POPULATION SIZE AND FACTORS AFFECTING AT-SEA DISTRIBUTIONS OF FOUR ENDANGERED PROCELLARIIDS IN THE TROPICAL PACIFIC[1]

LARRY B. SPEAR, DAVID G. AINLEY, NADAV NUR AND STEVE N. G. HOWELL
Point Reyes Bird Observatory, Stinson Beach, CA 94970

Abstract. We used at-sea censuses to quantify pelagic behavior, relationships between density and habitat variables, and to estimate population size of four taxa of procellariids in the eastern tropical Pacific: subspecies of *Puffinus auricularis* (Townsend's Shearwater, *P. a. auricularis,* and Newell's Shearwater, *P. a. newelli*) and subspecies of *Pterodroma phaeopygia* (Galapagos Dark-rumped Petrel, *Pt. p. phaeopygia,* and Hawaiian Dark-rumped Petrel, *Pt. p. sandwichensis*). All are considered threatened or endangered with extinction.

Birds commuting from colonies ranged 650 km (*P. a. auricularis*) to 1,300 km (*P. a. newelli* and *Pt. p. sandwichensis*). *P. a. auricularis* foraged at upwelling fronts in the Costa Rica Current over the continental slope of Mexico, while *P. a. newelli* preferred ocean fronts in the Equatorial Counter Current. Unlike the shearwaters, petrel densities correlated most strongly with distance to the colony and wind speed, although the two petrels each foraged in distinctly different current systems. Foraging behavior of the shearwaters was energy demanding, but they frequented highly productive feeding areas and rested often. The petrels appeared to forage more opportunistically and conserved energy by flying more efficiently. Foraging behavior was consistent with wing morphology of each group.

Pelagic population estimates (adults and subadults grouped) were 46,000 *P. a. auricularis,* confidence interval (CI) = 18,000 to 89,000; 84,000 *P. a. newelli,* CI = 57,000 to 115,000; 19,000 *Pt. p. sandwichensis,* CI = 11,000 to 34,000; and 88,000 *Pt. p. phaeopygia,* CI = 54,000 to 130,000. On the basis of breeder to non-breeder ratios in these and closely related species, we estimated breeding populations of 10,600, 18,000–19,000, 3,750–4,500, and 20,000 pairs, respectively. Calculation of minimal and maximum estimates indicated breeding populations larger than previously thought for *P. a. auricularis, P. a. newelli,* and *Pt. p. sandwichensis,* but similar for *Pt. p. phaeopygia.*

Key words: Townsend's and Newell's Shearwater; Dark-rumped Petrel; pelagic; population size; habitat; foraging; flight direction.

INTRODUCTION

Breeding locations of the Townsend's Shearwater (*Puffinus a. auricularis*), Newell's Shearwater (*P. a. newelli*), and two subspecies of Dark-rumped Petrel (Galapagos Island form: *Pterodroma p. phaeopygia* and Hawaiian Island form: *Pt. p. sandwichensis*) each consist of a single archipelago in the eastern and central Pacific (ECP). Locating colonies, and estimating population size of these birds is problematic because they are

active in their colonies at night only, and nest in widely spaced (20–100 m), deep (2–3 m) burrows in densely vegetated, steep terrain where censuses are extremely difficult (Harrison 1990, Ainley et al. 1995; see also Brooke 1990). Our best population estimates have consisted of extrapolation of burrow density over areas thought to include the colony boundaries. Even these estimates are tenuous because colony boundaries are usually uncertain and proportion of burrows that are active is difficult to assess.

P. a. newelli breed on the main Hawaiian Islands. Unknown numbers breed on Hawaii, and an estimated 6,000 pairs on Kauai (Harrison

1990), but colonies are being discovered regularly on that island (Ainley et al. 1995). They may breed on Oahu, Maui, Lanai, and Molokai (Harrison 1990). *P. a. auricularis* have bred on the three Revillagigedo Islands, Mexico (Islas Socorro, Clarion, and San Benedicto), but systematic censuses have not been conducted (reviewed in Collar et al. 1992). Jehl (1982) estimated 1,000 breeding on the south side of Isla Socorro based on calling birds heard at night; another colony was recently found on the north side (H. Walter and L. F. Baptista, pers. comm.).

Most recent population estimates for breeding *Pt. p. phaeopygia* ranged from 7,500 to 35,000 pairs (Coulter 1984, Tomkins and Milne 1991), although not all colonies have been found (Tomkins and Milne 1991). The breeding population of *Pt. p. sandwichensis* was estimated at 400–600 pairs on Maui (Harrison 1990). Breeding is confirmed on Hawaii, Kauai, and Lanai, but no censuses have been attempted (Harrison 1990). They may breed on Molokai.

Each taxon suffers from predation by introduced mammals (Coulter 1984, Harrison 1990, Howell and Webb 1990, Ainley et al. 1995). The petrels are listed as "endangered" (U.S. Dept. of Interior 1980), and the shearwaters as "threatened" (Collar et al. 1992, Ehrlich et al. 1992). Therefore, monitoring their populations is important. Because of difficulty at colonies, we used pelagic censuses to estimate densities, areal extent in the ECP, and population size including both breeders and nonbreeders. Nonbreeding population size is an important indicator of the status of the entire population (Klomp and Furness 1992). Similar efforts were made for the Barau's Petrel (*Pt. baraui*; Stahl and Bartle 1991) and Marbled Murrelet (*Brachyramphus marmoratus*; Piatt and Ford 1993), two other rare or threatened species difficult to census on the breeding grounds.

We also studied oceanographic affinities of each taxon. The pelagic range of *P. a. auricularis* is well known (Pitman 1986), but those of the other three taxa are not (see King and Gould 1967, Pitman 1986, Bartle et al. 1993). Furthermore, little information is available on oceanographic features preferred by these birds, either large scale (i.e., current systems or water-masses) or small scale (e.g., upwelling features, oceanic frontal zones; see Hunt and Schneider 1987, for definition of oceanographic scale). Feeding areas of each taxon have been indicated by casual observations of feeding birds and concentrations in oceanic regions. *P. a. newelli* are known to concentrate in two pelagic zones during the breeding season (King and Gould 1967), one within several hundred km of the Hawaiian Islands, and the other south of 10°N. *P. a. auricularis* have been seen feeding in coastal waters off Mexico (Au and Pitman 1986); *Pt. p. sandwichensis* showed a tendency to concentrate north of the main Hawaiian Islands at 25°N (King 1970); and *Pt. p. phaeopygia* concentrate primarily within 500 km of the Galapagos Islands (Pitman 1986). To examine the foraging range of breeding birds and provide additional information on important feeding areas we examined foraging incidence and flight direction relative to colony location of birds seen in different areas of the ranges of each taxon.

METHODS

SPECIES IDENTIFICATION

Field identification criteria for separating *P. a. auricularis* from *P. a. newelli* are given in Howell et al. (1994). We were unable to distinguish *Pt. p. phaeopygia* from *Pt. p. sandwichensis*, although data presented herein indicate a hiatus in ranges.

BREEDING CHRONOLOGY AND DEMOGRAPHY

Egg laying of *P. a. auricularis* occurs January to March, fledging in late-May to late-July (Jehl 1982). Egg laying of *P. a. newelli* on Kauai occurs late-May to early-June; young fledge in October to early-November (Berger 1972, Harrison 1990). Breeding by *Pt. p. phaeopygia* occurs throughout the year; chronology varies between islands (Cruz and Cruz 1990, Tomkins and Milne 1991). Egg laying of *Pt. p. sandwichensis* on Maui is in early-May, and the young fledge in the latter half of November (Berger 1972, Harrison 1990). On Kauai, fledging is two to three weeks later (Ainley et al. 1995).

We used information from two studies of species closely related (or the same) to those we studied to estimate proportions of breeders vs. nonbreeders. These included the Manx Shearwater (*P. puffinus*; sibling species of *P. auricularis*) studied by Brooke (1990), and *Pt. p. sandwichensis*, studied by Simons (1984). These authors assumed population stability, although this assumption was probably violated during our

study because of decreasing numbers of some, or all four, taxa (see Introduction).

Both *P. puffinus* and *Pt. p. sandwichensis* first bred on average at six years. Annual survival rate was 91% for *P. puffinus* and 93% for *Pt. p. sandwichensis*. We estimate 72% and 83%, respectively, of adults attempt breeding annually on the basis of observations of established adults not-observed breeding in one year but observed subsequently, and allowing for skipped breeders that died before being seen again. Survival rate of fledglings to breeding age was 33% in *P. puffinus* and 27% in *Pt. p. sandwichensis*. Hence, the proportion of pelagic populations estimated to be six years of age (i.e., breeders) was, for the shearwaters, 64% (spring; see model in Ainley et al. 1995) and 56% (autumn; allowing for emergence of fledglings; age-class = 0 yrs); and for the petrels, 56% and 48%. Allowing for incidence of nonbreeding by established individuals, an estimated 46% (spring) and 40% (autumn) of both shearwaters and petrels would have bred each year.

OCEANOGRAPHIC CHARACTERISTICS
OF THE STUDY AREA

Circulation of surface waters in the ECP is dominated by three current systems, the Equatorial Counter Current (ECC), North Equatorial Current (NEC) and South Equatorial Current (SEC; Fig. 1, from Wyrtki 1966). The ECC, which flows west to east, varies seasonally in strength and location. During the seasons that we censused birds in the ECP (late-March through June, and October through December) it is strong and lies at about 4°N to 10°N (Wyrtki 1966, p. 38). The NEC and SEC lie north and south, respectively, of the ECC, and flow east to west. The NEC extends to 25°N, and the SEC to 20°S, although the latter is strongest between 4°N and 10°S (Wyrtki 1966). Of the three current systems, the SEC has the lowest surface temperature and highest salinity; ECC the highest surface temperature and lowest salinity; and the NEC intermediate values. Temperature, salinity, thermocline depth and strength (definitions below; Censuses and Monitoring of Physical Variables), increase from east to west, and the reverse for primary productivity. The latter is highest east of 100°W at the Equator, and east of 115°W on the northern border of the ECC (Fiedler and Philbrick 1991).

Another important feature of the ECP is the Intertropical Convergence Zone, characterized by squalls, high winds and heavy rainfall (Philander 1989). This zone is often located at the northern boundary of the ECC (Wyrtki 1966).

During the study, El Niño occurred in 1986–1987 and 1991–1992. La Niña occurred in 1988. Although distributions of some seabird taxa changed during El Niño (Ribic et al. 1990), preliminary analyses indicated an insignificant effect by year on distributions of the four taxa we studied (ANOVAs, $P > 0.2$).

CENSUSES AND MONITORING OF
PHYSICAL HABITAT VARIABLES

Our data are from 22 cruises, 1980–1994 (although only one of the cruises was in 1980, the remaining 21 in 1984–1994), in the ECP between 30°N and 20°S, and between 170°W and the Americas. This area includes the entire range of *P. a. auricularis* (Jehl 1982, Pitman 1986, this study), but the ranges of *P. a. newelli* and *Pt. phaeopygia* extend beyond it. *P. a. newelli* occur to about 300 km north of Kauai during the breeding season, but are absent from waters within several hundred km of the Hawaiian Islands in autumn and winter (King and Gould 1967, Gould 1983). In the central Pacific, *Pt. phaeopygia* were most regularly sighted north of the main Hawaiian Islands at the northern boundary of the study area (25°N latitude; King 1970) during spring and summer, although they were absent from the vicinity of the islands during autumn and winter (see also Gould 1983). They have been sighted rarely in the North Pacific to 50°N (reviewed in Pyle et al. 1993).

In the South Pacific, *P. a. newelli* appearing birds have been sighted regularly near the Marquesas, Tuamotu and Samoan islands (Pitman 1986; R. Seitre, pers. comm; Spear et al., this study), and a specimen was obtained on Tutuila, American Samoa (Grant et al. 1994). They have also occurred southwest of Hawaii to the Marianas, Johnston Atoll, and Wake Island (one bird at each location; King 1967). One *Pt. phaeopygia* was recorded near the Moluccas (King 1967). There are no confirmed sightings of either species south of our study area (Murphy 1936; PRBO, unpubl. data).

With two or three persons observing simultaneously, we conducted continuous strip-transects from dawn to dusk while the ship was underway. Each transect lasted one half hour, except those terminated when the ship arrived on station. Birds seen within a 90° quadrant on one

side of the ship were counted. Strip-widths were 250–600 m, varying according to height above sea level of the observation platform. The latter was 3–16 m. Strip-width was calibrated after Heinemann (1981), periodically validated with ship's radar. Sighting birds in the outer area of the 600 m quadrant zone was not a problem because of our height above the sea, and because we scanned with binoculars the outer area every 30 to 45 sec per observer; we also scanned quadrants of lesser width. By noting ship speed (km per hr), we calculated surface area of ocean censused during each transect, which averaged 7.45 km², SD = ±1.23 km², n = 11,070 for 30 min transects. We observed for 5,825.3 hrs within the ECP study area and censused 85,933 km² of ocean, 44,586 km² in spring and 41,347 km² in autumn (seasons defined in section above).

We adjusted observed numbers to correct for bird flux; i.e., the effect of bird movement (Spear et al. 1992). For each sighting we noted behavior: resting on the water, feeding (including scavenging) or circling over a potential food source, or directional flight. For the latter behavior, we noted flight direction to the nearest 10°.

Data also recorded for each transect were ship position and course, water depth (m), sea-surface temperature (°C) and salinity (ppt), thermocline depth (m) and "strength" (see below), wind and wave direction (nearest 10°), wind speed (km per hr), wave height (nearest 0.3 m), and cloud cover (in eight subdivisions, or oktas). Thermocline depth and strength, indices of mixing in the water column, were monitored every four to six hours with expendable bathythermographs (XBTs). Thermocline depth refers to the point where the warm surface layer meets cooler water below; i.e., the shallowest inflection point as determined from XBT printouts plotting temperature as a function of depth. Exceptions occurred when there was no inflection point, in which case the thermocline is at the ocean surface, or the XBT profiles showed more than one inflection. In the latter case we assumed that the thermocline began at the depth of the strongest inflection. We measured thermocline strength as the temperature difference (nearest 0.1°C) between the thermocline to a point 20 m below the thermocline. A region with strong upwelling or a strong front had a shallow, weak thermocline, and the reverse where little mixing occurred.

Habitat variables also included three geographic variables: (1) "colony distance," the distance from the nearest known colony of a given taxon to the central point in a given "pelagic block" (see Statistical Analyses; Fig. 1); and for *P. a. auricularis* (a more coastal subspecies), (2) ocean depth and (3) "distance from the continental slope break," i.e., the distance from the 200 m isobath to the central point of a given block.

STATISTICAL ANALYSES

RELATIONSHIP BETWEEN DENSITY AND PHYSICAL HABITAT VARIABLES

We used Principal Component analysis (CRC; Computing Resource Center 1992) to identify important habitat variables and to delineate habitat differences among the four taxa. We also used Sidak multiple comparison (CRC 1992), an improved version of the Bonferroni test (SAS Institute, Inc. 1985), to statistically compare each habitat variable among taxa.

We divided most of the study area into a grid of 5° latitude × 5° longitude blocks (Fig. 1). Exceptions included blocks lying along the American coasts and those lying between 4°N and 10°N, and between the Equator and 4°N. The former were given dimensions of 5° × 6° to conform to boundaries of the ECC, the latter dimensions of 5° × 4°.

Because *P. a. auricularis* were concentrated over the continental slope off Mexico, and were sparse in southern offshore blocks, we designated three smaller blocks in the nearshore area. Each included an area from the 200 m isobath (i.e., the top of the continental slope) to 100 km offshore, which included the entire continental slope within the pelagic range of this shearwater. These blocks did not include waters inshore of the 200 m contour because we observed no *P. a. auricularis* there. In two cases, we combined blocks (two each) in the southern offshore area because of low *P. a. auricularis* density.

Densities for each block were calculated, by season, using the observed number of birds (corrected for flux) divided by the ocean area (km²) censused within the respective block. We do not report densities for blocks where less than 75 km² was censused in a given season because coverage less than 75 km² often led to anomalous densities, either zero or very high.

We used univariate and multivariate regression (CRC 1992) to model bird density as related to habitat variables observed within the range of
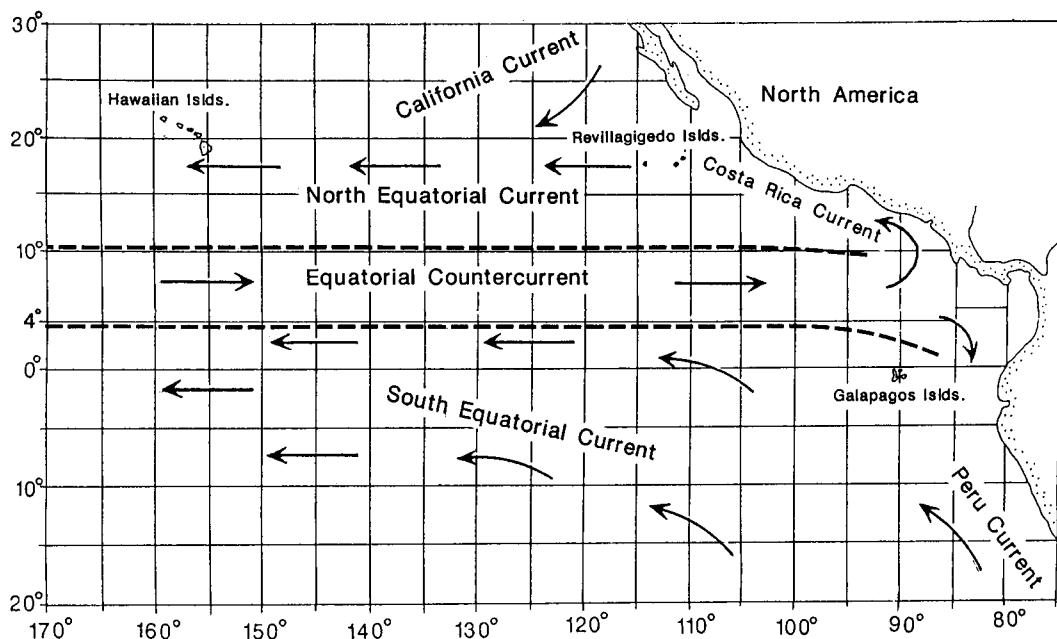
FIGURE 1. Study area, including major current systems and designated blocks. Blocks are 5° latitude × 5° longitude, except those lying along the American coasts and between 4°N and 10°N, and between the Equator and 4°N (See Methods; Relationship Between Density and Physical Habitat Variables).

each taxon. The sample unit was one block. Block densities were weighted by surface area of ocean censused within respective blocks to control for difference in census effort. For multivariate analyses, all habitat variables (an average value for all transects per block; see below for justification) were entered into the model. Insignificant terms were dropped. Because terms may be correlated, importance of some may be masked by others. Therefore, we tested for effects of eliminated terms by putting them, one at a time, back into the model. We also tested for non-linearity in the relationship of density to covariates by including quadratic terms for independent terms. The model was complete if no terms could be added or dropped. Circularly distributed variables including wind and wave direction, were omitted.

Although habitat varied appreciably within the study area, variation within each block was considerably less because each was located within a current system with relatively distinct habitat (except during El Niño; Ribic et al. 1990). Therefore, we assumed that using averaged habitat values for each block in regression analyses was justified.

We present results of univariate and multivariate analyses to distinguish direct effects from those due to confounding with other variables (see Richardson 1978). Habitat variables with significant multivariate effects are likely true influences, but stronger univariate than multivariate effects suggest confounding. Univariate analyses for densities of *P. a. newelli* and *Pt. p. sandwichensis* included season: (1) spring and (2) autumn. Due to poor coverage of the pelagic ranges of *P. a. auricularis* and *Pt. p. phaeopygia* in autumn, only spring data were analyzed for habitat use. We normalized block density using the square-root transformation, which is considered appropriate for data following a Poisson distribution, such as that usually obtained from counts (Kleinbaum et al. 1988). Residuals (produced in regression analyses) of the transformed data met assumptions of normality (CRC 1992; Skewness/ Kurtosis Test for Normality of Residuals, $P > 0.05$).

We used Pearson correlation analyses to examine relationships between all pairs of habitat variables. Comparisons of behavioral allocation, foraging location, and flight direction were by Chi-square test. Tests were performed on num-

bers, not percentages. Significance was assumed at $P < 0.050$. Means $\pm$ one standard deviation are reported.

POPULATION ESTIMATES

The population estimate for each taxon is the back-transformed mean density of all blocks in the observed range multiplied by the total ocean area of all respective blocks. When calculating overall study area density for each taxon, density observed in each block was weighted by the total surface area of the respective block to control for difference in block area.

We used the "Regression Estimator" method (Thompson 1992), followed by the procedure of Sokal and Rohlf (1980; p. 148), to calculate 95% confidence intervals of population estimates. Standard deviations of density were calculated as the root mean square error (RMSE) of density in multiple regression analyses that included all habitat variables significantly related to density. RMSE is equal to the square root of the mean square error of the residual variation (i.e., unexplained variation; CRC 1992) remaining after fitting a regression model. In other words, RMSE provides a measure of variability after the statistical model has taken explained variation into account, and thus reflects only unexplained variation.

To calculate upper and lower estimates of number of breeding pairs, we multiplied 95% confidence limits of the pelagic population by upper and lower estimates, respectively, for proportion of breeders in the pelagic population. For the shearwaters, upper and lower estimates of proportion of breeders were 0.60 and 0.30, compared to best estimates of 0.46 (spring) and 0.40 (autumn); see above, Breeding Chronology and Demography. The two estimates were 0.56 and 0.26 for the petrels, where best estimates were 0.46 and 0.40. Upper estimates are the highest possible estimates consistent with known survivorship and age-of-first- breeding. Lower limits are based on information indicating that, with proportion of breeders <0.30, or 0.26, respectively, populations of both species would rapidly go extinct (Ainley et al. 1995).

FLIGHT BEHAVIOR

Under the null hypothesis that birds fly in random directions relative to colony location, an expected 11% would be oriented toward the col-

ony; a value including birds on a direct course plus those flying $\pm 20°$ of a direct course, i.e., a flight path encompassing 40°. Similarly, 11% would be headed away, leaving 78% that would fly in directions oriented otherwise. Hence, 22% of the birds would fly toward or away from the colony. We used a 20° leeway to allow for random deviation from a direct course. A significantly higher proportion flying toward or away from the breeding colony would indicate commuting, We subdivided pelagic ranges relative to distance from the colony, with the objective of examining foraging ranges of birds attending the colony.

In calculating flight direction relative to wind direction we adjusted for nautical protocol where wind direction is the compass direction *from* which the wind is blowing, and flight direction is the direction *toward* which the bird is flying (i.e., relative directions are reversed 180°). Categories were: (1) flight into the wind (difference between bird course and wind direction 0° to 020°); (2) flight across a head-wind (direction difference between bird and wind 030° to 060°); (3) flight direction across the wind (difference 070° to 110°); (4) flight direction across a tail-wind (difference 120° to 150°); and (5) flight direction with the wind (difference 160° to 180°). If bird flight direction was not related to wind direction, the proportion of birds flying in each of the five directions would be 3:4:5:4:3, respectively (or 0.16, 0.21, 0.26, 0.21, and 0.16). Significant deviation from those ratios would indicate association between wind direction and flight direction. Data associated with wind <5 km/hr were not used in these analyses.

We also examined the possibility that relationships between flight direction and colony location were confounded with flight direction relative to wind direction. We analyzed contingency tables that, for each of the five categories of flight direction relative to wind direction, included the number of birds observed flying towards or away from the colony vs. the number expected to be oriented to or from the colony under the null hypothesis of no commuting. The latter were calculated as the total number seen oriented in one of the five categories of flight direction relative to wind direction (i.e., the number flying towards/away from the colony or otherwise), multiplied by 0.22 (see above). Significant deviation from the observed vs. expected ratios would indicate confounding between the effects of colony location and wind direction on flight direction.
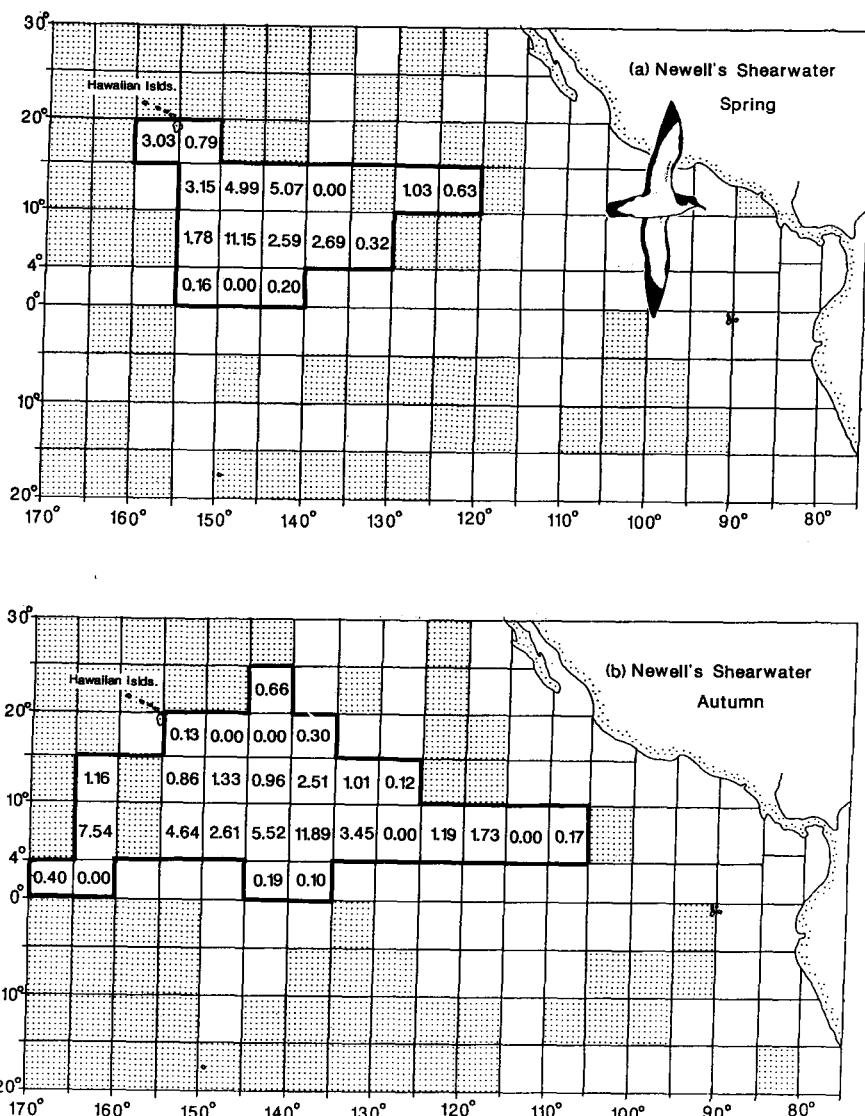
FIGURE 2. Densities (birds per 100 km² of ocean surface censused within a given block) of Newell's Shearwaters during spring (a) and autumn (b). The darkened border surrounds the observed pelagic range. Stippled blocks are those for which no density was calculated due to inadequate census coverage (i.e., <75 km² of ocean censused).

WING MORPHOLOGY

We measured *P. a. newelli* killed from striking power lines the previous night on Kauai. All measurements follow Pennycuick (1989), and included mass (kg), wing span (m; length from tip to tip of the fully expanded wings) and wing area (m²), which includes the area of the body between the wings. Values for *Pt. phaeopygia* are from Warham (1977). Warham's values for wing loading were calculated without including body area between the wings with wing area. Therefore, we adjusted Warham's *Pt. phaeopygia* value for wing loading by multiplying it by 0.842, based on the relationship found in 182 Juan Fernandez Petrels *Pt. externa* (Spear and Ainley, unpubl. data), a sibling species of the former, where wing area with body area between wings averaged 1041 cm², and wing area without body area averaged 877 cm².
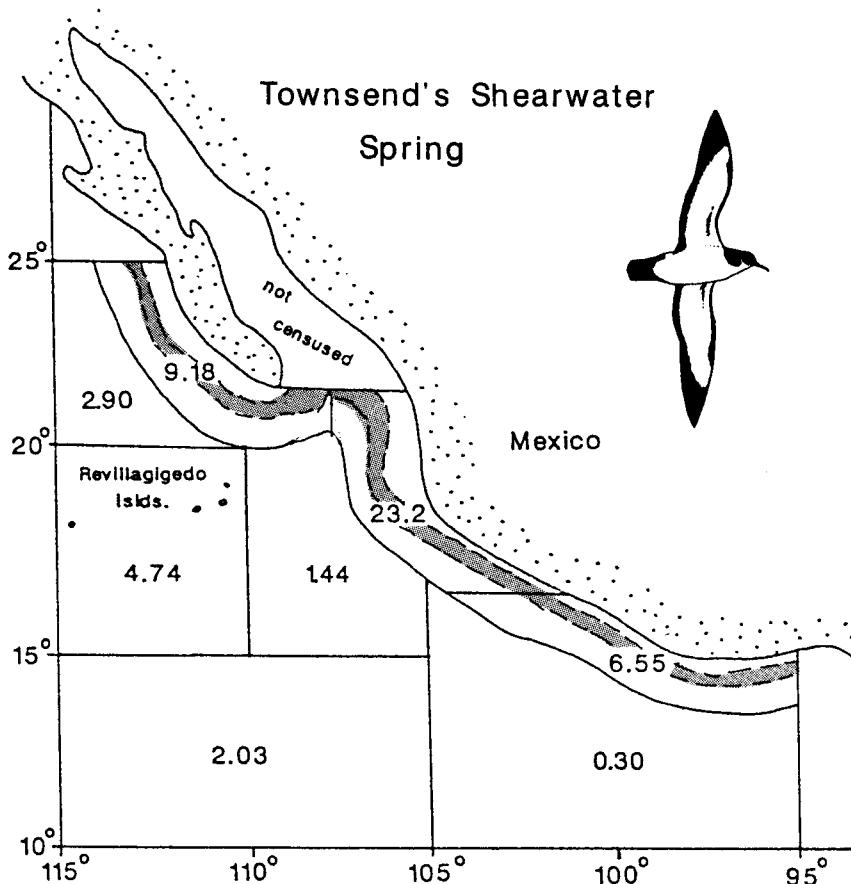
FIGURE 3. Densities (birds per 100 km² of ocean surface censused within a given block) of Townsend's Shearwaters in spring, within the observed pelagic range. Shading denotes the continental slope (including waters extending from the 200 m isobath to the 4,000 m isobath).

RESULTS

NUMBER OF SIGHTINGS AND DISTRIBUTIONAL RANGE

The adjusted number of sighted *P. a. newelli,* after correction for flux, was 627.9 (raw number = 673). We observed *P. a. newelli* near Hawaii, southeast to 106°W (at 9°N; Figs. 2a, b), south to the Equator (at 140°W; out of transect). We also recorded one *P. a. newelli* near the Marquesas Islands (12°S, 142°W). We did not census the full extent of the range of *P. a. newelli* north and west of Hawaii (but see Discussion).

We sighted 243 *P. a. auricularis* (adjusted number = 211.3), including birds near the Revillagigedos, west to 114°25'W, east to 97°48'W, north to 24°27'N, and south to 10°58'N (Fig. 3; see also Pitman 1986 for similar observations).

We sighted 311 Dark-rumped Petrels (adjusted number = 275.6), including birds near Hawaii and Galapagos Islands, south to 17°S (at 75°W; Figs. 4a, b), but not during eight cruises in pelagic waters off Chile (see also Murphy 1936, Jehl 1973). West of 120°W, we observed these birds south to 3°N. We did not census the full extent of the range north and west of Hawaii.

We saw most petrels either within 1,500 km of the Galapagos, or within 2,200 km of Hawaii (Figs. 4a, b). Ranges of the two taxa may overlap, but the low number (*n* = 2) seen in the 1,050 km wide area between 120°W to 130°W (and south of 10°N) indicated little overlap (see Bartle et al. 1993, for same conclusion). Therefore, birds seen west of 130° and north of 10°N were considered as *Pt. p. sandwichensis* (110 sighted; adjusted = 99.7), and those east of 120°W as *Pt. p. phaeopygia* (201 sighted; adjusted = 175.9).
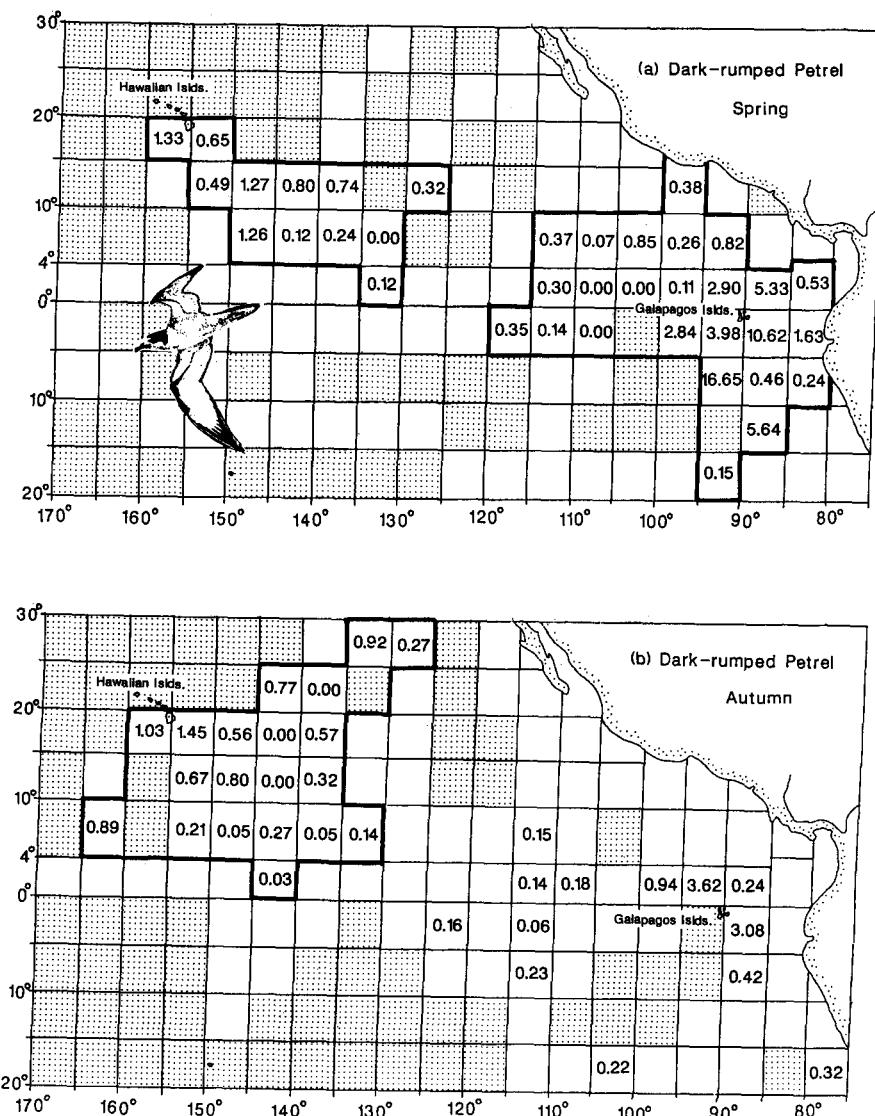
FIGURE 4. Densities (birds per 100 km² of ocean surface censused within a given block) of Dark-rumped Petrels in spring (a) and autumn (b), within the observed pelagic range (darkened border). Stippled blocks same as for Figure 2.

OCEANOGRAPHIC HABITAT COMPARED AMONG TAXA

When compared to *P. a. newelli* during spring, *P. a. auricularis* occurred in significantly cooler waters with a shallower, weaker thermocline and lower associated wind speed, wave height and cloud cover (Table 1, Fig. 5). Thus, *P. a. auricularis* was associated with more upwelled, less-stratified waters, but with less turbulent meteorological features than was *P. a. newelli*.

Compared to *Pt. p. sandwichensis, Pt. p.* *phaeopygia* occurred in waters having a significantly shallower thermocline, and lower wind speeds and wave heights (Fig. 5). None of the other habitat variables differed significantly between them.

Although *P. a. newelli* and *Pt. p. sandwichensis* occurred over similar habitat in spring (when they differed only for two variables), they differed significantly for five of seven during autumn; only salinity and wave height were similar (Table 1, Fig. 5). *P. a. newelli* was found in warmer waters

TABLE 1. Ocean habitat characteristics (mean ± one SD) of subspecies of procellariids in the central and eastern tropical Pacific, by season, 1980–1994. Values of n are the number of birds sighted.

	Sea-surface temperature (°C)	Sea-surface salinity (ppt)	Thermocline depth (m)	Thermocline strength (°C change)	Wind speed (km/hr)	Wave height (m)	Cloud cover (oktas)
Spring							
Newell's Shearwater (n = 284)	26.8 ± 1.15	34.52 ± 0.22	76 ± 21.3	7.2 ± 3.27	33 ± 4.9	1.6 ± 0.59	4.9 ± 2.46
Townsend's Shearwater (n = 198)	24.9 ± 3.68	34.34 ± 0.30	45 ± 25.3	2.6 ± 2.07	19 ± 6.2	1.1 ± 0.4	2.6 ± 2.76
Hawaiian Dark-rumped Petrel (n = 50)	26.2 ± 1.15	34.46 ± 0.25	68 ± 26.0	5.8 ± 3.81	33 ± 5.0	1.5 ± 0.49	4.2 ± 3.05
Galapagos Dark-rumped Petrel (n = 176)	25.4 ± 2.39	34.56 ± 0.81	22 ± 15.5	5.5 ± 2.50	19 ± 4.2	1.1 ± 0.53	3.5 ± 2.88
Autumn							
Newell's Shearwater (n = 389)	27.6 ± 0.70	34.43 ± 0.43	88 ± 37.7	4.5 ± 2.00	26 ± 5.3	1.2 ± 0.69	5.5 ± 2.48
Hawaiian Dark-rumped Petrel (n = 60)	26.7 ± 1.40	34.43 ± 0.35	56 ± 28.6	3.6 ± 1.47	31 ± 5.5	1.4 ± 0.75	4.2 ± 2.61

with deeper, stronger thermocline, lower wind speeds and more cloud cover than *Pt. p. sandwichensis*; i.e., in areas with less mixing in the water column and where Trade Winds were less developed.

Principal component (PC) analyses on the four taxa for sightings during spring, and that related them to seven oceanographic variables, indicated close relationships between *P. a. newelli* and *Pt. p. sandwichensis* and between *P. a. auricularis* and *Pt. p. phaeopygia* (Fig. 6). This pairing is not surprising because the former two occurred mostly in the NEC and ECC (Figs. 1, 2a, 4a), and the latter two in the most eastern sectors of the ECP (Figs. 3, 4a). Specifically, *P. a. auricularis* inhabited the Costa Rica Current, and *Pt. p. phaeopygia* inhabited the northern boundary of the Peru Current, southern end of the Costa Rica Current, and the eastern extremities of the SEC and ECC. Important oceanographic variables relating the four taxa during spring were, for the first two PCs, in order of importance: PC axis 1 — thermocline depth and strength, and wind speed; and PC axis 2 — wave height, sea-surface temperature, and wind speed (Table 2).

During autumn, *P. a. newelli* and *Pt. p. sandwichensis* (*P. a. auricularis* and *Pt. p. phaeopygia* excluded from autumn analysis due to inadequate data) were more distantly separate in relation to oceanographic variables than in spring (Fig. 6, see also below). Important variables were, in order of importance: PC1 — sea-surface salinity, thermocline strength, and sea-surface temperature; and PC2 — wave height, thermocline depth, and wind speed (Table 2).

RELATIONSHIP BETWEEN BIRD DENSITY AND PHYSICAL VARIABLES

A number of significant correlations existed between pairs of physical variables (Table 3). These results are considered when assessing models on the relationship between density and habitat variables.

For univariate analyses, densities of *P. a. newelli* increased significantly with increase in cloud cover and wave height (Table 4a). A significant positive effect of sea-surface temperature in autumn was absent during spring. A significant curvilinear (quadratic) relationship between density and sea-surface salinity (Fig. 7a) resulted from higher densities of *P. a. newelli* associated with moderate salinity, compared to waters of low or high salinity.

	spring		autumn	
	Low	High	Low	High
Sea surface temperature	To Ga Ha Ne		Ha Ne	
	<0.001 <0.001 <0.001		<0.001	
Sea surface salinity	To Ha Ne Ga		Ha Ne	
Thermocline depth	Ga To Ha Ne		Ha Ne	
	<0.001 <0.001		<0.001	
Thermocline strength	To Ga Ha Ne		Ha Ne	
	<0.001 0.003		0.001	
Wind speed	To Ga Ha Ne		Ne Ha	
	<0.001		<0.001	
Wave height	Ga To Ne Ha		Ne Ha	
	0.001			
Cloud cover	To Ga Ha Ne		Ha Ne	
	0.007 0.001		0.001	

FIGURE 5. Comparisons between Townsend's Shearwaters (TO), Newell's Shearwaters (NE), Hawaiian Dark-rumped Petrels (HA), and Galapagos Dark-rumped Petrels (GA) for association with seven oceanic variables. Spring analyses by Sidak multiple comparison test; autumn analyses by t test. Lines connecting taxa indicate insignificant differences, with P values below line breaks.

The full multivariate model explained 78% of the variation in the density distribution of *P. a. newelli* (Table 4a). With exception of sea-surface temperature (which covaried with cloud cover; Table 3), relationships between densities and salinity, cloud cover and wave height also were found in the multivariate analysis (Table 4a, Figs. 7a–c). One difference, however, was that the linear effect of salinity (not significant in univariate model) was highly significant in the multivariate model. In addition, while controlling for the latter three variables and distance to the colony, a highly significant, positive effect of thermocline depth appeared (Fig. 7d). Finally, a quadratic effect of colony distance (Fig. 7e) resulted from low densities within 1,000 km of Hawaii, density increase at distances up to 2,000 km, and then density decline. These results indicate preference for the ECC.

For univariate analyses, densities of *P. a. auricularis* increased significantly with decreasing ocean depth and distance to the continental slope (Table 4b). A quadratic relationship between density and wind speed resulted from high densities found at low wind speed, low densities at moderate wind speed, followed by an increase in density at high wind speed. Multivariate analysis, however, indicated that ocean depth was the only significant variable, explaining 78% of *P. a. auricularis* density variation (Table 4b, Fig. 7f). Lack of an effect of distance to the continental slope resulted from covariation of the latter with depth (Table 3). These results indicate preference for waters over the continental slope.

For univariate analyses, densities of *Pt. p. sandwichensis* correlated negatively and significantly with distance from Hawaii, sea-surface temperature and cloud cover, and positively with wind speed (Table 4c). Only sea-surface temperature and wind speed were significant in the multivariate analysis (Figs. 7g, h), explaining 49% of the variation in density. The effect of temperature was quadratic due to higher densities in waters of moderate temperature compared to where it was lower or higher. Lack of an effect by colony distance in this model resulted from covariance
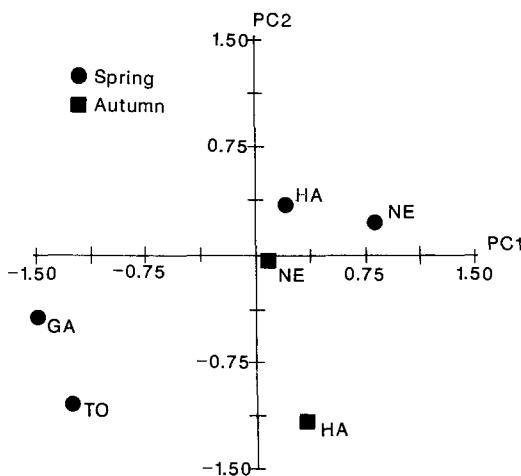
FIGURE 6. Principal component analysis on the relationship of habitat variables among Townsend's Shearwaters (TO), Newell's Shearwaters (NE), Hawaiian Dark-rumped Petrels (HA), and Galapagos Dark-rumped Petrels (GA) during spring and autumn.

of the latter with wind speed (Table 3). These results are consistent with higher densities in the NEC (which surrounds the main Hawaiian Islands), where waters were cooler and Trade Winds stronger, than in the ECC.

Univariate and multivariate models for *Pt. p. phaeopygia* were similar; the latter explaining 61% of the variation in densities (Table 4d). The models indicated a strong negative relationship with colony distance, although the effect was quadratic due to leveling of density beyond 1,000 km (Fig. 7i). An effect of wind speed was also quadratic due to increase in density with wind

speed to 45 km/hr, followed by a decrease at higher speeds (Fig. 7j). When controlling for colony distance, the linear effect of wind speed was positively and significantly related to density (Table 4d). These results are consistent with high density near the Galapagos (the far eastern sector of the SEC), where wind systems were more developed than to the north in the eastern edge of the ECC and Costa Rica Current off Central America; and less well developed than farther south, or farther west along the Equator.

POPULATION ESTIMATES

All blocks in the observed range of *P. a. auricularis* were censused during spring (Table 5). We estimated the pelagic population to be 46,400 birds (CI = 17,500–89,000). No estimate for autumn was made because censuses were too few for inshore areas.

We made observations over 75 km² or more of ocean surface in 94% and 93% of the blocks in the observed range of *P. a. newelli* in spring and autumn, respectively (Table 5). We estimated that the ECP study area held a population of 84,000 *P. a. newelli* in both spring and autumn (95% CI = 57,000–115,000 for spring, and 58,000–113,000 for autumn).

We observed 75 km² or more of ocean surface in 92% of the blocks in the observed range of *Pt. p. sandwichensis* in spring, and 87% in autumn (Table 5). We estimated an at-sea population of 16,300 birds for spring (CI = 10,600–23,300), and 22,700 for autumn (CI = 13,500–34,400).

We observed 75 km² or more of ocean area in 93% of the blocks in the observed range of *Pt. p. phaeopygia* in spring (Table 5). We estimated

TABLE 2. Principal component (PC) analyses: including (a) eigenvalue (cumulative) proportions of variance explained by (b) seven habitat variables associated with the occurrence of Townsend's and Newell's Shearwaters, and Hawaiian and Galapagos Dark-rumped Petrels during spring. Only habitat variables associated with Newell's and Hawaiian Dark-rumped Petrels were included in the autumn analysis. Sample sizes are given in Table 1.

(a)			(b)				
	Eigenvalue Cumulative proportion			Eigenvector loadings:			
				Spring		Autumn	
PC	Spring	Autumn	Habitat variable	PC1	PC2	PC1	PC2
1	0.30	0.26	Sea surface temperature	0.401	−0.466	−0.402	0.322
2	0.52	0.49	Sea surface salinity	−0.102	0.398	0.653	0.113
3	0.66	0.62	Thermocline depth	0.508	0.185	0.398	0.503
4	0.79	0.74	Thermal strength	0.464	−0.255	−0.478	0.079
5	0.91	0.85	Wind speed	0.426	0.455	0.139	−0.454
6	0.96	0.95	Wave height	0.279	0.499	0.024	0.510
7	1.00	1.00	Cloud cover	0.309	−0.264	−0.078	0.397

TABLE 3. Relationship between oceanographic and geographic variables within the pelagic ranges of four procellariids in the central and eastern tropical Pacific. Data taken within each lat. × long. block were averaged; values are the adjusted r (correlation coefficient); * = $P < 0.05$.

Newell's Shearwater, n = 43 blocks

	Sea-surface temperature	Sea-surface salinity	Thermal depth	Thermal strength	Wind speed	Wave height	Cloud cover	Ocean depth	Distance to continental shelf
Sea-surface salinity	-0.322	—							
Thermal depth	-0.175	0.537*	—						
Thermal strength	0.446*	-0.471*	-0.266	—					
Wind speed	-0.052	0.028	-0.127	-0.061	—				
Wave height	0.002	0.239	0.089	-0.330*	0.079	—			
Cloud cover	0.363*	-0.399*	0.033	0.227	-0.023	-0.012	—		
Distance to colony	0.257	-0.450*	-0.063	0.508*	-0.452*	-0.578*	0.260		

Townsend's Shearwater, n = 8 blocks (Spring only)

	Sea-surface temperature	Sea-surface salinity	Thermal depth	Thermal strength	Wind speed	Wave height	Cloud cover	Ocean depth	Distance to continental shelf
Sea-surface salinity	-0.702	—							
Thermal depth	0.430	-0.772*	—						
Thermal strength	0.628	-0.900*	0.869*	—					
Wind speed	-0.665	0.702	-0.554	-0.640	—				
Wave height	-0.567	0.755*	-0.506	-0.725*	0.719*	—			
Cloud cover	0.353	0.235	0.007	-0.061	-0.315	-0.013	—		
Depth	0.492	0.178	-0.243	-0.175	0.085	0.105	0.638	—	
Distance to shelf	0.484	0.090	0.032	0.032	0.175	0.129	0.582	-0.885*	—
Distance to colony	0.442	-0.803*	0.578	0.686	-0.676	-0.838*	-0.209	-0.213	-0.314

Hawaiian Dark-rumped Petrel, n = 32 blocks

	Sea-surface temperature	Sea-surface salinity	Thermal depth	Thermal strength	Wind speed	Wave height	Cloud cover	Distance to colony
Sea-surface salinity	-0.345	—						
Thermal depth	-0.030	0.337	—					
Thermal strength	0.528*	-0.388*	-0.021	—				
Wind speed	-0.048	-0.275	0.194	-0.018	—			
Wave height	-0.264	-0.001	0.235	-0.194	0.109	—		
Cloud cover	0.084	-0.424*	-0.016	0.443*	0.186	0.096	—	
Distance to colony	-0.200	0.145	0.029	0.249	-0.354*	0.191	0.247	

Galapagos Dark-rumped Petrel, n = 25 blocks (Spring only)

	Sea-surface temperature	Sea-surface salinity	Thermal depth	Thermal strength	Wind speed	Wave height	Cloud cover	Distance to colony
Sea-surface salinity	-0.749*	—						
Thermal depth	0.213	-0.018	—					
Thermal strength	0.676*	-0.413*	0.375	—				
Wind speed	-0.393	0.336	0.478*	0.132	—			
Wave height	-0.336	0.610*	0.432*	0.033	0.496*	—		
Cloud cover	0.186	-0.379*	0.523*	0.312	0.202	0.106	—	
Distance to colony	-0.130	0.465*	0.632*	0.144	0.540*	0.747*	0.073	

TABLE 4. Regression models describing significant physical habitat variables associated with four procellariids in the ECP. The term, season, included in models for Newell's Shearwaters and Hawaiian Dark-rumped Petrels, contributed insignificantly to variance explained. Density values, the dependent variable, were square root transformed. Values for linear terms were calculated after respective quadratic terms had been dropped from the model. The asterisk denotes interaction between season and independent term. All numerator df = 1.

Term	Coefficient × 100	SE × 100	F-value	P-value	Variance explained
a) Newell's Shearwater: Sample n = 43 blocks for each model.					
Univariate analyses:					
Sea surface temperature					
*season	—	—	4.98	0.031	9.7
Spring	0.0174	0.0247	0.49	0.5	3.4
Autumn	0.543	0.0178	9.27	0.005	27.1
Sea surface salinity					
Linear	−0.0492	0.0392	1.57	0.2	3.9
Quadratic	−0.255	0.0554	21.19	<0.001	33.8
Cloud cover	0.0486	0.0114	18.31	<0.001	31.5
Wave height	0.110	0.0459	5.74	0.021	12.6
Multivariate analyses: Model $F[8,34]$ = 14.71, P < 0.001, R^2 = 0.776.					
Distance to colony					
Linear	−1.38e⁻⁵	1.54e⁻⁵	0.80	0.4	0.8
Quadratic	−1.96e⁻⁸	5.18e⁻⁹	14.31	0.001	9.4
Sea surface salinity					
Linear	−0.160	0.0368	18.99	<0.001	13.8
Quadratic	−0.121	0.0561	4.63	0.039	3.1
Thermocline depth	0.00274	0.000575	22.78	<0.001	15.0
Cloud cover	0.0194	0.00955	4.14	0.050	2.7
Wave height	0.123	0.0353	12.11	0.001	8.0
b) Townsend's Shearwater: Sample n = 8 blocks for each model.					
Univariate analyses:					
Ocean depth	−0.00267	5.80e⁻⁵	21.12	0.004	77.9
Distance to continental shelf	−0.00312	0.000108	8.20	0.028	57.7
Wind speed					
Linear	−0.00690	0.0106	0.42	0.5	6.5
Quadratic	0.00330	0.000920	12.83	0.016	67.3
c) Hawaiian Dark-rumped Petrel: Sample n = 32 blocks for each model.					
Univariate analyses:					
Distance to colony	−1.94e⁻⁵	8.31e⁻⁶	5.44	0.027	15.7
Sea surface temperature	−0.0255	0.00849	9.00	0.006	24.9
Wind speed	0.00406	0.00146	7.70	0.010	22.1
Cloud cover	−0.0110	0.0145	6.08	0.020	17.2
Multivariate analyses: Model $F[4,27]$ = 4.89, P = 0.002, R^2 = 0.489.					
Sea surface temperature					
Linear	0.973	0.394	6.11	0.021	16.2
Quadratic	−0.0185	0.00734	6.36	0.018	13.0
Wind speed	0.00358	0.00133	7.24	0.013	14.8
d) Galapagos Dark-rumped Petrel: Sample n = 25 blocks for each model.					
Univariate analyses:					
Distance to colony					
Linear	−9.10e⁻⁵	3.20e⁻⁵	8.10	0.009	26.0
Quadratic	1.86e⁻⁷	6.96e⁻⁸	7.10	0.014	18.1

TABLE 4. Continued.

Term	Coefficient × 100	SE × 100	F-value	P-value	Variance explained
Wind speed					
Linear	0.00632	0.00387	2.66	0.12	10.4
Quadratic	−0.00144	0.000681	4.49	0.046	15.2
Multivariate analyses: Model $F[4,20] = 7.71$, $P = 0.001$, $R^2 = 0.607$.					
Distance to colony					
Linear	$-8.32e^{-5}$	$2.94e^{-5}$	8.02	0.010	20.5
Quadratic	$1.08e^{-7}$	$1.60e^{-8}$	7.40	0.013	14.6
Wind speed					
Linear	0.00254	0.00175	2.09	0.16	5.1
Quadratic	−0.00131	0.000542	5.85	0.025	11.5

88,000 birds (CI = 54,000–130,000). In spring, we did not census a section of southwestern part of this bird's range (Fig. 4a; Pitman 1986). We made no estimate for autumn because of poor coverage around the Galapagos.

Our best estimates for number of breeding pairs, as well as lowest and highest estimates, are given in Table 6. The lower estimates are higher than previous estimates for *P. a. auricularis, P. a. newelli,* and *Pt. p. sandwichensis* (1,000, 6,000, and 600 pairs, respectively; see Introduction). Low and high estimates for *Pt. p. phaeopygia* are similar to the previous estimates (7,500–35,000).

PELAGIC BEHAVIOR

Varying significantly among taxa was allocation of behaviors resting on the water, foraging, and flying directionally (χ^2 test, df = 6, $P < 0.0001$, Fig. 8). *P. a. auricularis* foraged more often, and flew directionally less often, than the others. *P. a. newelli* flew directionally less often, and rested more often, than *Pt. p. sandwichensis* or *Pt. p. phaeopygia* (χ^2 tests, df = 2, $P < 0.0001$, and 0.005, respectively). Behavior of the petrels was similar (χ^2 test, $P > 0.4$).

To examine the possibility that taxa had preferred feeding areas we divided the pelagic ranges of each into three non-a priori, large-scale segments. For *P. a. newelli* and *Pt. p. sandwichensis,* segments were defined relative to distinct oceanographic regions: the ECC (<10°N), the southern NEC (10–15°N), and offshore Hawaii (>15°N). For *P. a. auricularis,* segments were defined relative to distance from the continental slope, the most important feature affecting their distributions (see above), such that similar numbers of birds were included in each. For *Pt. p. phaeo-*

pygia, segments were defined as a function of colony distance (the major factor affecting their distribution), with each segment having similar numbers of birds.

P. a. auricularis foraged more often, and flew directionally less often, when within 100 km of the 200 m isobath than when >100 km from it (categories <51 km and 51–100 km from 200 m isobath grouped; χ^2 test, df = 1, $P < 0.0001$; resting birds excluded from this and the following analyses, Fig. 9a). Foraging birds were seen mostly over the eastern slope of the Mexican Trench, over depths averaging 2,524 m ± 1,325 m, range; 200–4,255 m, n = 103 birds.

P. a. newelli foraged more often, and flew directionally less often, when south of 10°N (i.e., in the ECC) than when north of 10°N (i.e., in the NEC and offshore Hawaii, grouped); χ^2 test, df = 1, $P < 0.0001$, Fig. 9b).

Behavioral allocation of *Pt. p. sandwichensis* was similar throughout its observed range (χ^2 test, df = 2, $P > 0.8$; Fig. 9c).

Pt. p. phaeopygia foraged more often, and flew directionally less often, when >250 km from the colony than when closer (categories 251–500 km and >500 km grouped; χ^2 test, df = 1, $P = 0.023$, Fig. 9d). For birds observed ≥250 km from the colony, the proportion foraging (as opposed to flying directionally) varied little between those found south or north of the colony (χ^2 test, df = 1, $P > 0.6$).

FLIGHT DIRECTION RELATIVE TO COLONY LOCATION

We used a priori distributional divisions according to results above indicating preferred feeding areas as a preliminary step towards determining
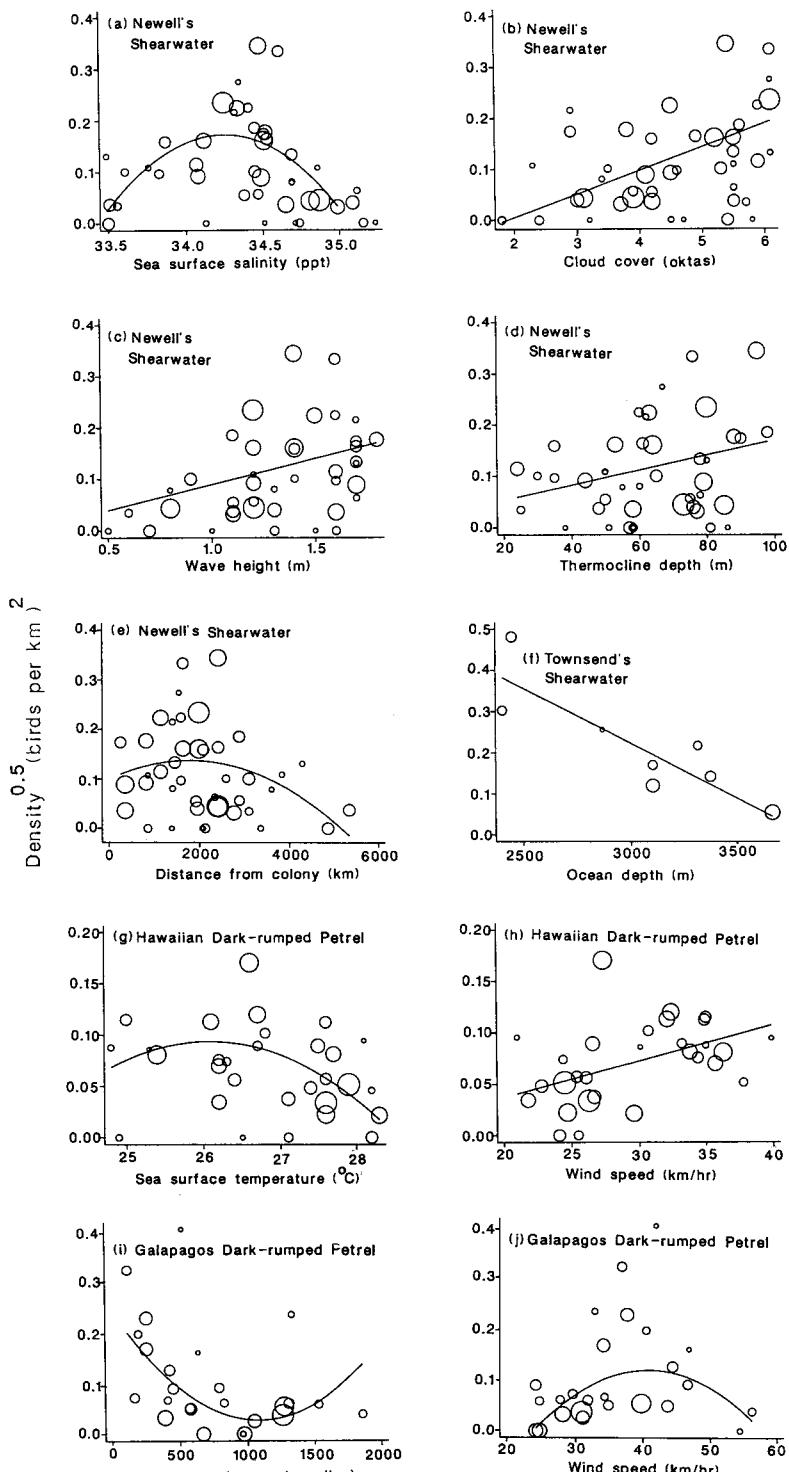
FIGURE 7a–j.   Relationships between shearwater and petrel densities (birds per 100 km² of ocean surface censused per block)$^{0.5}$ and habitat variables. Size of points proportional to weighting for area censused within respective blocks.

TABLE 5.   Mean pelagic densities, population estimates, and 95% of confidence intervals of Townsend's and Newell's Shearwaters, and Hawaiian and Galapagos Dark-rumped Petrels.

	Blocks in pelagic range	Blocks cen- sused[a]	Area censused (km^2)	Range area[b] (km^2)	Mean density[c] $\bar{x} \pm$ SD	Population estimate[d]	95% confidence limits
Townsend's Shearwater							
Spring							
NORMAL[e]	8	8	3,271	1,900,619	0.15621 ± 0.071990		
B-TRANS[f]					0.02440	46,378	17,522–89,008
Newell's Shearwater							
Spring							
NORMAL	17	16	11,157	4,928,401	0.13035 ± 0.042172		
B-TRANS					0.01699	83,739	57,360–115,093
Autumn							
NORMAL	29	27	13,989	8,111,337	0.10150 ± 0.042677		
B-TRANS					0.01030	83,565	58,046–113,298
Hawaiian Dark-rumped Petrel							
Spring							
NORMAL	13	12	8,404	3,516,619	0.06814 ± 0.020786		
B-TRANS					0.00464	16,328	10,611–23,271
Autumn							
NORMAL	23	20	11,651	5,946,632	0.06184 ± 0.030415		
B-TRANS					0.00382	22,741	13,477–34,415
Galapagos Dark-rumped Petrel							
Spring							
NORMAL	27	25	12,920	7,785,920	0.10624 ± 0.055410		
B-TRANS					0.01129	87,879	53,710–130,419

[a] The number of blocks in the subspecies observed pelagic range for which ≥ 75 km^2 ocean was censused.
[b] The summed area for all blocks in the pelagic range.
[c] Mean density (birds per km^2) is the average density among all blocks censused in the observed range of respective subspecies; square root transformed (see footnote e) or back-transformed (see footnote f). Density values for each block were weighted for total area of respective blocks to control for difference in block area.
[d] Population estimate equals the back-transformed mean density (B-TRANS value) multiplied by the range area.
[e] NORMAL refers to normalized values that had been square root transformed.
[f] B-TRANS refers to the back-transformed values (i.e., the squared NORMAL values).

if adults "commuted" directionally between colony and feeding local.

Number of birds seen flying toward ±20° vs. away ±20° from the colony varied insignificantly: *P. a. newelli,* 61.9 toward vs. 64.5 away; *P. a. auricularis,* 16.0 vs. 9.1; *Pt. p. sandwichensis,* 15.0 vs. 23.0; *Pt. p. phaeopygia,* 11.2 vs. 13.1 (χ^2 tests, df = 1, P = 0.9, 0.3, 0.4, and 0.8, respectively; decimal values resulted from correction for flux). These results indicate that birds were moving toward or away from the colony in similar numbers.

TABLE 6.   Estimates for number of breeding pairs of four taxa of procellariids. Best estimates are those derived directly from pelagic population estimates multiplied by the proportion of breeders (vs. nonbreeders). Autumn estimates adjusted for emergence of fledglings. See Methods: Breeding Chronology and Demography; Population Estimates, for calculation of proportion of breeders, upper and lower estimates, respectively.

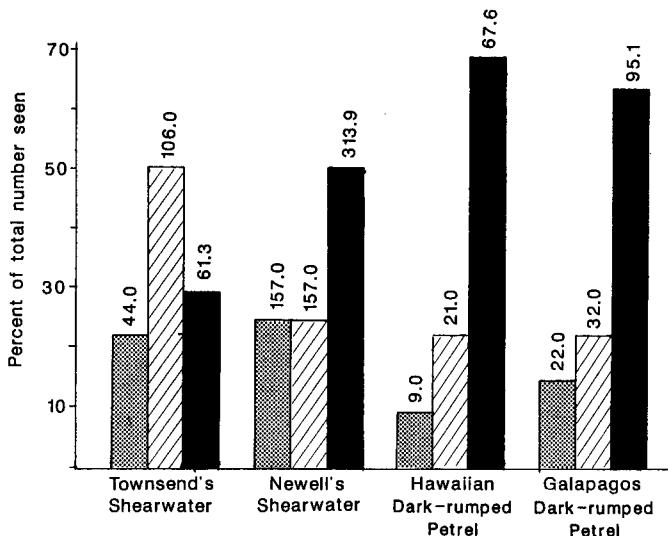|	Townsend's Shearwater	Newell's Shearwater		Hawaiian Dark-rumped Petrel		Galapagos Dark-rumped Petrel
	Spring	Spring	Autumn	Spring	Autumn	Spring
Number of breeding pairs						
Best estimate	10,600	19,300	16,700	3,750	4,500	20,200
Lower estimate	2,600	8,600	7,500	1,400	1,500	7,000
Upper estimate	26,700	34,500	29,200	6,500	8,300	36,500

FIGURE 8.   Temporal allocation of pelagic behavior: resting on water (dotted bar), foraging (striped bar), and flying directionally (solid bar). Sample *n*, denoted above each bar, and are not always whole numbers because of adjustment for bird flux among birds flying directionally.

Flight direction of *P. a auricularis* seen within 100 km of the continental slope indicated little movement to and from the Revillagigedos (x^2 test, df = 1, *P* = 0.4, Fig. 10a); however, the reverse was found for birds >100 km from the slope (x^2 test, df = 1, *P* = 0.031).

P. a. newelli seen flying over both the ECC and NEC showed significant movement towards or away from Hawaii (x^2 tests, df = 1, *P* < 0.0001 and 0.006, respectively, Fig. 10b). Alignment was greater among birds flying over the NEC (52.8%) compared to birds farther south (34.0%, df = 1, *P* = 0.001).

Flight direction of *Pt. p. sandwichensis* showed significant alignment with Hawaii (x^2 test, df = 1, *P* < 0.0001, Fig. 10c).

Flight direction of *Pt. p. phaeopygia* was not significantly aligned with the Galapagos, when either within 250 km, or further away (x^2 tests, df = 1, *P* = 0.14 and *P* = 0.5, respectively, Fig. 10d). However, a higher proportion of birds <251 km from the islands were aligned (38.5%) than were those farther out (16.6%; df = 1, *P* = 0.013). Small samples were problematic in *Pt. p. phaeopygia* and the *P. a. auricularis* analyses for near-colony and near-shore sectors, respectively.

EFFECT OF WIND DIRECTION ON
FLIGHT DIRECTION

Winds within 500 km of the Revillagigedos were mainly north and northwest, and within 500 km

of the Galapagos, mainly from the south (Fig. 11). Wind direction in the ECP north of 10°N, and west of 120°W, was predominantly from the northeast and east.

Wind direction was significantly related to flight direction of *P. a. newelli, Pt. p. sandwichensis* and *Pt. p. phaeopygia*, but not *P. a. auricularis* (x^2 tests, all df = 4; *P* < 0.0001, 0.002, 0.021, and 0.2, respectively, Fig. 12). Relationships resulted mostly from lower than expected proportions of birds flying with tail-winds or quartering across tail-winds, in conjunction with higher numbers flying across the wind or quartering across head-winds.

Flight direction relative to wind direction varied significantly among the taxa (x^2 test, df = 12, *P* = 0.024, Fig. 12), mainly because of different proportions of birds flying into head-winds and across the wind. *P. a. auricularis* flew against head-winds more often than *P. a. newelli* or *Pt. p. sandwichensis*, but not when compared to *Pt. p. phaeopygia* [df = 1, *P* = 0.012, 0.006, and 0.12, respectively; number flying into head-winds were compared with the number flying in all other directions (grouped)]. Petrels (grouped) flew more often across the wind than shearwaters (grouped; df = 1, *P* = 0.001).

Relationships between flight direction and colony location were not confounded with the effect of wind direction in *P. a. auricularis, P. a. newelli*, and *Pt. p. sandwichensis* (x^2 tests for inter-
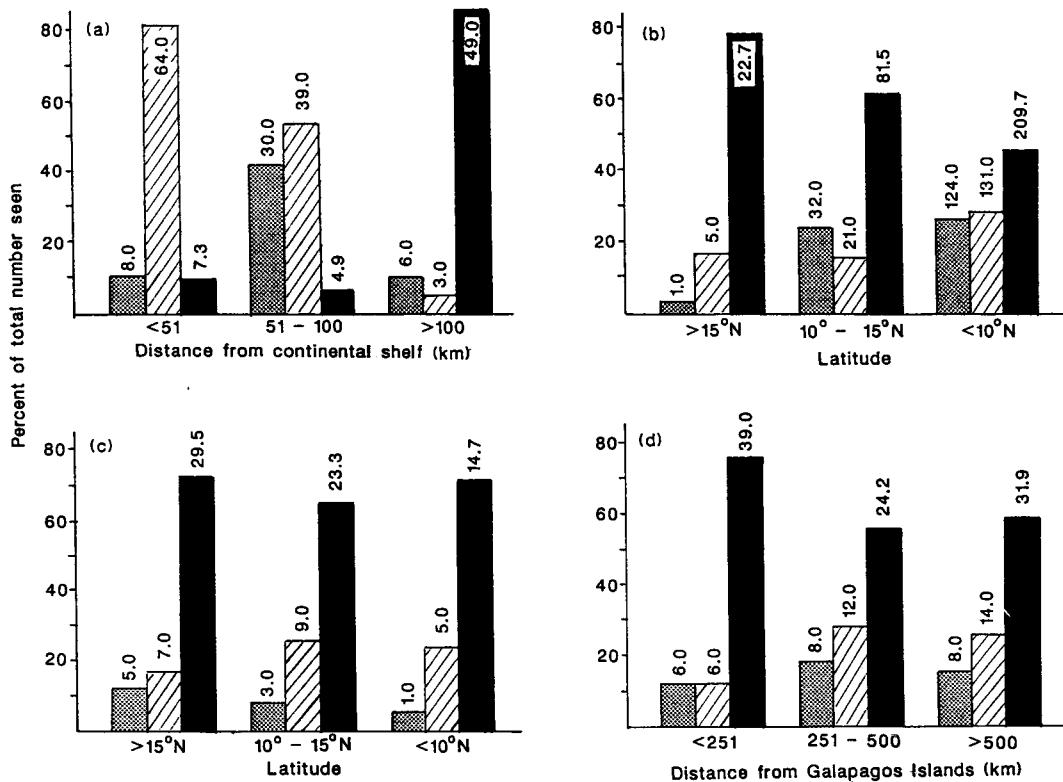
FIGURE 9. Allocation of pelagic behavior relative to location for: (a) Townsend's Shearwater, (b) Newell's Shearwater, (c) Hawaiian Dark-rumped Petrel, and (d) Galapagos Dark-rumped Petrel. See Figure 8 for denotation of patterns on bars, and *n* values.

action between colony location and wind direction on flight direction; all df = 4, except *Pt. p. sandwichensis* with df = 3; *P* = 0.9, 0.5, and 0.6, respectively, Figs. 13a–c), and marginally so in *Pt. p. phaeopygia* (df = 4, *P* = 0.057, Fig. 13d). This result indicates flight to and from the colony independent of wind direction. Small samples were problematic for *P. a. auricularis* and the two petrels.

WING MORPHOLOGY

Mean mass, aspect ratio and wing loading of 18 *P. a. newelli* was 378 ± 30.5 g, 10.3 ± 0.45, and 60 ± 5.3 N/m², respectively. Thus, the aspect ratio of *P. a. newelli* is lower, and wing loading higher, than those (11.2, and 44 N/m², respectively; Warham 1977; wing load adjusted to include the area of the body between the wings; See Methods—Wing Morphology) of the similarly-sized (390 g; Harris 1970, Tompkins and Milne 1991) *Pt. phaeopygia*. Values for *P. a. newelli* and *Pt. phaeopygia* are similar to those of

other species of *Puffinus* of the "Manx shearwater group," and *Pterodroma* of similar mass, respectively (Warham 1977; Spear and Ainley, unpubl. data).

DISCUSSION

FORAGING RANGE

Densities of *P. a. auricularis* were not related to distance to the breeding colony; those of *P. a. newelli* were quadratic, being highest in the central part of their range. Evidence suggests that breeding shearwaters commuted long distances between colonies and preferred foraging habitat. Minimum commuting range of *P. a. auricularis* would be 450 to 635 km (depending on island of origin and feeding location) from the Revillagigedos to waters over the 2,000 m isobath off Mexico. Assuming that the estimated breeding population of 36,000 *P. a. newelli* fed as near to their colonies as possible, and that no nonbreeders were intermingled, breeders would have for-
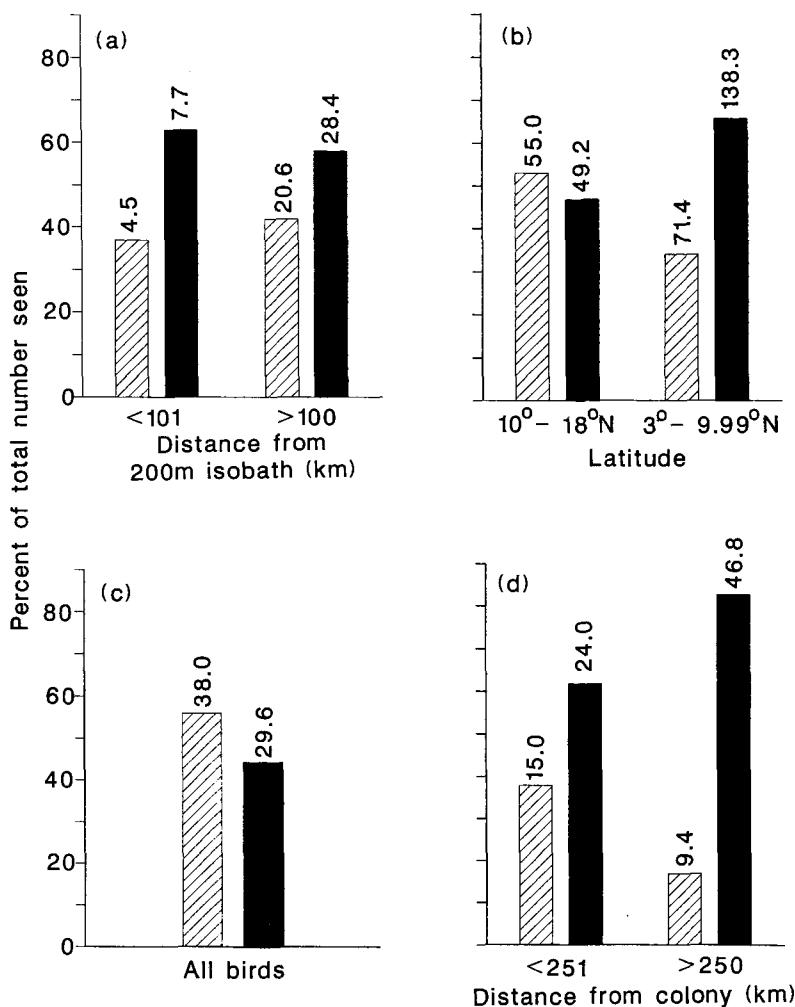
FIGURE 10. Flight direction as related to location for: (a) Townsend's Shearwater, (b) Newell's Shearwater, (c) Hawaiian Dark-rumped Petrel, and (d) Galapagos Dark-rumped Petrel. Flight direction towards or away from colony ±20° (striped bar); or not towards or away from colony (solid bar). See Figure 8 for notes on *n* values.

aged 1,000 km south and east of Hawaii, and 1,300 km south and east of Kauai (range would increase with intermingling of nonbreeders).

Apparent commuting ranges of *P. a. auricularis* and *P. a. newelli* are 1.6 to 3.3 times greater (maximum = 400 km) than for the closely related Manx Shearwater (Brooke 1990). Brooke's estimates were based on a two-day interval between chick feedings by a given parent, and a 45 km/hr flight speed. The contrast in flight range between these species may invoke other life-history differences. Average incubation and fledging periods of *P. a. newelli* are 62 days and 93 days, respectively (Byrd et al. 1984, Telfer 1986), com-

pared to 51 and 71 days for Manx Shearwaters (Brooke 1990). Incubation and chick fledging periods of procellariids are inversely related to feeding rates (reviewed in Warham 1990), and thus directly related to foraging trip duration and flight distance of foraging breeders (see also Weimerskirch et al. 1993). In other words, a longer chick-feeding interval for *P. a. newelli* compared to Manx Shearwaters is consistent with differences in their fledging periods. Ocean habitat used by the two species may explain these differences. Tropical/subtropical waters, like those surrounding the Hawaiian Islands, are less productive than temperate waters, which surround the British Isles
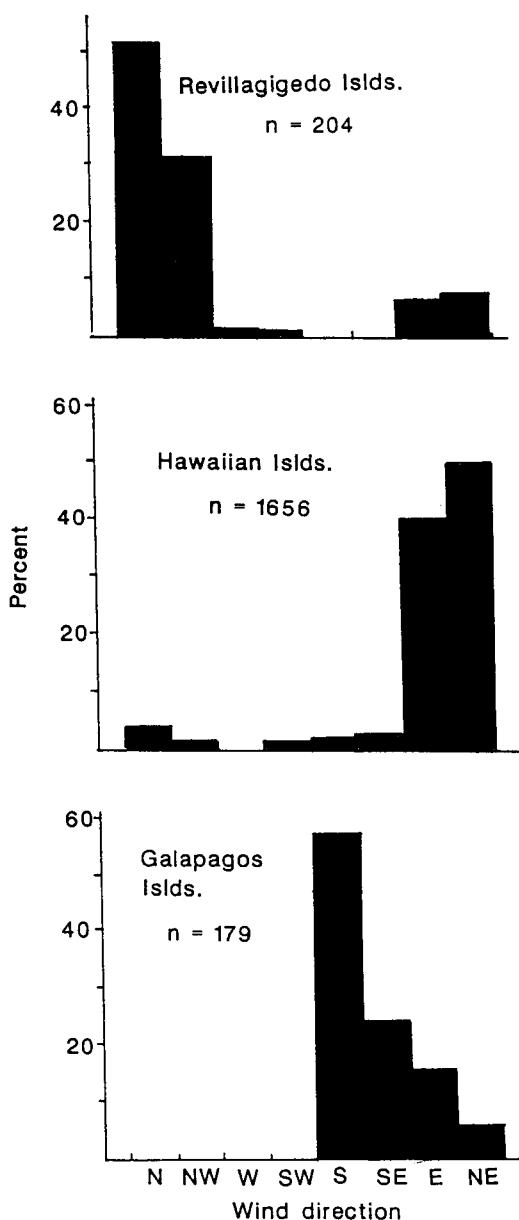
FIGURE 11. Wind direction noted during pelagic transects within (a) 500 km of the Revillagigedos Islands, (b) latitudes >10°N and between 120°W longitude and 165°W, and (c) 500 km of the Galapagos islands. Values of *n* denote number of transects.

(Brooke's study site; reviewed in Ainley and Boekelheide 1983). The above applies also to *P. a. auricularis,* which feeds in subtropical and tropical waters.

In contrast to the shearwaters, densities of *Pt. p. sandwichensis* and *Pt. p. phaeopygia* decreased significantly with distance from the colony. Furthermore, whereas densities of shearwaters were highest in areas where foraging incidence was highest, densities of the petrels were not. Breeding *Pt. p. sandwichensis* would have had a foraging range of 1,000 to 1,300 km, based on the same assumptions for distributions of breeders as given above for *P. a. newelli*. This range is nearly the same as that observed in the closely related Barau's Petrel (Stahl and Bartle 1991). A tendency for commuting by *Pt. p. phaeopygia* was insignificant; however, our results indicate that breeding birds would have foraged within some 375 km of the Galapagos, a range shorter than that of the other three taxa. Lack of evidence for commuting in this taxon may have been related to lack of breeding synchrony (Cruz and Cruz 1990, Tompkins and Milne 1991).

FLIGHT DIRECTION RELATIVE TO
WIND DIRECTION

Location of the breeding colony likely explains more frequent into-the-wind flight by *P. a. auricularis* compared to *P. a. newelli* or *Pt. p. sandwichensis*. Flight direction from the Revillagigedos to the continental slope off Baja California would be north, into prevailing winds, as would flight to the colony from the continental slope off mainland Mexico. *P. a. newelli* flew less often into the wind than *P. a. auricularis,* perhaps because head-wind flight was less often necessary during foraging commutes. *P. a. newelli* also flew further to feeding areas, perhaps made possible by avoiding flight into head-winds. More frequent head-wind flight by *Pt. p. phaeopygia* compared to the Hawaiian race was also consistent with a shorter foraging range. Another factor may have been lower wind speeds where *Pt. p. phaeopygia* and *P. a. auricularis* occurred, compared to the Trade Wind zone where *Pt. p. sandwichensis* and *P. a. newelli* occurred.

Avoidance of flying with tail winds by all four taxa is likely related to dynamics of soaring. Birds such as *Pterodroma,* that slope soar on rising air pushed in front of sea waves, must fly at the same speed as that of the waves to remain in the area of slope lift (Pennycuick 1975). Minimum flight speed will not allow this: they must soar faster by moving at an angle along the wave front. *Pterodroma* also soar on lift generated from lateral movement of wind (Spear and Ainley, pers. ob-
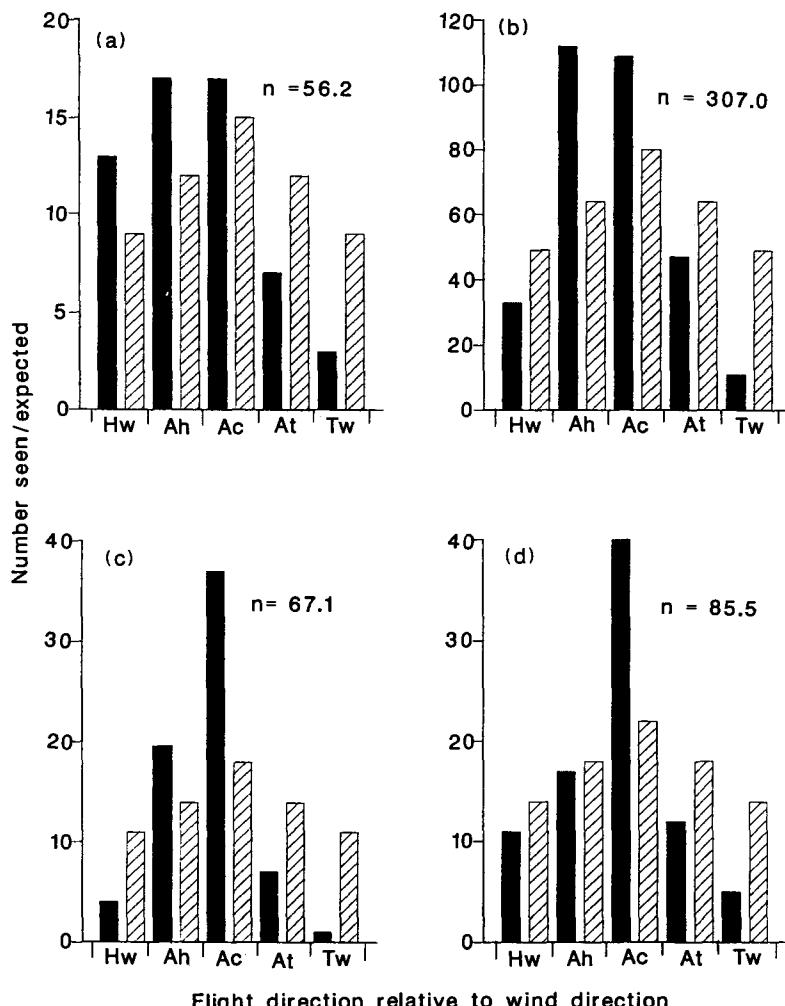
FIGURE 12. Flight direction relative to five categories of wind direction among (a) Townsend's Shearwater, (b) Newell's Shearwater, (c) Hawaiian Dark-rumped Petrel, and (d) Galapagos Dark-rumped Petrel. Solid bars represent numbers observed and hatched bars represent numbers expected. Flight directions designated as: Hw = flight into head-wind, Ah = flight across head-wind, Ac = flight across the wind, At = flight across tail-wind, Tw = flight with tail-wind. Values of n are the number seen, and are not whole numbers because of adjustment for bird flux.

serv.). Wind soaring would also be difficult in a tail wind because lift is achieved from force applied perpendicular to the wing surface (Pennycuick 1989).

Barau's Petrels also appeared to avoid flight with, or into, the southeast winds predominating in seas surrounding the breeding colony at Reunion Island (Stahl and Bartle 1991). When moving to and from the colony, these birds flew primarily to the south and west of a southeastern course (see also Weimerskirch et al. 1993, for similar response to wind direction in Wandering Albatrosses *Diomedea exulans*).

HABITAT AFFINITIES

P. a. auricularis and *P. a. newelli* preferred distinctly different but productive waters. *P. a. auricularis* found suitable foraging in waters over the continental slope of Mexico. When feeding, they were often associated with "upwelling fronts" accompanied by flotsam, slicks, and changes in water color (pers. observ.). Attraction of *P. a. auricularis* to "upwelling and coastal areas" was also noted by Au and Pitman (1986), who, like us, saw them feeding in association with multispecies bird flocks on prey forced to the surface
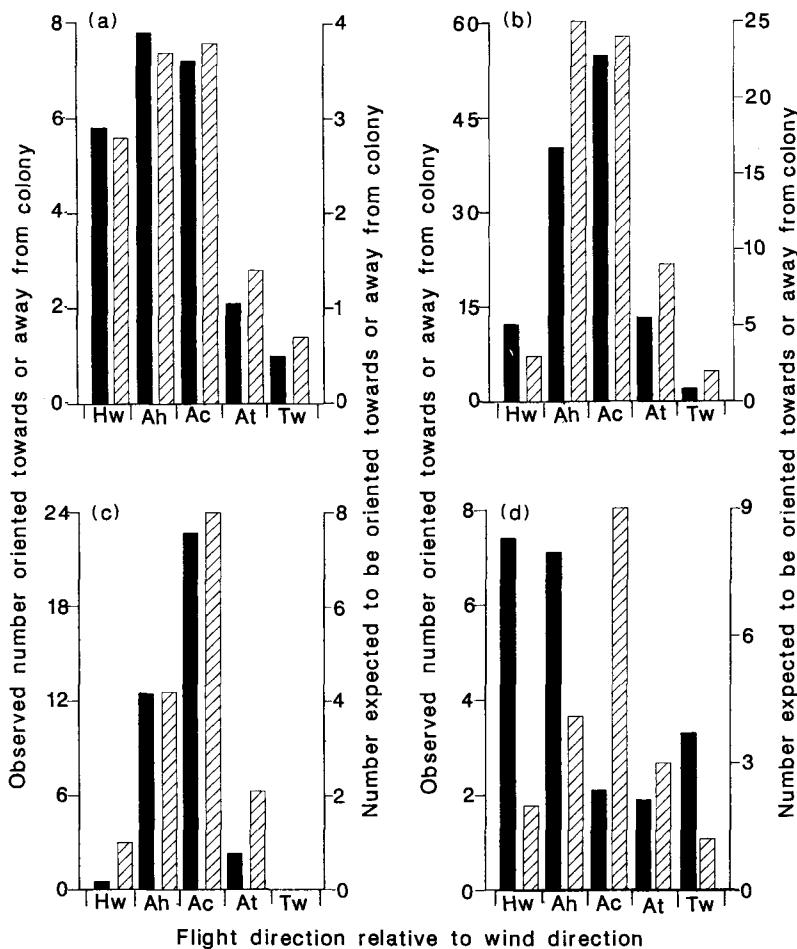
FIGURE 13.   Relationship between flight direction relative to colony location and flight direction relative to wind direction: (a) Townsend's Shearwater, (b) Newell's Shearwater, (c) Hawaiian Dark-rumped Petrel, and (d) Galapagos Dark-rumped Petrel. See Figure 12 for definitions of abbreviations. See Methods; Flight Behavior, for calculation of expected and observed values.

by dolphin (Family: Delphinidae). Use of highly productive waters associated with upwelling systems on the continental slope, and to a lesser degree the continental shelf, has been observed in four of the five other taxa of the Manx group (Hutton's Shearwater *P. huttoni* and Fluttering Shearwater *P. gavia,* Halse 1981, Wragg 1985; Manx Shearwater, Brooke 1990; and Black-vented Shearwater *P. opisthomelas,* Jehl 1974, Pitman 1986).

The sixth taxon, *P. a. newelli,* is apparently unique among the Manx group in having highly pelagic foraging affinities. These birds found suitable foraging over tropical waters of the ECC, and more specifically, the Inter-tropical Convergence Zone (i.e., similar to findings of King and Gould 1967). Frequent squalls, high winds,

turbulence and "ocean fronts" in this zone (see Murphy and Shomura 1972, Woods et al. 1977) may affect behavior and/or availability of prey and/or behavior of tunas (*Thunnus* spp.) on which *P. a. newelli* rely to drive prey to the ocean surface. Murphy and Shomura (1972), studying tunas in the ECP, found that the ECC, when compared to the NEC and SEC, held the highest densities of schooling, surface-feeding (smaller) tunas, the highest density of ocean "fronts," and a strong association between them. Gould (1974), King (1974) and Pitman (1986) also found the ECC important to seabirds.

Densities of the petrels covaried positively with wind speed, a result dissimilar to the shearwaters, but consistent with patterns reported for Northern Fulmars (*Fulmarus glacialis,* a petrel-

like procellariid) in the North Atlantic (Coulson and Horobin 1971, Manikowski 1971). Lack of a relationship between density and oceanographic factors (i.e., those likely to affect prey distribution) in *Pt. p. phaeopygia* may have been related to opportunistic foraging, or uniform prey distribution. The negative density/sea-surface temperature relationship in *Pt. p. sandwichensis* was independent of colony distance, indicating preference for cooler waters of the NEC. In fact, and in contrast to *P. a. newelli,* the evidence suggest that a major concentration of *Pt. p. sandwichensis* feed north of the main Hawaiian Islands in spring (King 1970). This, and disparity we observed in habitat use by the two species in autumn (when few occur north of Hawaii; King and Gould 1967, Gould 1983) suggests partitioning of foraging habitat.

WING MORPHOLOGY AND FORAGING HABITS

Difference in foraging habits of *P. a. auricularis* and *P. a. newelli* vs. the petrels were consistent with differences in wing morphology. Shearwaters of the Manx group feed by pursuit diving (Murphy 1936, Brooke 1990, Wood 1993). Furthermore, they use their wings, not their feet, to propel themselves while diving. Thus, high wing loading is likely a result of reduction of wing area (to allow wing-propelled swimming; see Pennycuick 1987), and increase in body density (to reduce buoyancy) facilitating more efficient diving, which in turn demands more rapid, energy demanding flight than the (non-diving) *Pt. phaeopygia.* This idea is consistent with flight styles. The shearwaters use a series of rapid wingbeats on stiff wings interspersed with short glides, and fly more directly (often into the wind) than the petrels. In contrast, the petrels fly mostly in wheeling arcs while soaring (see above). Although shearwater flight appeared more energy expensive, they flew to highly productive feeding areas and also rested more often than the petrels. In contrast, the petrels appeared to have foraged more opportunistically (i.e., their densities were affected little by oceanographic variables) while conserving energy through more efficient use of the wind and sea waves.

POPULATION ESTIMATES

Based on demographic parameters (see Methods), our estimates for number of breeding pairs of *P. a. auricularis, P. a. newelli, Pt. p. sandwichensis* and *Pt. p. phaeopygia* are 10,600, 18,000–19,000, 3,750–4,500, and 20,000, respectively. Estimates of *P. a. newelli* and *Pt. p.*

sandwichensis may be lower than true numbers because we did not census waters north and west of Hawaii. Estimates of *Pt. p phaeopygia* also may be low because we lacked coverage of a sector in the southwest part of their range (see Pitman 1986). On the other hand, on-going mammalian predation is likely to be causing population decline of all four taxa because these highly K-selected species are especially vulnerable to even a slight increase in adult mortality (see Simons 1984, Mougin et al. 1987, Wooller et al. 1989, Brooke 1990). This factor would act to inflate our estimates because our data were collected over an 11-year period.

Three other studies used at-sea censuses to estimate seabird populations (Ainley et al. 1984, Stahl and Bartle 1991, Piatt and Ford 1993), although 95% confidence intervals were not calculated. In our study, 95% CIs for pelagic population estimates were broad for *P. a. auricularis* (upper limit >4 times lower limit), less so for taxa of *P. phaeopygia,* and narrower for *P. a. newelli* (upper limit twice lower limit). This level of precision may seem low compared to CIs developed for other biological traits (e.g., metric characters, clutch size), however, population size is intrinsically more variable than many other traits because it is dynamic, fluctuating in both time (within year and between year variations) and space (Seber 1982). Even in studies such as ours, with extensive coverage of the pelagic range, CIs of seabird populations from at-sea censuses will always have large associated uncertainty because of the bird's extremely patchy patterns of occurrence (cf. Hunt 1990, 1991). Nevertheless, similarity of estimates obtained in both spring and autumn (i.e., in two independent samples) for *P. a. newelli* and *Pt. p. sandwichensis* suggests that our pelagic estimates are reliable. Regarding breeding populations, even when using the most pesimistic scenario, our minimum estimates for *P. a. auricularis, P. a. newelli,* and *Pt. p. sandwichensis* (2,600, 7,500, and 1,400 pairs, respectively) are greater than previous estimates (1,000, 6,000, and 600 pairs). Our minimum and maximum estimates (7,000–36,500 pairs) for *Pt. p. phaeopygia* are similar to previous estimates (7,500–35,000).

Demographic assessment notwithstanding, censuses west and north of the Hawaiian Islands, and information from this study could, for the first time, provide complete population estimates of *P. a. newelli* and *Pt. p. sandwichensis.* We would not expect large numbers of *P. a. newelli* or *Pt. p. sandwichensis* to fly far to the south-

west or west because this would usually require heading downwind on out-going trips, a flight direction they avoid (see above). Indeed, King and Gould (1967) reported concentrations of *P. a. newelli* only to the south, and few west of 170°W. Although an appreciable number of *P. a. newelli* and especially *Pt. p. sandwichensis* may feed north and northwest of Kauai during spring and summer, few birds of either species occur in near-to-Hawaii waters during autumn (King and Gould 1967, King 1970, Gould 1983). Thus, we censused nearly all of the area where these species appear to be concentrated in the non-breeding season.

ACKNOWLEDGMENTS

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