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SEABIRDS IN SOUTHEASTERN HAWAIIAN WATERS

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Waters within 200 nautical miles (370 km) of North America and the Hawaiian Archipelago (the exclusive economic zone) are considered as within North American boundaries by bird records committees (e.g., Erickson and Terrill 1996). Seabirds within 370 km of the southern Hawaiian Islands (hereafter referred to as Hawaiian waters) were studied intensively by the Pacific Ocean Biological Survey Program (POBSP) during 15 months in 1964 and 1965 (King 1970). These researchers replicated a trackline each month and provided considerable information on the seasonal occurrence and distribution of seabirds in these waters. The data were primarily qualitative, however, because the POBSP surveys were not based on a strip of defined width nor were raw counts corrected for bird movement relative to that of the ship (see Analyses). As a result, estimation of density (birds per unit area) was not possible.

From 1984 to 1991, using a more rigorous survey protocol, we resurveyed seabirds in the southeastern part of the region (Figure 1). In this paper we provide new information on the occurrence, distribution, effect of oceanographic factors, and behavior of seabirds in southeastern Hawaiian waters, including density estimates of abundant species. We also document the occurrence of six species unrecorded or unconfirmed in these waters, the Parasitic Jaeger (*Stercorarius parasiticus*), South Polar Skua (*Catharacta maccormicki*), Tahiti Petrel (*Pterodroma rostrata*), Herald Petrel (*P. heraldica*), Stejneger's Petrel (*P. longirostris*), and Pycroft's Petrel (*P. pycrofti*).

STUDY AREA AND SURVEY PROTOCOL

Our study was a piggyback project conducted aboard vessels studying the physical oceanography of the eastern tropical Pacific. Our transects were

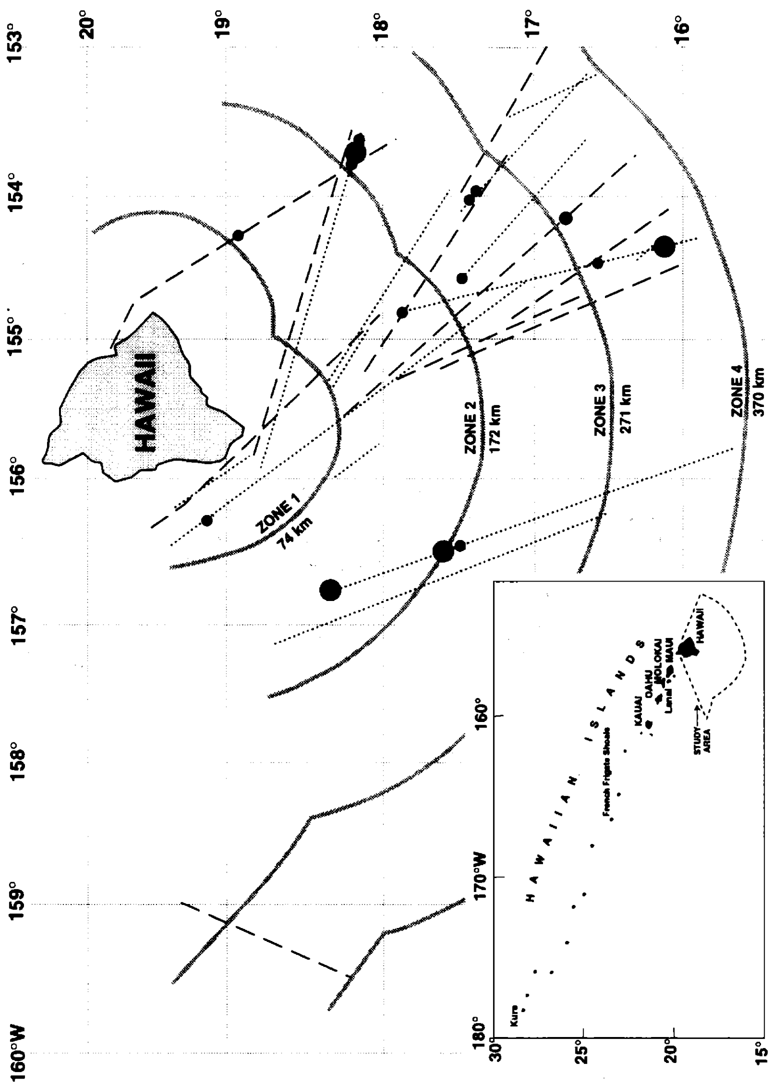

Figure 1. Study area in southeastern Hawaiian waters showing zones 1–4 and cruise tracks over which seabird surveys were conducted. Dotted lines, spring cruises; dashed lines, autumn cruises; small dots, locations of feeding flocks of 5 to 50 birds; medium-sized dots, flocks of 50 to 100 birds; large dots, flocks of >100 birds.

concentrated south and southeast of the island of Hawaii (Figure 1). While the ship was underway during daylight, at least two persons surveyed seabirds simultaneously from the flying bridge. Using the strip-transect survey method (see Spear et al. 1992a), they counted all seabirds seen within a strip of given width off the forequarter offering the best observation conditions. Strip width, determined as per Heinemann (1981), was 500 or 600 m depending on height of the flying bridge of the three vessels used (14 and 15 m above sea level). Alternating between observers, we used hand-held binoculars to scan the outer portion of the transect strip nearly constantly for birds missed with the unaided eye. We used a 25 × 150 mm mounted binocular to aid species identification. We recorded behavior and, for birds flying in a steady direction, recorded flight direction to the nearest 10°. We also recorded species and numbers of birds in feeding flocks (>4 birds pursuing prey) that passed within 2000 m.

Every 0.5 hr we recorded the ship's position, speed, and course. We conducted 289 transects, each of 0.5 hr except those terminated when the ship stopped, and calculated the area surveyed as the survey period multiplied by strip width and ship speed. Our effort comprised 72.1 hrs of surveys over 971.6 km^2 during spring (18 April through 27 June), and 71.9 hrs covering 1156.8 km^2 during autumn (7 October through 20 November), 1984–1991 (Table 1). Surveys were not conducted in spring 1985 or autumn 1986 and 1988.

Each 0.5 hr we also recorded sea-surface temperature and salinity, thermocline depth and "slope" (see below), wind direction (nearest 10°), wind speed, and distance from land. Thermocline depth and slope, indices of mixing in the water column, were monitored with expendable bathythermographs. Thermocline depth is the point where the warm surface layer meets cooler water below; i.e., the shallowest inflection point determined from bathythermograph plots of temperature with depth. Exceptions were when there was no inflection point, indicating that the thermocline was at the surface, or there was more than one inflection, when we assumed that the thermocline began at the depth of the strongest inflection. We measured thermocline slope as the temperature difference between the thermocline and a point 20 m below the thermocline.

ANALYSES

To estimate bird densities, we corrected observed (raw) numbers for the effect of flight speed and direction of birds relative to the ship's speed and course (Spear et al. 1992a; flight speeds from Spear and Ainley 1997). Without these corrections, densities from at-sea survey data are usually overestimated, particularly for fast fliers. The correction also is required because any patterns in bird or ship direction will bias analyses. For example, if birds flew east and west at the same speed and in equal numbers, uncorrected counts from a ship traveling west would show greater numbers flying east because the observer would count more that were flying east than west.

We calculated densities for each transect by dividing the corrected count by the number of square kilometers surveyed and report densities as birds

Table 1 Survey Effort in Hawaiian Waters by Date

Year	Day	Hours of survey	Area surveyed (km^2)
1984	8 May	6.5	85.9
1984	9 May	2.0	25.8
1984	18 May	5.0	55.8
1984	19 May	1.0	12.8
1984	5 Nov	5.5	79.2
1985	16 Oct	8.5	132.6
1985	30 Oct	8.5	120.8
1986	18 Jun	4.5	60.7
1987	31 May	2.5	39.0
1987	7 Oct	5.5	92.9
1988	4 Jun	5.8	85.8
1988	19 Jun	5.0	83.1
1989	2 May	9.0	143.2
1989	27 Jun	8.5	107.8
1989	17 Nov	7.0	122.1
1989	20 Nov	6.5	105.2
1990	21 Apr	10.8	101.0
1990	7 Nov	5.4	91.8
1990	15 Nov	8.5	134.7
1991	18 Apr	4.0	66.9
1991	25 Apr	7.5	106.6
1991	12 Nov	11.0	194.8
1991	19 Nov	5.5	82.7
Total			
8	23	144.0	2128.4

per 100 km^2 of ocean surface. For predominant species (definition given below), unless noted otherwise, all abundance estimates pertain to corrected counts, with variance given as one standard error. We report only raw numbers in accounts of less frequent species. The POBSP calculated abundance differently; precluding between-study comparisons of absolute abundance.

We recognized three species groups: "breeding residents," species that breed on the Hawaiian Islands, "nonbreeding residents," species that do not breed on the Hawaiian Islands but reside in the study area as prebreeders or during the nonbreeding season, and "migrants," species that migrate across the study area when traveling between breeding and wintering areas.

We divided the study area into four zones (Figure 1): zone 1, 0 to 73 km from Hawaii; zone 2, 74 to 172 km; zone 3, 173 to 271 km; and zone 4, 272 to 370 km. Respectively by zone, we surveyed 130.8 (10.8 hrs), 289.7 (22.0 hrs), 291.4 (22.3 hrs), and 259.7 km^2 (17.0 hrs) of ocean surface during spring, and 140.9 (9.0 hrs), 324.1 (19.9 hrs), 362.4 (22.5 hrs) and 329.1 (20.5 hrs) km^2 during autumn. During April, May, June, October, and November, we surveyed 274.5, 359.7, 337.4, 346.3, and 810.5 km^2 of ocean surface, respectively.

Using the STATA program (STATA Corp. 1995), we used multiple-regression analyses and Sidak multiple-comparison tests (an improved version of the Bonferroni test; SAS Institute 1985) to compare seabird densities by zone, season, and species group. The sample unit was one 0.5-hr transect. We also use log-likelihood ratio (G) tests to examine proportional differences.

We log-transformed densities to satisfy assumptions of normality (skewness/kurtosis test for normality of residuals, $P > 0.05$). Because no birds were seen during 87 (30%) of the 289 transects, densities included values of zero. As a result, transformations were calculated as the log (density + 1). Experimentation with different modifications [e.g., log (density + 0.5)] showed no appreciable effect of choice of modifications on probabilities (P). All analyses of variance were of the log-transformed density values. Normality was not achieved in all analyses, but least-squares regression (ANOVA) is considered to be very robust with respect to non-normality (Seber 1977, Kleinbaum et al. 1988). Although regression analyses yield the best linear unbiased estimator relating density to independent variables, even in the absence of normally distributed residuals, P values at the lower levels of significance must be regarded with caution (Seber 1977). Therefore, to reduce the chances of committing a Type I error, we assumed significance for ANOVAs at $P \leq 0.02$. We included two- and three-order polynomials in regression analysis to test for curvilinearity.

Unless noted otherwise, species accounts pertain only to transect data; i.e., they do not include feeding flocks seen outside the transect zone. All references to the POBSP refer to King (1970). Seasons are defined as in the northern hemisphere.

RESULTS

Seasonal Distributions

We recorded 32 species, including 15 species of breeding residents, 11 nonbreeding residents, and six migrants (Table 2). During spring, densities of breeding residents were significantly higher than those of nonbreeding resident; those of migrants were significantly lower (Sidak tests, all $P < 0.01$, Figure 2). During autumn, densities among the three groups differed insignificantly (Sidak test, all $P > 0.1$). During spring, densities of breeding residents were significantly higher, those of migrants significantly lower than during autumn (Sidak tests, df = 287, both $P < 0.01$, Figure 2). Between the two seasons, densities of nonbreeding residents differed insignificantly (Sidak test, $P = 0.3$).

During spring, densities were significantly higher in zones 1 and 4 than during autumn (Sidak tests, both $P < 0.01$, Figure 3), but in zones 2 and 3 they did not differ significantly (both $P > 0.6$). The lack of a significant difference in the latter two zones resulted in a marginally insignificant difference (ANOVA, $F[1,287] = 4.88$, $P = 0.028$) in overall density between spring (52.5 ± 10.20 birds per 100 km^2, $n = 145$ transects) and autumn (32.2 ± 6.12 birds per 100 km^2, $n = 144$), controlled for zone. Thus, for a given zone, there was a marginally insignificant trend for densities to be greater during spring than autumn.

Table 2 Raw and Corrected Counts and Status of Seabirds Recorded in Southeastern Hawaiian Waters, 1984–1991

Species	Raw	Corrected[a]	Status[b]
Diomedeidae			
Black-footed Albatross, *Phoebastria nigripes*	3	3.0	BR
Procellariidae			
Newell's Shearwater, *Puffinus newelli*	27	17.0	BR
Christmas Shearwater, *P. nativitatis*	1	0.4	BR
Sooty Shearwater, *P. griseus*	164	105.7	MI
Buller's Shearwater, *P. bulleri*	2	2.0	MI
Wedge-tailed Shearwater, *P. pacificus*	202	175.3	BR
Juan Fernandez Petrel, *Pterodroma externa*	41	40.1	NO
White-necked Petrel, *P. cervicalis*	18	23.1	NO
Dark-rumped Petrel, *P. phaeopygia*	29	24.8	BR
Tahiti Petrel, *P. rostrata*	2	1.2	NO
Kermadec Petrel, *P. neglecta*	8	5.6	NO
Murphy's Petrel, *P. ultima*	1	1.0	MI
Herald Petrel, *P. heraldica*	3	2.3	NO
Mottled Petrel, *P. inexpectata*	58	31.7	MI
Black-winged Petrel, *P. nigripennis*	94	81.2	NO
Pycroft's Petrel, *P. pycrofti*	5	7.6	NO
Stejneger's Petrel, *P. longirostris*	7	5.0	MI
Bulwer's Petrel, *Bulweria bulwerii*	59	49.2	BR
Oceanitidae			
Leach's Storm-Petrel, *Oceanodroma leucorhoa*	35	41.2	NO
Harcourt's Storm-Petrel, *Oceanodroma castro*	2	2.2	BR
Phaethontidae			
Red-tailed Tropicbird, *Phaethon rubricauda*	4	4.0	BR
White-tailed Tropicbird, *Phaethon lepturus*	8	6.0	BR
Sulidae			
Red-footed Booby, *Sula sula*	1	0.4	BR
Fregatidae			
Great Frigatebird, *Fregata minor*	3	1.2	BR
Laridae			
South Polar Skua, *Catharacta maccormicki*	1	0.6	NO
Pomarine Jaeger, *Stercorarius pomarinus*	9	13.5	NO
Parasitic Jaeger, *Stercorarius parasiticus*	2	2.5	NO
Sooty Tern, *Sterna fuscata*	238	231.6	BR
Arctic Tern, *Sterna paradisaea*	7	4.3	MI
White Tern, *Gygis alba*	14	19.1	BR
Brown Noddy, *Anous stolidus*	1	1.0	BR
Black Noddy, *Anous minutus*[c]			BR

[a] See Methods, Analyses.

[b] BR, breeding resident; NO, nonbreeding resident; MI, migrant.

[c] Seen in feeding flocks only.

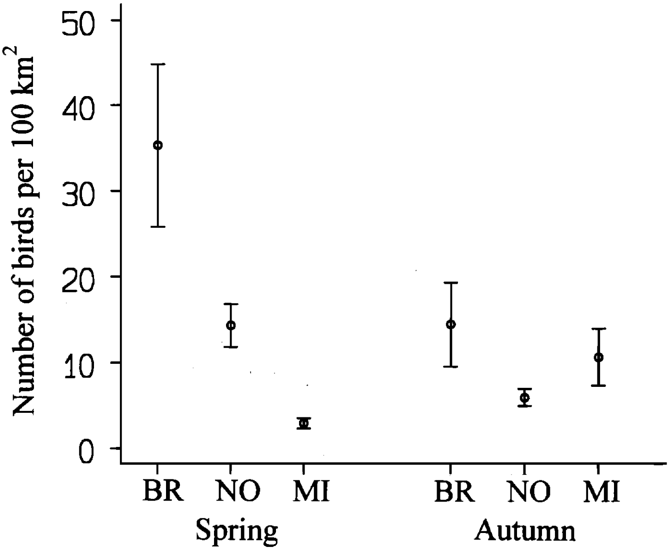

Figure 2. Estimated densities (mean ± standard error) of breeding residents (BR), nonbreeding residents (NO), and migrants (MI) with respect to season. Sample sizes during spring and autumn were 145 and 144 transects, respectively.

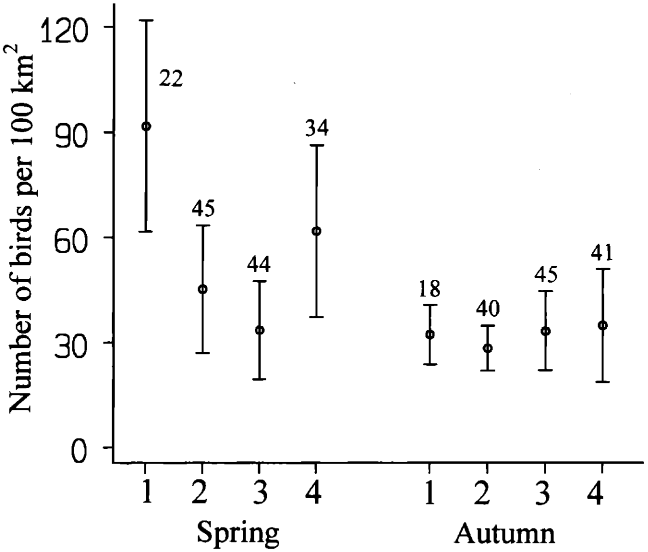

Figure 3. Estimated densities (mean ± SE) of seabirds with respect to distance from Hawaii (see Figure 1 for locations of zones). Numbers accompanying each error bar are sample sizes (number of transects).

Predominant Species

Predominant species (corrected counts > 15 birds, Table 2) were, in order of decreasing abundance, the Sooty Tern, Wedge-tailed and Sooty shearwaters, Black-winged and Bulwer's petrels, Leach's Storm-Petrel, Juan Fernandez, Mottled, White-necked, and Dark-rumped petrels, White Tern, and Newell's Shearwater.

During spring, the Sooty Tern was the most abundant species in all zones except zone 2, where it ranked second, and the Wedge-tailed Shearwater was second most abundant in all zones except 2, where it ranked first (Table 3). The Leach's Storm-Petrel and Bulwer's Petrel were third and fourth most abundant in zones 1 and 2, and the Black-winged and Juan Fernandez petrels ranked among the five most abundant species in zones 3 and 4.

During autumn, the Sooty Tern ranked among the two most abundant species in zones 2 and 4, the Wedge-tailed Shearwater in zones 1 and 3, and the Mottled Petrel in zones 1 and 2 (Table 3). The Black-winged Petrel was second to fourth most abundant in all four zones, and the Sooty Shearwater was variably abundant in all four zones during each season except spring, when its density was <1 bird per 100 km^2 in zone 4.

Breeding Residents: Predominant Species

Sooty Tern. A very abundant breeder throughout the tropical Pacific (Harrison 1983) and the most abundant seabird breeding on the Hawaiian Islands (Harrison 1990). Harrison (1990) estimated that a minimum of 975,750 pairs breed on the northwestern Hawaiian Islands (i.e., islands west of Kauai or 160° W), 70,000 on the main islands. Egg laying from March to July, fledging to late October.

As did the POBSP, we found the Sooty Tern the most abundant species during both spring and autumn (Table 4). Densities were significantly higher during spring than in autumn, a difference due mostly to high densities in June and especially in May (Figure 4). The POBSP also observed peak numbers in May.

A significant interaction between the effects of distance from Hawaii and season reflected a significant decline in densities of Sooty Terns with distance during spring, compared to a significant increase with distance during autumn (Table 5). This difference resulted primarily from the very high densities in zone 1 during spring, in marked contrast to autumn, when these terns where not seen in zone 1 and their densities peaked in zone 4 (Figure 5). A quadratic effect of distance in both spring and autumn (Table 5) resulted from stable, low densities in zones 2 and 3, compared to higher densities in zones 1 and 4 (spring) or higher densities only in zone 4 (autumn; Figure 5). Densities decreased with increase in water temperature (Table 6).

Adults composed 90% of the 54 Sooty Terns whose age we recorded during spring, 86% of 28 birds in autumn. In spring and autumn, 66% of 143 birds and 55% of 89, respectively, were feeding. Of these, 95% (137) were feeding in flocks capturing prey forced to the surface by tuna (*Thunnus* spp.; hereafter "feeding over tuna"); seven were solitary.

Table 3 Relative Abundance of More Common Seabirds[a] by Distance From Hawaii

	Spring		Autumn	
Rank	Species	Estimated density[b]	Species	Estimated density
Zone 1 (0–73 km offshore)				
1	Sooty Tern	32.7	Wedge-tailed Shearwater	17.0
2	Wedge-tailed Shearwater	22.9	Mottled Petrel	6.3
3	Bulwer's Petrel	18.6	Sooty Shearwater	6.1
4	Leach's Storm-Petrel	6.2	Black-winged Petrel	1.3
5	White-tailed Tropicbird	2.2	White-tailed Tropicbird	1.2
6	Dark-rumped Petrel	2.0		
7	Black-winged Petrel	1.6		
8	Newell's Shearwater	1.1		
9	Sooty Shearwater	1.0		
Zone 2 (74–172 km offshore)				
1	Wedge-tailed Shearwater	14.4	Mottled Petrel	6.4
2	Sooty Tern	11.2	Sooty Tern	5.8
3	Leach's Storm-Petrel	8.1	Black-winged Petrel	4.4
4	Bulwer's Petrel	3.5	Wedge-tailed Shearwater	3.1
5	Sooty Shearwater	2.5	Sooty Shearwater	2.6
6	Black-winged Petrel	1.9	White Tern	1.4
7			Dark-rumped Petrel	1.0
Zone 3 (173–271 km offshore)				
1	Sooty Tern	7.3	Sooty Shearwater	16.7
2	Wedge-tailed Shearwater	6.2	Wedge-tailed Shearwater	5.7
3	Black-winged Petrel	3.7	Black-winged Petrel	4.6
4	Juan Fernandez Petrel	2.9	Sooty Tern	2.4
5	Sooty Shearwater	2.9		
6	Newell's Shearwater	2.9		
7	Bulwer's Petrel	2.1		
8	Pomarine Jaeger	1.9		
9	Leach's Storm-Petrel	1.2		
10	Parasitic Jaeger	1.0		
Zone 4 (272–370 km offshore)				
1	Sooty Tern	13.7	Sooty Tern	18.5
2	Wedge-tailed Shearwater	10.6	Black-winged Petrel	4.9
3	Juan Fernandez Petrel	7.7	Dark-rumped Petrel	2.4
4	White-necked Petrel	7.4	White Tern	2.2
5	Black-winged Petrel	4.5	Juan Fernandez Petrel	2.0
6	Bulwer's Petrel	4.5	Wedge-tailed Shearwater	1.6
7	Newell's Shearwater	2.2	Sooty Shearwater	1.0
8	Pomarine Jaeger	2.1		
9	White Tern	2.1		
10	Dark-rumped Petrel	1.5		
11	Pycroft's Petrel	1.5		
12	Leach's Storm-Petrel	1.2		

[a] Estimated density ≥ 1 bird per 100 km^2.

[b] Birds per 100 km^2, extrapolated after correction for ship speed and direction and species' average flight speed and direction.

Table 4 Estimated Densities with Standard Errors of Predominant Species by Residence Status and Season

Species	Density[c] Spring	Density[c] Autumn	P^a
Breeding residents			
Sooty Tern	13.8 ± 4.67	7.7 ± 3.93	0.005[b]
Wedge-tailed Shearwater	11.7 ± 5.06	5.2 ± 1.50	0.1
Bulwer's Petrel	5.6 ± 1.39	0.0	0.001[b]
Dark-rumped Petrel	0.8 ± 0.43	1.1 ± 0.34	0.06
White Tern	0.6 ± 0.51	1.0 ± 0.68	0.5
Newell's Shearwater	1.7 ± 0.58	0.1 ± 0.08	0.001[b]
Nonbreeding residents			
Black-winged Petrel	3.0 ± 0.96	4.2 ± 0.88	0.008[b]
Leach's Storm-Petrel	4.1 ± 1.07	0.5 ± 0.23	0.001[b]
Juan Fernandez Petrel	2.7 ± 0.91	0.8 ± 0.33	0.02[b]
White-necked Petrel	1.9 ± 0.96	0.0	0.001[b]
Migrants			
Sooty Shearwater	2.0 ± 0.52	7.0 ± 2.83	0.01[b]
Mottled Petrel	0.1 ± 0.08	2.7 ± 1.05	0.001[b]

[a] Probabilities from a t test comparing the difference in densities (log-transformed) between seasons. Sample sizes (number of transects) were 145 in spring and 144 in autumn.

[b] Difference between seasons significant at $P \leq 0.02$.

[c] Birds per 100km^2.

Wedge-tailed Shearwater. Breeds in subtropical to temperate waters throughout the Pacific Ocean (Harrison 1983, Everett and Pitman 1993). Berger (1972) estimated that 98% of the Wedge-tailed Shearwaters breeding on the Hawaiian Islands are of the light phase. Most dark-phase birds breed in the southern hemisphere (Warham 1990). Harrison (1990) estimated that a minimum of 176,575 pairs breed on the northwest Hawaiian Islands, 38,165 pairs on the main islands. Egg laying in mid-June, fledging in November.

This was the second and third most abundant species during spring and autumn, respectively (Table 4). There was an insignificant tendency for densities to be greater during spring than autumn. As found by the POBSP, abundance peaked during May (Figure 4).

Densities decreased significantly with distance from Hawaii Island; the effect differed little between spring and autumn (Table 5, Figure 5). There was a quadratic effect of distance. In spring, this resulted from a gradual decline in density from zone 1 to 3, followed by an increase in zone 4. In autumn, density declined abruptly from zone 1 to 2, then stabilized in zones 2 to 4. Abundance increased with decrease in wind speed (Table 5) and increase in water salinity (Table 6).

The proportion of dark-phase birds was 7.8% of 115 in spring, 5.0% of 60 birds in autumn; the difference was insignificant ($G = 0.51$, df = 1, $P =$

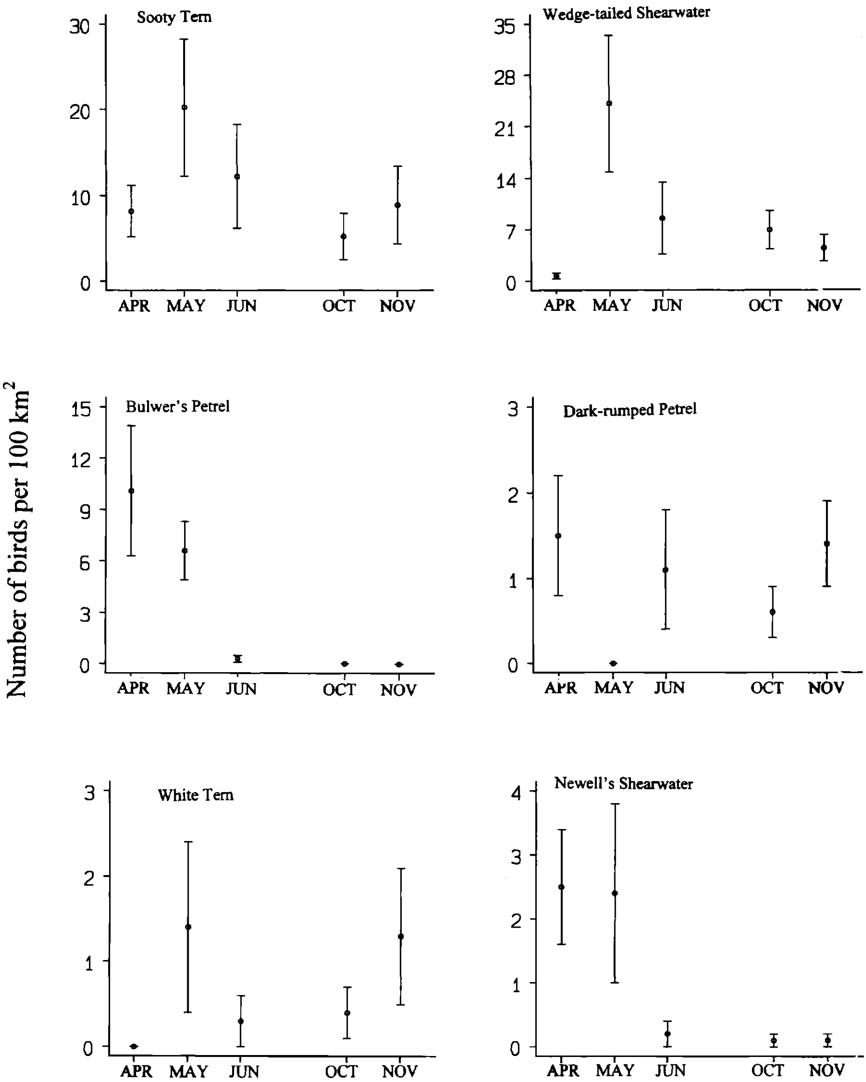

Figure 4. Densities (mean ± standard error) by month of predominant species of seabirds breeding on the Hawaiian Islands. Sample sizes (number of transects) for each month were 45, 52, 48, 45, and 99, respectively.

0.5). In contrast, the POBSP observed 17.1% (n = 6640 birds) dark phase during spring, a proportion significantly greater than ours in spring (G = 8.28, P = 0.005) and a proportion significantly greater than theirs in autumn (3.3%, n = 421 birds; G = 75.81, $P < 0.001$).

Table 5 Multiple-Regression Analyses of Relaionships between Estimated Bird Density[a] and Distance from Hawaii and Wind Speed[b]

		Seasons combined		Spring		Autumn		
	Distance × season[c]	Distance	Distance^2[d]	Distance	Distance^2	Distance	Distance^2	Wind speed
Breeding residents								
Sooty Tern	0.003	—	—	(–)[e] 0.002[f]	(+) 0.01	(+) 0.02	(+) 0.02	ns[g]
Wedge-tailed Shearwater	ns	(–) 0.001	(+) <0.001	—	—	—	—	(–) 0.01
Bulwer's Petrel	0.001	—	—	(–) 0.01	(+) 0.001	—	—	ns
Dark-rumped Petrel	0.02	—	—	ns	ns	(+) 0.02	ns	ns
White Tern	ns	ns	ns	—	—	—	—	ns
Newell's Shearwater	ns	(+) 0.01	ns	—	—	—	—	(+) 0.02
Non-breeding residents								
Black-winged Petrel	ns	(+) 0.001	ns	—	—	—	—	ns
Leach's Storm-Petrel	0.01	—	—	(–) 0.01	(–) 0.001	ns	ns	(+) 0.001
Juan Fernandez Petrel	0.007	—	—	(+) 0.001	ns	ns	ns	ns
White-necked Petrel	0.003	—	—	(+) 0.001	ns	—	ns	ns
Migrants								
Sooty Shearwater	ns	ns	ns	—	—	—	—	(–) 0.001
Mottled Petrel	0.001	—	—	ns	ns	(–) 0.001	ns	(–) 0.001

[a] Transformed as log(birds/100 km^2). The sample size for each species was 289 transects.

[b] Wind speed and distance from land analyzed as continuous variables.

[c] Interaction between the two terms in the effect on density.

[d] Squared terms denote quadratic effects (no quadratic effects of wind speed were significant).

[e] Signs given in parentheses denote signs of the regression coefficient, i.e., a positive or negative slope. A negative slope indicates higher densities nearer Hawaii; a positive slope indicates higher densities farther from Hawaii.

[f] Values following coefficients are P values; significance accepted at $P \leq 0.02$.

[g] ns, not significant.

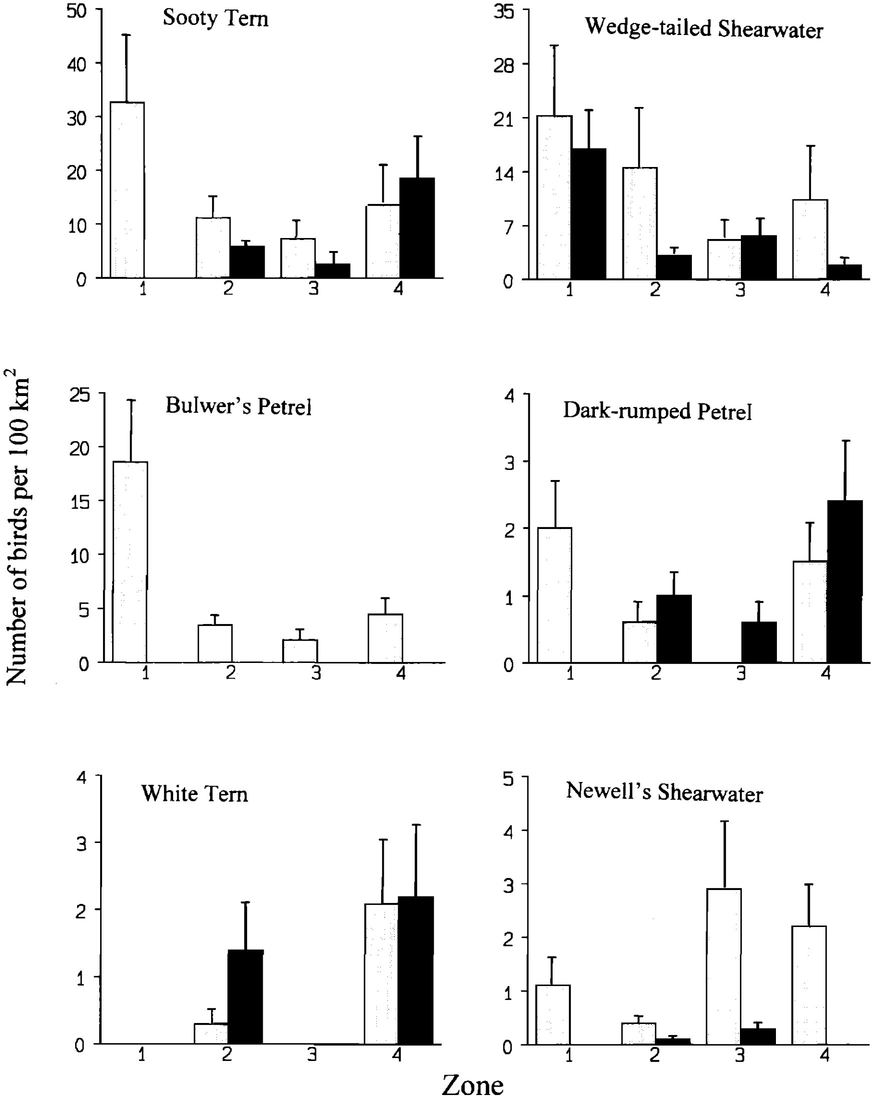

Figure 5. Densities (mean ± standard error) by season and zone of predominant species of seabirds breeding on the Hawaiian Islands. Light bars, spring; dark bars, autumn. Lines above the bars are standard errors. See Figure 1 for location of zones, Figure 3 for sample sizes.

Table 6 Regression Analyses of Relationships between Estimated Bird Density[a] and Oceanographic Variables[b]

	SST	SST^{2}[c]	SAL	TDPT	TDPT^{2}	TSLP	TSLP^{2}
Breeding residents							
Sooty Tern	(-)[d] 0.02[e]	ns[f]	ns	ns	ns	ns	ns
Wedge-tailed Shearwater	ns	ns	(+) 0.01	ns	ns	ns	ns
Bulwer's Petrel	(-) 0.001	ns	(-) 0.001	(+) 0.002	ns	(-) 0.005	ns
Dark-rumped Petrel	ns	ns	ns	(-) 0.003	ns	ns	ns
White Tern	ns	ns	ns	ns	ns	ns	ns
Newell's Shearwater	(-) 0.001	ns	(-) 0.02	ns	ns	ns	ns
Nonbreeding residents							
Black-winged Petrel	(+) 0.001	ns	(+) 0.02	(-) 0.001	(+) 0.01	ns	ns
Leach's Storm-Petrel	(-) 0.001	ns	(-) 0.001	ns	ns	ns	ns
Juan Fernandez Petrel	ns	(-) 0.05	ns	(-) 0.001	(+) 0.001	(-) 0.003	ns
White-necked Petrel	ns	ns	ns	(-) 0.001	(+) 0.001	(-) 0.001	(+) 0.002
Migrants							
Sooty Shearwater	ns	ns	ns	ns	ns	(-) 0.01	ns
Mottled Petrel	ns	ns	(+) 0.01	ns	ns	ns	ns

[a] Transformed as log(birds/100km^{2}). The sample size for each species was 289 transects.

[b] SST, sea-surface temperature; SAL, sea-surface salinity; TDPT, thermocline depth; TSLP, thermocline slope. All independent terms analyzed as continuous variables.

[c] Squared terms denote quadratic effects (no quadratic effects for salinity).

[d] Signs given in parentheses denote signs of the regression coefficient, i.e., a positive or negative slope. A positive slope indicates an increase in density with increase in value of the variable.

[e] Values following coefficients are P values; significance accepted at $P \leq 0.02$.

[f] ns, not significant.

During spring and autumn, 83% of 95 birds and 23% of 14, respectively, were feeding. Of the 109 feeding birds, 97% were in flocks feeding over tuna, 3% were scavenging squid.

Bulwer's Petrel. Breeds throughout the tropical Pacific (Harrison 1983). Harrison (1990) estimated that a minimum of 76,555 pairs breed on the northwestern Hawaiian Islands, 335 pairs on the main islands. Egg laying from late May to early June, fledging in September.

Like the POBSP, we observed Bulwer's Petrel only during spring, when it was the third most abundant species (Table 4). We observed peak densities in June (Figure 4), the POBSP in May.

Densities of Bulwer's Petrels decreased with increase in distance from Hawaii (Table 5, Figure 5). A quadratic effect of distance resulted from an abrupt decline in density from zone 1 to 2, then stabilization in zones 2 to 4. Densities increased with decrease in water temperature, salinity, and thermocline slope and with increase in thermocline depth (Table 6).

Of the 49 birds, 11 were feeding. Eight were solitary and three were in a feeding flock.

Dark-rumped Petrel. An endemic taxon, with an estimated 3750 to 4500 pairs breeding at high elevations on the main Hawaiian Islands (Spear et al. 1995). Egg laying in early May, fledging in October and November (Simons 1985, Ainley et al. 1995).

This was the sixth most abundant species during autumn (Table 4); between the two seasons densities differed insignificantly. We observed highest densities in April (Figure 4); the POBSP counted highest numbers in May.

In spring, densities were significantly higher in zone 1 than in zones 2 and 3. In autumn, densities were significantly higher in zone 4 than in zones 1, 2, or 3 (Sidak tests, $P < 0.02$, Figure 5). Density decreased with increase in thermocline depth (Table 6).

Seven of the 25 petrels were feeding. Five were in flocks feeding over tuna; two were feeding over tuna but were not in a flock.

White Tern. Relatively small populations breed on islands throughout the tropical Pacific (Harrison 1983). Harrison (1990) estimated that 7445 pairs breed on the northwestern Hawaiian Islands, 50 pairs on Oahu. On Oahu the breeding season is protracted and varies much from year to year (Berger 1972, Miles 1986).

This was the seventh most abundant species during autumn (Table 4). Densities differed insignificantly by season and month (Table 4; Sidak tests for monthly comparisons, all $P > 0.02$, Figure 4). The POBSP likewise recorded similar numbers throughout the year.

These terns were seen only in zones 2 and 4 (Figure 5). There were no relationships between densities and distance from Hawaii or oceanographic variables (Tables 4 and 5). Of the 19 terns recorded, 52% were feeding. Nine were feeding in flocks and one was solitary.

Newell's Shearwater. An estimated 18,000 to 19,000 pairs breed on the main Hawaiian Islands (Spear et al. 1995), to which the bird is endemic. Egg laying in late May or early June (Harrison 1990), fledging in October and November (Berger 1972).

This was the ninth most abundant species during spring (Table 4). Densities were significantly higher in spring than in autumn. As did the POBSP, we recorded the majority in April and May (Figure 4).

Densities increased with distance from Hawaii and wind speed (Table 5, Figure 5; see also Spear et al. 1995). Densities also increased with decrease in water temperature and salinity (Table 6).

Four of the 17 birds (24%) were feeding, all in flocks over tuna.

Nonbreeding Residents: Predominant Species

Black-winged Petrel. Breeds in abundance in the temperate South Pacific on islands off New Zealand and Australia (Falla et al. 1967). Egg laying in December and January, fledging in late April.

This was the fifth and fourth most abundant species during spring and autumn, respectively (Table 4); densities were significantly higher in autumn. We observed it during each of the five months except April; densities were highest in June (Figure 6). The POBSP observed highest numbers from May to November, with a peak in October.

Densities increased significantly with increase in distance from Hawaii at both seasons (Table 5, Figure 7); densities differed insignificantly by season

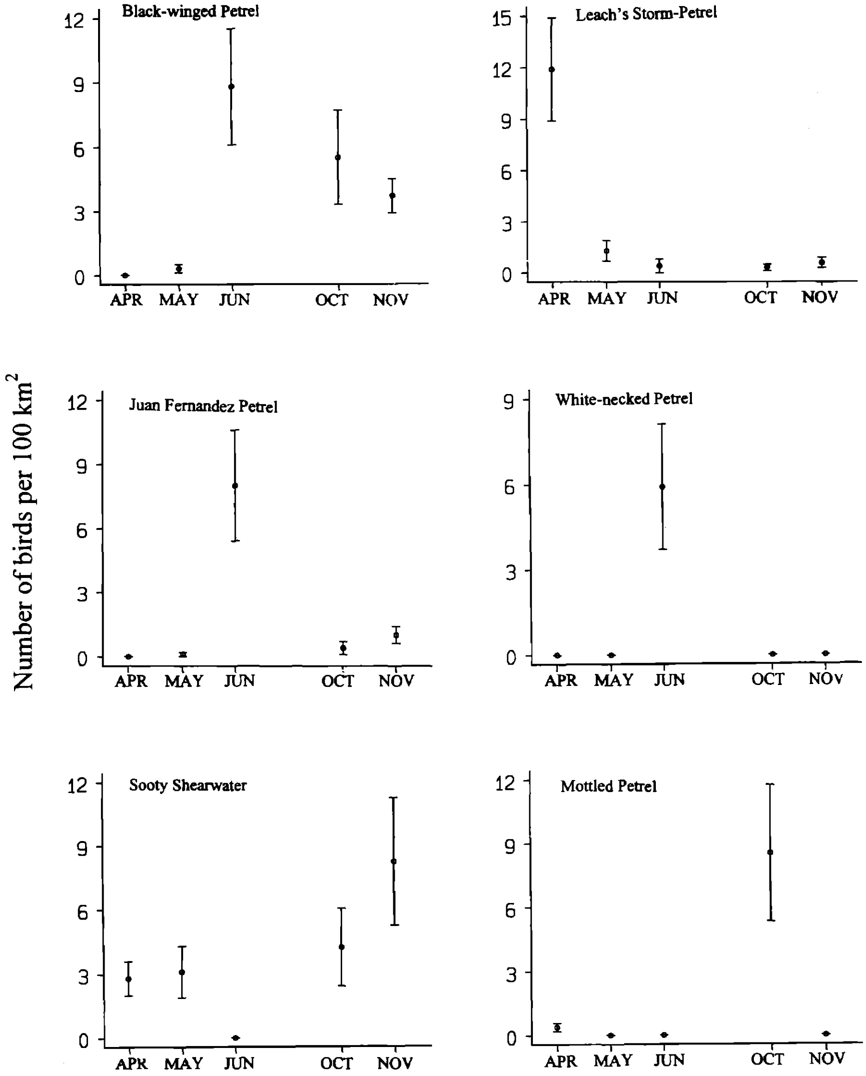

Figure 6. Densities (mean ± standard error) by month of predominant species of seabirds not breeding in the Hawaiian Islands. Sample sizes (number of transects) for each month were 45, 52, 48, 45, and 99, respectively.

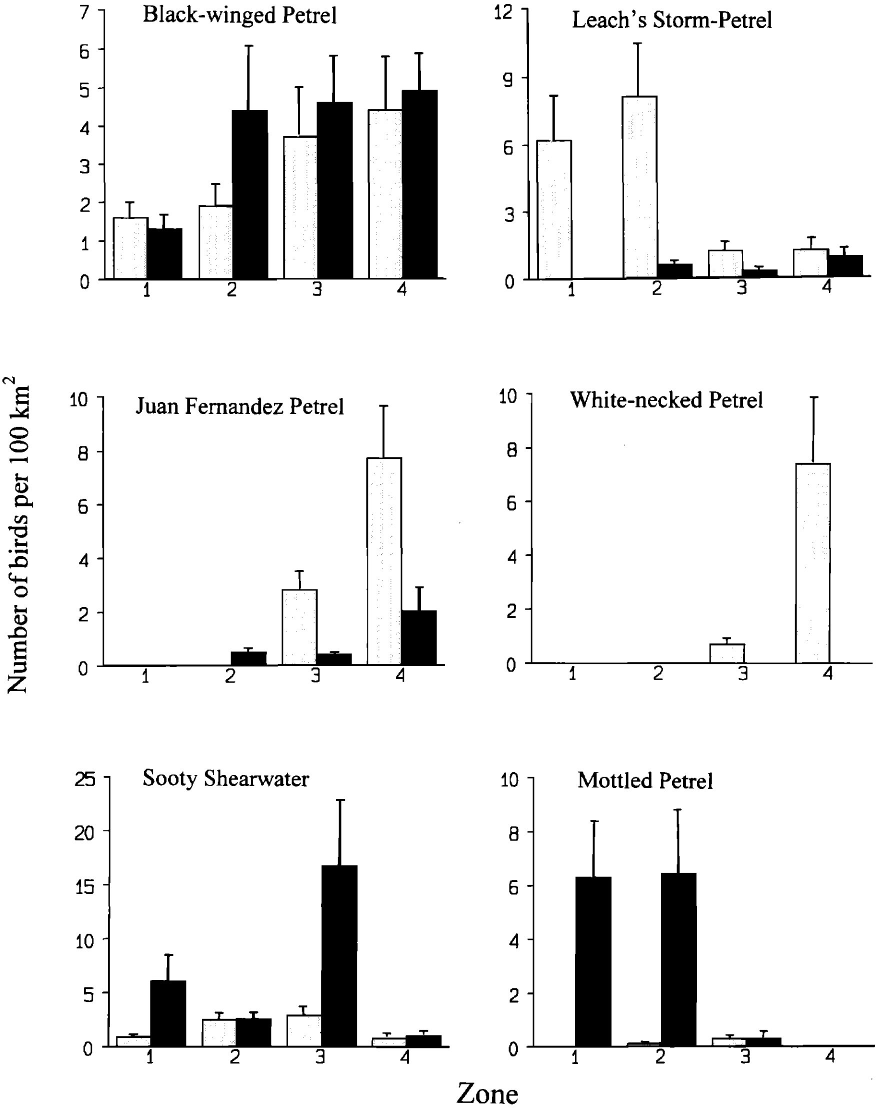

Figure 7. Densities (mean ± standard error) by season and zone of predominant species of seabirds not breeding on the Hawaiian Islands. Light bars, spring; dark bars, autumn. Lines above the bars are standard errors. See Figure 1 for location of zones, Figure 3 for sample sizes.

in each of the four zones (Sidak tests, all $P > 0.02$). Densities increased significantly with increase in water temperature and salinity and with decrease in thermocline depth (Table 6). The effect of thermocline depth was quadratic because of stabilization of density at depths >50 m (Figure 8).

During spring and autumn, 21% of 33 birds and 10% of 49, respectively, were foraging. Of the 12 foraging petrels, five were feeding in flocks over tuna; seven fed alone on the water.

Leach's Storm-Petrel. A very abundant breeder around the North Pacific (Crossin 1974, Ainley 1980); winters throughout the eastern tropical Pacific (Pitman 1986).

This was the fourth most abundant species during spring, when the only species in higher densities were those breeding on the main Hawaiian Islands (Table 4). Densities of these storm-petrels were significantly higher in spring than autumn. We observed them each month (Figure 6), although densities were highest during April. The POBSP also observed highest numbers in April.

A significant interaction between the effects of distance from Hawaii and season on density was due to a significant decrease in density with increase in distance during spring, compared to an insignificant effect of distance during autumn (Table 5, Figure 7). During spring, most of these petrels occurred in zones 1 and 2. A cubic effect of distance in spring ($P < 0.02$) resulted from stabilization of density in zones 1 and 2, followed by an abrupt decline in zone 3 and stabilization in 4. Densities increased with increase in wind speed (Table 5) and decrease in water temperature and salinity (Table 6).

Of the 41 birds recorded, 31% were feeding, all alone. In spring, flight direction was mostly northwest to north (75%).

Juan Fernandez Petrel. An estimated 1 million pairs breed on Mas Afuera Island, Chile; egg laying in late December and early January (Brooke 1987). Fledging is probably in May, if the chicks develop like those of the closely related Dark-rumped Petrel (Harris 1970).

This was the sixth most abundant species during spring (Table 4). Densities were higher in spring than in autumn because of very high densities in June (Figure 6; it was not abundant earlier in the spring). In contrast, the POBSP observed highest numbers in October and about half as many in June.

A significant interaction between the effects of distance from Hawaii and season on density was due to a significant increase in density with increase in distance in spring; during autumn the effect was insignificant (Table 5, Figure 7). In spring, densities were significantly higher in zone 4 than in other zones (Sidak tests, all $P < 0.02$, Figure 7). These petrels were not seen in zone 2 in spring or in zone 1 at either season.

Densities increased significantly with decrease in thermocline depth and slope (Table 6). A quadratic effect of water temperature was due to higher densities at temperatures of 26° to 27°C and lower densities at temperatures of 24° and 28°C (Figure 8). A quadratic effect of thermocline depth reflected a drop in density at depths greater than 50 m, followed by density stabilization at greater thermocline depths.

Of the 40 birds recorded, 43% were foraging. Of the 17 feeding birds, 15 (88%) were in flocks feeding over tuna, and two were scavenging squid.

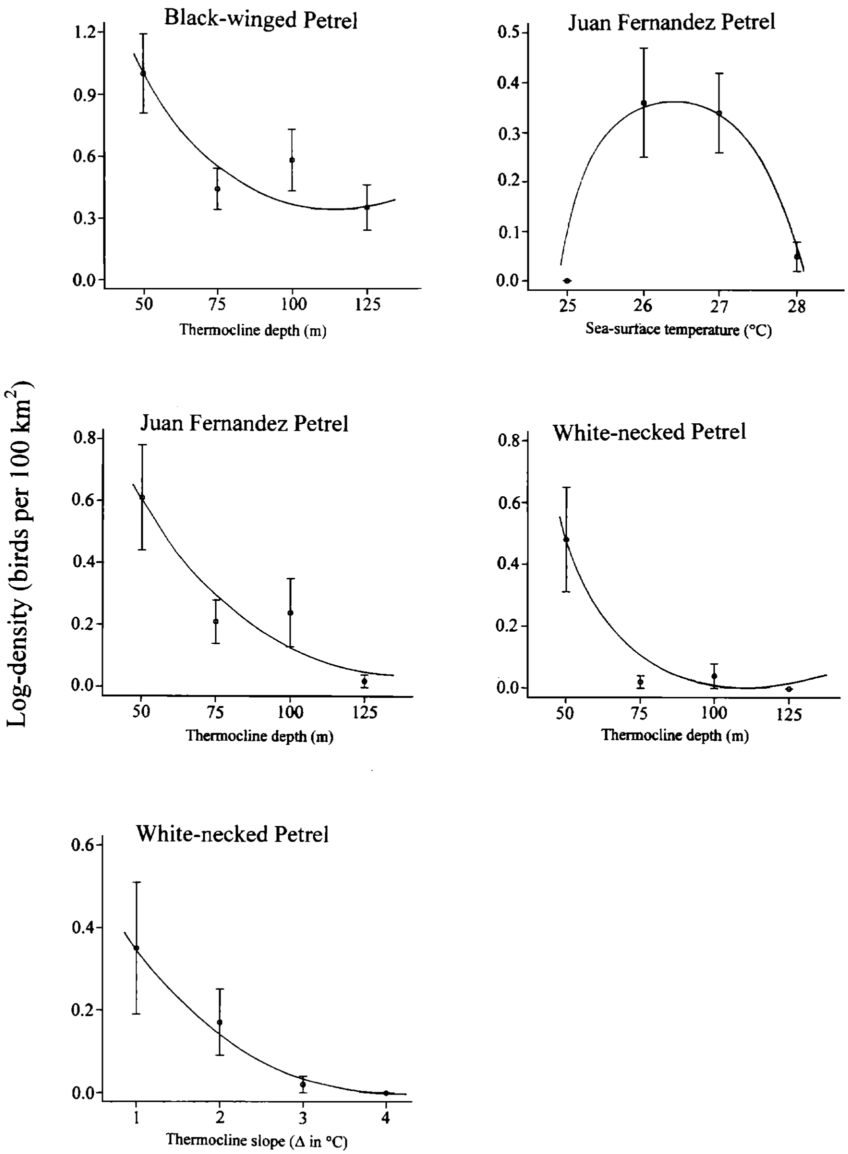

Figure 8. Results of multiple-regression analyses for density of seabirds (log-transformed) with oceanographic variables having a nonlinear effect. Shown are the means of seabird density (log-transformed) ± one standard error (vertical lines). Samples sizes for sea-surface temperature, from left to right, were 62, 89, 103, and 35, for thermocline depth 51, 109, 54, 75, for thermocline slope 40, 74, 114, 61.

White-necked Petrel. An estimated 50,000 pairs breed on Macauley Island, north of New Zealand (Tennyson et al. 1989), on a schedule similar to that of the Juan Fernandez Petrel (Falla et al. 1967, Brooke 1987). A major wintering area of these petrels is in the transition zone of the western North Pacific (Tanaka and Inaba 1977, Pyle and Eilerts 1986).

All sightings occurred during spring (only in June), when this was the eighth most abundant species (Table 4, Figure 6). We saw them only during La Niña in 1988 and in 1989 (13.1 and 0.4 birds per 100 km^2, respectively). We do not compare our results for this species with those of the POBSP because the latter sometimes combined counts of White-necked and Juan Fernandez petrels (King 1970; see Spear et al. 1992b for identification problems).

Densities increased with increase in distance from Hawaii (Table 5, Figure 7); most birds were seen in zone 4. This species' densities increased with decrease in thermocline depth and slope (Table 6). A quadratic effect of thermocline depth was due to a marked drop in density at depths >50 m, followed by density stabilization (Figure 8). Similarly, a quadratic effect of thermocline slope reflected a gradual drop to very a low density with increase in slope to 3°, followed by leveling of density at slopes of 4° (Figure 8). One of the 23 birds recorded was in a flock feeding over tuna.

Migrants: Predominant Species

Sooty Shearwater. Millions breed on islands off southern New Zealand and Chile; many winter in the North Pacific (Everett and Pitman 1993, Warham and Wilson 1982) and Peru Current (Murphy 1936). Eggs are laid from mid-November to early December; fledging is in late May and early June.

This was the seventh and second most abundant species during spring and autumn, respectively (Table 4); densities were significantly higher in autumn. We saw it in each month except June, with peak densities in November (Figure 6). The POBSP had highest counts in April and October.

The seasonal difference in abundance reflected densities in zones 1 and 3 being higher in spring than in autumn (Sidak tests, both $P < 0.002$, Figure 7). In both seasons, density differed insignificantly with distance from Hawaii, although densities in zone 3 were very high in autumn (Table 5, Figure 7). Density decreased with increase in wind speed and thermocline slope (Tables 4 and 5).

During spring and autumn, one of 85 birds and four of 21, respectively, were foraging. Of these, four were in flocks feeding over tuna and one appeared to be scavenging. Flight direction was mostly northwest in spring, and southwest in autumn.

Mottled Petrel. Breeds on islands south of New Zealand. Egg laying in December and January, fledging in May (Warham et al. 1977). Winters in subpolar waters of the North and South Pacific (reviewed in Bartle et al. 1993).

This was the fifth most abundant species during autumn, when densities were significantly higher than in spring (Table 4). We observed 55 in October and three in April (Figure 6). This chronology is similar to that seen by the POBSP, which logged the species in October (50 birds), November (2), December (2), April (10), and May (1). Our greatest numbers were on 16 October, when we estimated 15.9 birds per 100 km^2; peak counts by the POBSP were on 18 October.

Densities decreased with increase in distance from Hawaii in spring, but there was little effect of distance in autumn (Table 5, Figure 7). Nearly all birds were seen in zones 1 and 2, southeast of Hawaii Island, where densities were significantly higher than in zones 3 and 4. Densities decreased with increase in wind speed (Table 5) and water salinity (Table 6). We saw none feeding. Flight direction was southwest to southeast in autumn and north in spring.

Breeding Residents: Non-Predominant Species

Our counts of the following species were too low for distributional analysis (see Table 2). Numbers in parentheses are Harrison's (1990) estimated minima of pairs breeding on the northwestern and main Hawaiian Islands, respectively: Black-footed Albatross (36,260; 0); Christmas Shearwater (2245; 40), Harcourt's Storm-Petrel (<100 on Kauai; unknown number on Hawaii), White-tailed Tropicbird (0; 890), Red-tailed Tropicbird (8760; 92), Red-footed Booby (4540; 1100), Great Frigatebird (8115; 0), Brown Noddy (76,700; 16,005), and Black Noddy (6565; 615). The last we saw only in feeding flocks near Hawaii (see Feeding Flocks).

We identified two Harcourt's Storm-Petrels, one each at 18° 28′ N, 155° 47′ W, 50 km off Hawaii on 21 April 1990, the other at 18° 25′ N, 155° 27′ W, 65 km off Hawaii, on 18 April 1991. We distinguished the species from Leach's by its more square (less forked) tail, darker color, narrower band-shaped sharply demarcated white rump-patch. The difference from the V-shaped rump patch of the Leach's is best seen through a 20× binocular when the bird is flying directly away. In addition, Harcourt's usually fly with wings angled back towards the tail more so than do Leach's.

Nonbreeding Residents: Non-Predominant Species

Kermadec Petrel. Breeds in the South Pacific with a prolonged or year-round breeding season (Murphy and Pennoyer 1952). We observed it in June (4 birds) and November (4; for identification criteria see Herald and Murphy's petrels). The POBSP recorded 76 Kermadec Petrels; numbers were greatest from June to January. The POBSP recorded the light morph more often than the dark. In June, we saw three dark morphs and one intermediate; in November all were light. Kermadec Petrels were seen in zones 2 (2 birds) and 3 (6 birds). Three of the eight birds were in a feeding flock foraging over small tuna.

Herald Petrel. Breeds in the South Pacific with a prolonged or year-round breeding season (Murphy and Pennoyer 1952, Pyle et al. 1990). On the basis of molecular evidence and assortative mating between the light and dark morphs, Brooke and Rowe (1996) split them, recognizing the light-bellied morph as the Herald Petrel (*P. heraldica*), the dark-bellied birds as the Henderson Petrel (*P. atrata*), both distinct from the polymorphic form breeding on South Trinidad in the Atlantic Ocean and Round Island in the Indian Ocean (*P. arminjoniana*).

We saw three Herald Petrels at 16° 40′ N, 154° 08′ W, at 16° 53′ N, 154° 19′ W, and at 15° 56′ N, 154° 28′ W on 12 November 1990 (first two petrels) and 15 November 1991. The birds were 311, 281, and 364 km, respectively, from Hawaii. We distinguished them from the light-morph Kermadec Petrel by the lack of white primary shafts on the dorsal surface and the longer, wedge shaped tail, differing from the short, square tail of the Kermadec. These birds had indistinct M-patterns on the upper surface of the wings and back, a feature absent in the Kermadec Petrel. The Herald Petrels also had a slimmer appearance than the Kermadec. Relative to body size, they had longer, more slender wings (see Spear and Ainley 1998) and a less robust body.

The POBSP may have seen it but confused it with other similar species, and color morph was not reported. Gould (1971) stated that this species was an "uncommon, winter, nonbreeding visitor," but did not give identification criteria or report color. Finally, Amerson (1971) reported a specimen in the U.S. National Museum (USNM 543342) collected by R. B. Clapp, 14 March 1968, as it flew over Tern Island in the northwestern Hawaiian Islands (this is the only record listed by the AOU 1983), but did not report color. To further confound the problem, the USNM specimen was, as we write this, unavailable for examination because of museum remodeling.

Tahiti Petrel. Breeds on islands in the tropical South Pacific (Harrison 1983). The POBSP observed 12 birds identified as Tahiti or Phoenix (*P. alba*) petrels, and Gould (1971) reported one Tahiti Petrel but gave no identification criteria. The AOU (1983; Appendix A) lists the Tahiti under "sight records" based on information from W. B. King (no reference given) for a bird reported from Hawaiian waters in 1964, but identification criteria are not available.

The Tahiti and Phoenix petrels can be distinguished by bill size and pronounced differences in the wing profile of flying birds (Spear et al. 1992b). Many Tahiti Petrels also have a light rump contrasting with the darker back and tail, a feature absent in the Phoenix.

We recorded two sightings of the Tahiti Petrel on 5 November 1984, at 18° 25′ N, 159° 22′ W and 18° 37′ N, 159° 16′ W, 244 and 233 km from Hawaii, respectively. The first petrel was headed north, the second south. The interval between the two sightings was 1 hr, so there is a reasonable chance that these sightings were of the same bird.

Pycroft's Petrel. Breeds in relatively low numbers on islands off northern New Zealand (Dunned 1985). Egg laying in November and December, fledging in May.

This petrel had not been recorded away from the breeding grounds before our study (Spear et. al. 1992b, Howell et al. 1996). We collected a specimen on 2 May 1987 (Los Angeles County Museum [LACM] 103973) on the equator, 125° W, followed by four more between 1988 and 1991 (LACM 104342, USNM 597200, 597201, and 597202). A bird collected at 9° 00′ N, 140° 00′ W, was about 750 km from the study area. We collected no seabirds in Hawaiian waters. The POBSP recorded no Pycroft's Petrels despite extensive collecting in the central Pacific, but Gould and Piatt (1993) reported sightings (without identification criteria) from north of the Hawaiian

Islands in the transition zone (32° to 43° N) of the central North Pacific.

This petrel is regular in the eastern tropical Pacific (Spear et al. 1992b, Spear and Ainley unpubl. data). A possible reason for the lack of prior records is confusion of this species with Cook's (*P. cooki*) and Stejneger's petrels, which also occur in the eastern tropical Pacific (Spear et al. 1992b). Cook's Petrels occur between 125° and 150° W in autumn during migration to their New Zealand breeding grounds. We have not recorded them there during spring. At sea, the more extensively gray hind neck of Pycroft's Petrel separates it from Cook's (Howell et al. 1996); i.e., Cook's Petrels show appreciably more white in the "face." Pycroft's is smaller with shorter wings and longer tail, relative to body size, than Cook's (Spear et al. 1992b). The lighter gray crown and nape of Pycroft's Petrel distinguish it from Stejneger's Petrel, in which these features are sooty gray (see Spear et al. 1992b, Howell et al. 1996). Nevertheless, the last difference may not be apparent in poor light. This, in combination with the nearly identical body size and shape of Stejneger's and Pycroft's, make these two species the more likely of the trio to be confused in such conditions (Spear and S. N. G. Howell pers. obs.).

We sighted five Pycroft's Petrels, all in June and only during La Niña of 1988 and in 1989. On 19 June 1988, we saw three Pycroft's Petrels at 16° 45′N, 153° 22′W, at 16° 50′N, 153° 27′W, and at 16° 56′N, 153° 34′W, about 330 to 350 km from Hawaii. On 27 June 1989, we saw two at 15° 42′ N, 154° 17′ W and 17° 17′ N, 154° 43′ W, 361 and 230 km from Hawaii. One of the Pycroft's Petrels was feeding in a flock over small tuna.

In June 1986, we observed two Pycroft's/Cook's Petrels that, in retrospect, were probably Pycroft's. Pyle and Eilerts (1986) reported Cook's Petrels around the northwestern Hawaiian Islands that also may have been Pycroft's.

Pomarine Jaeger. These jaegers breed in the Arctic (Furness 1987) but are present in the eastern tropical Pacific throughout the year, most abundantly in winter (Spear and Ainley 1993).

Eight of nine birds were seen in spring, the other in autumn. We observed them in April (3 birds), May (5), and October (1). Spring birds comprised six adults (five light-phase, one dark) and two light-phase subadults; the autumn bird was a light-phase subadult. These birds were seen in zones 1 (2 birds), 2 (2), 3 (4), and 4 (1). Two were in a flock feeding over tuna. In spring, flight direction was northwest to northeast. The POBSP noted a similar pattern, and that most birds wintering in Hawaiian waters were within 50 km of land.

Parasitic Jaeger. Breeds in the Arctic (Furness 1987). Wintering chronology in the eastern tropical Pacific is similar to that of the Pomarine Jaeger (Spear and Ainley 1993, unpubl. data).

This species had not been recorded in Hawaiian waters. We recorded two, a dark-phase subadult (second or third year) on 27 June 1989, at 16° 36′N, 154° 32′ W, and a light-phase adult on 12 November 1991, at 16° 46′ N, 154° 13′ W (latter record in Pyle 1992). These were distinguished from the Long-tailed Jaeger (*S. longicaudus*) by the distinctive shape of the central rectrices. We saw three light-phase first-year jaegers on 2 May 1989, at 17° 40′ N, 156° 35′ W, that were either Parasitic or Long-tailed jaegers. All were in flocks feeding over tuna.

South Polar Skua. Breeds in Antarctica from December to April (Ainley et al. 1990) and winters in low numbers throughout the eastern tropical Pacific (Spear and Ainley 1993, unpubl. data).

The POBSP recorded eight skuas, listing them as the Great (*Catharacta skua*). Gould (1983) reported a South Polar Skua in Hawaiian waters at 24° 18′ N, 158° W, in November 1976 but gave no identification criteria. Thus the South Polar Skua was unconfirmed in Hawaiian waters before we sighted and photographed a flying bird on 7 October 1987 at 18° 05′ N, 155° 01′ W (see Pyle 1988). The identification was based on the extensive golden hackles on the nape, a feature absent in the Great Skua and Chilean Skua (*C. chilensis*; Harrison 1983, Furness 1987, Ainley and Spear pers. obs). We suspect that the skuas seen by the POBSP were South Polar Skuas. All skuas that we have identified in the eastern tropical Pacific have been of this species.

Migrants: Non-Predominant Species

Buller's Shearwater. Breeds in New Zealand and winters in the North Pacific (Falla et al. 1967, Wahl 1985). Egg laying in November and December, fledging in April.

We observed four on 13 November 1989 at 17° 54′ N, 154° 53′ W, two sitting on the water and two in a feeding flock. Five earlier records from Hawaiian waters include three sightings by the POBSP in March and April 1964–1965 and two on 3 November 1984 (Pyle and Eilerts 1986).

Murphy's Petrel. Breeds during summer in the subtropical South Pacific (Harrison 1983) and migrates to the North Pacific (Bartle et al. 1993). Four specimens have been collected in Hawaiian waters: Kure Atoll (7 October 1963), French Frigate Shoals (9 September 1966), Kauai (25 November 1986), and at sea 13 km off Oahu (29 October 1966; Gould and King 1967, Clapp 1974, R. L. Pyle; SIGHTINGS Data Base, Bishop Museum, Honolulu). On 27 June 1989 we saw another flying south at 16° 09′ N, 154° 24′ W. The bird lacked white patches on the underside of the forewings and white primary shafts, distinguishing it from Solander's (*P. solandri*) and Kermadec petrels, and was sooty gray with an indistinct M-pattern on the dorsal wings and back, distinguishing it from the uniform darker (nearly black like the Christmas Shearwater) Henderson Petrel (see Herald Petrel).

Stejneger's Petrel. Breeds on Mas Afuera Island, Chile (Brooke 1987) and winters in the northwestern Pacific (Tanaka et al. 1985). Egg laying in December and January (Brooke 1987), fledging in April and May.

This species was recorded on Lanai in 1914, when a partially eaten bird was found (Clapp 1984). Two possible sighting were made in Hawaiian waters in the 1990s (R. L. Pyle, SIGHTINGS Data Base, Bishop Museum, Honolulu). We saw seven: 5 November 1984 (1 bird), 16 October 1985 (3), 30 October 1985 (2), and 18 June 1986 (1), three in zone 2 and two each in zones 3 and 4. The bird seen in June was flying northwest; those in autumn were flying south to southeast. Identification was based on criteria in Spear et al. (1992b); see also Pycroft's Petrel.

Arctic Tern. Breeds in the Arctic and winters in the Antarctic. We observed seven, two on 21 April 1990 and five on 25 April 1991, dates consistent with observations by the POBSP. None were feeding. Flight direction was northward.

Feeding Flocks

We recorded 16 flocks of seabirds foraging over tuna (Figure 1); the fish were from 0.3 to about 0.6 m in length. Thirteen (81%) of the flocks were seen during spring. Numerically, they were dominated by Sooty Terns (62% of all individuals recorded) and Wedge-tailed Shearwaters (20%; Table 7), i.e., findings similar to those of the POBSP. The species composition of flocks was 92.5% breeding residents, 6.0% nonbreeding residents, and 1.4% migrants.

The ratio of the number of feeding birds to the distance the ship traveled (= survey effort for flocks) for each zone indicated a higher incidence of feeding in zone 4 than in 1, 2, or 3 (*G* tests, all $P < 0.001$, Table 7) and in zones 1 and 2 than in 3 (both $P < 0.010$). The ratio between zones 1 and 2 did not differ ($P = 0.4$). These differences resulted mainly from variation in numbers of Sooty Terns.

The mean number of species per flock differed insignificantly among zones (ANOVA, $P = 0.9$, Table 7), as did the ratio of number of species to survey effort ($G = 3.36$, df = 3, $P = 0.3$). However, of the 17 species recorded, the number recorded in zone 3 (15 species) was over twice that in zones 1 and 4 (7), and 1.7 times higher than in zone 2 (9 species). The differences were mainly due to the presence of four species of nonbreeding resident *Pterodroma* seen feeding only in zone 3. Low numbers of flocks preclude detailed comparisons.

DISCUSSION

Although our survey effort was not extensive (surveys covered 2128.4 km^2 of ocean area on 23 days over eight years), we show that many findings of the POBSP have changed little between 1964–1965 and 1984–1991. We report the first quantitative estimates for these waters of bird abundance based on a rigorous survey protocol and document the occurrence of several species unreported or unconfirmed from Hawaiian waters.

Species Status

Species predominant in southeastern Hawaiian waters and breeding on the Hawaiian Islands, were, in decreasing order of abundance, the Sooty Tern, Wedge-tailed Shearwater, Bulwer's Petrel, Dark-rumped Petrel, White Tern, and Newell's Shearwater. Predominant nonbreeding residents were, in decreasing numerical importance, the Black-winged Petrel, Leach's Storm-Petrel, Juan Fernandez Petrel, and White-necked Petrel. Predominant migrants comprised the Sooty Shearwater and Mottled Petrel.

Our records of the Tahiti, Herald, Pycroft's, and Stejneger's petrels, South Polar Skua, and Parasitic Jaeger, species we classify as nonbreeding residents, are the first records for Hawaiian waters, although a dead Stejneger's Petrel was found on Lanai in 1914 (Clapp 1984) and confirmation of the Herald Petrel collected on French Frigate Shoals in 1968 (USNM 543342;

Table 7 Number of Individuals, Number of Participant Species, and Species Composition of 16 Feeding Flocks, 1984–1991[a]

	Distance from Hawaii									
	Zone 1 (*n* = 2)		Zone 2 (*n* = 4)		Zone 3 (*n* = 7)		Zone 4 (*n* = 3)		All zones (*n* = 16)	
Individuals[b]	38.0 ± 7.1		38.3 ± 16.3		14.4 ± 7.7		101.0 ± 118.9		39.0 ± 50.5	
Species per flock[b]	4.5 ± 2.1		4.0 ± 2.6		4.6 ± 1.1		4.3 ± 2.5		4.4 ± 1.8	
Species composition[c]										
Breeding residents										
Dark-rumped Petrel	2	2.6	0	—	1	1.0	7	2.3	10	1.6
Bulwer's Petrel	0	—	2	1.3	1	1.0	0	—	3	0.5
Wedge-tailed Shearwater	20	26.3	38	25.5	35	35.0	33	10.9	126	20.1
Newell's Shearwater	0	—	19	12.8	1	1.0	0	—	20	3.2
Great Frigatebird	2	2.6	1	0.7	1	1.0	0	—	4	0.6
Sooty Tern	45	59.2	80	53.7	28	28.0	236	78.1	389	61.9
White Tern	3	3.9	1	0.7	8	8.0	15	5.0	27	4.3
Black Noddy	3	3.9	0	—	0	—	0	—	3	0.5
Nonbreeding residents										
Juan Fernandez Petrel	0	—	0	—	8	8.0	8	2.6	16	2.5
White-necked Petrel	0	—	0	—	4	4.0	0	—	4	0.6
Kermadec Petrel	0	—	0	—	4	4.0	0	—	4	0.6
Black-winged Petrel	0	—	0	—	1	1.0	0	—	1	0.2
Pycroft's Petrel	0	—	0	—	1	1.0	0	—	1	0.2
Pomarine Jaeger	1	1.3	2	1.3	1	1.0	1	0.3	5	0.8
Parasitic Jaeger	0	—	0	—	0	—	2	0.7	2	0.5
jaeger spp.	0	—	0	—	3	3.0	0	—	3	0.6
Migrants										
Buller's Shearwater	0	—	4	2.7	0	—	0	—	4	0.6
Sooty Shearwater	0	—	2	1.3	3	3.0	0	—	5	0.8
Total	76	99.8	149	100.0	100	100.0	302	99.9	628	100.1

[a] Zones given with respect to distance from Hawaii (see Figure 1). Values of *n* under zones denote number of feeding flocks.

[b] Mean plus or minus standard deviation.

[c] Number of individuals, followed by percentage of total number of all birds recorded in flocks.

Amerson 1971) awaits re-opening of the specimen collection at the museum. The six species were uncommon (Herald, Pycroft's, and Stejneger's petrels and Parasitic Jaeger) or rare (Tahiti Petrel and South Polar Skua) during our study.

Particularly noteworthy was the Pycroft's Petrel, which is not listed among species occurring in North America (AOU 1983), and the Black-winged Petrel, which was the fourth and fifth most abundant species (and most abundant *Pterodroma*) during spring and autumn, respectively—see King (1970) for similar findings—but which is considered by the AOU (1983) as "accidental" in Hawaiian waters.

During spring, species breeding on the Hawaiian Islands were significantly more abundant in southeastern Hawaiian waters than nonbreeding residents or migrants, and migrants were significantly less abundant than nonbreeding residents. In autumn, however, abundance differed little among the three groups because of decrease in densities of breeding species, stabilization in densities of nonbreeding residents, and increase in migrants. The decrease in breeders was most marked in the Bulwer's Petrel, which was the third most abundant species during spring but not recorded in autumn [see also King (1970) for similar results].

The marked increase in migrants during autumn was due to southward movement through Hawaiian waters of Sooty Shearwaters and Mottled Petrels. In spring, these birds migrate to the North Pacific from breeding sites near New Zealand, returning in autumn (Warham 1996). The lower number in the study area during spring was likely because these birds' migration routes follow the predominant wind systems (see Spear and Ainley, in press), which move clockwise in the North Pacific. EvidentYy most Sooty Shearwaters and Mottled Petrels migrate north along the western side of the Pacific (west of Hawaii) in spring, move from west to east to the northeastern Pacific in summer, and follow the southwesterly trade winds through the study area in autumn.

The concentration of Mottled Petrels in zones 1 and 2 off the eastern side of Hawaii Island was the highest that we encountered during extensive surveys in the eastern tropical Pacific. We suspect that the Hawaiian Islands disrupt the migration front moving from the north or northeast toward the southwest, deflecting birds southward around the islands. The combined data from our study and the POBSP for the Mottled Petrel suggest a very synchronous migration across Hawaiian waters during early to mid-October. The consistent flight direction of the Sooty Shearwater, Stejneger's Petrel, Arctic Tern, Leach's Storm-Petrel, and Pomarine Jaeger (the latter two classified as nonbreeding residents because of the presence of birds near the Hawaiian Islands in summer; King 1970) also indicate direct migration through Hawaiian waters, as do our observations of Buller's Shearwaters elsewhere in the eastern tropical Pacific (Spear and Ainley, unpubl. data).

Seabird Abundance in Relation to Oceanographic Factors

Lower sea-surface temperature, higher salinity, and a shallow, less stratified thermocline are evidence of mixing in the water column due to fronts (upwelling and/or divergences/convergences; reviewed in Owen 1981, Fiedler et al. 1991). These conditions increase primary productivity and the food of higher-order predators. It was not surprising, therefore, that densities of each predominant species except the White Tern were correlated with one or more of these variables and that most correlations indicated preference for more productive surface waters. The Wedge-tailed and Newell's shearwaters, Bulwer's and Black-winged petrels, Leach's Storm-Petrel, and Sooty Tern preferred low temperatures or high salinity, and the Dark-rumped, Black-winged, Juan Fernandez, White-necked, and Bulwer's petrels preferred shallow and/or less stratified thermoclines. Consistent with these findings, we saw the White-necked and Pycroft's petrels in Hawaiian waters only in 1989 and especially 1988. Oceanographically, La Niña 1988 was a year of unusual conditions in the study area, with the coolest surface water, shallowest thermocline, and most mixed thermal structure encountered during the 8-year study (Ainley and Spear, unpubl. data).

The high densities of seabirds during spring in the southernmost region (zone 4) were due mostly to the abundance of "tuna-birds," the Sooty Tern, Wedge-tailed Shearwater, and Juan Fernandez and White-necked petrels (see King 1970 for similar results). High densities of these species in these waters in spring were consistent with the significantly higher number of feeding flocks foraging on prey forced to the surface by tunas. This finding was probably related to the proximity of these waters to the enriched surface layer along the northern boundary of the east-flowing Equatorial Countercurrent (Wyrtki 1966, Fiedler et al. 1991, Ballance et al. 1997). During May and June this current reaches its northern apex, with divergence at about 10° N, where surface waters escape and move north into the west-flowing North Equatorial Current (Wyrtki 1966). Consistent with this idea, Murphy and Shomura (1972) found that the Equatorial Countercurrent has higher densities of schooling surface-feeding smaller tunas than the North Equatorial Current. Other studies also have noted the importance of the Equatorial Countercurrent as a seabird feeding area (Gould 1974, King 1974, Au and Pitman 1986, Spear et al. 1995, Ballance et. al. 1997).

Among breeding species, the Sooty Tern, Wedge-tailed Shearwater, and Bulwer's Petrel *decreased* significantly in abundance with increase in distance from Hawaii during the breeding season in spring (see King 1970 for similar results). In contrast, in autumn, densities of the former two *increased* with distance from Hawaii, and the Bulwer's Petrel disappeared. During autumn, a similar pattern of increased density with distance from Hawaii was also seen in the Dark-rumped Petrel (during spring, the distribution of this species was bimodal). These results indicate that in autumn feeding conditions also were better in the southern part of the study area and, in turn, suggest that, to facilitate breeding, some species may have been constrained to feed in less productive waters near the Hawaiian Islands.

Additional evidence indicating better food supply in the more southern waters was the density increase with increase in distance from Hawaii during spring in the Black-winged, Juan Fernandez, and White-necked petrels (nonbreeding residents that nest in the South Pacific; see King 1970 for similar results), and Newell's Shearwater, a breeding species. A likely explanation for use by the shearwater of more southern waters during the breeding season is that it is a very fast flier, capable of breeding on Hawaii while foraging at greater distances (Spear et al. 1995, Spear and Ainley 1997).

Thus, of the 10 predominant species (excluding migrants), the White Tern was the only breeder with no distributional patterns relative to island distance. Similarly, the Leach's Storm-Petrel, with densities decreasing with increase in distance from Hawaii in spring, was the only nonbreeder not conforming to the idea that unconstrained species should forage in more southern waters. The inshore distribution of the Leach's Storm-Petrel (a planktivore) in spring, and moderately high incidence of feeding over tuna by seabirds in waters near Hawaii (zones 1 and 2), is consistent with an "island effect" (Murphy and Shomura 1972). These authors found that Skipjack Tuna (*Katsuwonus pelamis*; a smaller, surface-feeding tuna), as well as smaller Yellowfin Tuna (*Thunnus albacares*), were abundant just offshore of mid-Pacific archipelagos.

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LITERATURE CITED

Ainley, D. G. 1980. Geographic variation in Leach's Storm-Petrel. Auk 97:837–853.

Ainley, D. G., Ribic, C. A., and Wood, R. C. 1990. A demographic study of the South Polar Skua *Catharacta maccormicki* at Cape Crozier. J. Anim. Ecol. 59:1–20.

Ainley, D. G., Podolsky, G. R., DeForest, L., and Spencer, G. 1995. The ecology of Newell's Shearwater and Dark-rumped Petrel on the island of Kauai. Final Rep., Task 2, Seabird Ecology Study. Electric Power Res. Inst., 3412 Hillview Ave., Palo Alto, CA 94304.

Amerson, A. B. 1971. The natural history of the French Frigate Shoals, Northwestern Hawaiian Islands. Atoll Res. Bull. 150:1–383.

American Ornithologists' Union. 1983. Check-list of North American Birds, 6th ed. Am. Ornithol. Union, Washington, D.C.

Au, D. W. K., and Pitman, R. L. 1986. Seabird interactions with dolphins and tunas in the eastern tropical Pacific. Condor 88:304–317.

Ballance, L. T., Pitman, R. L., and Reilly, S. B. 1997. Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. Ecology 78:1502–1518.

Bartle, J. A., Hu, D., Stahl, J. C., Pyle, P., Simons, T. R., and Woodby, D. 1993. Status and ecology of gadfly petrels in the temperate North Pacific, in The Status, Ecology, and Conservation of Marine Birds of the North Pacific (K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey, eds.), pp. 93–100. Spec. Publ. Can. Wildlife Serv., Ottawa.

Berger, A. J. 1972. Hawaiian Birdlife. Univ. of Hawaii Press, Honolulu.

Brooke, M. De L. 1987. Population estimates and breeding biology of the petrels *Pterodroma externa* and *P. longirostris* on Isla Alejandro Selkirk, Juan Fernandez Archipelago. Condor 89:581–586.

Brooke, M. De L., and Rowe, G. 1996. Behvioural and molecular evidence for specific status of light and dark morphs of the Herald Petrel *Pterodroma heraldica*. Ibis 138:420–432.

Clapp, R. B. 1974. Specimens of three species of *Pterodroma* from the North Pacific. Ardea 62:246–247.

Clapp, R. B. 1984. First records of Juan Fernandez (*Pterodroma e. externa*) and Stejneger's (*Pterodroma longirostris*) Petrels from Hawaii. 'Elepaio 44:97–98.

Crossin, R. S. 1974. The storm-petrels (Hydrobatidae), in Pelagic studies of seabirds in the central and eastern Pacific Ocean (W. B. King, ed.), pp. 154–203. Smithsonian Contr. Zool. 158.

Dunnet, G. M. 1985. Pycroft's Petrel in the breeding season at Hen and Chickens Islands. Notornis 32:5–21.

Erickson, R. A., and Terrill, S. B. 1996. Nineteenth report of the California Bird Records Committee: 1993 records. W. Birds 27:93–126.

Everett, W. T., and Pitman, R. L. 1993. Status and conservation of shearwaters in the North Pacific, in The Status, Ecology, and Conservation of Marine Birds of the North Pacific, (K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey, eds.), pp. 93–100. Spec. Publ. Can. Wildlife Serv., Ottawa.

Falla, R. A., Sibson, R. B., and Turbot, E. G. 1967. Birds of New Zealand. Houghton Mifflin, Boston.

Fiedler, P. C., Philbrick, V., and Chavez, F. P. 1991. Oceanic upwelling and productivity in the eastern tropical Pacific. Limnol. Oceanogr. 36:1834–1850.

Furness, R. W. 1987. The Skuas. T. & A. D. Poyser, Calton, England.

Gould, P. J. 1971. Interactions of seabirds over the open ocean. Ph.D. dissertation, Univ. Arizona, Tucson.

Gould, P. J. 1974. Sooty Tern (*Sterna fuscata*), in Pelagic studies of seabirds in the central and eastern Pacific Ocean (W. B. King, ed.), pp. 6–52. Smithsonian Contr. Zool. 158.

Gould, P. J. 1983. Seabirds between Alaska and Hawaii. Condor 85:286–291.

Gould, P. J., and King, W. B. 1967. Records of four species of *Pterodroma* from the central North Pacific. Auk 84:591–594.

Gould, P. J., and Piatt, J. F. 1993. Seabirds of the central North Pacific, in The Status, Ecology, and Conservation of Marine Birds of the North Pacific, (K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey, eds.), pp. 27–38. Spec. Publ. Can. Wildlife Serv., Ottawa.

Harris, M. P. 1970. The biology of an endangered species, the Dark-rumped Petrel (*Pterodroma phaeopygia*), in the Galapagos Islands. Condor 72:76–84.

Harrison, C. S. 1990. Seabirds of Hawaii: Natural History and Conservation. Cornell Univ. Press, Ithaca, N.Y.

Harrison, P. 1983. Seabirds: An Identification Guide. Houghton Mifflin, Boston.

Heinemann, D. 1981. A range finder for pelagic bird censusing. J. Wildlife Mgmt. 45:489–493.

Howell, S. N. G., Webb, S., and Spear, L. B. 1996. Identification at sea of Cook's, de Filippi's, and Pycroft's Petrels. W. Birds 27:57–64.

King, W. B. 1970. Pelagic studies of seabirds in the central and eastern Pacific Ocean. Smithsonian Contr. Zool. 158.

King, W. B. 1974. Wedge-tailed Shearwater (*Puffinus pacificus*), in The Status, Ecology, and Conservation of Marine Birds of the North Pacific (K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey, eds.), pp. 53–95. Spec. Publ. Can. Wildlife Serv., Ottawa.

Kleinbaum, D. G., Kupper, L. L., and Muller, K. E. 1988. Applied Regression Analysis and Other Multivariable Methods. PWS-KENT Publ., Boston.

Miles, D. H. 1986. White Terns breeding on Oahu, Hawaii. 'Elepaio 46:171–175.

Murphy, R. C. 1936. Oceanic Birds of South America. Macmillan, New York.

Murphy, R. C., and Pennoyer, J. M. 1952. Large petrels of the genus *Pterodroma.* Am. Mus. Novitates 1580:1–42.

Murphy, G. L., and Shomura, R. S. 1972. Pre-exploitation abundance of tunas in the equatorial central Pacific. Fish. Bull. 70:875–913.

Owen, R. W. 1981. Fronts and eddies in the sea: Mechanisms, interactions, and biological effects, in Analysis of Marine Ecosystems (R. Longhurst, ed.), pp. 197–233. Academic Press, London.

Pitman, R. L. 1986. Atlas of seabird distribution and relative abundance in the eastern tropical Pacific. Admin. Rep. LJ-86-02C, Southwest Fisheries Center, P. O. Box 271, La Jolla, CA 92038.

Pyle, P., and Eilerts, B. 1986. Pelagic seabird observations from northwest Hawaiian Island waters. 'Elepaio 46:181–183.

Pyle, P., Spear, L. B., and Engbring, J. 1990. A previously unreported population of Herald Petrel on Ta'u Island, American Samoa. Colonial Waterbirds 13:136–138.

Pyle, R. L. 1988. Checklist of the birds of Hawaii—1988. 'Elepaio 48:95–106.

Pyle, R. L. 1992. Checklist of the birds of Hawaii—1992. 'Elepaio 52:53–62.

SAS Institute, Inc. 1985. SAS user's guide: Statistics, 5th ed. SAS Inst., Inc., Cary, N.C.

Seber, G. A. F. 1977. Linear Regression Analysis. Wiley, New York.

Simons, T. R. 1985. Biology and behavior of the endangered Hawaiian Dark-rumped Petrel. Condor 87:229–246.

Spear, L. B., and Ainley, D. G. 1993. Kleptoparasitism by Kermadec Petrels, jaegers, and skuas in the eastern tropical Pacific: Evidence of mimicry by two species of *Pterodroma*. Auk 110:222–233.

Spear, L. B., and Ainley, D. G. 1997. Flight speed of seabirds in relation to wind speed and direction. Ibis 139:234–251.

Spear, L. B., and Ainley, D. G. In press. Migration routes of Sooty Shearwaters in the Pacific Ocean. Condor.

Spear, L. B., and Ainley, D. G. 1998. Morphological differences relative to ecological segregation in petrels (family: Procellariidae) of the Southern Ocean and tropical Pacific. Auk 115:1017–1033.

Spear, L. B., Nur, N., and Ainley, D. G. 1992a. Estimating absolute densities of flying seabirds using analyses of relative movement. Auk 109:385–389.

Spear, L. B., Howell, S. N. G., and Ainley, D. G. 1992b. Notes on the at-sea identification of some Pacific gadfly petrels (genus: *Pterodroma*). Colonial Waterbirds 15:202–218.

Spear, L. B., Ainley, D. G., Nur, N., and Howell, S. N. G. 1995. Population size and factors affecting at-sea distributions of four endangered procellariids in the tropical Pacific. Condor 97:613–638.

STATA Corporation. 1995. STATA reference manual: Release 3.1, 6th ed. Stata Corp., College Station, TX.

Tanaka, Y., and Inaba, F. 1977. The distribution and migration of the White-necked Petrel, *Pterodroma externa cervicalis*, in the west area of the North Pacific and Japanese waters. J. Yamashina Inst. Ornithol. 13:61–68.

Tanaka, Y., Kaneko, Y., and Sato, S. 1985. Distribution and migration of smaller petrels of the genus *Pterodroma* in the northwest Pacific. J. Yamashina Inst. Ornithol. 17:23–31.

Tennyson, A., Taylor, G., and Scofield, P. 1989. Another visit to Macauley Island. Ornithol. Soc. N. Z. News 52:4–5.

Wahl, T. R. 1985. The distribution of Buller's Shearwater *Puffinus bulleri* in the North Pacific Ocean. Notornis 32:109–117

Warham, J. 1990. The Petrels: Their Ecology and Breeding Systems. Academic Press, London.

Warham, J. 1996. The Behaviour, Population Biology and Physiology of the Petrels. Academic Press, London.

Warham, J., and Wilson, G. J. 1982. The size of the Sooty Shearwater population at the Snares Islands, New Zealand. Notornis 29:23–30.

Warham, J., Kelley, B. R., and Wilson, G. J. 1977. Breeding of the Mottled Petrel. Auk 94:1–17.

Wyrtki, K. 1966. Oceanography of the eastern equatorial Pacific Ocean. Annu. Rev. Oceanogr. Mar. Biol. 4:33–68.

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