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SOOTY SHEARWATERS OFF CALIFORNIA: DISTRIBUTION, ABUNDANCE AND HABITAT USE[1]

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Abstract. Sooty Shearwaters (*Puffinus griseus*) migrate to waters of the North Pacific Ocean each spring after nesting on colonies in the South Pacific. Their numbers and habitat affinities off California were investigated during 60 aerial and 24 ship surveys in 1975 to 1978 and 1980 to 1983. Population densities computed monthly indicated arrival throughout California waters in late March and departure of most birds from southern California one to two months earlier than in waters to the north. Peak densities exceeded 10 birds km^{-2} over the shelf and upper continental slope off central California for two to six months each year but reached these levels on only a few occasions in northern and southern California. Densities in all areas generally were highest in late spring and reached secondary peaks in mid- to late summer after variable declines from the spring peak. Populations are estimated to total 2.2 to 4.2 million birds in May, June, or July, depending on year and method of calculation. Population turnover may be rapid; total numbers of birds migrating through the area may be much higher than the "instantaneous" population. Shearwaters concentrated in relatively shallow, cool waters, especially where strong thermal gradients marked the edges of upwellings.

Key words: Sooty Shearwaters; Puffinus griseus; *California; seabirds; migration; population density.*

INTRODUCTION

Sooty Shearwaters (*Puffinus griseus*) nest on offshore islands of New Zealand, Australia, and Tierra del Fuego. Richdale (1963) studied their breeding biology in southern New Zealand, but virtually nothing is known of numbers or nesting phenology of the South American populations (Murphy 1936, Palmer 1962). During the austral winter, some Sooty Shearwaters remain in cool waters of the southern hemisphere (Jehl 1973, Brown et al. 1975, Ainley et al. 1983), but many migrate northward as far as Alaska in the Pacific Ocean and Greenland in the Atlantic (Bourne 1956, Phillips 1963). Some banding has been done on New Zealand colonies (Richdale 1963, Warham 1964), but there are few returns and the migration routes remain controversial (Phillips 1963, Ainley 1976, Guzman and Myres 1982). Along the west coast of North America, Sooty Shearwaters are reported to be among the most numerous of all seabirds from May through September (Sanger 1972; Wiens and Scott 1975; Briggs and Chu, in press).

During multiyear studies of seabirds and marine mammals off California, we focused attention on the Sooty Shearwater as a key species in overall seabird trophic dynamics. This paper presents our estimates of shearwater population density throughout the year and examines environmental conditions at sites of shearwater concentrations. Related studies of diet and fat accumulation and results of computer modeling of Sooty Shearwater energy demands are reported in Chu (1984) and Briggs and Chu (in press).

STUDY AREA AND METHODS

Our data come from two studies conducted at sea: 1975 to early 1978 in the Southern California Bight, and 1980 to early 1983 in central and northern California. Additional observations were made in 1979 in Monterey Bay, where large numbers of Sooty Shearwaters have traditionally been reported (Loomis 1900, Beck 1910, Stallcup 1976).

STUDY AREA

The surveyed area extended westward 185 to 400 km from the California coast and covered about 215,000 km^2 within the California Current System (Fig. 1). The California Current arises at about 40° to 44°N as the southward-flowing extension of the West Wind Drift (or North Pacific Subarctic Current). As it flows southward off California it carries a mixture of cool, relatively fresh subarctic waters and cool, salty, nutrient-rich waters advected from upwelling regions along the coast. A limb of the current recurves counterclockwise at about 33°N to flow northward as the Southern California Countercurrent. This large, quasi-permanent eddy centers along the undersea ridge extending 200 km southeast from Point Conception and affects productivity off southern

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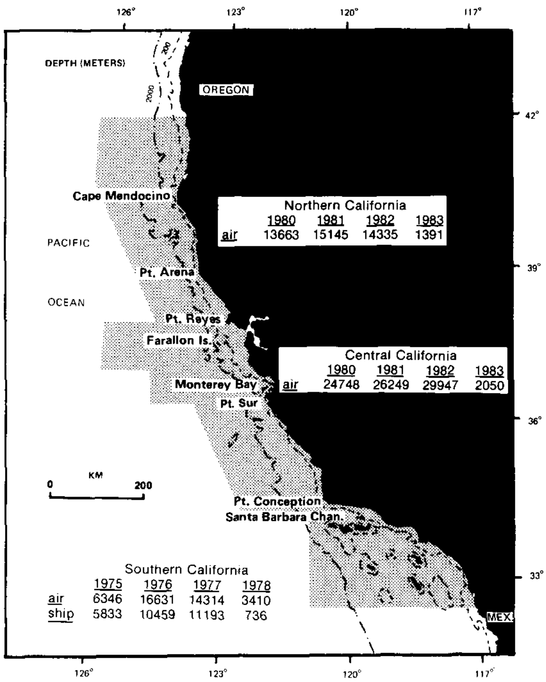

FIGURE 1. Map of the California coast showing shelf and slope topography and surveyed areas (shaded). Total coverage each year (linear km) is indicated for each type of survey.

California (Owen 1980). Off southern California, continental shelf topography is complex. The seafloor consists of a series of basins and ridges, some capped by islands, and is termed the continental borderland to distinguish it from less complex regions (Emery 1960). The main continental slope (Patton Escarpment) lies some 200 km off San Diego. Farther north, off central and northern California, the shelf varies from 5 to about 75 km in width.

Waters are generally coolest and least saline offshore, in the north. Coastal upwelling, brought on by pulses of north winds, occurs at almost any time over the shelf, generally reaching maximum development in the south earlier in the year (April–May) than farther north (June–July; Bakun and Nelson 1977). Upwellings enhance local food web productivity (Hickey 1979, Cox et al. 1982). Major upwellings are associated with promontories such as Cape Mendocino, Point Arena, Point Reyes, Point Sur, and Point Conception. Waters upwelled over the shelf may be entrained by eddies, injecting coastal plankton populations offshore into the California Current (Haury 1984, Mooers and Robinson 1984). Where this occurs, abrupt horizontal gradients in physical and chemical properties often prevail. Coastal upwellings, offshore eddies, and the often strong, meandering thermal fronts lying between persist for periods ranging from days to weeks (Breaker 1983, Fiedler 1983). We discuss below the relationship of shearwater concentrations to thermal fronts associated with upwellings.

METHODS

We made ship and aerial surveys 48 times in southern California and 36 times in central and northern California. To estimate bird density (individuals km^{-2}) we used standardized strip-transect techniques (50-m-wide transects at 60 to 65 m altitude for aerial counts, and 400-m transects on both sides of a vessel moving at 18 to 22 km hr^{-1}). Our techniques are described and analyzed in Briggs et al. (1981, 1983, and 1985a, 1985b).

For birds as large as shearwaters, the ship and aerial protocols yielded density estimates that were statistically homogeneous. That is, although observers on neither platform could count or identify all birds present, on a regional basis (10,000+ km^2) mean density values calculated from ship and aerial data did not differ significantly (Briggs et al. 1985b). Thus, for this paper we pooled ship and aerial results for our southern California studies. In many months, however, we had done both types of survey. For these months, we averaged all samples taken in each cell of a 5′ latitude-longitude grid. On the other hand, the ship did not regularly visit the rough waters within 40 km of Point Conception (a center of Sooty Shearwater abundance), and no matching aerial data for southern California are available for the months of July and September 1975, April and August 1976, and August 1977. Because we undersampled this area of high bird density, our population estimates for these months may be low.

Sampling tracks followed for the southern California studies appear in Briggs et al. (1981); aerial transects surveyed in central and northern California are shown in Briggs et al. (1983, 1984). The total coverage achieved by each type of survey is shown for three latitudinal regions in Figure 1. For the most part, sampling took place during the last week of each month and required three to six days.

After calculating shearwater density for each geographic grid cell visited, we averaged densities to produce monthly means for five depth/latitude regions. Offshore areas include only waters deeper than 2,000 m; waters shallower than 1,999 m we labeled shelf-slope. Depth is highly correlated with distance from the mainland in central and northern California but poorly correlated to about 150 km off southern California. Our sampling routinely included offshore waters in central and northern California but not in the south.

Numerous sightings were logged at the generic level. During our study, Sooty Shearwaters could be confused with Short-tailed and Flesh-footed shearwaters (*P. tenuirostris* and *P. carneipes*) but, because of differences in back color, flight pattern, and size, generally not with co-occurring Pink-footed (*P. creatopus*) or Buller's shearwaters (*P. bulleri*). The Short-tailed may be the predominant shearwater in central and northern California during winter (Stallcup 1976), when shearwater numbers are very low. During aerial surveys, sightings were recorded at the species level primarily when underwing pattern and color were clearly visible (which happened quite often, due to startling of flocks by approach of the aircraft). Observers on vessels used the field marks discussed in Stallcup (1976) to distinguish the species. We observed no Short-tailed Shearwaters during numerous vessel surveys off southern California in spring through early autumn and encountered none among the 160 collected there and in Monterey Bay in the same months. Similar paucity of the Short-tailed has been reported for Monterey Bay collections comprising many hundreds of birds (Morejohn et al. 1978; D. Croll, pers. comm.). On these bases, we assigned unidentified shearwater sightings to the various species according to the proportions of shearwaters positively identified at the same location, provided we had identified more than half of the birds seen at that location. Where shearwaters were mostly unidentified (for example, if glare had been severe), we did not assign them to species and do not report them here. For this reason, our figures may underestimate the actual densities in central and northern California, where all data come from aerial counts (which are critically affected by glare), and the numbers of unidentified birds accounted for a larger portion (31% of all sightings) than in the south (18% of all sightings).

To examine relations of shearwater density to selected environmental parameters, we used hydrographic charts to characterize each sampled grid cell (approximately 80 km^2) for water depth and distance from various points. About 299 and 103 grid cells were visited per survey in central and northern California and in southern California, respectively. Surface temperatures were obtained by through-hull and bucket thermometers aboard ship and by using an infrared radiation thermometer mounted through the aircraft floor (Briggs et al. 1984). Where temperatures were not directly available (equipment malfunction), we have used satellite infrared images (NOAA 6 and 7 satellites) to contour thermal features onto the surveyed track lines. Satellite-contoured temperatures represent 5% of values for northern California; they were calibrated by data from adjacent aerial lines, ship data, or NOAA buoy data (Piltz 1982, this study).

Relationships among habitat variables were investigated with Principal Components Analysis (PCA) applied to values for each sampled grid cell (SAS 1982). Because some environmental variables in central and northern California were highly correlated, we preferred PCA to multiple regression analysis, which assumes uncorrelated, independent variables. Habitat variables included water depth, distance from the mainland, and distance from the nearest point on the shelf break (defined as 200-m depth). Surface water temperature and gradients in temperature were also considered. Gradients were calculated as temperature difference divided by distance measured between center points of adjacent $5' \times 5'$ grid cells. The maximum gradient value was selected for each combination of adjacent cells. This was a conservative index that changed more rapidly in the cross-shelf direction than parallel to the coast. Thermal features smaller than 8 km generally were not resolved by this gradient index. Values of latitude in the north and latitude-longitude in the south provided a general index to the pattern of transition of surface water properties (temperature, salinity, and nutrients) occurring from north to south along the axis of the California Current (Bernal and McGowan 1981). Longitude was included for the south because of the northwest–southeast orientation of the southern California coastline. Components were rotated orthogonally and the criterion for significance was set at an eigenvalue ≥ 1.0. By this procedure, we identified a small number of consistently significant components (two or three) explaining much of the variation in monthly environmental data. In separate analyses, we then assessed the correlation between shearwater density and values of the first three principal components at each sampled location. To control variance, shearwater density was transformed by taking the log, after adding 0.01 (Sokal and Rohlf 1981). This emphasized presence-absence of the birds rather than variations in density. These analyses focused on habitat characteristics with scales corresponding to aggregations of bird flocks but are unsuitable for determining the fine scale characteristics of feeding sites (tens to a few hundred m).

RESULTS

REGIONAL AND SEASONAL VARIATION IN DENSITY

Throughout California, Sooty Shearwater populations were highest from May through Au-

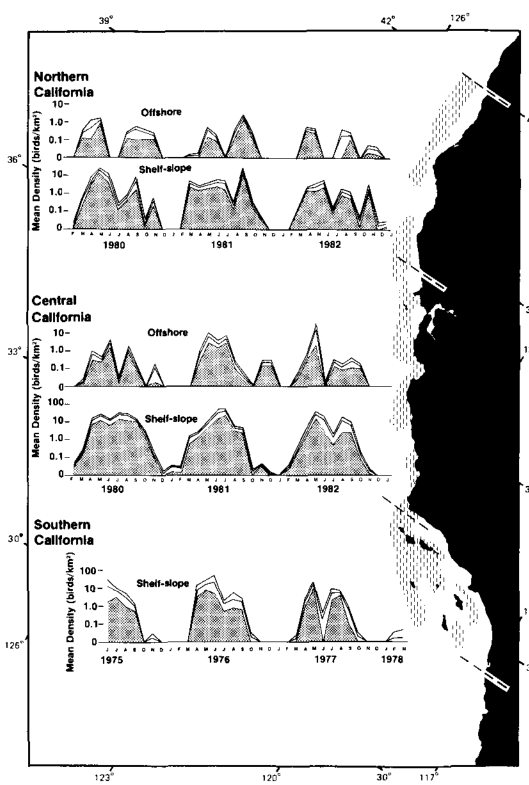

FIGURE 2. Annual curves of Sooty Shearwater population density for five geographic/depth regions off California. For each region three curves represent the mean (center) ± 1 SE. Shaded areas lie more than 1 SE below the mean. Hatched areas on the map depict locations where annual mean shearwater density exceeded 20 birds km^{-2} during April through September.

gust or September and were distinctly concentrated in shelf and slope waters. Population density on the southern California shelf and slope reached values as high as 1 bird km^{-2} in June through September 1975, April through September 1976, and April, May, and July through September 1977 (Fig. 2). Density there exceeded 10 birds km^{-2} in June 1975 and 1976 and in May 1977. Over the shelf and slope in central California density exceeded 1 bird km^{-2} during April through September each year; in the same depth region of northern California, density oscillated somewhat in late summer and exceeded 1 bird km^{-2} each April, May, and June. Density was high (>10 birds km^{-2}) in central California shelf and slope waters for two to six months each year but reached these levels only twice off northern California. The highest density values in each shelf/slope region were: 18 birds km^{-2} in southern California (June 1976), 50 birds km^{-2} in central California (July 1981), and 26 birds km^{-2} in northern California (September 1981). Each of the shelf/slope regions is large (>28,000 km^2), and much local variation in density is masked by our averaging procedures. Local densities (in 10′ by 10′ latitude-longitude grid cells) exceeded 1,000 birds km^{-2} six times in the south and eleven times in central California. These concentrations occurred near San Miguel and Anacapa islands (at either end of Santa Barbara Channel), in Monterey Bay, and in the Gulf of the Farallones. Sightings of isolated flocks of 1,000 to 20,000 birds were logged on 27 occasions (some of these away from transects used in density calculations), and in one instance (21 June 1981), we made 75 aerial photographs of a flock covering at least 4 km^2 in Monterey Bay. Analysis of these photographs led to an estimated 631,000 birds, the most spectacular sighting in our six years of study.

Sooty Shearwater density was low in offshore areas, attaining mean values above 1 km^{-2} in only six months in central California and only once in the north (June 1981).

Annual curves were bi- or trimodal in most cases; initial peaks in spring were followed by midsummer dips and one or more late summer or autumn peaks. The differences in density between peaks and troughs were greatest in the two offshore areas and over the shelf and slope in the north; seasonal curves were smoother over the shelf and slope in central California. Abrupt peaks and troughs probably represent passage of major segments of migrating populations. Complexities such as multiple peaks over the shelf in the north may indicate pulsed southward movements of different segments of the population summering in the Gulf of Alaska or movement of some birds to the north from central California. The broad, unimodal curve in the shelf/slope region of central California during 1981 may have arisen by one or more of a variety of processes: migration may have been very prolonged; birds migrating both north and south may have intermingled in summer; or the peaks associated with migrations may have been masked by the presence of a large, sedentary summering population.

We can make regional comparisons of migration dates between 1975 and 1981, which had similar prevailing temperature regimes, and 1976 and 1982, the two years coinciding with onset of *El Niño* episodes in the tropical Pacific (Lynn 1983). Aligning data from these years suggests that Sooty Shearwaters arrive about the same time in each region (late March), but the late summer departure from southern California is more abrupt than elsewhere.

Over 10,000 records for flight directions obtained throughout southern California in 1976 and 1977 indicate no seasonal change in the predominantly northwest (upwind) flight direction (K. T. Briggs, unpubl.). This was true even as late as August, when other authors have supposed birds to be migrating south out of California waters (Guzman and Myres 1982). In central and northern California, flight direction data were affected by potential startling of birds by the survey aircraft and predominance of north winds. Nevertheless, over 79% of 6,621 sightings in August and September show north or northwest flight. In recent studies, we have found Sooty Shearwaters to fly predominantly upwind, even if it means moving south in June (K. T. Briggs and D. G. Ainley, pers. obs.).

NUMBERS OF BIRDS OFF CALIFORNIA

Since Sooty Shearwaters are one of the most important avian predators in the North Pacific, it makes sense to estimate the numbers of birds that might be present off California at one time. This can be done in three general ways. First, we can compute monthly averages for each of the geographic-depth regions, multiply these by the appropriate areas, and combine them to yield an average, so-called "instantaneous" population. Doing so gives a maximum of about 2.6 million Sooty Shearwaters off California in May, with about 80% of the population in the central and southern shelf-slope regions. Combined numbers fall below 1.0 million after the end of July; most birds are still concentrated in the central coastal area.

A second procedure simply entails adding the maximum values for each region for each month; this would give us population estimates corresponding to environmental conditions conducive to large populations. Doing so for our data yields maximum monthly populations of more than 4.0 million in May and 2.7 million in June and July. These high added populations derived from data taken in years of heavy upwelling and high plant, plankton and fish productivity (cf. Smith and Eppley 1982).

Third, we can match different years on the basis of similar environmental conditions, such as temperature, that correlate with and probably influence shearwater migrational dynamics (see discussion below). The summers of 1975 and 1981, for example, were characterized by strong upwelling and temperatures at or below 20-year mean values (Fig. 3). These were followed by summers with anomalously warm water coinciding with *El Niño* episodes in the tropical Pacific. In both episodes, while oceanographic anomalies, including temperature, became evident off California during late summers of 1976 and 1982, maximum anomalies followed about four months after the

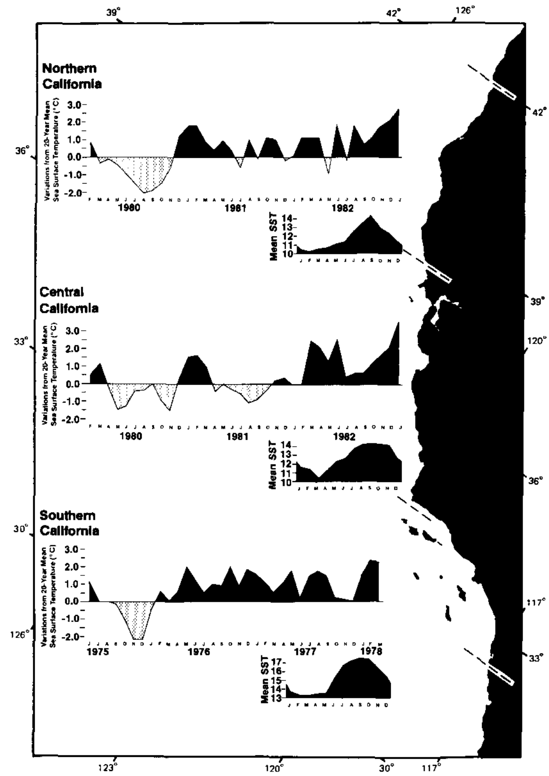

FIGURE 3. Mean monthly sea surface temperatures (small graphs; 20-year means) and monthly departures from the mean (large graphs) for each of three latitudinal sectors off California. Means are adapted from Auer (1981–1983) and monthly anomalies are based on measurements made during this study and adapted from Auer (1981). Persistent warm anomalies in autumn 1976 and 1982 coincided with onset of *El Niño* conditions in the tropical Pacific.

shearwater population would normally have migrated south (Lynn 1983, Simpson 1983). Combining population estimates from these cool and warm years reveals that the population was greatest in May, June, or July of the cool years, reaching a level of about 2.3 to 2.7 million. In the warm *El Niño* years (1976 and 1982), the population was high in May (3.5 million), dropping quickly to less than 1.0 million after June. Thus, warm environmental conditions may have hastened shearwater migration or at least departure from California. Although our systematic sampling ended before the normal arrival dates for Sooty Shearwaters in 1983, we noted that when *El Niño* conditions reached peak in summer 1983, Monterey Bay populations were greatly reduced compared with other years (A. Baldridge, pers. comm.; KTB, pers. obs.).

We stress that our estimates produce instantaneous totals for the state, not estimates of the total number of birds that might pass through. Since the rates of population turnover during migration and the proportion of birds

TABLE 1. Principal components analysis of environmental variables in 294 grid cells sampled in July 1980. Significant loadings (multiple r) are underlined.

Variable	Component I	Component II	Component III
Water depth	0.948	0.090	−0.055
Distance to mainland	0.862	−0.007	−0.107
Distance to shelf break	0.924	0.196	−0.064
Latitude	−0.059	−0.963	−0.010
Water temperature	0.232	0.917	−0.069
Temperature gradient	−0.180	−0.047	0.982
Variance explained	43.2%	30.3%	16.5%
Shearwater density	0.381	0.239	0.406

that stays in California to feed during summer are unknown, we cannot reliably estimate the total numbers of shearwaters that may use California waters at some time during the year. Given the flight speeds typical of this species (20 to 50 km hr^{-1}), and estimates of up to 12 to 35 million birds in the Gulf of Alaska during summer (Gould et al. 1982), the numbers of shearwaters migrating through or summering off California might be an order of magnitude higher than our instantaneous estimates of 2 to 4 million.

ENVIRONMENTAL CORRELATES OF DENSITY

Principal components analysis of northern and central California habitat data revealed the importance of two (occasionally three) habitat gradients, or components, that together explained an average of 76% of standardized variance. For example, data from July 1980 show (Table 1) high cross-shelf correlation between water depth, distance to the mainland, water temperature, and distance to the shelf-break (Component I). Because we sampled almost the same areas each month, these depth and distance correlations did not vary, but there was seasonality in temperature. Water temperature significantly correlated with distance from shore (multiple r = 0.23 to 0.64, n = 299) in April through November each year but not in winter. Component II, explaining 30% of variance, reflected the prevalence of cool temperatures at higher latitudes. Temperature gradients contributed significantly to Component II in data from winter 1981 and winter to spring 1982: large, cross-shelf temperature gradients (averaging 0.1–0.2°C km^{-2}) prevailed at these times in the warm waters south of Monterey Bay. Component III mostly comprised the unique variance in the gradients variable, and generally explained about 19% of the total.

Variation in shearwater density correlated significantly (r = 0.35 to 0.45) with Component I in spring to summer 1980 and 1982 and with Component III (multiple r = 0.23 to 0.68) in almost all months (April through September) when birds were abundant. Bird density seldom correlated with variation in Component II (latitude-temperature).

These same patterns also characterized the southern California data. On Component I, there was little significant contribution from water temperature, but temperature gradients varied significantly as the inverse of depth and distance from shore (i.e., strong thermal gradients bordered upwellings in the shallow waters near the mainland and on the "aprons" of the islands). Component II consisted mainly of the inverse variation of temperature on latitude-longitude, reflecting the influence of advection of cool water from the north and heavy upwelling in the San Miguel Island area. In 11 of 18 surveys made in April through September, we found a significant inverse correlation of shearwater density with Component I (up to r = −0.59 in midsummer 1976 and 1977) and in 9 of 18 surveys a significant positive correlation with Component II (up to r = 0.77 in September 1975).

Overall, these analyses point to an affinity of Sooty Shearwaters for cool waters near the coast. However, whereas Sooty Shearwaters concentrated in the coolest waters of the Southern California Bight, they shunned the coolest waters off northern California. Coastal upwellings from Point Arena to Cape Mendocino, where surface temperatures were 7 to 10°C in summer, were little visited by shearwaters; the birds instead concentrated in the south in warmer waters from 30 to 70 km offshore (Fig. 2). Heaviest concentrations throughout the state were encountered in waters 11 to 14°C, within or south of active upwellings.

Interestingly, Sooty Shearwaters also made little use of the vast expanse of the eastern half of the California Current (seaward of coastal upwellings) for feeding or migration, or they did so only for short periods. Our sampling routinely extended 185 km offshore; relatively few birds ever were seen more than 100 km from the coast, even where sea temperatures were low. During transects to 400 km off Monterey Bay in June, August, and September 1982, we found an average of only 0.04 birds km^{-2} more than 100 km offshore, and no birds from 200 to 400 km. Unless our routine sampling missed significant migration much farther offshore, or distribution among habitats in 1982 was extremely atypical, then the preferred habitat for Sooty Shearwaters includes the coastal upwelling zone, but not California Current waters seaward of the central continental slope. Additionally, however, presence of bird concentrations at some distance removed from the coldest upwelled waters indicates that temperature by itself is an unreliable indicator of the suitability of feeding areas. It is much more likely that feeding shearwaters make use of such optical cues as slicks, color discontinuities, and shoals of bait, which in turn are differentially common within and near upwelling centers (cf. Briggs et al. 1984, Laurs et al. 1984). These cues may prevail where physical processes (e.g., current shears or convergences) act to concentrate seabird prey.

DISCUSSION

During spring, Sooty Shearwaters arrive in the eastern North Pacific at about the same time across a broad front. They arrive off California in late March and reach densities over one bird km^{-2} a month later. Arrival dates for other north Pacific areas include late March to early April off Japan (Palmer 1962), mid-March in the Gulf of Alaska (Gould et al. 1982), early April off Vancouver Island (Guzman and Myres 1982), and February to April in the central Gulf of California (D. W. Anderson, in litt.). King (1970) and D. G. Ainley (in litt.) reported that Sooty Shearwaters fly north past the Hawaiian Islands in March and April.

With some annual and geographic variation, shearwater density off California peaked in April through July, usually in May or June. In southern California, this peak was followed by declines of 50% or more and a later (July, August, or September), lower peak. Density curves in central California were somewhat broader, and the late summer populations were much higher than in the south. In northern California, substantial peaks were also observed in late summer and early autumn; in one case (September 1981), fall densities eclipsed those of spring.

DISTRIBUTIONS OF SHEARWATER PREY

The pattern of early population declines in the south and persistence of dense populations later in summer at higher latitudes parallels that seen in several other seabird populations (e.g., Black-footed Albatross, *Diomedea nigripes,* and Brown Pelican, *Pelecanus occidentalis*) and correlates with several aspects of food availability and prey behavior (Sanger 1974, Anderson and Anderson 1976). Chu (1984) reported that Sooty Shearwaters eat predominantly juvenile rockfish (*Sebastes* spp.), euphausiids, market squid (*Loligo opalescens*), and northern anchovies (*Engraulis mordax*). Despite the abundance of anchovies in southern California, they were not a primary Sooty Shearwater food in the samples reported by Chu (1984). We think this is due to anchovy behavior during the late spring peak of shearwater abundance; the fish occur in wary, dispersed spawning schools (Mais 1974). In summer, post-spawning anchovies occasionally form large, near-surface schools in the day near the southern California coast. But, by the time these schools become common, and thus susceptible to heavy shearwater predation (the peak occurs in October), most Sooty Shearwaters already have left the northeastern Pacific for the breeding grounds. Rockfish juveniles and euphausiids, which are both abundant in the northwestern Southern California Bight (Brinton 1976, Parrish et al. 1981) are the mainstays of the Sooty Shearwater diet until upwelling tapers off after June, and shearwater populations begin to dwindle.

In contrast, shearwater food resources in central California may be more diverse, more persistently available through spring and summer, and perhaps locally more abundant. Among primary shearwater prey species, rockfish are the predominant resident pelagic spawners; euphausiids are abundant in spring and summer (probably more so than to the south; Mais 1974, Brinton 1976), and squid are exceptionally abundant and available in midsummer at shallow water spawning centers such as Monterey Bay (Morejohn et al. 1978, Parrish et al. 1981, Chu 1984).

Contrasting with the situation in the south, the ecology of anchovies in central California invites heavy predation by shearwaters. Here, post-spawning fish occur in dense daytime schools very close to shore, particularly from Morro Bay to Point Arguello, in Monterey Bay, and in the Gulf of the Farallones; anchovies also average larger than in the south (Mais 1974). In late summer, shearwaters fatten and complete their premigratory molt at the same time they feed on energy-rich anchovies (Chu 1984).

North of Cape Mendocino, prey availability may be greatest after midsummer. Large numbers of Sooty Shearwaters occurring sporadically off extreme northern California probably make use of rockfish and squid, which are much more abundant there than off southern California (Mais 1974). Additionally, an ecologically distinct anchovy population spawns in midsummer in the Columbia River Plume off Oregon (Richardson 1981). In part, the large shearwater concentrations seen off Oregon in

August (Wiens and Scott 1975) and off northern California in August through October (this study) may form in response to feeding opportunities on these southward-drifting anchovies. Comparative studies of diet north of Monterey Bay would be most instructive.

We believe that concentration of Sooty Shearwaters over the shelf and upper continental slope rather than in waters farther offshore (particularly north of Point Conception) relates to two general aspects of prey availability. First, three important prey species are distributed close to shore in summer: rockfish, squid, and anchovies. Second, prey far offshore in California Current waters may be more difficult to find and capture. During April through September, offshore waters in the California Current exhibit more stable vertical stratification than those in and near upwelling centers (e.g., Huyer 1983, Brink et al. 1984). Concentrations of phytoplankton and associated zooplankton tend to be found near or below the thermocline by day (30 to 100 m); because of nocturnal vertical migration of zooplankton and nekton, prey are found nearer the surface but are dispersed through a greater vertical range at night. While this in no way rules out nighttime surface feeding by shearwaters, it does imply that prey will be found in lower concentrations. As noted by D. G. Ainley (in litt.) fur seals (*Callorhinus ursinus*) and other diving mammals are quite successful predators on small fish and squid in these offshore waters in some seasons. This reinforces the idea that prey may be concentrated too deep for shearwater exploitation. Surface waters are also much clearer seaward of the continental slope. Thus, even where prey are concentrated at depths typically reached by diving shearwaters (5 to 10 m, Brown et al. 1981), water clarity abets avoidance by the prey.

Beyond this, except where eddies entrain upwelled water, surface convergences, often marked by abrupt thermal gradients, are less common offshore than near the shelf break. Convergent fronts are often found at the seaward edges of upwellings and can concentrate macroplankton and their fish (and bird) predators. These features may be relatively long-lived (several weeks or more for features of 50 to 200 km extent), thus providing some continuity in feeding conditions. Outer Monterey Bay and the shelf-break region for 100 km south of Pt. Reyes are examples of areas where thermal fronts are persistent and shearwater numbers were large. We have found upwelling fronts to mark the offshore limits of distribution for some coastal bird species (e.g., Common Murre, *Uria aalge,* and Western Gull, *Larus occidentalis*) as well as the near-coast limits for some offshore species (e.g., Leach's Storm-Petrel, *Oceanodroma leucorhoa,* and Buller's Shearwater). Phalaropes (*Phalaropus fulicarius* and *P. lobatus*), pelicans, and Cassin's Auklet (*Ptychoramphus aleuticus*) share the Sooty Shearwater's affinity for the frontal zone per se (Briggs et al. 1983, 1984). Recently, Cory's Shearwaters (*Callonectris diomedea*) have been shown to closely associate with shelf-break fronts of the Gulf Stream (Haney and McGillivary 1985).

ANNUAL POPULATION VARIATIONS

Ainley (1976) noted the occasional decline in abundance of Sooty Shearwaters off California during years of environmental warming. We surveyed populations during two such events: the relatively weak 1976 to 1977 episode and the early phase of the strong one of 1982 to 1983. Sooty Shearwaters occurred in fairly large numbers during spring in 1976 and 1982, but densities then declined unusually rapidly from midsummer onward. Shearwaters were fairly abundant off southern California during the height of the thermal anomaly in summer 1977. We did not make standard surveys during summer 1983, when the ocean off central California was at its warmest and least productive in almost twenty years. However, our own brief observations on Monterey Bay and conversations with other observers indicated that Sooty Shearwaters were scarce. Off British Columbia, Vermeer and Rankin (1984) found these birds to be an order of magnitude more numerous in 1983 than in limited previous or subsequent surveys. This suggests that the population that normally summers off California may have shifted a thousand or more km northward.

UNRESOLVED QUESTIONS

Several questions about Sooty Shearwater distribution remain unresolved. Our data show primarily northwestward (upwind) flight in all seasons, including the period of presumed southward migration (late summer). Except for the suggestions of early authors and the observations of R. L. Pyle and R. L. DeLong (unpubl.), the route(s) of southward migration thus remain unclear. It may be that most birds depart across a broad front away (southwest) from the coast rather than along it, thereby avoiding the warm coastal waters of southern California and Mexico (which average 18 to 25°C during August and September).

Population turnover rates during migration are still unknown, yet we need them to determine the total population that might pass through California (Guzman and Myres 1982). Resolution of this problem may require marking or telemetric tracking at various stages of the annual cycle.

The origin of birds that visit California is also uncertain (Ainley 1976, Guzman and Myres 1982). Opinions range from solely South American origin, to origin in the southwestern Pacific, to mixtures of the two. Migrations over equatorial regions may be more or less rigorous (thus affecting numbers of migrants), and final summer feeding locations may shift according to meteorological conditions or food availability along the route. In fact it is possible that bimodal peaks in abundance off California result from arrival of birds from different nesting grounds. And California populations might also vary in composition from year to year, depending on stages of the *El Niño* episodes. Only analyzing several years of observations in the tropics (e.g., Ainley and Boekelheide 1983) and perhaps recoveries of banded birds from different colony areas will provide answers.

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