into the Gulf region and, of so, to what extent.

It was assumed that point (3) could be determined by taking specimens of marked individuals from the pool of birds banded (more than 1.8 million) by POBSP in the central Pacific (King, 1974). In fact, few central Pacific species were seen and no marked birds from there were recovered on these cruises. However, much was learned about (1) seabird presence, numbers, and timing in the Gulf of Panamá, and (2) the role of the Gulf in eastern Pacific seabird distribution over that yearly cycle.

TABLE 1. A summary of cruise statistics

Cruise	• Observation		# Spp seen	Total # birds seen	All birds seen/hr	Less Black Tern seen/hr
	Time (Hrs)	Distance (N. Mi.)				
1968						
15—18 Aug	33.0	198	13	1896	57.5	32.6
17—20 Sep	26.5	152	14	1771	66.8	56.1
11—15 Oct	39.5	260	20	2949	74.6	40.0
02—04 Nov	27.0	170	21	6959	257.7	46.6
17—20 Dec	24.0	142	14	8560	356.6	65.0
1969						
24—27 Jan	28.5	174	11	2410	84.6	37.8
28 Feb—2 Mar	26.0	173	14	11758	452.2	65.5
25—28 Apr	33.5	223	16	2964	88.4	32.6
19—22 Jun	33.0	241	17	1467	44.5	41.3
29—31 Aug	19.0	156	12	686	36.1	32.4
ALL	290.0	1889	24	41420	142.8	44.2

METHODS

From August 1968 through August 1969, 10 seabird survey cruises of 3 to 5 days duration were made at roughly equal intervals in the Gulf of Panamá. All surveys were made from craft of about 14 m length. Observations were begun and ended seaward of the sea buoy 11 km southeast of the Balboa Harbor entrance. Continuous watch was kept in daylight hours while the ship was under way; no nocturnal observations were attempted. Ship speed was kept at about 8 km/h on all cruises. Observers rotated watches at the stern, from where all of the horizon except a small arc dead ahead could be viewed. Birds were usually located with the eye, then binoculars were used for closer viewing. Specimens were collected selectively and were iced or frozen for preparation ashore. Occasionally, artificial slicks of cooking oil and galley wastes were spread on the sea surface, primarily to attract storm-petrels though other species often came to them.

Following POBSP procedures (King *et al.* 1967), each seabird sighting with related data was entered separately by time of observation on a daily log sheet. Latitude and longitude of each sighting were later reckoned by interpolating time of sighting with the ship's cruise track. Sea and weather conditions were recorded at 4-hour intervals, and air and water temperatures recorded at least daily. All field data were later transcribed onto magnetic tape and were deposited in POBSP files at the Division of Birds, U.S.

National Museum of Natural History (USNM), along with copies of the original field logs and individual cruise reports. Specimens collected were distributed about equally between USNM and the Gorgas Memorial Laboratory, Panamá, R.P.

RESULTS

Table 1 is a summary of cruise statistics. Table 2 lists the species of seabirds identified and number of each seen per hour of observation on each cruise and all cruises combined. In the tables and text, "birds seen" refers to *at sea* observations, excluding counts on and about islands unless specifically indicated. Abbreviations used include: N, E, S, W, the respective compass directions; *I* for island or *Isla*, *Is* for islands or *Islas*; months, by first three letters, e.g., Aug. A few data included in this paper have been incorporated into POBSP reports in the context of Pacific-wide species analyses (e.g., Crossin 1974). Some "first specimen" and other records are included in Ridgely & Gwynne's (1989) *Guide to the Birds of Panama*; these are cited in the species accounts.

The Black Tern (*Chlidonias niger*) was by far the most common seabird seen in the Gulf of Panamá from Oct. through Apr., and constituted more than 80% of all seabirds seen on the Nov., Dec. and Feb./Mar. cruises (Table 2). Even in Jun., "summering" Black Terns made up 7% of all birds seen. Such large numbers of this one species tended to obscure the relative importance

and position of other species in this study. Therefore, in certain discussions and tables, totals and averages are given from which Black Tern numbers have been subtracted. Such usages are clearly indicated.

SPECIES ACCOUNTS

Diomedeiidae

Diomedea sp. One albatross was seen near Bahía Piñas in Jun. Wetmore (1965) listed 3 species as reported from the Panamá Pacific. Two of these, *D. exulans* and *D. chrysostoma*, breed in the subantarctic and are rarely seen in tropical waters or farther northward. The third species, *D. irrorata*, breeds on Is Galápagos and off Ecuador; Blake (1977) termed it the only exclusively tropical albatross. Ridgely & Gwynn (1989) give two reports of this species for the area. The bird seen on the Jun. cruise was provisionally identified as *D. irrorata* (Waved Albatross), casual in the Gulf of Panamá.

Procellariidae

Puffinus griseus (Sooty Shearwater). This species was seen Jun. through Sep., most frequently in Aug. (Table 2). Other reports (Wetmore 1965) were all within these months except for one in Feb. E Pacific Sooty Shearwaters breed off subantarctic South America. After breeding season, they move rapidly through the tropics, reaching subtropical and subarctic waters off North America by Jun.; return migration begins in Aug. (Harrison 1983). Sooty Shearwater sightings in the Gulf indicated a relatively light northward through-migration, with largest numbers present on the southward (Aug.) lap.

Puffinus lherminieri (Audubon's Shearwater). This species was seen in two distinct periods — Apr.—Aug. and Oct.—Dec. (Table 2). Peak abundance was in Apr. and Oct.—Nov. Other reports for the Gulf (Wetmore 1965) fall within these two periods. Wetmore identified a cruise specimen (USNM 544844) as *P. l. subalaris*, which

TABLE 2. Seabird species and numbers of each seen per hour at sea on each cruise and all cruises together.

Species	CRUISE DATES											
	1968				1969							Cruise Year
	15-18 Aug	17-20 Sep	11-15 Oct	02-04 Nov	17-20 Dec	24-27 Jan	28 Feb -2 Mar	25-28 Apr	19-22 Jun	29-31 Aug		
Unident Albatross									<0.1	<0.1		
<i>Puffinus griseus</i>	1.6	0.3							0.1	0.4	0.2	
<i>P. lherminieri</i>	<0.1		6.5	4.5	0.3			2.1	0.5		1.4	
Unident shearwaters	<0.1	<0.1	0.9	0.2	0.1	0.1	<0.1				0.1	
Unident petrels			0.1	<0.1					<0.1		<0.1	
<i>Oceanites oceanicus</i>										<0.1	<0.1	
<i>Oceanodroma tethys</i>	3.6	0.7	0.3	1.2				0.1	3.1	4.2	0.7	
<i>O. melania</i>	0.1	0.1	<0.1	1.2	0.1		0.4	0.4	1.2	0.1	0.4	
<i>Halocryptena microsoma</i>			<0.1	0.1	0.6	0.6	9.7	14	0.3	2.1	2.7	
<i>Phaethon aethereus</i>		<0.1	<0.1								<0.1	
<i>Pelecanus occidentalis</i>	1.3	7.0	0.8	1.2	1.8	9.8	21	0.1	1.8	0.6	4.5	
<i>Sula dactylatra</i>		<0.1	0.2	0.1				<0.1	2.2		0.3	
<i>S. nebovicii</i>	0.2	<0.1	0.2	0.4	1.0	0.2	0.3	0.2	0.6	0.8	0.4	
<i>S. leucogaster</i>	22	13	19	21	10	7.9	10	4.0	28	12	14.7	
<i>Fregata magnificens</i>	1.8	4.9	3.1	3.8	9.5	2.3	2.2	4.0	3.2	3.3	3.8	
<i>Phalaropus lobatus</i>	1.5	29	4.3	7.7			0.1			8.8	5.1	
All jaegers			<0.1	0.5		0.2	0.7	0.3			0.2	
<i>Larus atricilla</i>				<0.1	15	16	13	1.8	<0.1		4.6	
<i>Xema sabini</i>			0.5	0.2	13		3.6	3.1	0.3		2.1	
<i>Chlidonias niger</i>	25	11	35	211	292	47	387	56	3.2	3.7	107.1	
<i>Sterna hirundo</i>	0.4	0.7	1.5	<0.1	14	0.1	4.0	0.1	0.2		2.1	
<i>S. anaethetus</i>		0.1	1.5	0.8	0.1					<0.1	0.3	
<i>S. albifrons</i>			0.2	1.8							<0.1	
<i>Thalasseus maximus</i>	<0.1		<0.1	0.3	<0.1	0.2	<0.1	<0.1			0.1	
<i>Anous stolidus</i>			<0.1	1.2				1.6	0.1		0.3	

breeds on Is Galápagos and is the only E Pacific population of this species. Its bimodal occurrence in the Gulf suggests migration to and from breeding grounds. However, Snow (1965) found that Audubon's Shearwater breeds continuously on the Galápagos and on a non-annual (9 months) cycle. He did note peaks and troughs in egg-laying, however. In the Oct.—Nov. cruises, this species was common in feeding and resting flocks of up to 40 birds, and often in mixed feeding flocks with Black Terns, Brown Boobies and Brown Noddies. Larval fishes spilled from the bill of a bird collected from one such mixed flock.

Unidentified procellariids. A few unidentified shearwaters were seen on every cruise except Apr. and Jun. (Table 2). Most were provisionally identified as *Puffinus pacificus* (Wedge-tailed Shearwater). That species, which in the E Pacific breeds off Baja California, has been collected once in the Gulf (Wetmore 1965) and there have been several other sight reports (Ridgely & Gwynne 1989). Petrels, seen on Oct. and Jun. cruises, were most probably *Pterodroma phaeopygia* (Dark-rumped Petrel), known from three other sight reports in the Gulf (Ridgely & Gwynne 1989).

Hydrobatidae

Oceanites oceanicus (Wilson's Storm-Petrel). A single specimen was collected in Aug. 1969, the first record for Panamá (Ridgely & Gwynne 1989) and the only one recorded on these cruises. E. Eisenmann (*in litt.*) identified it as *O. o. chilensis* (*O. o. magellanicus* in Blake 1977; the Panamá specimen referred to by Blake is this specimen). This E Pacific population breeds on islets off Cape Horn, normally winters N to Perú and was thought to be only casual northward of there (Blake 1977). However, Jehl (1974) found Wilson's Storm-Petrel (presumably of this form) to be regular though uncommon offshore between Guatemala and Michoacán, México.

Oceanodroma tethys (Wedge-rumped Storm-Petrel). This species was seen Apr. through Nov., peaking in Jun.—Aug. (Table 2). Other reports (Wetmore 1965) extend its known occurrence in the Gulf to Feb.—Nov. There are two subspecies of Wedge-rumped Storm-Petrel: *O. t. tethys* from Is Galápagos, and *O. t. kelsalli* from guano islands off Perú. Both have been recorded off

Panamá (Wetmore 1965). Specimens from these cruises were identified as *kelsalli* (Wetmore, *in litt.*).

Oceanodroma melania (Black Storm-Petrel). Some individuals of this species were seen on every cruise except Jan., though they were most numerous Feb./Mar.—Jun. and especially Nov. (Table 2). Other reports for the area (Wetmore 1965) include Jan. This species breeds off S California and Baja California (Harrison 1983). The two peaks of abundance seen suggest periods of through-migration in the Gulf. However, some individuals apparently spent most of boreal winter there, while a few non-breeding birds remained in the Gulf through the breeding season.

Halocypena microsoma (Least Storm-Petrel): Individuals of this species were seen on every cruise except Aug. 1968 and Sep. (Table 2), with notable peaks in Feb./Mar.—Apr. (9.7—14.5/hr) and Aug. 1969 (2.2/hr). Seasonally, this species was the most abundant and ubiquitous storm-petrel seen on these cruises. This contrasts sharply with the few previous records from the Gulf; Wetmore (1965: 45—47) listed only 5 reports for the area, all in Feb.—May. The boreal spring peak noted suggests a substantial flight from the S through the Gulf to its breeding grounds off Baja California; post-breeding migration through the Gulf was not nearly so marked. Some summering individuals remained in the Gulf through the breeding period.

Phaethontidae

Phaethon aethereus (Red-billed Tropicbird). A total of 3 immature birds were seen in Sep.—Oct. cruises, all well offshore. The Red-billed Tropicbird had previously been reported only once from Panamá Pacific waters (Wetmore 1965). An immature bird collected on the Sep. cruise (USNM 544841, *P. a. mesonauta*, identified by Wetmore) was the first Panamá Pacific specimen (Ridgely & Gwynne 1989). In the E Pacific, this species nests from México to Perú, including Is Galápagos where some breeding occurs throughout the year (Harris 1969). I Malpelo, some 460 km SW of Panama, contains the nearest known Pacific breeding colony (Blake 1977).

Pelecanidae

Pelecanus occidentalis (Brown Pelican). This

common breeding bird in the Gulf of Panamá is highly coastal-oriented, so that frequency of birds seen at sea in these cruises did not reflect adequately their actual abundance within the general region. Montgomery & Martínez (1984) state that more than 50 000 Brown Pelicans migrate into the Bay of Panamá (i.e., the area near the mainland) after beginning of dry season (Jan. into May), adding to a substantial resident population. Inspection of Table 2 does show a rise in frequency of birds at sea in Jan. and Feb./Mar. cruises, but hardly enough to suggest the massive immigration indicated by Montgomery & Martínez for coastal waters. Notably, birds seen in Apr. and Jun., when adults plus yearlings might be expected to be present, were at pre-dry season frequencies. On these cruises, no evidence of breeding on offshore islands was noted until Feb./Mar.; pelicans were then found nesting in large numbers thereafter through the dry season.

Sulidae

Sula dactylatra (Masked Booby). Masked Boobies were seen in Sep.—Nov. and Apr.—Jun., usually in small numbers (Table 2). On the Jun. cruise, however, 71 birds (2.2/hr) were found along the track between Is Perlas and Bahía Piñas. Previously, there had been only 2 reports of this species from Panamá Pacific waters (Wetmore 1965). A specimen collected in Sep. (USNM 544840, *S. d. granti*, identified by Wetmore) was the first for Panamá. This population breeds from México S to Is Galápagos and I Malpelo, and off the South American coast to Chile (Harrison 1983). I Malpelo is the nesting ground nearest Panamá.

Sula nebouxii (Blue-footed Booby). Small numbers of this species were seen at sea on every cruise (Table 2). On the islands, they increased notably Dec. through Jun., presumably breeding there, though no nests and only one fledgling were noted. Wetmore (1965) listed breeding records, but also indicated several dry season island reports in which nesting was not clearly evident. Thus, a fraction of Blue-footed Boobies in the Dec.—Jun. peak may have been seasonal, non-breeding visitors. There was an "invasion" of up to 10 000 Blue-footed Boobies from elsewhere, possibly Is Galápagos, I Malpelo or Is Lobos off Perú, into the Gulf during the

1982—1983 El Niño event (Aid *et al.*, 1985; N. G. Smith, *in litt.*).

Sula leucogaster (Brown Booby). This breeding resident was the second most abundant species seen on these cruises (Table 2). Only Black Terns seasonally occurred in greater numbers. Brown Boobies were observed at breeding activities Oct. through Apr., with condition of nestlings seen indicating that some breeding activity had been in progress before and would continue after that period. Landings were made on I Galera and I Camote in Mar., where Brown Boobies were in early stages of a nesting peak, most nests with eggs or recently hatched young. On I Galera, nests were found on the ground at the fringes of cane patches and beneath tall broad-leafed evergreen trees; most were made of fallen leaves. Some nests undoubtedly had been used previously, for they were about 0.5 m high. On treeless I Camote, nests were built in clumps of tall grass and were largely made of that material.

Fregatidae

Fregata magnificens (Magnificent Frigatebird). This species was seen at sea in fair numbers on every cruise (Table 2). Large feeding flocks over unusually abundant fish shoals accounted for relatively high numbers in Dec.; otherwise they were found scattered along cruise tracks alone or in small groups. Birds were numerous on islands at every visit, but indications of breeding were not noted until Dec. Nesting was at peak in Feb./Mar. In non-breeding months (Jun.—Nov.), few adult males were seen at sea or on the islands. This abruptly changed in Dec., with the appearance of ballooning adult males and reduction in numbers of subadult-plumaged birds in the area.

Phalaropodidae

Phalaropus lobatus (Red-necked Phalarope). This species was seen in the Gulf in Aug.—Nov., often in very large flocks, peaking at 29 birds/hr in Sep.; and once in Feb./Mar. (Table 2). This clearly reflected a heavy post-breeding migration of this boreal breeder through the Gulf that cruise year, moving on later presumably to wintering waters off South America, and with very little passage through the Gulf on its northward return flight. E. Eisenmann (personal commu-

TABLE 3. Probable breeding provenance and non-breeding quarters of seabirds observed on the Gulf of Panama cruises.

Species	Probable breeding area	Probable "winter quarters"
A. Subantarctic Zone		
<i>Puffinus griseus</i>	Off S Chile	Calif. to Alaska
<i>Oceanites oceanicus</i>	Off Cape Horn	N to Peru
B. Southern Subtropic Zone		
<i>Oceanodroma tethys</i>	Off Peru	Ecuador N to Pma
C. Tropic Zone		
<i>Puffinus lherminieri</i>	Galapagos	Tropical E Pacific
<i>Phaethon aethereus</i>	I Malpelo, Galapagos	Tropical E Pacific
<i>Pelecanus occidentalis</i>	Gulf of Panama	Gulf of Panama
<i>Sula dactylatra</i>	I Malpelo, Galapagos	Tropical E Pacific
<i>Sula neboxii</i>	Gulf of Panama	Gulf of Panama
<i>Sula leucogaster</i>	Gulf of Panama	Gulf of Panama
<i>Fregata magnificens</i>	Gulf of Panama	Gulf of Panama
<i>Sterna anaethetus</i>	Central America	Tropical E Pacific
<i>Anous stolidus</i>	Galapagos	Tropical E Pacific
D. Northern Subtropic Zone		
<i>Oceanodroma melania</i>	S & Baja California	Peru to I Galapagos
<i>Halocyptena microsoma</i>	Baja California	Colombia & Ecuador
<i>Larus atricilla</i>	E U.S. coast	Panama S to Chile
<i>Sterna albifrons</i>	S & Baja California	Ecuador & Peru
<i>Thalasseus maximus</i>	S Calif & NW Mexico	Panama S to Peru
E. Subarctic Zone		
<i>Chlidonias niger</i>	Interior N. America	Panama S to Chile
<i>Sterna hirundo</i>	Int. & E coast N. Am.	Panama S to Peru
F. Arctic Zone		
<i>Phalaropus lobatus</i>	Circumpolar Pacific	At sea off Peru
<i>Stercorarius</i> spp.	Circumpolar Pacific	Off S Am. to c. 50°S
<i>Xema sabini</i>	Circumpolar Pacific	Colombia S to Peru

nication) thought this 1968–69 period to be highly unusual for the Red-necked Phalarope off Panamá. Previously, the species was scarcely known from there; Wetmore (1965) listed only a single record for the Panamá Pacific. Ridgely & Gwynne (1989) presently consider it an irregular but occasionally common transient in the Gulf. In the Sep. cruise, flock after flock were seen feeding over shoaling fish, hovering and "surface plunging" (Ashmole 1971) much like Black Terns. They were in simple flocks and in mixed flocks with Black Terns and Brown Pelicans. On other occasions, they were seen feeding in their more usual manner, sitting on the water and "surface seizing" prey with quick dips of the bill.

Stercorariidae

Jaegers. Subadult jaegers seen at sea (and at times in the hand; see below) are very difficult to iden-

tify; and most of the jaegers seen on these cruises were subadult. Though individuals of all three species were positively identified, most birds were simply recorded as "jaegers". Jaegers (including those birds identified) were seen on Oct.—Nov. and Jan.—Apr. cruises (Table 2). Previously, there had been few reports of any jaegers from the Gulf (Wetmore 1965). The bimodal appearance of these boreal breeders indicated a small and relatively compact southward migration through the Gulf and an early-starting and more prolonged northward passage through the Gulf from wintering waters off S South America.

Stercorarius pomarinus (Pomarine Jaeger). Individuals of this species were positively identified on Oct.—Nov. cruises. Wetmore (1965) listed two reports but no specimens for the Gulf.

Stercorarius parasiticus (Parasitic Jaeger). Two subadult jaegers were collected together on the

Mar. cruise. Wetmore (*in litt.*) identified one (USNM 544850) as *S. parasiticus*, the other (USNM 544851) a *S. longicaudus*. E. Eisenmann (in a note found attached to the museum specimen) reexamined both specimens and concluded that USNM 544851 also was *S. parasiticus*. Wetmore apparently concurred, for the museum label now reads "*Stercorarius parasiticus* AW". Wetmore (1965) listed only one sight report of this species from Panamá Pacific waters. Ridgely & Gwynne (1989) mention subsequent reports, including a sighting of 900 to 1300 individuals off Punta Mala in 1970.

Stercorarius longicaudus (Long-tailed Jaeger). A jaeger collected in Nov. (USNM 544846) was identified by Wetmore (*in litt.*) as *S. parasiticus*. However, this specimen was later reidentified on the basis of molt pattern by R.R. Viet (per specimen label) as *S. longicaudus*. Wetmore (1965) listed no report of this species from Panamá Pacific waters.

Laridae

Larus atricilla (Laughing Gull). This species occurs near mainland Panamá in every month of the year and in large numbers, those in boreal summer being non-breeding young birds (Wetmore 1965). However, Laughing Gulls were not seen at sea on these cruises until a single bird was noted in Nov. From Dec. through Feb./Mar. it was abundant, often in large feeding flocks; a few birds remained in May–Jun., but none were

seen at sea thereafter (Table 2). Thus, this boreal breeder was a major winter resident in the open Gulf of Panamá, arriving there late in northern autumn and most having departed by early northern spring.

Xema sabini (Sabine's Gull). This species was seen in the Gulf Oct.–Dec. and in Feb./Mar.–Jun. (Table 2). There were only 2 previous reports of this gull from Panamá (Wetmore 1965). A bird collected on the Oct. cruise (USNM 544843) was the first specimen for Panamá. On these cruises, Sabine's Gull was, when present, both common and abundant, with flocks of 50 or more often in sight. Evidently, these arctic breeders entered and lingered in the Gulf of Panamá on post-breeding migration, passing on to pelagic winter quarters off the central Pacific coast of South America (Harrison 1983), with smaller numbers transiting the Gulf on the northward return flight.

Chlidonias niger (Black Tern). The most abundant bird in the Gulf of Panamá, Black Terns were seen commonly on every cruise. They were present in greatest numbers Oct. through Apr., peaking in Feb./Mar. with 287 birds/hr (Table 2). In northern midwinter months, simple or mixed feeding flocks of 1000 or more Black Terns were not unusual; at least 3000 were seen in one mixed flock working over huge shoals of fish in Dec. Large numbers of subadult birds regularly remain in these tropical waters through the year (Wetmore 1965), while

TABLE 4. Percentage composition by provenance of seabirds seen in the Gulf of Panama for each cruise and all cruises together.

Cruise	Provenance							
	Austral		Tropical (Non-Gulf)		Tropical (Local)		Boreal	
	con*	sin*	con	sin	con	sin	con	sin
Aug 68	9.2	16.3	< 1.0	< 1.0				
Sep	1.5	1.8	< 1.0	< 1.0				
Oct	< 1.0	< 1.0	10.7	19.4				
Nov	< 1.0	2.6	2.6	14.5				
Dec			< 1.0	< 1.0				
Jan 69								
Feb/Mar								
Apr	1.0	< 1.0	4.2	11.1				
Jun	7.2	7.7	6.1	6.5				
Aug	12.8	14.2	< 1.0	< 1.0				
ALL	1.3	3.4	2.2	5.6				

* CON, percent of all species seen in cruise; SIN, percent of all species seen less Black Tern.

the Gulf is obviously a major wintering area for the species. However, a dip in numbers in the Jan. cruise (coincident with fewer fish shoals seen) suggested that wintering populations may wander widely.

Sterna hirundo (Common Tern). Some Common Terns were seen on every cruise except Aug. 1969 (but present Aug. 1968); they were most numerous Sep.—Oct. and Dec.—Feb./Mar. (Table 2). Common Terns are regularly present near the mainland in larger numbers than were noted at sea on these cruises; subadults occur throughout the year (Wetmore 1965).

Sterna anaethetus (Bridled Tern). This species was seen in fair numbers in Aug.—Dec. cruises, peaking in Oct.—Nov. (Table 2). Previous reports of Bridled Terns for Panamá Pacific waters were few (Wetmore 1965), but those included a Feb. 1956 sighting of large numbers about Los Frailes del Sur, emergent rocks 9 km off the S coast of SE Azuero Peninsula and some 110–130 km SW of the nearest area surveyed in these cruises. Wetmore believed the terns were breeding there. Similarly large flocks have since been seen near Los Frailes (Ridgely & Gwynne 1989), but breeding is undocumented to date (N.G. Smith, personal communication). The known breeding range of the Bridled Tern in the E Pacific is from México (Harrison 1983) to Costa Rica (Stiles 1984). In the absence of sightings from the E Gulf of Panamá on Jan.—Jun. cruises, any Bridled Terns concentrated and possibly breeding off Los Frailes did not penetrate into the Gulf in that period. However, the Oct.—Nov. peak seen suggested migration in those months W through the Gulf in the direction of Los Frailes and breeding areas beyond.

Sterna albifrons (Least Tern). A few Least Terns were seen at sea in Oct.—Nov. (Table 2), among feeding flocks of Black Terns. One immature was collected (USNM 544848, *S. a. browni*, identified by Wetmore), the first Least Tern specimen for Panamá. That population breeds from central California S to Baja California. Wetmore (1965) had no report of this species for the Panamá Pacific. Ridgely & Gwynne (1989) presently consider it uncommon to sometimes fairly common there; they also discuss other small Neotropical terns, unreported but possible in the Gulf, with which Least Terns might be confused in the field.

Thalasseus maximus (Royal Tern). A few Royal Terns were seen at sea in Nov.—Dec. and Aug. (1968) (Table 2), usually in mixed feeding flocks dominated by Black Terns. They are much more regular and abundant near the mainland, where some are present throughout the year (Wetmore 1965).

Anous stolidus (Brown Noddy). This species was seen on Oct.—Nov. and Apr.—Jun. cruises (Table 2). Wetmore (1965) listed only 2 earlier reports for the Gulf proper. There are two other records from nearby Los Frailes del Norte, islets about 4 km offshore of SE Azuero Peninsula (Ridgely & Gwynne 1989). Wetmore thought that Brown Noddies might nest on Los Frailes, but to date breeding there has not been proved. A specimen taken on the Nov. cruise (USNM 544847, *A. s. galapagensis*, identified by Wetmore) was the first for Panamá Pacific waters. There are two tropical E Pacific breeding populations (Harrison 1983): *A. s. ridgwayi* of offshore islands from México to Central America (including I Cocos); and *A. s. galapagensis* of Is Galápagos and Rocas Octavia near Punta Marzo, Colombia, close to the Panamá border (Ridgely & Gwynne 1989). Wetmore's identification indicates a southern origin for individuals seen on these cruises.

DISCUSSION

An upwelling induced by offshore trade winds in dry season (Jan. through Apr.) creates conditions in the Gulf of Panamá favorable for planktonic growth and, as a result, for increased abundance of fish and of seabirds to eat those fish (Schaefer *et al.* 1958). However, abundance of fish and seabirds is not limited to dry season months in the Gulf. Total seabirds seen (excluding Black Terns; see above) on these cruises in wet season ranged from 32.4 to 65.0 birds/hour, as compared with 32.8 to 65.5 birds/hour in dry season (Table 1). Frequency of birds seen from cruise to cruise or from day to day tended to vary with frequency of shoaling fish (and feeding flocks) encountered, which in turn was not a clear function of season generally. Dry season was, however, the peak of nesting for locally breeding species in this cruise year, in keeping with observations by Montgomery & Martínez (1984), Wetmore (1965) and others.

Of 24 species positively identified on these cruises, only 4 breed in the Gulf of Panamá; the rest are seasonal or casual visitors. Where do these seabirds come from? What is the relative importance of seabirds of different provenances in the Gulf avifauna? Table 3 presents the probable origin by breeding areas of seabirds seen on these cruises, and their probable terminal non-breeding-season ("wintering") quarters. Here, these seabirds are grouped by the latitudinal oceanic zones (Ashmole 1971) of their respective breeding grounds.

Only 3 species seen were *austral breeders* (Subantarctic and Southern Subtropic Zones). Of these, one was a through-migrant, one may winter in part in the Gulf, and one was only casual or accidental there. Four of the 9 *Tropic Zone species* were breeding residents in the Gulf (though some individuals may enter the Gulf only to breed, e.g., Brown Pelicans). The 5 non-breeding tropical species include one through-migrant, 2 "wintering" birds, and 2 casuals. *Boreal breeders* (Northern Subtropic, Subarctic, and Arctic Zones) numbered 12. Five of these northern birds wintered in the Gulf; 7 were through-migrants, though 2 of these were absent in northern winter months only in Jan. There were no boreal casuals.

Table 4 presents the percentage composition by provenance of seabirds seen on these cruises. *Gulf resident species* comprised just under a quarter of all birds recorded, or half of all birds excluding Black Terns. Three quarters of all birds seen were *boreal breeders*; without Black Terns they made up about a third of all birds seen. Local and boreal breeders together comprised 96.4% of all seabirds seen. If Black Terns are excluded, these two categories still made up 91% of birds seen.

Austral and visiting tropical seabirds were generally minor constituents of the Gulf avifauna in that cruise year: 1.3% (3.4% less Black Terns) and 2.2% (5.6% less Black Terns), respectively, of all birds seen. However, austral birds did show increased numbers seasonally: 9.2% and 12.8% of birds seen (14.2% and 16.3% less Black Terns) on the Aug. 1968 and 1969 cruises, respectively, and 7.2% (7.7% less Black Terns) on the Jun. cruise. Non-resident tropical species likewise exhibited peaks that were significant

fractions of all birds seen on certain cruises: 10.7% and 2.6% (19.4% and 14.5% less Black Terns) in Oct. and Nov.; and 4.2% and 6.1% (11.1% and 6.5% less Black Terns) in Apr. and Jun. No austral breeders were seen on Dec. through Feb./Mar. cruises nor were any non-resident tropical seabirds seen in Jan.—Feb./Mar. months of austral summer when these birds (tropical species too?) presumably were in their breeding quarters.

Diamond (1983) compared and discussed characteristics of tropical *versus* temperate seabird communities. However, Haney (1986) found that structure and turnover of seabird populations seen off the southeastern United States continental shelf suggested that the concept of a seabird "community" may not apply in some marine environments. In this Gulf of Panamá survey, the seabirds encountered appeared most often to reflect seasonally fluctuating assemblages of subpolar, temperate and tropical species in Haney's sense, rather than integrated communities.

In terms of numbers, biomass, residence time, and impact on resources, the core seabird "assemblage" in the Gulf of Panamá that year probably comprised the Black Tern, Brown Booby, Brown Pelican and Magnificent Frigatebird, in that order. Of lesser significance but seasonally important were the Laughing Gull, Least Storm-Petrel, Common Tern and (that year, at least) Sabine's Gull and Red-necked Phalarope. The remaining species seen might be considered marginal in the avifauna; neither the status of other species nor of the resources of the Gulf should likely be affected substantially by the presence or absence, the successes or failures, of those species in the Gulf of Panamá.

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REFERENCES

- Aid, C.S., G.C. Montgomery & D.W. Mock. 1985. Range extension of the Peruvian Booby to Panamá during the 1983 El Niño. *Colonial Waterbirds* 8: 67–68.
- Ashmole, N.P. 1971. Sea bird ecology and the marine environment, pp 223–286 in Farner, D.S., J.R. King & K.C. Parkes (eds.). *Avian Biology*, Vol. I. Academic Press, London.
- Blake, E.R. 1977. *Manual of Neotropical Birds*, Vol. I. Univ. Chicago Press, Chicago.
- Crossin, R.S. 1974. The storm-petrels (Hydrobatidae). Pp 154–205 in King, W.S. (ed.). *Pelagic studies of seabirds in the central and eastern North Pacific Ocean*. *Smiths. Contrib. Zool. No. 158*.
- Diamond, A.W. 1983. Feeding overlap in some tropical and temperate seabird communities. *Stud. Avian Biol.* 8: 24–46.
- Haney, J.C. 1986. Influence of Gulf Stream eddies on seabirds. Abstract no. 448, XIX Congr. Internatl. Ornith. Abstracts-Resumés.
- Harris, M.P. 1969. Breeding seasons of seabirds in the Galápagos Islands. *J. Zool. London* 159: 145–165.
- Harrison, P. 1983. *Seabirds, an identification guide*. Houghton Mifflin Co., Boston.
- Jehl, J.R. 1974. The near-shore avifauna of the Middle American west coast. *Auk* 91: 681–699.
- King, W.B. (ed.). 1974. *Pelagic studies of seabirds in the central and eastern Pacific Ocean*. *Smiths. Contrib. Zool. No. 158*.
- King, W.B., G.E. Watson, & P.J. Gould. 1967. An application of automatic data processing to the study of seabirds. I. Numerical coding. *Proc. Natl. Mus.* 123, 3609: 1–29.
- Montgomery, G.G., & M.L. Martínez. 1984. Timing of pelican nesting on Taboga Island in relation to upwelling in the Bay of Panamá. *Colonial Waterbirds* 7: 10–21.
- Ridgely, R.S., & J.A. Gwynne. 1989. *A guide to the birds of Panama with Costa Rica, Nicaragua and Honduras*. Princeton Univ. Press, Princeton.
- Schaefer, M.B., Y.M. Bishop, & G.V. Howard. 1958. Some aspects of upwelling in the Gulf of Panama. *Bull. Inter-Amer. Tropical Tuna Comm.* 3: 79–131.
- Snow, D.W. 1965. The breeding of Audubon's Shearwater (*Puffinus lherminieri*) in the Galápagos. *Auk* 82: 591–597.
- Stiles, F.G. 1984. Status and conservation of seabirds in Costa Rican waters. Pp 223–229 in Croxall, J.P., P.G.H. Evans & R.W. Schreiber (eds.). *Status and conservation of the world's seabirds*. ICBP Tech. Publ. No. 2, Cambridge.
- Wetmore, A. 1965. *The Birds of the Republic of Panama*. Part 1. — Tinamidae (Tinamous) to Rynchopidae (Skimmers). *Smiths. Misc. Coll.*, Vol. 150.