

MIGRATION ROUTES OF SOOTY SHEARWATERS IN THE PACIFIC OCEAN¹

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Abstract. During 17 cruises, 1983 to 1991, we recorded flight directions and densities of Sooty Shearwaters (*Puffinus griseus*) migrating across the equatorial Pacific, between the Americas and 170°W. Sooty Shearwaters breed in New Zealand and Chile in winter (seasons given as “boreal”), migrate to the North Pacific during spring, and return south in autumn. A two-fold increase in numbers seen flying northwest from the Peru Current in spring compared to the number flying southeast on return in autumn, and a six-fold increase in numbers flying southwest towards New Zealand during autumn compared to the number migrating northeast during spring, indicates that many completed a figure-eight route (ca. 40,500 km) each year. This route would involve easterly flight from New Zealand to the Peru Current in winter, northwesterly flight to the western North Pacific in spring, eastward movement to the eastern North Pacific during summer, and southwest flight to New Zealand during autumn. We suggest that most shearwaters using this route are nonbreeders, possibly from both the New Zealand and Chilean populations. Many birds, probably breeders from both populations, likely use shorter routes to and from the North Pacific (ca. 28,000 to 29,000 km). Annual variation in the number of transequatorial migrants was positively correlated with a progressive, annual increase in sea-surface temperature, due to large-scale ocean warming in the eastern Pacific. A progressive increase in number of shearwaters migrating to the North Pacific mostly reflected increased migration from the Peru Current, consistent with a concurrent sharp decline of these birds in the California Current. These results indicate a distributional shift in feeding location during the nonbreeding period, from the eastern boundary currents to the central North Pacific, which has been exhibiting a cooling trend.

Key words: *El Niño*, migration routes, ocean warming, Pacific Ocean, *Puffinus griseus*, Sooty Shearwater.

INTRODUCTION

The Sooty Shearwater (*Puffinus griseus*) is one of the most abundant seabirds of the Pacific Ocean, with breeding colonies on islands near New Zealand, Chile, and Australia (Everett and Pitman 1993, Warham 1996). The New Zealand population numbers in the millions, including an estimated 5.5 million birds in the Snares Islands population alone (Warham and Wilson 1982). The only Chilean colony for which a population estimate is available (200,000 birds) breeds on Guafo Island (Clark et al. 1984a), although other colonies are numerous (Clark et al. 1984b, Marin 1984). Colonies near Australia are small (Lane and White 1983); the largest includes an estimated 2,000 birds (Brothers 1979).

Sooty Shearwaters from New Zealand and Australia (hereafter “New Zealand”) are transequatorial migrants, and during summer (seasons refer to the “boreal” time frame throughout), are distributed across the North Pacific be-

tween Japan and North America (Shuntov 1974, Gould and Piatt 1993, Warham 1996). Prior to the 1990s, very large concentrations summered in the California Current (Briggs et al. 1987, Veit et al. 1997). The northward migration occurs in March to May, and the southward return occurs in September to December. Migration routes in the Pacific are not well known, although much information was assembled by Shuntov (1974) from studies on seasonal occurrence at-sea, including a 10-year study, 1959–1968, by the Russian Scientific Research Institute. One of their findings was that the migration occurs along a broad front extending 8,000 km across the Equator between 120°W and 170°E (see also King 1967, Pitman 1986).

It has been suggested that birds from the Chilean population migrate northward into the North Pacific along a narrow front off the coast of the Americas, possibly to as far north as British Columbia (Shuntov 1974, Guzman and Myres 1983, Warham 1996). However, this migration route is in question because sightings of this species off Central America are rare (Jehl 1974).

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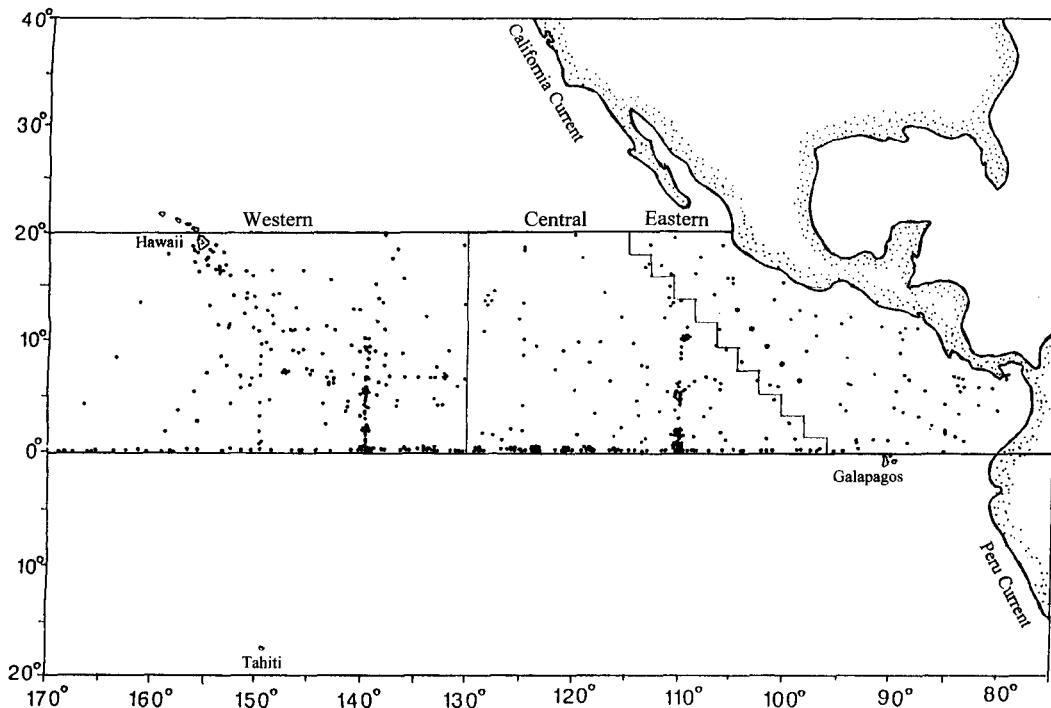


FIGURE 1. Study area in the equatorial Pacific, including the three designated sectors. Dots denote noon-day positions during seabird surveys at sea.

Indeed, the possibility that Chilean birds perform transequatorial migrations at all is questionable (Warham 1996) because many feed in the Peru Current during the period of, and just following, the postnuptial migration (March–July; Jehl 1973, Duffy 1981).

During at-sea surveys in the equatorial Pacific from 1983 to 1991 (Fig. 1), we gathered information on migration of Sooty Shearwaters. Our primary objective was to test for differences in flight direction between seasons and locations to provide insight on migration routes used by each population, Chilean and New Zealand. We assumed that birds flying northwest had originated from the Peru Current, and that flight towards the northeast indicated movement from New Zealand. This assumption is valid because (1) the two populations are separated by 8,500 km, one southeast of our study area and the other southwest, (2) before and during the postbreeding migration, Sooty Shearwaters do not occur in pelagic waters of the temperate to subtropical South Pacific that are not on the normal migration routes (references above; Spear and Ainley, unpubl. data), and (3) they pass quickly across

the equatorial Pacific to foraging areas in the North Pacific.

We also examined the relationship between extent of transequatorial movement and the occurrence of El Niño.

METHODS

STUDY AREA AND SURVEY PROTOCOL

The study area included waters lying between 20°N and the Equator, and from the coast of the Americas west to 170°W. From 1983 to 1991, we made 17 cruises in that area, each lasting one to three months. With exception of 1983 (one cruise during autumn), cruises were made twice each year, one in spring (18 April–27 June) and one in autumn (22 September–20 November). During daylight, while the ship was underway, we conducted observations from the flying bridge (14–15 m above sea level), and counted all Sooty Shearwaters passing within 500–600 m (depending on platform height) of the fore-quarter offering the best observation conditions. Two observers watched together during 90% of the surveys; one, three, or four observers

watched during the remainder. The outer portion of the transect area was scanned nearly constantly with hand-held 8 to 10 \times binoculars to detect shearwaters missed with the unaided eye.

Behaviors recorded for each sighting were: (1) resting on the water, (2) foraging (feeding or milling over a potential food source), and (3) flying in a steady direction. For the latter behavior, we recorded flight direction to the nearest 10 $^\circ$.

Although surveys were usually conducted continuously while the ship was underway during daylight, we divided the survey period into 30-min transects. Each half-hour we recorded ship's position, speed and course, wind speed and direction, and sea-surface temperature (SST). We conducted 1,826.5 hr of surveys during spring, and 1,660 hr during autumn. The total area surveyed, calculated for each transect as the survey period multiplied by ship speed and transect width, was 27,282 km 2 during spring and 25,785 km 2 during autumn.

We collected 37 Sooty Shearwaters, 11 during spring and 26 during autumn. Each was weighed, examined for molt, and sexed by examination of gonads. To compare fat loads, L. B. Spear scored subcutaneous fat of each after skinning them. Fat was scored as: 0 = no fat or traces, 1 = light deposit near hind limbs and abdomen but absent over the pectorals, 2 = light deposit continuous or mostly continuous over the pectoral, 3 = moderate deposit throughout, 4 = heavy deposit throughout (see Spear and Ainley 1998, for validation of this method).

DATA ANALYSES

We divided the study area into three sectors: eastern, central (western edge of the eastern sector to 129 $^\circ$ 59.9'W), and western (130 $^\circ$ W to 170 $^\circ$ W; Fig. 1). For each sector, by season and year, our survey effort averaged 1,041 \pm 758.5 km 2 ($n = 51$, range 95–3,320 km 2). We recorded 912 Sooty Shearwaters (see Discussion for evaluation of number recorded relative to the number expected). Of these, 783 birds were flying in a steady direction (migrating), or 429.8 after adjusting counts for the effect of bird movement relative to that of the ship (Spear et al. 1992; using flight speeds for this species given in Spear and Ainley 1997b), with an overall count of 558.8 birds. The latter adjustment is required in studies of flight direction from a moving vessel because any patterns in bird/ship direction

will bias analyses. For example, if birds flew east and west in equal numbers, unadjusted counts from a ship transiting west would show greater numbers flying east because the observer would count more that were flying east compared to those flying west. This adjustment is particularly important for fast fliers, such as Sooty Shearwaters. We calculated densities for each transect by dividing the adjusted count by the number of km 2 surveyed. Hereafter, all shearwater enumerations pertain to adjusted counts.

We used log-likelihood *G*-tests to test for behavioral differences (significance assumed at $P < 0.05$). We used multiple regression analyses performed with STATA (STATA Corp. 1995) to test for trends in shearwater densities (the dependent variable) as related to year and SST. Sidak multiple comparison tests (an improved version of the Bonferroni test; SAS Institute 1985) and *t*-tests were used to compare densities among sectors and use of different flight directions. The sample unit was one 30-min survey transect, each weighted for the area surveyed.

We log-transformed density to satisfy assumptions of normality (skewness/kurtosis test for normality of residuals, $P > 0.05$). Because densities (birds 100-km $^{-2}$) included values of zero, transformations were calculated as the log (density + 1). Experimentation with different modifications (e.g., log [density + 0.5]) demonstrated no appreciable effect of choice of modifications on quantitative outcomes of respective analyses. All ANOVAs and *t*-tests were of the log-transformed density values, although densities presented in figures are nontransformed data except for figures showing density comparisons among years. Normality was not achieved in all analyses, but least-squares regression analysis (ANOVA and *t*-tests) are 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 and *t*-tests at $P < 0.02$. We included two- and three-order polynomials in regression analysis to test for curvilinearity.

Because Sooty Shearwaters feed little in the

TABLE 1. Behavior of Sooty Shearwaters recorded during at-sea surveys in the equatorial Pacific, with respect to season and ocean sector (definitions given in Methods). "Enroute" denotes actively migrating birds who were flying in a steady direction.

Sector	Spring			Autumn		
	On water <i>n</i> (%)	Foraging <i>n</i> (%)	Enroute <i>n</i> (%)	On water <i>n</i> (%)	Foraging <i>n</i> (%)	Enroute <i>n</i> (%)
Eastern	0 (0.0)	6 (37.0)	10.2 (63.0)	1 (34.5)	1 (34.5)	0.9 (31.0)
Central	0 (0.0)	13 (21.2)	48.2 (78.8)	3 (9.6)	1 (3.2)	27.1 (87.1)
Western	24 (16.2)	11 (7.4)	113.1 (76.4)	61 (20.4)	8 (2.7)	230.3 (76.9)
Total	24 (10.6)	30 (13.3)	171.5 (76.1)	65 (19.5)	10 (3.0)	258.3 (77.5)

equatorial Pacific (see Results), we did not expect them to have responded directly to oceanographic conditions in the study area, such as SST, that may relate to food supply (Polovina et al. 1994, Roemich and McGowan 1995). However, we used SST in the South Equatorial Current (SEC) as a surrogate for SST in the eastern boundary currents to the northeast (California Current) and southeast (Peru Current). Like the SEC, these current systems are affected strongly by wind-driven upwelling of cool, deep waters. Processes that affect upwelling in the SEC are propagated to the east (then north and south) in warming events such as El Niño (Kessler and Taft 1987, Philander 1989, McPhaden and Hayes 1990). Therefore, we confined the regression analysis relating shearwater densities to SST to that part of the study area lying within the SEC, i.e., waters between 0° and 4°N (Wyrki 1966); the purpose was to eliminate confounding effects that could result from differences in SST in the SEC vs. the North Equatorial Countercurrent and North Equatorial Current. The latter also lie within the study area, but have warmer SST than the SEC. We also included "longitude" in these models to control for the east-to-west increase in SST in the SEC. We tested the null hypothesis that shearwater abundance did not increase with increase in SST, where rejection would indicate that more shearwaters migrated to the North Pacific during periods of ocean warming in the eastern Pacific.

TABLE 2. Body mass (g) and fat score (mean ± SE), by season, of female and male Sooty Shearwaters collected in the equatorial Pacific. Comparisons by *t*-tests. See Methods for scoring fat load. Sample sizes: spring, 2 females and 9 males; autumn, 9 females and 17 males.

	Mass			Fat score		
	Spring	Autumn	<i>P</i>	Spring	Autumn	<i>P</i>
Females	603 ± 43	778 ± 17	<0.001	1.5 ± 0.5	4.0 ± 0.0	<0.001
Males	683 ± 35	845 ± 23	<0.001	2.3 ± 0.5	3.8 ± 0.2	<0.001

RESULTS

BEHAVIOR AND BODY CONDITION

During both spring and autumn, 76–78% of the observations of Sooty Shearwaters involved birds that were actively migrating (Table 1). However, allocation of behaviors differed significantly between seasons (sectors grouped; $G_2 = 26.8$, $P < 0.001$). Higher proportions of birds foraging/feeding were recorded during spring, and higher proportions of birds resting on the water were recorded during autumn. Only 3% of the shearwaters were foraging during autumn compared to 13% during spring.

During spring, behavior differed between the three sectors ($G_2 = 24.4$, $P < 0.001$, Table 1). The difference resulted from a higher proportion resting on the water in the western sector compared to a higher proportion foraging in the eastern and central sectors. Shearwater behavior did not differ significantly between sectors during autumn ($G_2 = 2.3$, $P > 0.5$).

Of the 40 birds recorded as foraging, 5% were scavenging dead squid and 95% were pursuit plunging for live prey in mixed-species flocks over tuna.

Weight and fat load of both males and females were significantly greater during autumn compared to spring (Table 2). None of the 37 specimens were molting body or flight feathers.

FLIGHT DIRECTION

The proportion of shearwaters flying in a steady direction (i.e., migrating vs. resting on the water and foraging) differed little between seasons (Table 1). Therefore, between-season comparison of densities of birds flying in different directions was a valid assessment of seasonal differences in the use of different migration routes. Nevertheless, density values used in these analyses are not absolute, because migrants resting on the water or foraging were excluded.

During spring, 87.0% of the shearwaters recorded as flying in a steady direction were headed northwest (300° to 350°) or northeast (10° to 60°). During autumn, 79.9% of the directional flyers were headed southwest (190° to 240°) or southeast (120° to 170°).

During spring, density indices of shearwaters migrating northwest increased from east to west (Sidak test comparing densities among sectors, all $P < 0.001$, Fig. 2A). Densities of those migrating northeast increased in a similar way (Sidak test, $P < 0.01$, Fig. 2A), except that the difference between the eastern and central sectors was nonsignificant ($P > 0.3$). These results indicate that birds from the Peru Current flew to the central and western North Pacific, and that the New Zealand birds recorded during spring were migrating to the eastern North Pacific.

During autumn, density indices of shearwaters headed southwest increased from east to west (Sidak test, all $P < 0.01$, Fig. 2B), indicating that they were enroute from the eastern North Pacific to the vicinity of New Zealand. Density indices of birds flying southeast towards the Peru Current also increased from east to west, indicating that they had come from the central or western North Pacific (Sidak test, all $P < 0.01$, Fig. 2B).

During spring, density indices of shearwaters compared within each sector were significantly greater among those headed northwest than birds headed northeast (Sidak test, all $P < 0.02$, Fig. 2A). In fact, when grouping the three sectors, densities of shearwaters moving northwest in spring were 15 times greater than densities of birds moving northeast (Fig. 3). These results indicate that, within the study area, the vast majority of birds crossing the Equator in spring originated from the Peru Current.

During autumn, density indices of shearwaters compared within each sector were signifi-

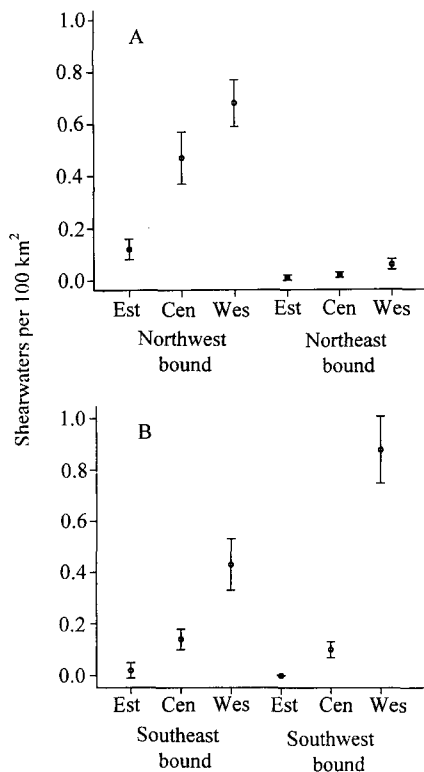


FIGURE 2. Density indices (mean \pm SE) of Sooty Shearwaters seen flying in different directions in the eastern (Est), central (Cen), and western (Wes) sectors of the eastern tropical Pacific during (A) spring and (B) autumn, 1983–1991. Number of transects were: 629, 1,266, and 1,758 for eastern, central, and western sectors, respectively, in spring; 464, 1,026, and 1,830, respectively, during autumn. Sector locations shown in Figure 1.

cantly greater among those headed southwest than birds headed southeast in the western sector (Sidak test, $P < 0.001$, Fig. 2B), but not the central or eastern sectors (both $P > 0.6$). When grouping the sectors, densities of shearwaters migrating southwest in autumn were 1.8 times greater than those of birds moving southeast (Fig. 3). These results indicate that the majority of birds crossing the Equator in autumn were migrating toward New Zealand.

The density index for shearwaters migrating on a northwest heading from the southeast Pacific during spring was 2.0 times greater than that recorded for birds returning on a southeast heading during autumn (unpaired $t_{6,971} = 6.0$, $P < 0.001$, Fig. 3). In contrast, the densities recorded for shearwaters migrating on a northeast

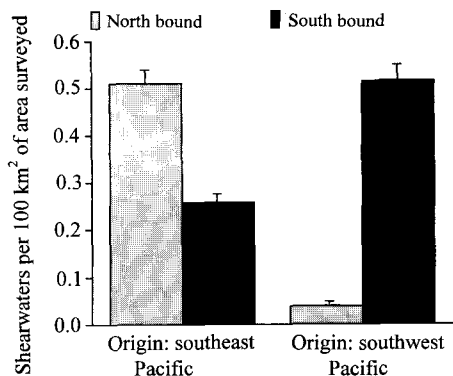


FIGURE 3. Density indices (mean + SE) of Sooty Shearwaters migrating from the southeast and southwest Pacific to the North Pacific, and returning from the North Pacific to respective locations in the South Pacific. Indices of shearwaters migrating from, and returning to, the southeast Pacific are those migrating northwest during spring, and southeast during autumn, respectively. Indices of shearwaters migrating from, and returning to, the southwest Pacific are those migrating northeast during spring, and southwest during autumn, respectively. Density values are not absolute values because, when seen, some birds in migration were sitting on the water, foraging, or flying in other directions, and were not included in the calculations. Samples sizes (number of transects) were 3,653 transects in spring and 3,320 in autumn.

heading from the southwest Pacific during spring, was 12 times less than densities returning on a southwest heading in autumn ($t_{6,971} = 8.6$, $P < 0.001$; Fig. 3). These results indicate that, within the study area, more birds migrated from the Peru Current to the North Pacific in spring than returned to the Peru Current in autumn, and the opposite among birds from New Zealand.

ANNUAL TRENDS IN NUMBER OF MIGRANTS

Densities increased significantly with year during both spring and autumn when analyzed across sectors (see "All sectors" in Table 3, Fig. 4). During spring, the relationship was curvilinear due to a slight decline in density during 1984 to 1986, followed by leveling to 1988, and then an abrupt increase during 1989 to 1991.

During spring, a curvilinear relationship between shearwater densities and year, similar to that of the combined data, was evident in the western sector (Table 3, Fig. 5). There also was a significant linear increase in density with year in the central sector, but not in the eastern sector. No shearwaters were observed in the eastern sector during spring 1985 and 1988; spring 1986

and 1990 were the only years in which appreciable numbers were seen (Fig. 5). Thus, increased movement in the western sector, where most shearwaters were flying northwest (Fig. 2A), was primarily responsible for the overall increase in density with year during spring.

During autumn, densities of Sooty Shearwaters increased significantly with year in the central sector (Table 3, Fig. 5). The relationship was curvilinear due to low, stable densities during 1983 to 1988, followed by a marked and progressive increase during 1989 to 1991. No shearwaters were recorded in the central sector during autumn 1984, 1985, 1987, or 1988. There were no significant relationships between densities and year in the eastern and western sectors (Table 3, Fig. 5). During autumn, no shearwaters were recorded in the eastern sector during six of the nine years. Thus, the annual increase during autumn was primarily due to increase in the central sector, where densities of birds moving southeast and southwest were similar (Fig. 2B).

SHEARWATER DENSITIES IN RELATION TO SEA-SURFACE TEMPERATURE (SST)

There were significant, positive relationships between shearwater densities and SST in the SEC during both spring and autumn (Table 4, Fig. 6). Thus, for a given longitude, densities increased with SST. Warmest SSTs occurred during El Niño 1986–1987 and 1990–1991 (El Niño timing in Trenberth and Hoar 1996, Trenberth 1997), and during non El Niño 1989 (Fig. 6).

DISCUSSION

Our total count of 912 Sooty Shearwaters may seem low, considering the abundance of this species and our claim that we surveyed a large section of the migration front. However, a more accurate perspective is obtained when considering the shearwater count in relation to the width of the transect strip (500–600 m) and the total area surveyed (53,067 km²), relative to the area over which the shearwaters migrated (study area = 19.25 million km²). Hence, with an average (corrected) density of 0.00827 birds km⁻² recorded during spring, an estimated average of 3.8 to 5.7 million Sooty Shearwaters crossed the study area each spring, assuming that the migration period lasted 60 to 90 days (see Introduction), and that, with an average flight speed of 47 km hr⁻¹ (Spear and Ainley 1997b), 2.5 days were required for a shearwater to cross the study

TABLE 3. Regression analyses for annual trend in density of Sooty Shearwaters migrating across three sectors in the equatorial Pacific, 1983–1991. For these analyses, the dependent variable was log-density, or log-birds per 100 km². Year was analyzed as a continuous term. See Figure 1 for sector locations; Figure 4 for sample sizes.

	Regression coefficient \pm SE	F-value	P
Spring			
Eastern sector			
year	-0.005 ± 0.007	0.0	>0.9
Central sector			
year	0.018 ± 0.007	5.8	<0.02
Western sector			
year, linear	0.044 ± 0.008	29.9	<0.001
year, quadratic	0.019 ± 0.004	27.9	<0.001
All sectors			
year, linear	0.024 ± 0.005	26.9	<0.001
year, quadratic	0.007 ± 0.002	9.3	<0.002
Autumn			
Eastern sector			
year	-0.004 ± 0.005	1.0	>0.2
Central sector			
year, linear	0.033 ± 0.005	41.1	<0.001
year, quadratic	0.014 ± 0.002	33.6	<0.001
Western sector			
year	-0.006 ± 0.008	0.6	>0.3
All sectors			
year	0.019 ± 0.004	18.9	<0.001

area. Similarly, the corrected mean density of 0.01293 birds km⁻² recorded during autumn, equates to an estimated 6 to 9 million migrants per annum. These numbers are well within the expected range when considering population size, seasonal differences in migration routes of Chilean and New Zealand populations (see below), and that both adults and subadults were involved.

BEHAVIOR AND BODY CONDITION

The Sooty Shearwaters we saw in the equatorial Pacific were clearly migrating, based on their consistent flight direction. However, these birds also rested (16%) and foraged (7%). Although the proportion flying directionally differed little between seasons, they foraged more often during the postbreeding, spring migration (13%) than during the prenuptial movement (3%). This may not be surprising. These birds were heavier and fatter during the prebreeding migration. Chu (1984) also noted that Sooty Shearwaters in the California Current fattened considerably before migrating south. Therefore, feeding during the prenuptial migration may be unnecessary.

Higher feeding incidence in eastern and central sectors was probably related to the increased productivity west-to-east in the equatorial Pacific (Fiedler et al. 1991). Thus, feeding opportunities were likely to have occurred more often in the more eastern regions. The fact that more shearwaters migrated through the western sector where feeding incidence was lowest, also indicates that feeding was not a high priority during migration through the equatorial Pacific.

MIGRATION ROUTES

Consistent with Shuntov (1974), our results indicate that, during spring, relatively few Sooty Shearwaters from New Zealand migrated northeast across the equatorial Pacific. This finding, in conjunction with a 12-fold increase in the number of autumnal migrants heading southwest on return to New Zealand, indicates that most spring migrants from New Zealand flew to the

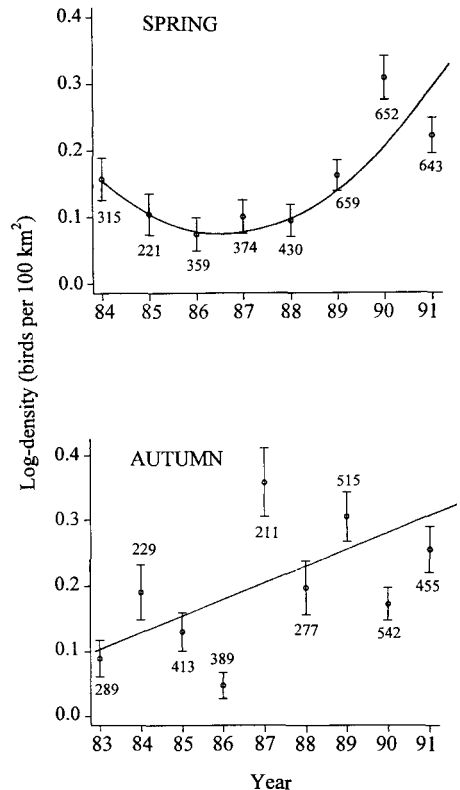


FIGURE 4. Annual densities (mean \pm SE, log-transformed) of Sooty Shearwaters (sectors combined) migrating across the equatorial Pacific. Numbers adjacent to data are sample sizes.

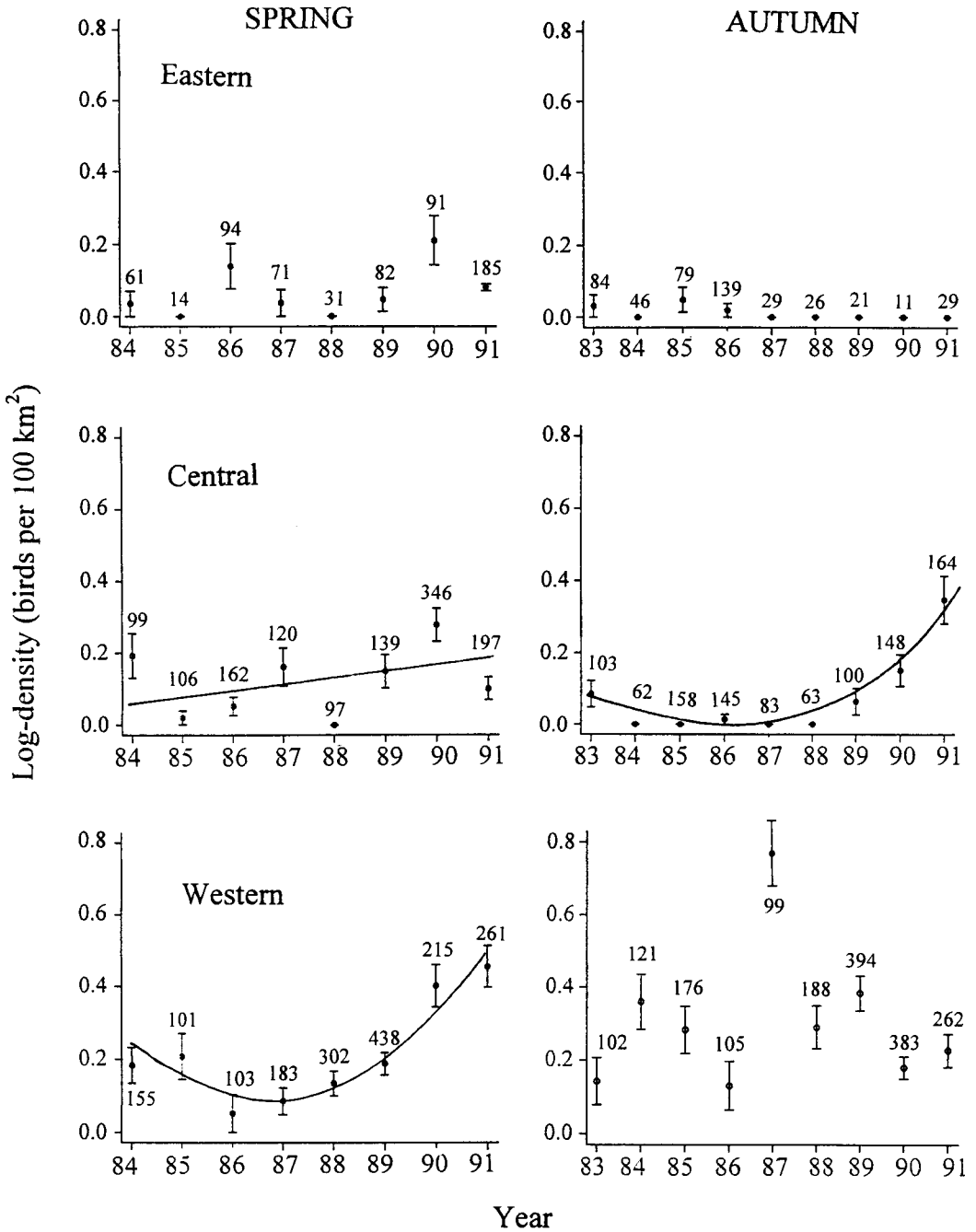


FIGURE 5. Annual density (mean \pm SE, log-transformed) of Sooty Shearwaters, shown by season and sector. Numbers adjacent to data are sample sizes. See Figure 1 for sector locations.

TABLE 4. Regression analyses for the relationship between Sooty Shearwater density (log-shearwaters per 100 km²) and sea-surface temperature (SST), controlling for longitude. This analysis pertains only to data collected within the South Equatorial Current. The sample in units of 30-min survey transects was 1,709 for spring and 1,291 for autumn. All numerator df = 1. Spring: model $F_{2,1706} = 16.1$, $P < 0.001$; Autumn: model $F_{2,1288} = 13.0$, $P < 0.001$.

	Regression coefficient \pm SE	F-value	P
Spring			
SST	0.022 \pm 0.008	7.3	<0.01
Longitude	0.003 \pm 0.001	25.2	<0.001
Autumn			
SST	0.020 \pm 0.007	8.3	<0.01
Longitude	0.003 \pm 0.001	10.6	<0.001

western North Pacific on a northern or north-western course west of our study area; that is, west of 170°W (Fig. 7A; see Shuntov 1974, for similar conclusions). The large concentration of shearwaters migrating southwest across the study area from the eastern North Pacific during autumn also supports the idea that, during summer, many moved west-to-east across the North Pacific (Phillips 1963, Shuntov 1974). It also is likely that New Zealand birds who remained in the western North Pacific during summer flew south across waters to the west of our study area when returning to New Zealand during autumn (Fig. 7A; see Shuntov 1974).

During spring, most Sooty Shearwaters flew northwest and crossed the Equator in the western sector of our study area, indicating migration from the Peru Current to the central or western North Pacific. There, between Japan and 160°E, this species is particularly abundant during spring (Shuntov 1974). Interestingly, the number of shearwaters migrating from the Peru Current to the North Pacific during spring was twice as great as the number returning from the North Pacific in autumn. Two explanations are possible. First, members of the New Zealand population, probably nonbreeders or failed breeders, migrated from New Zealand to the Peru Current during autumn and winter (Fig. 7A). A likely route would include southward flight from New Zealand to the Southern Ocean during autumn (reviewed in Shuntov 1974, Warham 1996), followed by easterly and northeasterly flight, with arrival in the Peru Current during winter or spring. Second, nonbreeders from the Chilean

population also may have used the “figure-eight” route proposed above for the New Zealand population. Serventy (1953) suggested that the closely related Short-tailed Shearwater (*P. tenuirostris*) also uses a figure-eight route as a consequence of wind regimes (see below), albeit a different route than the one we suggest for the Sooty Shearwater.

Movement of Sooty Shearwaters from New Zealand to the Peru Current would not be surprising. The Peru Current is one of the world's most productive ocean systems (Glantz and Thompson 1981), and a diverse group of other Procellariiformes breeding in New Zealand migrate there. These are the Salvin's (*Thalassarche salvini*), Chatham (*T. eremita*), and Buller's Mollymawks (*T. bulleri*); Westland (*Procellaria westlandica*), Parkinson's (*P. parkinsoni*), Cook's (*Pterodroma cooki*), and White-headed Petrels (*P. lessonii*); Buller's Shearwater (*Puffinus bulleri*), and White-faced Storm-Petrel (*Pelagodroma marina*; Murphy 1936, Pitman and Ballance 1992, Howell and Webb 1995, Spear et al. 1995, Howell et al. 1996).

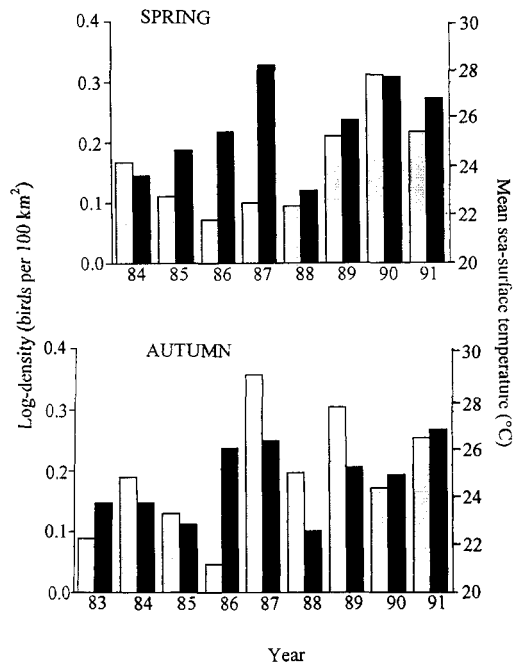


FIGURE 6. Mean density (log-transformed) of Sooty Shearwaters (light bar) in relation to mean sea-surface temperature (dark bar) recorded during surveys in the South Equatorial Current. Numbers above bars are sample sizes.

The idea that the Chilean birds migrate north along the coast of the Americas to the California Current, and then back to the Peru Current (Shuntov 1974, Warham 1996), is not supported by our results. First, the nearly complete absence of Sooty Shearwaters migrating south along the coast of Central America during autumn indicates that few breeders from the Chilean population occurred in the California Current. Second, densities of shearwaters moving north in the eastern sector were low during spring. These results indicate that most Sooty Shearwaters found in the California Current had flown there from the western or central North Pacific, and that most Sooty Shearwaters found off the west coast of North America originate from New Zealand.

These results also indicate that Chilean birds that migrated in spring to the central or western North Pacific remained there until autumn (i.e., they did not move to the eastern North Pacific before returning to Chile). However, because subadults remain at sea for several years before returning to the natal colony (reviewed in Warham 1996), there is a possibility that some Chilean birds also used the figure-eight route apparently used by the New Zealand population (Figs. 7A, B). This would be consistent with factors related to wind regimes (see below).

MIGRATION ROUTES IN RELATION TO WIND DIRECTION

Based on wind regimes in the Pacific Basin, and using the proposed migration routes, Sooty Shearwaters migrating north from New Zealand would be oriented across-wind, or across tailwinds (i.e., with the wind on one rear quarter; Figs. 7A, C). The same would be true during spring for birds migrating to the North Pacific from the Peru Current (Figs. 7B, C). During autumn, however, birds returning to colonies near Chile would be headed into the wind, or across headwinds, after crossing the Equator. This would not be true for birds returning to New Zealand, which always would be flying with quartering tailwinds or across-wind.

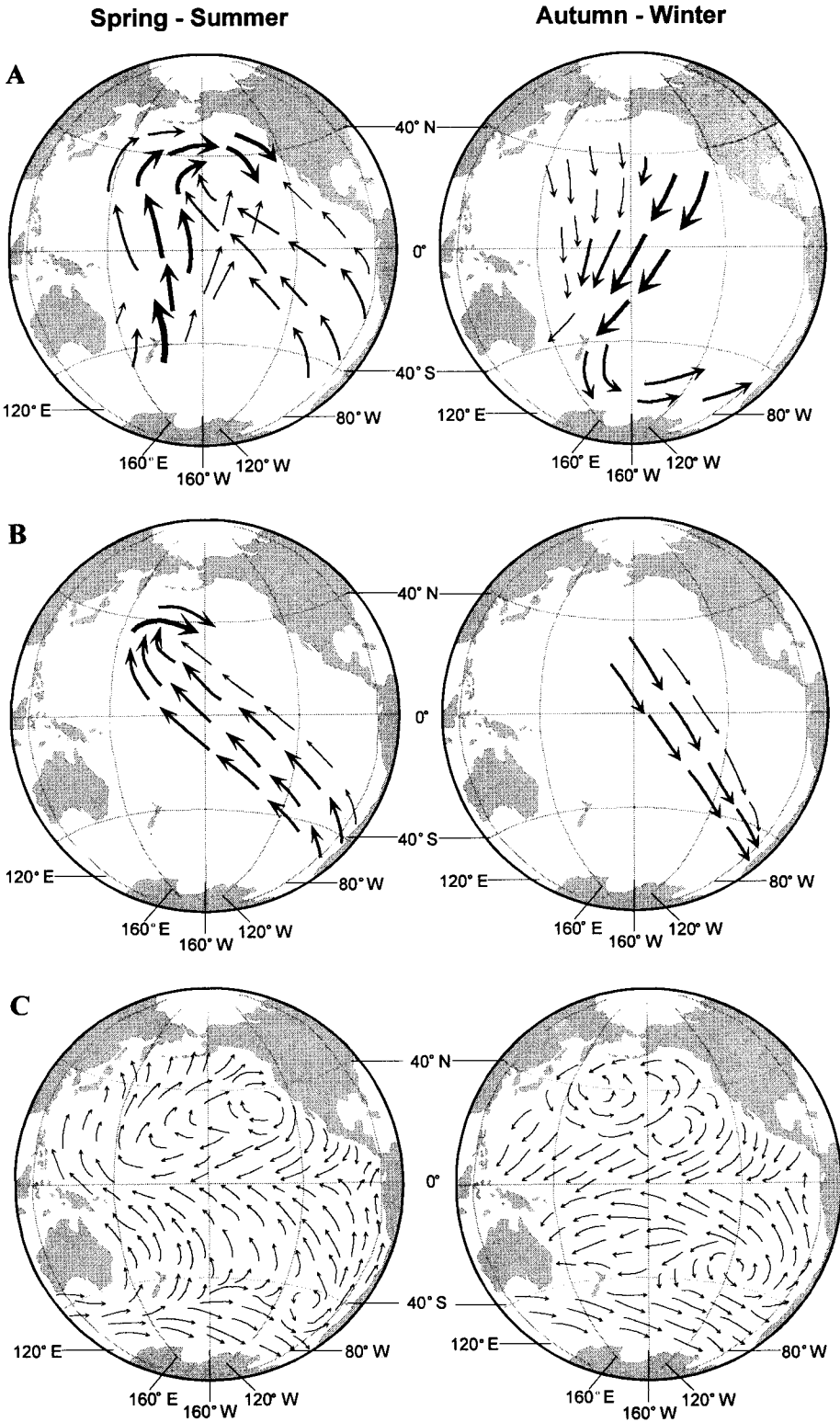
Spear and Ainley (1997a) found that cross-wind flight was preferred by this species, which also flew regularly into the wind and across headwinds; tailwind and across-tailwind flight was avoided. In that earlier study, in which most data were gathered in the California and Peru Currents where the shearwaters were foraging, we concluded that headwind flight maximized the chance of detecting prey. Specifically, because air speed for downwind flight must be greater than wind speed (especially in birds like Sooty Shearwaters, which must fly fast due to high wing loading; Pennycuik 1989, Spear and Ainley 1997a), ground speeds obtained when flying downwind are likely too great to allow adequate time to detect and capture mobile prey on the flight path. Alternatively, the higher ground speeds obtained during flight across tailwinds increases the migration rate over waters unfavorable for feeding (such as the tropics).

Consistent with this idea, our results indicate that headwind flight occurred among migrating Sooty Shearwaters only during autumn, and primarily among birds of Chilean origin. This, in addition to the fact that the Peru Current is, in most years, a highly productive system where feeding opportunities are usually favorable, might explain the large number of Sooty Shearwaters who spend the nonbreeding season in the Peru Current (Bourne and Dixon 1973, Jehl 1973, Duffy 1981, Spear and Ainley, unpubl. data). The headwind flights during the prenuptial migration in autumn could be facilitated by the larger body mass and, thus, wing loading (22.5% and 19.2% increase among females and males, respectively; Table 2) of breeders, compared to post-breeders migrating in spring. Higher wing loading enhances capabilities for headwind flight (Pennycuik 1989).

MIGRATION DISTANCE COMPARED WITH THAT OF OTHER AVIAN SPECIES

The distances flown by Sooty Shearwaters using the figure-eight route (ca. 40,500 km) would probably differ little from migration distances flown by Arctic Terns (*Sterna paradisaea*), the

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 FIGURE 7. Suggested migration routes of Sooty Shearwaters from colonies near (A) New Zealand and Australia, and (B) Chile. Sizes of vectors reflect differences in the number of shearwaters, as suggested by Shuntov (1974; Figs. 17, 18) and densities recorded in this study for various sectors and seasons in the equatorial Pacific (see Fig. 2). (C) Wind regimes of the Pacific Ocean during the two seasonal periods (from Gentilli 1966).



species thought to have the longest migrations of any avian species (e.g., Gill 1995). The Arctic Tern breeds in the arctic to 80°N (Harrison 1987), and winters in the Southern Ocean to about 75°S (Ainley et al. 1984, Gudmundsson et al. 1992, Stahl et al. 1996). Although migration routes are not well known, based on band returns and observations at sea, Arctic Terns breeding in Scandinavia likely complete a route which, at maximum, includes flight to and from waters south of Australia and New Zealand (details in Stahl et al. 1996). The round-trip flight would be about 46,000 km, or 5,500 km (12%) longer than the figure-eight proposed for Sooty Shearwaters.

MIGRATION IN RELATION TO OCEANOGRAPHIC FACTORS

Shearwater densities were correlated with SST in the SEC, where changes in oceanographic climate foretell El Niño conditions in the Peru and California Currents (Philander 1989, McGowan et al. 1998). A very strong El Niño occurred in 1990–1991 (Trenberth 1997). In concert, a significant increase occurred in the number of transequatorial migrant shearwaters. Interestingly, the increase mostly involved migrants from the Peru Current, but likely included birds from the Chilean and New Zealand populations (see above). The pattern is consistent with that of Sooty Shearwaters in the California Current. Previously, 3–5 million Sooty Shearwaters summered in that current system (Chu 1984, Briggs et al. 1987), but they declined by 90% during 1985 to 1994, primarily after 1989 (Ainley et al. 1995, Oedekoven 1997, Veit et al. 1997). The decline also correlated with ocean warming and decline in zooplankton (Roemich and McGowan 1995, McGowan et al. 1996). Our failure to detect a decrease in numbers of transequatorial migrants indicates that the decrease in the California Current was not due to a major population decline.

The California and Peru Currents, both eastern boundary currents, are very productive but are strongly affected by El Niño (McGowan 1990). The decline of Sooty Shearwaters in the California Current, concurrent with increased migration from the Peru Current, indicates analogous climate change in both systems. We propose that shearwaters have redistributed themselves in the Pacific Basin, including a shift from prevalence in eastern boundary currents to more

pelagic waters of the western and central North Pacific. This pattern would be consistent with a noted preference of Sooty Shearwaters for cold-water areas (Allen 1994, Warham 1996, Oedekoven 1997), and the compensatory cooling of the western and central North Pacific as the boundary currents warmed (McGowan et al. 1998).

In conclusion, migration routes of Sooty Shearwaters are more complex than previously suspected, and likely differ depending on population, breeding status, and environmental factors. This idea requires further investigation. We suspect, however, that the proposed figure-eight route, which is about 1.5 times longer than the relatively direct routes between the North Pacific and New Zealand (round-trip, ca. 29,000 km) or Chilean (ca. 28,000 km) breeding colonies (Figs. 7A, B), is used primarily by nonbreeders, perhaps from both populations. We also suspect that the proposed direct routes are used primarily by breeders.

The positive correlation between SST and density of shearwaters migrating to the North Pacific per annum has strong implications regarding the effects of large-scale ocean warming, particularly in the context of the four back-to-back El Niños that occurred since 1990 (Trenberth 1997). The results, indicating a major decline in numbers of Sooty Shearwaters using historically important foraging areas in the Peru and California Currents, also have strong implications regarding possible negative impacts by the recent, extended period of ocean warming on populations of species endemic to the eastern boundary currents. However, adequate monitoring programs for such species are sparse (California Current: Carter et al. 1992, Oedekoven 1997; Peru Current: Crawford and Jahncke, in press.)

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