BIRD COMMUNITIES AT SEA OFF CALIFORNIA: 1975 to 1983

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Cover Photograph: Adult (foreground) and first-winter Common Murres (*Uria aalge*) on Monterey Bay, California, September 1982. Photo by W. B. Tyler.

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GLOSSARY AND ACRONYMS

AFN/AB: Audubon Field Notes/American Birds.

CalCOFI: California Cooperative Oceanic Fisheries Investigations; an agency drawing personnel, direction and support from the National Marine Fisheries Service, the California Department of Fish and Game and the University of California. CalCOFI investigators have gathered much of the basic information available about fisheries, oceanography and biology of the California Current System.

CUZ: Coastal Upwelling Zone; the area under direct influence of coastal upwellings (not including areas influenced only by upwelled waters advected by offshelf eddies). On theoretical grounds the upwelling zone is limited to about 25 to 40 km from the coast.

Cyclonic (Anti-) Circulation: Circulation that follows the direction seen in atmospheric low-pressure systems (cyclones). In the northern hemisphere, cyclonic currents turn counterclockwise. Small to medium sized eddies of the California Current that have a relatively cool interior (cold-core eddies) have cyclonic circulation.

DML: Distance from the nearest point on the mainland shore, a variable included in analysis of bird habitat affinities.

ENSO: El Niño/Southern Oscillation; the quasi-periodic tropical ocean-atmosphere phenomenon leading to collapse of fisheries along the South American west coast around Christmas time. During the warm water phase of ENSO events, surface temperatures along the coast of Peru and northern Chile rise as much as 8°+C, the thermocline is very deep, and stratification and stability of the upper water column is strong. Due to decreased upwelling of organic nutrients to the photic zone, plankton productivity is low, and the food webs upon which seabirds depend may be greatly upset. Related, but less severe ocean/atmsophere anomalies occur along the North American Pacific Coast a few months after the peak of events near the equator; oceanographic conditions may be extreme, plankton productivity is low, and some seabird prey populations experience low growth and recruitment.

NOAA: The U.S. National Oceanographic and Atmospheric Administration; within NOAA, the Satellite Field Service Offices of the National Weather Service provide operational monitoring of ocean thermal conditions. NOAA also maintains a network of oceanographic data buoys that provided the basis for calibration of radiometric temperature data taken from airplanes in this study.

North Pacific Central Gyre: The vast mass of subtropical to temperate water occupying the central portion of the North Pacific Ocean. The Gyre is bounded by the California Current in the east, North Equatorial Current in the south, Kuroshio Current in the west and the North Pacific West Wind Drift in the north. Compared to the California Current, surface waters of the Gyre are relatively warm, clear, salty and well stratified in the vertical dimension.

PCA: Principal Components Analysis.

POBSP: The Pacific Ocean Biological Survey Program of the Smithsonian Institution. This far ranging field program included areas off California during the mid-1960s.

SCB: Southern California Bight.

SSS: Sea surface salinity.

SST: Sea surface temperature. During this study SST was measured by bucket or through-hull thermometers aboard ship and by radiometry from airplanes and polar-orbiting satellites.

Thermocline: The portion of the upper water column in the ocean where temperature changes rapidly in the vertical dimension. Above the thermocline, waters are warm and relatively well-mixed by wind, while below it, waters are cool and decrease very gradually in temperature. Off California thermocline depths range from a few meters near the coast to about 100 meters in central and western portions of the California Current. Thermal gradients from the top to the bottom of the thermocline are typically 1 to 4°C.

WD: Water depth.

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Abstract.—Seabird populations off California were studied during two three-year periods: southern California during 1975 through early 1978, and central and northern California during 1980 through early 1983. Aerial surveys provided almost all data in central and northern California and about half in the south; ship surveys provided the remainder. Periodic coastal surveys assessed proportions of populations ashore.

The seabird fauna is dominated by about thirty species that reached maximal abundance in the coastal upwelling zone. Biomass and density generally were highest off central California. At times of maximal abundance (fall and winter), estimated total numbers reached 4 to 6 million individuals. A drop in biomass occurred off central and northern California late in 1982 during onset of the intense "El Niño" event of 1982–1983; no such decline was observed off southern California during a weak "El Niño" episode in 1976. The decline in 1982 resulted from decreased visitation of birds nesting north of California (particularly alcids, fulmars, and gulls), and low populations of locally nesting diving birds such as the Common Murre (*Uria aalge*).

Consistent interspecific associations were seen between several species of *Larus* gulls, between several shearwaters (*Puffinus* spp.) and Northern Fulmars (*Fulmarus glacialis*), and between several members of an inner-shelf/nearshore fauna including loons, grebes, scoters, cormorants and pelicans. For the most part, gulls and shearwaters were avoided by other species, especially alcids and phalaropes (*Phalaropus* spp.). Leach's Storm-Petrel (*Oceanodroma leucorhoa*) consistently associated with no other species, was distinct in regional occurrence, and occupied a unique set of sites along measured habitat gradients.

Coastal upwellings, the upwelling frontal zone, and warm, clear, thermally stratified waters of the California Current constitute the three major divisions of open water habitat off California and support different species assemblages. Aggregations of gulls, terns, and storm-petrels extended over relatively large distances (40+ km), often in homogeneous patches of California Current habitat, whereas murres, auklets, and phalaropes aggregated over much shorter dimensions, mainly in the coastal upwelling zone. This suggests that different scale-dependent physical processes affected patches of seabirds and their prey in different habitats.

Species attaining estimated "instantaneous" populations in central and northern California exceeding one million individuals were murres and Cassin's Auklets (*Ptychoramphus aleuticus*) among the nesting residents and Sooty Shearwaters (*Puffinus griseus*) and phalaropes among the seasonal visitors.

KEYWORDS: seabird distribution, community analysis, species composition, species diversity, seabird habitats

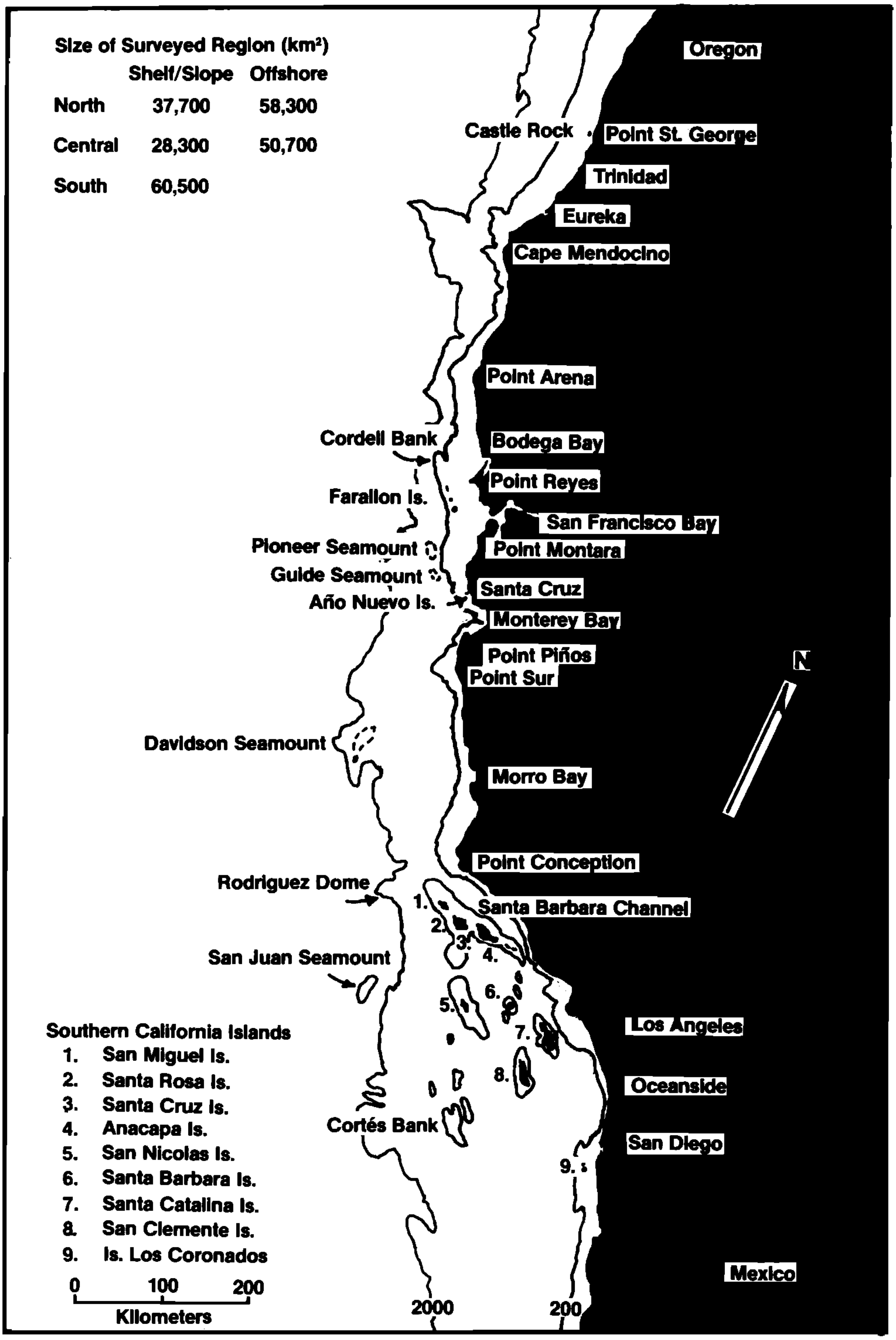
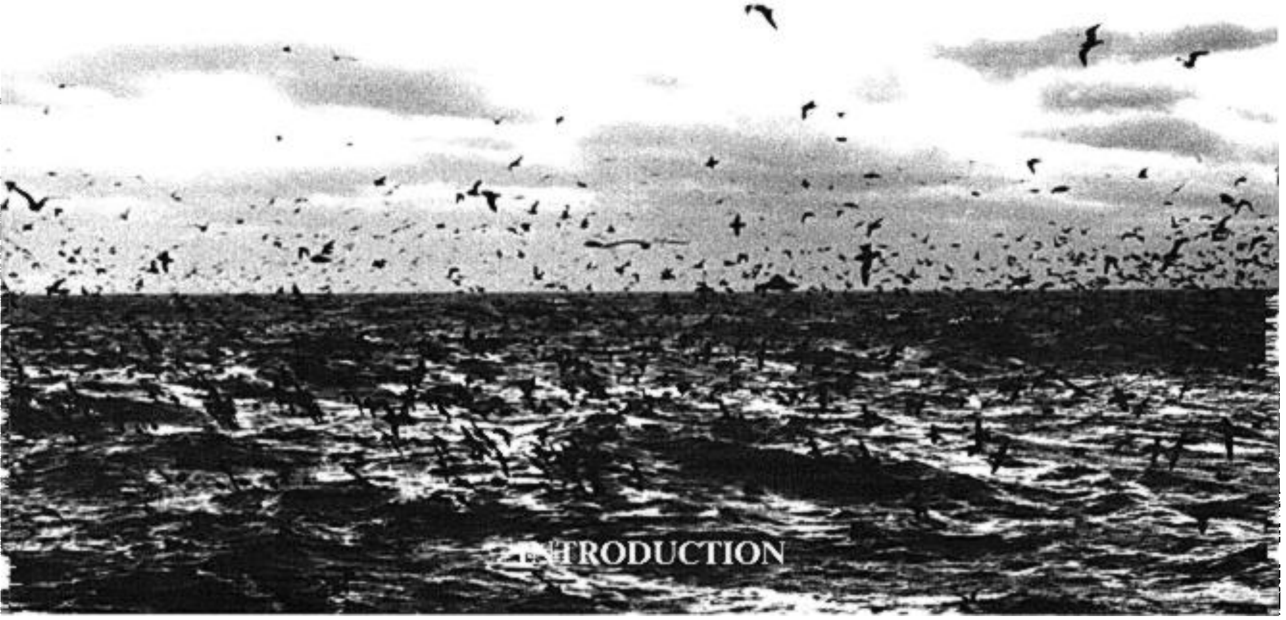


FIGURE 1. Map of the coast of California showing significant place names and undersea topography. The 200 and 2000 m isobaths delimit shelf and slope habitat divisions, respectively.



INTRODUCTION

Although it is widely recognized that seabirds "make their living" at sea, with individuals of many species spending more than half their lives away from land, there exists a strong terrestrial bias in our knowledge about characteristics and regulation of seabird communities. Simply put, we are only just beginning to appreciate how pattern and process in the marine environment affect these marine animals.

To a great extent this is attributable to difficulty of work at sea. While few major colony areas in the world now are beyond the reach of systematic study, ornithological coverage of many ocean areas has been infrequent and unsystematic; the oceans are too large and the available resources too limited to have permitted development of a 'mature' science of pelagic seabird biology. Still poorly understood are such basic questions as: How many seabirds species can coexist simultaneously in the same ocean habitat? To what extent do seabirds compete with each other for food? How closely do seabirds track changes in ocean conditions on various time and space scales? Do some species specialize in discrete kinds of habitat? What strategies are employed by seabirds to find suitable ocean habitat and what environmental features serve as cues for habitat choice? What significant life history consequences accrue to birds making different habitat choices? Resolution of some of these questions would provide an informative contrast to the body of descriptive and theoretical work concerning population regulation through processes affecting seabirds while ashore.

Until very recently, scientific resources were almost always inadequate to characterize the occurrence of whole marine bird faunas through space and time. Beyond this, studies of physical processes and food webs seldom coincided temporally or geographically with those of offshore bird populations. This has meant that patterns in bird communities at sea could not readily be explained by reference to bio-oceanographic processes. This has changed since about 1970, and several large-scale bird studies have benefitted from simultaneous oceanographic data collection (e.g., Ashmole 1971, Pocklington 1979, Brown 1980, Ainley and Jacobs 1981).

In this paper, we attempt to describe quantitatively the occurrence of seabirds in waters off California and relate patterns of abundance, seasonality, and community diversity to physical and biological characteristics of the ocean habitat. This is necessarily a descriptive task, one that must precede studies focused on mechanisms and consequences of habitat choice.

Our work took place within a period of intensive oceanographic study of the California Current. Driven initially by the need to understand the collapse of the California fishery for sardines (*Sardinops sagax*), government and academic research here since 1950 has focused on processes affecting biological productivity; until recently, physical oceanography received less attention. Programs supported since 1974 by the U.S. Department of Interior, Minerals Management Service, have gathered considerable information applicable to preservation of important wildlife and habitat resources during development of offshore oil and gas reserves. As part of that program, researchers at the University of California undertook studies in 1975 and 1979 to assess the status, numbers, distributions, and movements of all seabirds in California waters. The data resulting from this and complementary work carried out by the U.S. Fish and Wildlife Service and Point Reyes Bird Observatory now permit a basic understanding of the ways in which seabirds use California Current habitats, how this community is structured, and how variation in

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Top photo: Sooty Shearwaters (*Puffinus griseus*) on Monterey Bay, California, by D. B. Lewis.

some ocean processes affects bird populations at sea and on land.

We present results of standardized surveys made with consistent methods and replicate sampling. Our goal is to interpret distribution, seasonality, and community organization in relation to variability in the physical environment.

This paper comprises several sections, addressing different aspects of the general problem. First, we review the oceanography of the California Current System off California to set the stage for later analyses of seabird habitats. Next, the (present) status, numbers, and habitat affinities of California seabirds are discussed in the format of species accounts. This is followed by analyses of diversity and interspecific associations in several latitudinal/water depth regions. Habitat use is analyzed for numerically important species using a multivariate ordination (principal components) approach. We also describe patterns of patchiness and aggregation among numerically dominant species and relate these to dominant scales of variation in surface temperature.

Ours is not the first attempt to synthesize information about the seabirds off California but is the first to use replicate, quantitative sampling. With Grinnell and Miller's (1944) distributional summary of the state's avifauna, the general seasonality, relative abundance, and affinity for nearshore or oceanic waters were known for most species. The focus of the bulk of California seabird work before 1975 was the island colonies of southern and central California (Fig. 1). Most noteworthy is the century of ornithological investigation on the Farallon Islands (reviewed in Ainley and Lewis 1974, DeSante and Ainley 1980), which has been continued and greatly augmented by the Point Reyes Bird Observatory. Nesting biology of about a dozen species has been studied there during the past fifteen years. Lengthy time series of observations of nesting biology also exist for Brown Pelicans (*Pelecanus occidentalis*) at Anacapa Island (Anderson and Gress 1983) and for the Western Gull (*Larus occidentalis*) and the Xantus' Murrelet (*Synthliboramphus hypoleucus*) at Santa Barbara Island (Hunt et al. 1981; Murray et al. 1983). The locations and sizes of all seabird nesting colonies throughout the state were surveyed during 1975 to 1980 (Sowls et al. 1980, Hunt et al. 1981).

Systematic work at sea has been confined to only a few areas. Monterey Bay has been important as a collecting locality and site for birding trips since the beginning of the century (Loomis 1895, Beck 1910, Stallcup 1976), and the Gulf of the Farallones has been traversed and surveyed hundreds of times en route to the Farallones colonies (Ainley and Boekelheide in press). Despite the large numbers of fishing and pleasure boats in southern California, no systematic attempt was made to document seabird numbers and distribution in that area prior to the studies reported here. Waters lying 50 to 950 km west and south of Point Conception were visited about monthly in 1966 and 1967 by personnel of the Smithsonian Institution's Pacific Ocean Biological Survey Program (POBSP). Results of that program were partially reported more than a decade ago (King 1974), but much information remains unanalyzed in computer files or in unpublished cruise or data reports (e.g., Pyle and DeLong 1968).

Sighting records and seasonal status of seabirds in waters off the southern California coast were discussed by Garrett and Dunn (1981; some of these were based on incomplete records from the program upon which we report). A step toward analyses of the habitat affinities of important species was made by Small (1974) based on the then-available sightings from birdwatching trips made from several southern and central California ports. Ainley (1976) attempted to place some (order-of-magnitude) numerical interpretation on the reports published primarily in Audubon Field Notes/American Birds (AFN/AB), and also to relate patterns of seasonal abundance and geographic concentration to general cycles of ocean productivity, temperature, and salinity. For a number of pelagic species, Ainley identified thermal or salinity regimes that correlated with interannual variations in bird abundance or geographic concentrations in space.

METHODS

SAMPLING PLAN AND COVERAGE AT SEA

Our results derive from two studies designed to assess the abundance, distribution, and habitat affinities of all marine birds off California. From April 1975 through March 1978 the waters off southern California were surveyed from both ship and airplane. Our purpose was to repeatedly sample areas of inshore and offshore habitats with approximately monthly frequency to determine which bird species were most abundant, the locations of preferred feeding areas, and routes of migrations. Shipboard observers in southern California made 24 surveys totalling more than 27,000 linear km of predetermined trackline. This cruise track (depicted in Briggs et al. 1981b) emphasized waters inshore of the Santa Rosa-Cortés Ridge, which extends for 250 km southeast of Santa Rosa Island and approximates the offshore limits of the Southern California Bight (SCB). The waters of Santa Barbara Channel were not routinely visited by our vessels, except as part of related studies of seabird breeding biology (Hunt et al. 1981). Five vessel surveys reached waters of the California Current west of the Santa Rosa-Cortés Ridge during September 1975, January and October 1976, and January and April 1977; total offshore vessel coverage was about 3100 linear km.

Low altitude aerial surveys also were made 24 times in southern California. Aircraft followed primarily north-south tracks extending from the mainland to about 200 km offshore (Fig. 2 of Briggs et al. 1981b). The comparatively rough waters far offshore were undersampled by aerial surveys during 1975 but were reached routinely during subsequent years. Total aerial coverage was about 40,000 linear km, averaging 1800 km per survey.

Surveys of central and northern California (from Point Conception north) during February 1980 through January 1983 were conducted almost exclusively from aircraft. Monthly surveys were made along about forty lines oriented east-west and extending up to 185 km offshore. Initially, the lines were selected at random from among 92 possible tracks (every 5′ of latitude) with the stipulation that no more than two adjacent lines would be skipped. To the initial pool of about 30 selected transects, 10 lines were added to provide more resolution in five areas targeted for possible minerals leasing. The between-line spacing in the final set of transects averaged 19.8 km. Weather permitting, the same 40 to 42 lines were then sampled each month at least as far offshore as the base of the continental slope (arbitrarily 2000 m). Four pairs of lines were selected in central and northern California whereon sampling routinely extended to 185 to 200 km from shore (these were located at the northern edge of Santa Barbara Channel, off Monterey Bay, off Cape Mendocino and off Point St. George; in practice we usually were able to sample on four to six of these lines). This sampling scheme led to expenditure of 40% of total sampling effort each over waters of the continental shelf and slope and the remaining 20% in 'offshore' regions. Averaging about 3100 linear km per month, total aerial coverage was almost 83,000 km in central California and almost 45,000 km in northern California (north of 38°50′N; annual coverage is shown in Briggs and Chu 1986). Six half-day aerial surveys south of Monterey Bay provided synoptic observations of offshore populations during spring and summer 1983. Additionally, five vessel surveys were conducted in 1981 to determine species composition and habitat affinities of several groups of birds off central California; 950 km of trackline were surveyed. In all, we logged sightings of approximately 3.5 million birds of 74 species.

OBSERVATION PROTOCOLS

Our shipboard and aerial methods were described and analyzed previously (Briggs et al. 1981a, 1984, 1985a, b); only a few important features will be noted here. The aim of both techniques was to produce estimates of density (birds km^{-2} surveyed) for each species encountered. We sought to obtain large, replicate samples (spatially and seasonally) to facilitate statistical analyses. Observers scanned strips parallel to the path of the survey platform, noting lateral distance to sightings in terms of non-overlapping corridors or bands. Ship surveys featured 400-m, bow-to-beam corridors on each side of the vessel. Two experienced observers attempted to minimize recounts of birds following the vessel by noting bird numbers and identities at the stern every 10 to 20 minutes. The southern California ship track was divided into 106 segments, each of which was 7.4 km (4-nautical-mile) in length and was centered within a 5′ by 5′ latitude/longitude grid-cell; wherever possible, observations were made continuously from about an hour after sunrise to an hour before dark. Aerial observers scanned much narrower strips (50 m) and only made observations on the shaded side of the flight path; surveys were flown at 65 m altitude at approximately 165 km h^{-1} ground speed. Vessel observers recorded sightings on prepared forms, while those in aircraft made verbal tape recordings of similar data. In each case, sightings consisted of taxa, numbers, ages or plumage morphs, behavior, associations with other species, and environmental information. Data taken at the start and end of each transect line included position and time, observation conditions, environmental data, notes on observer fatigue, and reliability of navigational information (which occasionally was inadequate due to interference or malfunction of electronic aids).

In comparing and evaluating the strengths and weaknesses of the two methods, we found that our ship and aerial techniques produced similar estimates of bird density when data were matched for time and area (Briggs et al. 1985a). Under *ideal* survey conditions, aerial observers reported significantly higher densities of birds along selected, short (to 18.5 km) transects. However, the results of geographically broad counts under changeable viewing conditions indicated that density differences between the two types of platform were not significant compared to within-sample geographic variability or variations between months. In presenting southern California data, we emphasize the aerial because of comparability with data taken in central and northern California. Where southern California aerial sampling included gaps of more than a month, we have drawn from ship samples to smooth seasonal curves, recognizing the geographic (shelf/slope) biases in the ship track.

As might be assumed *a priori,* vessel surveys were more efficient at determining the detailed species composition of bird aggregations and at identifying rare or unusual birds. Aerial observers covered much broader areas in relatively shorter periods, reported more sightings at the generic or family level, and noted fewer unusual species (Briggs et al. 1985a).

SHORELINE METHODS AND COVERAGE

Numbers of individuals at sea often represent only a portion of a seabird population. Variable portions may be found on land or on waters near coastal roosts or colonies. To evaluate coastal bird numbers, we made systematic counts of birds along most sections of the coast, including islands, during most months (24 visits) in southern California and quarterly (twelve times) north of Point Conception. For the most part, this was done by aerial observers surveying at about 100 m altitude and 100 m away from the coast; one observer recorded all birds on shore while another surveyed offshore to about 200 m. Where large aggregations of birds were known to occur (e.g., the Farallon Island nesting colonies), observations were made from as far away as 400 m altitude and 300 m setback in order to minimize disturbance. Verbal recordings indicated locations to within 1 km, proportions of birds on land and in the water, and counts of each species. We made heavy use of 35-mm aerial tele-photography. Virtually every group of birds exceeding about fifteen individuals was photographed for later counts (from projected transparencies). This was especially important at large (10^4 to 10^5 birds) colonies and roosts where visual estimates of numbers would only have been useful for order-of-magnitude analyses. Where photographic quality permitted, each bird was counted on each frame. Counts were made from more than 40,000 photographs.

To augment information for the southern California coast, monthly censuses were made along 18–29 beaches representing about one-tenth the length of the coast; these included no harbors. Where we refer to these mainland counts, we have extrapolated observed numbers by factors appropriate to the percent of the coast covered (in linear km). These shoreline and surf censuses were made with the aid of binoculars and were most useful for grebes, cormorants, scoters, gulls, and terns.

ENVIRONMENTAL DATA

To determine the habitat affinities of seabirds and to limit data quality to the best attainable, observations of environmental conditions were made at the start and finish of every observational watch and whenever conditions changed. Minimally, this took place about every twenty minutes. Observers noted wind direction and speed, sea state, glare intensity and direction, and presence of fog or other detriments to viewing. Sea surface temperatures were noted at least every twenty-five minutes (approximately 7 km) using bucket or through-hull thermometers aboard ship. During aerial surveys of central and northern California, surface temperatures were recorded at least every 9 km (minimally, at intervals of 5′ of longitude) along tracklines by a Barnes Precision Radiation Thermometer. This instrument, coupled to a chart recorder and calibrated onboard against known black-body temperature, had a nominal accuracy of ±0.2°C. Periodic overflights of oceanographic data buoys provided additional means of calibration.

Additional information about the distribution and patterning of surface temperature was derived from monthly synopses prepared by the National Marine Fisheries Service for 1975 to 1978, by Auer for 1980 to 1983, and from satellite-sensed ocean-temperature images furnished by the National Weather Service and Scripps Ocean Visibility Laboratory. Frequent, non-quantitative comparisons of these satellite images with our *in situ* or remote (aerial) data assisted us in contouring of surface isotherms and in understanding the spatial relationships between habitats.

Because of their potential importance as cues to habitat qualities and presence of food, we took special notice along sampling tracks of occurrence of ocean color boundaries, slicks, current or wind shears, flotsam, kelp, and feeding animals of all types. Presence of fishing activities was noted as were apparent associations with aggregations of plankton or bait.

ANALYSES

Bird density

Transect data were recorded continuously and subsequently were partitioned geographically to permit analyses at different scales ranging from large regions down to individual sightings. To arrive at monthly estimates of bird density, the numbers of birds observed in each 5′ by 5′ latitude or longitude segment of ship or aerial tracks was divided by the area included within the transect. The resulting figures, which we call "grid cell densities," were averaged for all samples (ship and air, or multiple visits by the same type of platform) taken in each location. Monthly regional mean densities derived from sample sizes (visited grid cells) ranging from 86 to 144 for the southern California shelf/slope, and 42 to 116 for six geographic units north of Point Conception (shelf [0 to 199 m depths], slope [200 to 1999 m] and "offshore" [>1999 m] regions, respectively, in central and northern California). We extrapolated to estimated regional populations (approximate number of individuals) by multiplying regional mean densities by the appropriate regional areas. Adding these estimated ("instantaneous") regional populations for a given month provided an estimate for the total population. In no case did we know the rates of population turnover for migrating species. As a result, numbers of birds actually passing through California may have been several times larger than the "instantaneous" estimates that we present. Due to large standard errors in density estimates at sea, the error range typical of our monthly population estimates was ±25% to 40%. Accordingly, we report mean regional densities (±1 SE) and estimated total populations, and do not attempt to statistically assess the significance of differences in estimates between regions or months.

Bird densities were used in two types of further analyses: they were transformed into location-specific standing stock estimates (biomass per unit area), and they were used along with environmental variables to prepare matrices for principal components analyses. Transformation of bird density to biomass density (kg km^{-2}) was accomplished by multiplying grid-cell densities by a figure representing mass of each species or species group (Briggs and Chu 1987).

Species diversity

Two measures of species diversity are presented for each area and month: the raw number of species or groups recorded, and the Shannon Index of Diversity (Shannon and Weaver 1949):

$$H' = -\sum_{i=1}^{n} (P_i \cdot \ln P_i)$$

(where n is the number of species recorded and P_i is the proportion of total density contributed by species i). Diversity indices are sensitive to scale of measurement; i.e., the size of the sampling unit affects the value of the index. We estimated species diversity for several (nested) scales of measurement using aerial data from central and northern California: species lists were compiled and H′ calculated for progressively larger geographic units, starting with 5′ longitudinal (approximately 7.3 km) segments of aerial trackline. Focusing on the central California shelf/continental slope region, we then combined 5′ segments along 7 to 11 east-west tracklines, each of which was about 20 to 40 km in length (for example, all segments on the line extending west of Point Pinos), and recalculated species numbers and H′ for each line. Finally, we calculated diversity from all sightings in each region (e.g., ignoring grid cells and transect lines and compiling a species/abundance list from all sightings made in May 1980 on the central California shelf), for all of central California (shelf, slope, and offshore) and for all of central and northern California combined.

Species associations and scales of aggregation

We investigated the association between species over spatial scales ranging from the individual flock of two or more birds swimming or feeding together, to groups of flocks seen over tens of km. These analyses required different kinds of data and different kinds of statistical tools.

The consistency of association between species was estimated by examining sightings comprising more than one bird of one or more species either feeding together (useful primarily for surface-foraging species) or swimming or flying in close proximity (up to about 50 m). To obtain meaningful sample sizes, these analyses were limited to species having relatively high abundance.

Aerial observers frequently are unable to perceive the structure of bird aggregations that extend over several hundred meters along a trackline: the substructure of a flock may be seen but cohesiveness of the whole unit may go unnoticed. Compared to ship observations, during which a given bird flock may be in view for several minutes (a time-sample component), aerial data are much like a single frame out of a strip of movie film. The result is that aerial data underestimate the proportion of birds that associate with one another, and overestimate the proportion of non-associated and solitary individuals. Recognizing this bias, we selected only those aerial sightings pertaining to birds in association with one another (as compared with solitary birds) and calculated Cole's Coefficient of Association (Cole 1949). This index ranges from -1.0 (complete avoidance between two species) to $+1.0$ (complete association). Significance of the index is estimated by computing a Chi-square statistic from a 2×2 table in which the cells are: number of flocks containing species A and species B, number of flocks containing A but not B, flocks containing B but not A, and flocks containing neither.

We evaluated flock associations by season, using central and northern California data: the 'breeding' season included April through July, the 'post-breeding' season extended from August through November, and the 'winter' included December through March. Approximately 500 to 600 flock records were included in each seasonal analysis.

To compare the geographic scales of aggregations of birds (raw numbers were used; flocks and individuals were treated equivalently) found on the same transect lines, we followed a method first applied to marine bird data by Schneider and Duffy (1985). This method employs an index of patchiness (I′ of Ord 1972) and requires continuous transect data. Owing to the orientation of our transect lines, across-shelf variations could be resolved to about the scale of the smallest time increment routinely employed by observers (one minute of flight time or about 3 km), but patterns of aggregation along the shelf could be evaluated only at much larger scale, corresponding to the interval between flight lines (9 to 28 km). Aerial and ship sampling in central California in 1985 indicated that for several species, aggregations had different characteristic scales in the two directions (Briggs et al. in press). This is noted where it is known to occur. Because of this and the apparent richness of variation on scales shorter than could be resolved along the shelf, we limit our discussion to cross-shelf data. Information from southern California was not included because (1) in much of the region there is no clear-cut across-shelf or along-shelf orientation, and (2) topographic and island influences on water circulation patterns are very complex, potentially obscuring any simple pattern in bird aggregations that might result from relatively simple patterns in habitat structure. Additionally, concurrent satellite imagery of surface temperature patterns was not available for the (earlier) southern California studies, negating the possibility of simultaneously evaluating spatial variation in bird aggregations and this environmental parameter.

Among the several available indices for determining characteristic patch sizes in birds, we used the simple ratio I′ discussed by Ord (1972) in preference to more complex, and computationally intractable measures. Using bird numbers in each 3-km unit (bin) of continuous aerial transects (one minute of flight time), the mean and variance were computed and the index was plotted as a function of bin size. Bird numbers were successively aggregated into larger bins until only three such bins composed the entire transect. Variations in I′ are considered for different species, locations (near versus away from active colonies), and seasons.

The 3-km unit is coarse relative to the scale of actual bird flocks. However, Schneider and Duffy (1985) and Schneider and Piatt (in press) have used ship data to show that intensity of aggregation of a variety of seabirds is lower for bins of 1 to 3 km than for larger units. Thus, while our analysis does not apply to distances at which birds are typically in direct visual contact, we are able to examine intensity of aggregation over scales corresponding to large prey patches and different marine habitats.

Habitat characteristics

The relationships of selected bird species to various environmental features were analyzed by correlation and principal components analyses (PCA). Values for water temperature and depth, distance from the nearest point of land and from the nearest point on the continental shelf-break, bottom slope (maximum elevational disparity per km) were computed for each 5′ by 5′ geographic grid cell. Gradients in surface water temperature, which may help to define seabird habitats, were calculated from temperature values at the centerpoint of each visited grid cell. Surface temperature gradients were computed as temperature difference (°C) divided by distance measured between centerpoints of adjacent grid cells. Thus, a maximum of eight $\Delta T/\Delta D$ values were available for each sampled cell, assuming that all neighboring cells also were sampled. We selected the maximum gradient value for each cell.

After major habitat components were identified by PCA, we determined correlations between bird density variations and values of habitat components. We used orthogonal rotation of resulting axes and a minimum eigenvalue of 1.0 for inclusion in the model (SAS 1982).

Bird densities were log-transformed (Sokal and Rohlf 1981) to control variance, thus emphasizing order-of-magnitude variations in abundance. These analyses indicated which species' abundances most strongly correlated with variation along two or three major gradients in open-water habitats.

Our analysis of bird aggregations is complemented by examination of the scales of variation in surface thermal patterns. These were assessed via spatial autocorrelation, using satellite imagery obtained concurrently with sampling of bird populations. The maximum resolution of satellite data was about 1.1 km, and values were calibrated to ±0.3°C against aircraft radiometer data and against NOAA oceanographic buoy data.

Autocorrelation analysis typically is applied to residuals rather than raw data. Thus, we sought to remove a mean trend from each data set. Regression analysis indicated that only about 12% of variance in satellite temperature data was explained by the pattern of 20-year mean values for the same locations and months (modified from Auer 1982, 1983). Although statistically significant for the large sets of data used (400 to 500 data points), it appeared that a better fit to the satellite data (resulting in smaller residuals) could be obtained by using a linear regression of temperature against latitude and distance offshore. When this regression was fitted to September 1981 data, the model explained 17% of temperature variation. This procedure was adopted for de-trending data from three additional images. After removing the mean latitude/distance trends from the data, autocorrelations were computed at separations of 1 to 64 km in the west and north directions. These are reported separately for the cross-shelf and along-shelf directions, as well as for the combined data.

Because of the degree of processing required in computing autocorrelations from the satellite image data and potential aliasing due to time lags (up to 24 hours) between bird sampling and satellite imaging, we do not attempt to statistically compare autocorrelation patterns between regions or dates. Rather, we employ these analyses to determine whether certain bird species appear to aggregate on scales similar to those predominating in environmental data.

OCEANOGRAPHY OF THE STUDY AREA

The oceanography and, to a great extent, the climatology of the coast of California is dominated by influences of the California Current, its associated countercurrent, and by seasonal upwellings. Large scale processes affecting exploitable fish stocks have received a great deal of attention over the past several decades. Particularly well studied are the geographic and temporal variations in hydrographic parameters affecting populations of the northern anchovy (*Engraulis mordax*) and Pacific sardine as well as characteristics of plankton populations fed upon by these fish. With both resources and research interest concentrated in waters from northern Baja California to about Point Conception, researchers associated with the multi-agency California Cooperative Oceanic Fisheries Investigations (CalCOFI) program have monitored physical and biological variables with mixed intensity since the late 1940s.

Several authors have related aspects of the physical environment to seasonal and geographic patterns of seabird populations and distributions in the California Current System. Ainley (1976) drew upon existing CalCOFI data concerning thermal and salinity regimes off California to describe general population abundance for many seabird species in differing years, seasons, and temperature/salinity regimes. Somewhat more detailed descriptions have appeared for several species (Briggs et al. 1981b, 1983, 1984). Recent research and re-examination of older information have modified somewhat the pre-1970 perceptions of the characteristics and processes of the California Current System. As an update to this conceptual progress and a prelude to habitat analyses appearing later in this paper, we review here the oceanography of the California Current System.

BATHYMETRY

The coastline of California trends south from Oregon to Point Conception, then veers abruptly to the east and southeast forming the Southern California Bight (SCB). Major promontories include Cape Mendocino and points Arena, Reyes, Sur, and Conception. The continental shelf (depth 0–199 m) is very narrow (5 to 35 km) in much of northern and central California, but broadens to 50 to 75 km off Eureka, San Francisco, and Morro Bay. Deep submarine canyons dissect the shelf near Cape Mendocino and Monterey Bay, and sheltered embayments are present at Eureka, Bodega, Point Reyes, San Francisco, Monterey, Morro Bay, and San Diego. South of Point Conception, the seafloor is complex, consisting of a series of basins and ridges, some topped by islands. In contrast to waters north of Point Conception where only Año Nuevo, the Farallones, and Castle Rock could be considered as important island habitat, the SCB contains nine islands or island groups (including Islas Los Coronados just southwest of San Diego). Here, deep basins (> 1000 m) lie close-by rugged island chains and submerged banks, creating very complex circulation patterns. The main continental slope runs south from Point Conception and lies more than 200 km west of San Diego.

GENERAL CHARACTERISTICS OF SURFACE WATERS

Waters off California shallower than 200 m depth are relatively cool, fresh, and nutrient-rich compared with those at equivalent latitudes in the central or western Pacific, or those south of central Baja California, Mexico. Reid et al. (1958), Hickey (1979), and Bernal and McGowan (1981) point out the north-south trend in chemical and thermal conditions of surface waters: ignoring the strong, localized, seasonal variations imposed by coastal upwellings (discussed below), waters are coolest, freshest, and generally richest in organic nutrients north of Point Arena. Latitudinal gradients in temperature are greatest in late summer, when waters off extreme northern California may be 10°C cooler than those near the U.S./Mexico border. Sea surface temperatures (SSTs) range between about 8 to 9°C in the north during late winter and spring and more than 20°C near San Diego in late summer. Seasonal ranges in temperatures and variations from twenty-year means are presented for the waters sampled in this study by Briggs and Chu (1986).

It is noteworthy that, beginning in about mid-1976, a secular rise in temperatures prevailed over all areas and times included in this study. McLain (1983) discussed periodic fluctuations between relatively cool and relatively warm temperature regimes in this region, linking them to North Pacific Basin-wide shifts in meteorologic and oceanographic conditions lasting up to a decade. A previous 'hingepoint,' when conditions seemed to shift, occurred in 1957–1958.

The summer thermocline is shallower in the north than off southern California (roughly 10 to 20 m deep versus 30 to 60 m) and deepens with distance from shore to more than 80 m at the seaward limits of our study area. Phytoplankton concentration maxima often are found at the (deep) thermocline offshore but may peak near the surface over the shelf. Turbid waters over the shelf result from dense plant pigment concentrations, sediment discharges from rivers and coastal bays, and suspension of sediments by wave and current action.

Surface waters of the California Current flow in a southerly direction, with considerable short-term, localized variability. The fastest flows are in the range of 0.5 m sec^{-1} and center 200 to 500 km offshore. The California Undercurrent underlies and flows in the opposite direction to the California Current through most of the year. Its importance to bird populations and to their prey is that the Undercurrent surfaces near the coast from about Point Conception to at least southern Washington from approximately November through February. This northward coastal current, referred to as the Davidson Current, contains water that is warmer and saltier than California Current water at comparable depths. In spring and summer, when the Undercurrent flows at 100 to 300 m depth below the California Current, coastal upwelling appears to draw from the Undercurrent as replacement for surface waters that are advected seaward.

Between the southern California mainland (south of Los Angeles) and about 118°W, waters usually flow to the north from about May through February or March. Farther offshore, within the main axis of the California Current, flow is to the southeast through much of the year.

It is now appreciated that global and basin-wide shifts in meteorological and hydrographic conditions associated with El Niño-Southern Oscillation (ENSO) cycles lead to occasional weakening of southward flow within the the California Current, strengthening of the coastal countercurrent in winter, and deepening and stabilization of the surface layer (0 to 300 m) density structure. In years such as 1957–1958, 1969, 1972, 1976, and 1982–1983, strong coastal countercurrents in winter transported warm, salty water from offshore and south, creating a relatively stable surface layer through which upwelling of nutrients in the subsequent spring was impaired (Chelton 1980, McLain 1983). The profound effects of the strong 1982–1983 ENSO event in California have been examined by McLain (1983), McGowan (1984), Fiedler (1984), Ainley et al. (ms) and others. Bernal and McGowan (1981) and Chelton et al. (1982) have shown that annual variations in standing stock and productivity of plant and animal plankton in the California Current correlate with variations in transport of water from the north. In years of strong, southward transport, primary production is high (Smith and Eppley 1982), zooplankton standing stocks increase, and the productivity of anchovies and rockfish (*Sebastes* spp.) is at a peak. Ainley et al. (in press) and Hodder and Graybill (1985) relate annual changes in productivity to seabird nesting success on the Farallon Islands and Oregon, respectively. Years of low southward transport, particularly those with strong ENSO events, are characterized by low productivity in the plankton, as well as in fish and squid, upon which most seabirds feed.

UPWELLING

Upwelling is an extremely important, localized phenomenon along the Pacific coast. Its influences are seen not only in hydrographic characteristics of coastal waters but also in various aspects of food-web productivity and coastal meteorology. Prevalence of north- and northwesterly winds during spring and summer leads to offshore transport of coastal surface waters and replacement by waters drawn from depths to about 100 m. These upwelled waters are cool, salty, and rich in organic nutrients. In addition to augmenting ocean productivity, upwellings have several characteristics of significance to the seabird fauna. One such attribute is the formation of strong gradients in chemical and physical properties of seawater at the seaward edges, where upwelled waters intrude into the warmer, fresher, thermally stratified waters of the California Current. At these 'upwelling fronts' (which are usually 10 to 30 km in cross-shelf breadth), thermal gradients may exceed 0.5°C km^{-1} and may be accompanied by abrupt changes in ocean color (chlorophyll fronts), slicks, accumulations of flotsom and drift kelp, and sometimes by large concentrations of zooplankton and their predators (Briggs et al. 1984, Briggs and Chu 1986, 1987). These upwelling boundaries typically overlie the continental slope, are structurally complex, and may persist for several weeks. Fronts visible in satellite infrared images extend up to 300 km along and offshore of the shelf-break (Fig. 2).

Upwellings exert a strong influence on the composition of the prey base available to seabirds. Parrish et al. (1981) point out that among fishes heavily utilized by birds for food, there exists a marked difference between the dominant species spawning in the region of strongest upwelling (Point Conception to Cape Mendocino) and the species spawning in the SCB. For example, spawning and survival of young northern anchovies are favored by formation of large patches of (usually dinoflagellate) prey for the larvae. These conditions frequently prevail in southern California during late winter but are seldom seen off central or northern California, especially (due to turbulence) in the main upwelling season. Accordingly, anchovies do not spawn in large numbers between Point Conception and the California/Oregon border. In contrast, rockfishes and flatfishes spawn in large numbers in the region of maximum upwelling and are abundant in seabird diets through spring and early summer. Anchovy biomass, and we assume availability to seabird predators, is highest during spawning season in the south, and anchovies become an important component of bird diets in central California only later in summer, after the

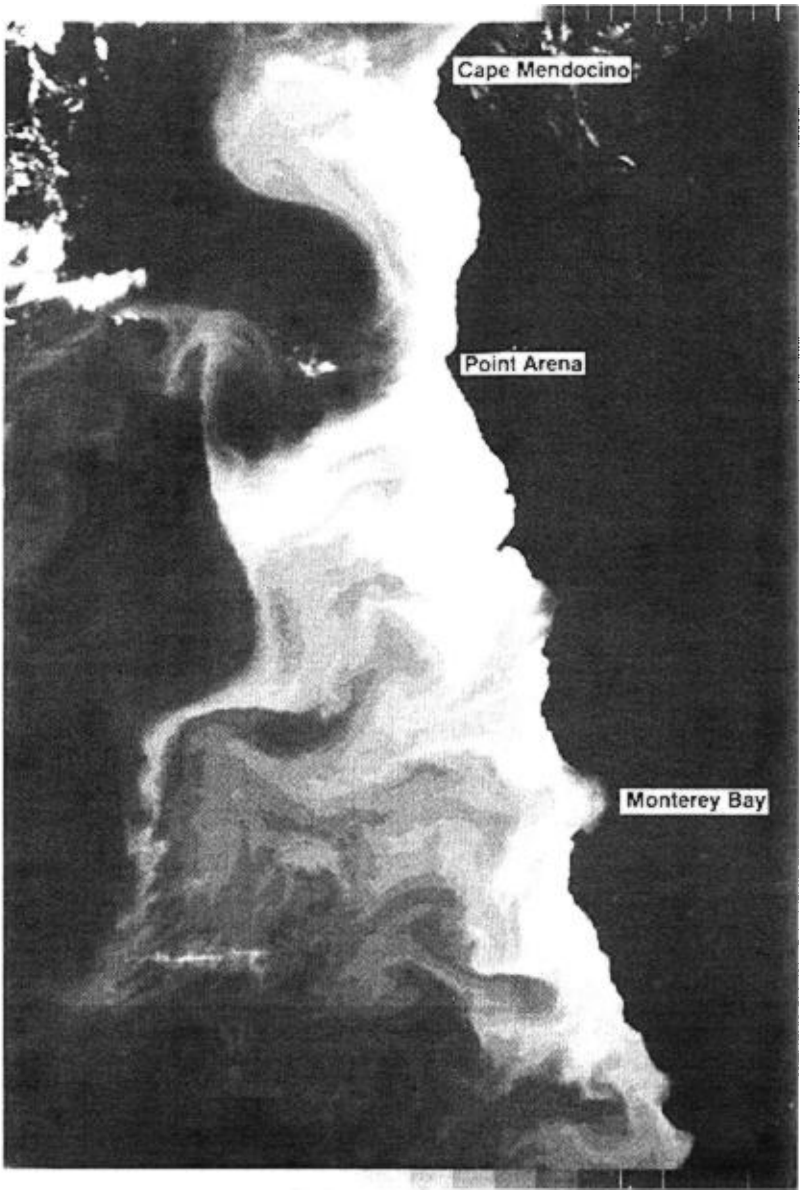

FIGURE 2. Satellite infrared image of sea surface temperature off California on 21 September 1981. The coolest waters, represented by light grey shades, are 9 to 11°C, whereas dark shades mark waters warmer than 16°C. Several filaments of upwelled (cool) water extend for 100s of km from major headlands (courtesy E. Daghir).

fish undertake post-spawning migration out of the SCB (see, for example, Briggs and Chu 1986, 1987).

Upwellings can occur in any season and almost everywhere along the California coast; however, the months of greatest extent and persistence are April through about September. Within each year, upwelling reaches greatest intensity earlier in the south (Nelson 1977). Peak upwelling occurs in northern Baja California from March through May, off Point Conception April through early June, off Cape Mendocino May through July, and off Oregon from June through late July or early August. In all areas, favorable winds tend to pulse; periods of heavy upwelling are interspersed with relative calms, during which surface waters may become heated by the sun and stratified, and offshore waters may move toward the coast. Centers of upwelling, where winds are strongest and persist in directions favorable for upwelling, and where surface waters become coolest, include Point St. George, Cape Mendocino, Point Arena, Point Reyes, Point Sur, and Point Arguello-Point Conception. In each of these locations, the coolest surface waters typically are found somewhat downstream (southward and offshore) of coastal promontories.

The general seasonality of hydrographic conditions was characterized for Monterey Bay by Bolin and Abbott (1963). Three main seasons were the Upwelling season (discussed above), the Oceanic season (when upwelling ceases and thermally stratified waters originating offshore move toward the coast, bringing with them elements of the 'oceanic' plankton), which lasts roughly from late summer until November, and the Davidson Current season (November through February) when coastal surface waters move north and coastal convergence or downwelling occurs. This scheme has been rather loosely applied to other areas of the state, assuming similarity of timing and conditions. However, studies completed recently in the Point Sur area, together with the large archive of satellite images of SST now available for the Pacific Coast show that upwelling can and does occur in all seasons. At Point Sur, Breaker (1983) found alternation of upwelling and nonupwelling regimes. The Oceanic season of Bolin and Abbott may in fact be peculiar to Monterey Bay and a few other sites where large, persistent, warm eddies of the California Current approach the coast with the general diminution of upwelling after about August. A warm eddy offshore of Monterey Bay can be seen in a large portion of available satellite SST images, but no such structure is consistently present near Point Sur, Point Conception, Point Reyes, or Point St. George. Conversely, large, warm eddies often approach the coast west of Eureka, near Point Arena, and south of Morro Bay.

IMPORTANT MESOSCALE FEATURES

Advances in the ability of oceanographers to rapidly assess the hydrographic (especially thermal) and optical characteristics of surface waters over large spatial scales (100s to 1000s of kms) has revealed that the California Current System is rich in meanders and eddies. Meanders are no less prevalent in the California Current than in more energetic western boundary currents (such as the Gulf Stream and the Kuroshio Current) and occur in all seasons (Hickey 1979, Huyer 1983, Mooers and Robinson 1984). Meander effects may include current jets running counter to the southward mean flow at speeds of up to 1.0 m sec^{-1} (Owen 1980, Simpson et al. 1984). The eddies studied to date have characteristic persistence scales varying with size from days to many months; some have been shown to exert an influence on subsurface hydrographic conditions to depths of a few hundred meters. The most permanent California Current eddies may be relatively fixed in place by bottom topography.

The largest and ecologically most important eddy-like structure is the so-called Southern California Eddy which forms south and east of Point Conception and influences hydrographic patterns through much of the SCB. Although commonly regarded as a cyclonic recurvature of the eastern limb of the California Current (Owen 1980), the western part of this structure appears in satellite imagery of temperature to be a cool, advected mass contiguous with the major upwellings at Point Conception. In contrast, waters east of the Santa Rosa-Cortés Ridge are subtropical in nature, and different from the cool waters transported away from the Point Conception upwelling. The boundary between these water types often lies just east of San Nicolas Island and may in fact be a zone of strong sheer between opposing currents. Effects of the "Southern California Eddy" on biological populations, including important habitat influences on spawning anchovies, are discussed by Owen (1980) and Parrish et al. (1981).

Another mesoscale oceanographic feature of apparent significance to seabirds is the tidal plume formed outside the Golden Gate on outgoing tides. This plume of turbid, estuarine waters often has a very sharp edge forming an arc extending as far offshore as 25 km into the Gulf of the Farallones, reaching maximum expression in late winter/early spring. Waters of the plume are less salty and of different temperature than ocean waters of the Gulf (depending on the season, the plume may be relatively warm or cool). Recent field studies suggest that both plankton (euphausiid) and fish populations differ between the areas normally included within the plume and those lying outside (S. E. Smith, P. B. Adams pers. comm.). Aggregations of seabirds along the edge of the plume are common, and certain species (such as shearwaters and Cassin's Auklets) avoid the turbid waters of the plume itself (K.T.B., D. G. Ainley unpubl. data).

RESULTS

SEABIRD NUMBERS AND STATUS

The California state list includes 103 species that make up the marine avifauna. These species obtain almost all their food from the sea and occur on salt water more than half the year. This total excludes the shorebirds except phalaropes, all anseriforms except scoters and brant, and all waders. We observed 74 marine species during the course of our studies. About 30 of these species were relatively numerous in their preferred habitats and seasons and accounted for the great majority of energy cycling through the California marine bird community (Briggs and Chu 1987). In the following 62 species accounts we emphasize data concerning the California nesting fauna and species whose estimated total populations exceeded 20,000 individuals. We do not consider species seen only once or a few times or those never observed away from the mainland shore.

Red-throated Loon, *Gavia stellata*

Loons are relatively easy to identify from above (during aerial surveys) when in the nuptial plumage (especially March through May). In autumn and winter, however, when immature birds are present and adults are in basic plumage, many Pacific and Common loons (*G. pacifica* and *G. immer*) cannot be distinguished. Red-throated Loons (*G. stellata*) are always much paler, appearing small, speckled and with a slender neck.

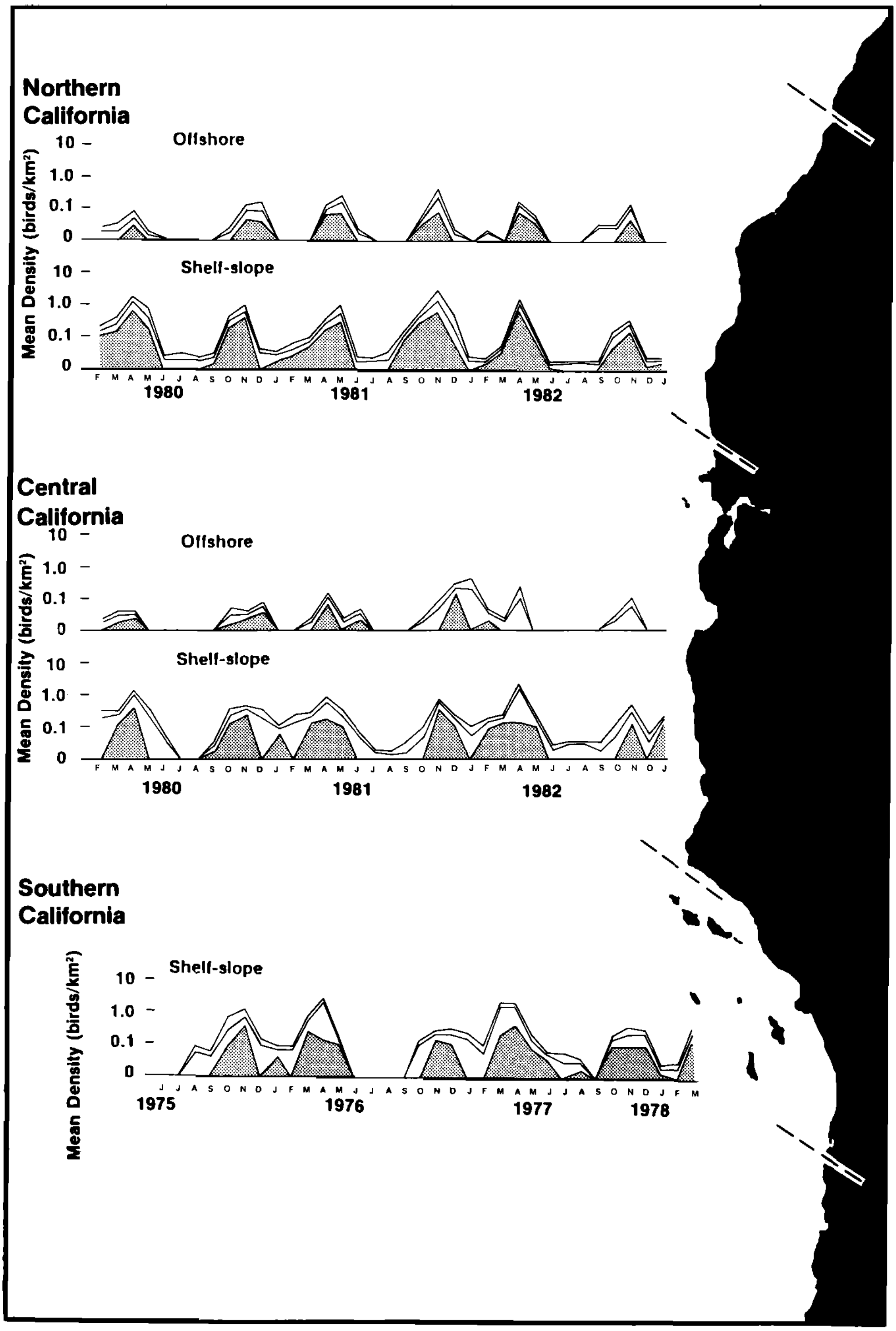

FIGURE 3. Comparison of monthly mean densities of Pacific Loons in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

Where we encountered substantial numbers of unidentified loons in winter, we arbitrarily apportioned them to species in the same ratio recorded among birds identified to species at the same general location.

The Red-throated Loon generally is far less numerous than the Pacific Loon and in migration is decidedly more coastal in distribution; as with other loons, peak numbers occur during migration and winter. There is some suggestion that Red-throated Loons migrate a few weeks earlier in spring and a few weeks later in fall than do other loons.

During our studies, Red-throated Loons were most numerous off central and northern California, particularly on the sheltered waters of Morro Bay, Monterey Bay, the Gulf of the Farallones, and Tomales Bay, and along the open coast from Eureka to Trinidad Head. Estimated populations north of Point Conception were on the order of 3800 to 16,000 in April and about a third less in autumn. Numbers dropped to about 2000 to 3000 in winter.

Within 0.5 km of the southern California mainland, we found Red-throated Loons to be more than ten times as numerous as Common or Pacific loons. Farther to seaward, they were relatively rare, with less than 100 seen near the Channel Islands at the peak of winter occupancy. Shelf waters at the eastern end of Santa Barbara Channel harbored estimated peak numbers of 1000 to 3000 birds.

Pacific Loon, *Gavia pacifica*

The Pacific Loon is the most abundant and widely distributed loon off California; the great majority of loons seen more than about 10 km from the mainland are of this species (Small 1974, Ainley 1976). Because of our fixed, monthly sampling in central and northern California, the exact timing of the autumn migration could not be determined. But, as was seen by DeSante and Ainley (1980) at the Farallones, peak counts always occurred in late-November. Peak numbers of fall migrants reached southern California in mid-December. Relatively small populations remained in California each winter with perhaps 10,000 to 15,000 birds, on average, coastwide, evenly distributed between northern, central, and southern California. Populations of birds remaining through summer were very small and concentrated from San Francisco northward.

Peak densities of Pacific Loons seen during migrations were 0.8 to 1.8 birds km^{-2} in central and northern California and 0.4 to 1.8 birds km^{-2} in the south (Fig. 3). Turnover rates in migration are unknown; however, we estimate that populations ranged from 75,000 to 287,000 at once in central and northern California and 40,000 to 60,000 in the south. Compared to these numbers, an eleven-week spring shoreline count from Pigeon Point in central California, produced a total of 432,000 migrating loons, 98% of which were Pacific Loons (Winter and Morlan 1977). The peak count of 46,770 birds came in late April 1977; these shoreline counts would have missed a sizeable number of birds migrating more than about 5 km from the coast.

Wintering numbers of Pacific Loons were much smaller, with 5000 to 19,000 birds estimated for central and northern California in January 1981, 1982, and 1983, and about 5000 in southern California during winter 1976, 1977, and 1978.

North of Point Conception, Pacific Loons migrated primarily over the continental shelf. During November surveys, we found more than ten times as many Pacific Loons over shelf waters than over the continental slope; most birds were found from 5 to 50 km offshore. Because of the northwest-southeast trend of the southern California coast, loons travelling southward from near Point Conception spread over a broad offshore area. We found them to be most common within 40 km of the southern California mainland, but they also occurred in densities above 1.0 birds km^{-2} as far offshore as 75 km. The farthest offshore that we saw Pacific Loons was 110 km west of Monterey and at Tanner Bank, 165 km southwest of Los Angeles (but only 65 km south of San Nicolas Island).

During winter, Pacific Loons occupied only relatively sheltered waters along mainland and island coasts; favored sites included Bodega and Tomales bays, the Gulf of the Farallones, Monterey Bay, and eastern Santa Barbara Channel (where densities occasionally rose to over 80 birds km^{-2} over the shallows northeast of Anacapa Island). The 300+ km stretch of coast north of Point Arena, where winter storminess is most severe, harbored only about 5% of the statewide winter total.

Spring migration took place in March through early June with a distinct peak at the time of our late-April counts. DeSante and Ainley (1980) noted a peak in late March at the Farallones, but our larger samples consistently indicated a later peak for central California. The pattern of spring migration looked like that in fall, except that we frequently saw hundreds or thousands of loons feeding or resting in shallow waters of the island passes of Santa Barbara Channel. Loons in breeding plumage occurred among them as late as 15 June (1975 and 1976).

Common Loon, *Gavia immer*

We noted migrating Common Loons from late March to late May and late October to mid-December, but data were too sparse to detect any seasonal peak or north-south trend in timing. DeSante and Ainley (1980) noted that peak migration dates at the Farallones were late October to mid-November.

Extrapolation from densities recorded in five April surveys (1976, 1977, 1980, 1981, 1982) suggests that the 'instantaneous' population of Common Loons was between 5000 to 10,000 birds at sea and about 1000 within 0.5 km from the coast. Common Loons were concentrated near the coast at Morro Bay, Monterey Bay, the Gulf of the Farallones, Tomales Bay, and north of Trinidad Head (the same areas as the Red-throated Loon), but undoubtedly were still more abundant on estuarine waters not included in our samples (e.g., San Francisco Bay).

This species was difficult to identify during winter aerial censuses of the coastline; however, Common Loons appear to have numbered less than 1000 statewide from December through March.

Eared/Horned Grebe, *Podiceps nigricollis/auritus*

Due to their narrow along-coast distribution and a tendency to dive at the approach of aircraft, small grebes (predominantly Eared Grebes, but also Horned Grebes) were difficult to identify and not adequately censused by our aerial survey techniques; in this account we refer to them collectively as Eared Grebes, noting that Horned Grebes probably accounted for less than 5% of all small grebes seen on open coastal waters. Ship surveys around the southern California islands provided reliable counts, but not all islands were visited each survey, and the mainland was not censused in this way.

Eared Grebes were sighted near the Santa Barbara Channel islands from September through June each year, with high counts in January or February (2834 were counted in February 1976). Along the mainland of southern California we saw far fewer birds; populations along the open coast were as low as 500 to 1000 birds during winter. Numbers throughout southern California dwindled for a month or two in late winter, then rose again in midspring, apparently as a result of birds moving into the area from the south (Eared Grebes are abundant in the Gulf of California through April; D. W. Anderson and K.T.B. unpubl. obs.). We counted up to 1800 small grebes during winter aerial surveys of central and northern California, most within Tomales Bay and at the entrance to San Francisco Bay; this figure may understate the actual numbers of these grebes present in the region by one or more orders of magnitude. Flocks of hundreds of Eared Grebes are seen during winter in the vicinity of the Farallon Islands; an estimated 3120 birds occurred there during fall and winter 1974–1975 and peak counts were attained from mid-December through mid-March (DeSante and Ainley 1980).

Western/Clark's Grebe, *Aechmophorus occidentalis/clarkii*

These two species were not distinguishable from the air and Clark's was not yet given species rank at the time of our southern California studies. For simplicity we collectively refer to both species as "Western" Grebes.

The Western Grebe is one of the predominant species in waters within 0.5 km of the mainland coast during October through May, and at least a few birds can be found on inshore waters throughout the year. This species shows a distinct preference for waters over sandy bottom less than 10 m deep (determined from coastal charts and direct observations from the air), especially downwind from major headlands.

Up to a few hundred birds appeared on saltwater in central and northern California by late September each year. Numbers of birds on coastal waters increased throughout fall, and peak populations occurred from November through January. Winter numbers were variable, probably reflecting movements to and from coastal estuaries in response to the passage of storms. A coastwide decline in numbers was seen after March, and populations were lowest from May through late August (Fig. 4).

Because Western Grebes occupied an extremely narrow band, within about 0.5 km of the coast, their numbers were poorly resolved by our offshore transects. Along-coast counts were relatively infrequent, and suspected weather-related population movements render even this technique somewhat inadequate. However, peak populations were on the order of 25,000 birds north of Point Conception and 27,000 to the south. Three areas of concentration in winter were evident: the coast from Trinidad Head to Point St. George, which was usually occupied by 4000 to 5000 birds; the waters from Bodega Bay to Monterey Bay, which harbored up to about 10,000 birds; and the shallows at the eastern end of Santa Barbara Channel, which supported an estimated 2000 to 27,000 birds (averaging 10,000 on three January surveys). Counts along the coast in summer were much lower: 1700 to 4100 in central and northern California during July 1980, 1981, and 1982, and perhaps 500 to 800 along the southern California coast during 1975 to 1977. Western Grebes were very uncommon offshore, even near island shores. They were scarce near the Channel Islands, and DeSante and Ainley (1980) have reported that fewer than ten birds occur at any given time at the Farallones. Interestingly, at the Farallones, these grebes reached

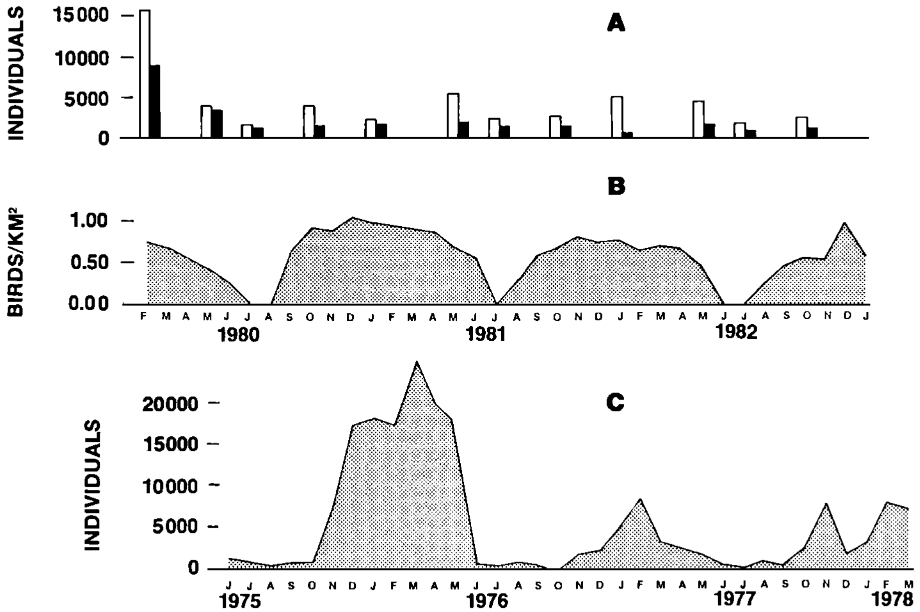

FIGURE 4. Shoreline counts and open-water densities of Western/Clark's Grebes. (A) Shoreline counts of grebes in northern California (open bars) and central California (solid) during 1980–1982. (B) Mean density of grebes in shelf waters of central and northern California (combined). (C) Estimated grebe populations throughout southern California extrapolated from mainland and island beach counts and aerial transects of eastern Santa Barbara Channel.

peak numbers in late September and early October and were much less numerous thereafter (DeSante and Ainley 1980), a pattern quite different from that characteristic of the mainland coast.

Black-footed Albatross, *Diomedea nigripes*

The Black-footed is the most numerous albatross on coastal waters of the U.S. Pacific coast and is present throughout the year. Peak abundance occurred from May through July, with an estimated 15,000 to 75,000 birds present in early summer. Numbers were lowest from October through February, during which period we estimate a population totalling only 500 to 1500 birds.

Various authors have commented on latitudinal patterns in Black-footed Albatross abundance and seasonality off California. Sanger (1974), analyzing observations gathered during 100 months of sampling by the CalCOFI program during the 1950s, showed a strong north-south gradient in numbers: Black-footed Albatross were two to ten times more abundant north of Point Conception than to the south. In central and northern California, Sanger detected no obvious east-west trend, but off southern California albatrosses were more numerous far offshore (i.e., in the California Current proper) than within about 100 km of the coast. These observations were based on counts made while ships were on station for hydrographic work, and coverage was quite variable between months and regions. Ainley (1976) examined accounts published in AFN/AB and also suggested that Black-footed Albatross were more numerous in central and northern California and less so farther south. He noted that the peak in sightings occurred later off southern California (August) than off central California (May–July).

Our data, which are based on replicated coverage in all seasons, show three trends with regard to seasonal distribution of this species: 1) In almost all cases, densities were much higher north of San Francisco than to the south (Fig. 5); 2) birds were more numerous over the continental slope than either the shelf or the waters farther to seaward (we did not sample some of the regions far offshore discussed by Sanger 1974); and 3) there was a *northward* seasonal withdrawal of the center of abundance from April onwards. Birds were concentrated north of San Francisco in all seasons, but in summer, at peak population, the largest numbers of birds were seen north of Cape Mendocino.

Off southern California, we noted peak numbers in May or June each year. By far, the largest portion of the 71 sightings there occurred within

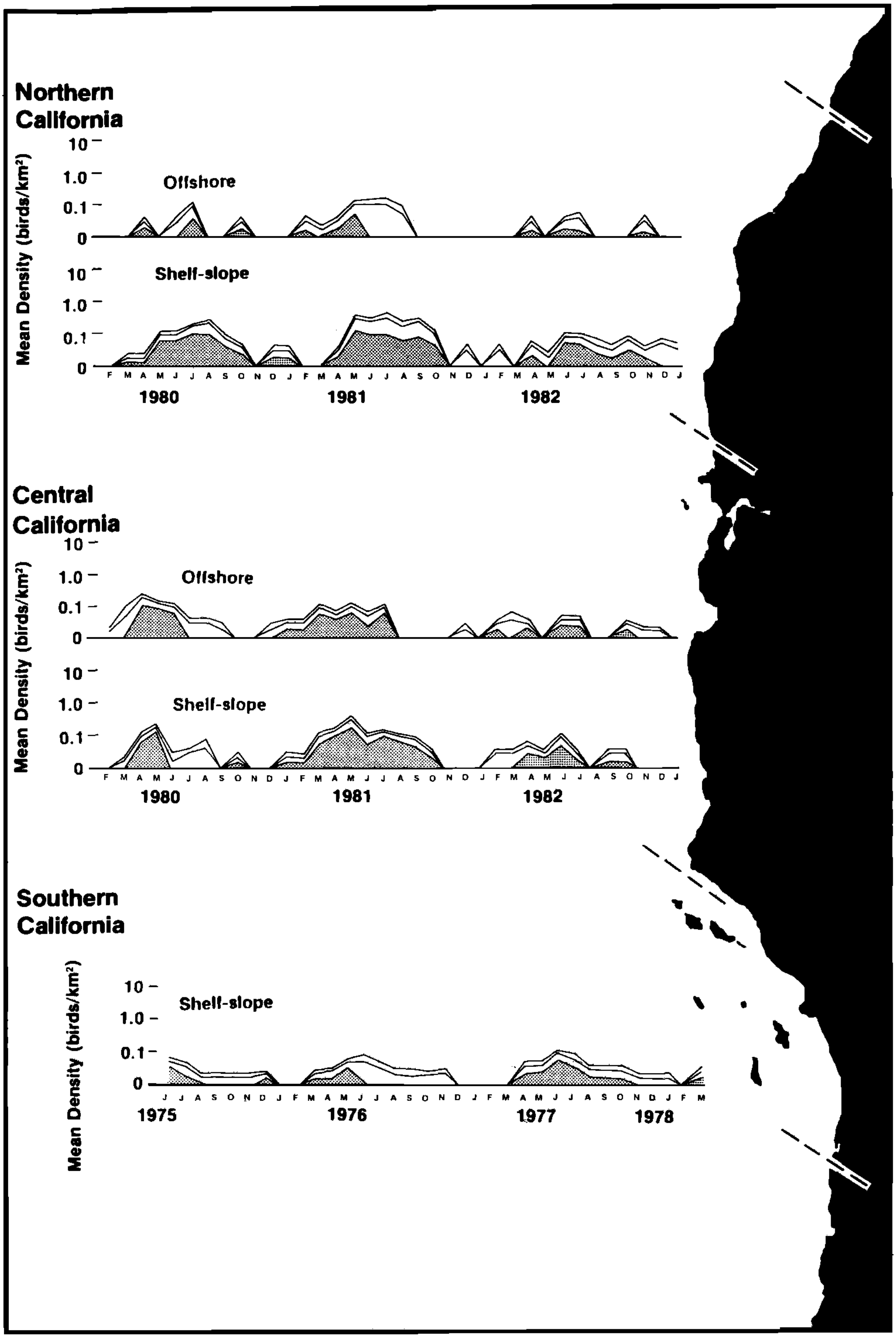

FIGURE 5. Comparison of monthly mean densities of Black-footed Albatross in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

25 km of the axis of the Santa Rosa-Cortês Ridge, especially near San Miguel Island and Tanner-Cortês Bank. These are the coolest and most productive waters off southern California. We think that the late-summer peak in sightings reported by Ainley (1976) is a function of seasonal and geographic bias in data from birdwatching trips originating at southern California ports: in spring and early summer these trips usually avoid the rough, cool, offshore waters where albatrosses actually concentrate.

Black-footed Albatross were most numerous along the upper continental slope from the Farallones to Eureka. Within these areas occur some very complex and dynamic interactions between upwelling filaments and warm, California Current eddies (Huyer and Kosro 1987). Albatross generally were found on the warmer, more translucent sides of color or thermal boundaries separating these two types of water. These areas also support important trawl fisheries that provide considerable quantities of fish offal to scavenging albatross.

Our southern California data are insufficient to ascertain much about interannual variability in numbers, but fewer birds were sighted in 1976, an ENSO year, than in 1975 or 1977. In central and northern California, numbers of Black-footed Albatross were 50% lower at the 1982 June peak than in the two previous years. And, densities were comparatively low from July 1982 onward. At about this time, oceanographers were noting atmospheric changes relating to the onset of the intense 1982–1983 ENSO episode. Sanger (1974) noted a similar decline in albatross numbers in central California coastal waters during the 1957 episode; farther offshore the pattern was not obvious.

Laysan Albatross, *Diomedea immutabilis*

We saw Laysan Albatrosses infrequently off central and northern California and rarely off southern California. Thirty-three sightings of single birds were logged in central and northern California; all but two (August 1982) were seen in November through April, and all but five were north of Monterey Bay. We saw one Laysan at Cortês Bank in January 1976, and six or more during an April 1977 cruise in the California Current off southern California (from 121° to 122°W). Most birds were seen over deep water seaward of the shelf.

Northern Fulmar, *Fulmarus glacialis*

Fulmars occurred off California in all seasons, but large numbers were seen only from October through March or April. We found that fulmars usually entered the area from the north in October and became abundant off southern California after about mid-November. In all regions, populations built to a late fall–early winter peak (November, December, or January north of Monterey, and December or January south of there), then dropped to a midwinter low, usually in February (Fig. 6). There followed another (lower) peak in abundance in March, then numbers dwindled through spring. We interpret this pattern to indicate movement through California of birds that winter off Mexico; the low in winter corresponds to the period when many birds are south of California or far offshore.

Extrapolations from regional density data indicate that combined, statewide populations reached about 225,000 to 360,000 birds in December–January, while only 35,000 to 95,000 birds were present at the winter low. In most months, fulmars attained highest densities at sea between Point Pinos and Bodega Bay. With little annual and regional variation, dark or medium-plumaged birds accounted for two-thirds or more of all birds for which plumage morph was noted (n = 1043 in 1975–1978 and 998 in 1980–1983).

Northern Fulmars were decidedly most numerous in waters seaward of the middle of the continental shelf (5 to 40 km from the mainland), and were recorded as far offshore as we surveyed (to 460 km, June 1982). Fulmars also were seen close to the mainland shore; in November 1981, about 200 fulmars were observed at Santa Cruz (Monterey Bay) feeding in the surf zone on the carcass of a juvenile sperm whale (*Physeter catodon*; W.B.T. unpubl. obs.).

Ainley (1976) noted a correspondence between large numbers of fulmars and periods of cool temperatures and high surface salinity. This general pattern helps to explain certain variations in numbers observed during our studies. During winter, fulmars were much more common in the cool waters west of the southern California islands than in the warm waters nearer the mainland. As the incidence of upwelling increased there during spring and early summer, the fulmars remaining off southern California concentrated in the coolest upwellings near Point Conception and San Miguel Island and avoided the warmer coastal waters to the southeast. Fulmars were about three times more numerous off southern California in 1975–1976, a cool-water winter, than in the warmer winter of 1976–1977.

Off central and northern California during winter, Northern Fulmars concentrated seaward of the zone influenced by freshwater runoff from land. After most birds departed in March and April, remaining birds shifted toward the coast and concentrated in upwelling centers (cool and saline water) during spring and early summer. Additionally, fulmars occupied the relatively warm neritic waters between Point Conception

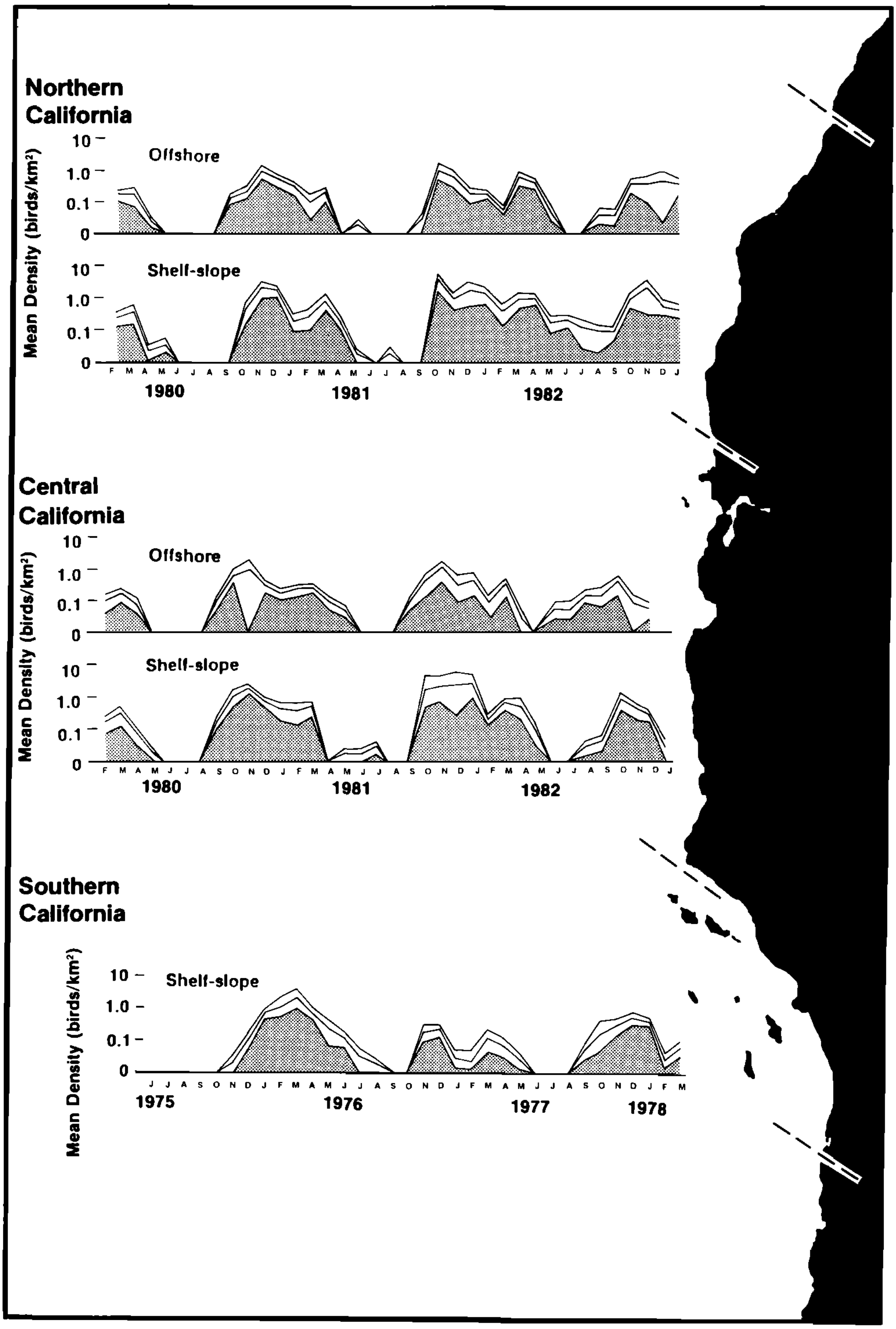

FIGURE 6. Comparison of monthly mean densities of Northern Fulmar in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

and Monterey Bay in large numbers during the cool winter of 1980–1981 but not in the warmer winters before and after. Further, on a larger scale, during the onset of ENSO conditions in fall 1982, fulmars were confined to a cool-water zone lying seaward of a wedge of warm water that was narrow (25 km) at Cape Mendocino but broader than 200 km off central California. In thermal satellite imagery it appeared that the habitat of the fulmar was 'wedged' offshore by strong northward coastal currents emanating from south of Point Conception.

After winters of high fulmar abundance (1976 and 1981), some birds lingered off California throughout summer. We recorded at least a few birds on every survey in both years, almost all near sites of upwelling (Point Conception, Point Reyes, Point Arena, and Cape Mendocino).

In light of these observations, we interpret the apparent large variations in prevalence of fulmars off California as reflecting regional redistributions of a population that may not vary tremendously in size between years (except in the extreme case of the 1982–1983 El Niño). Fulmars were present in greater numbers near the coast in years when waters were cool and salty. In other years, they remained offshore beyond the reach of single-day bird-watching trips.

Gadfly Petrels, *Pterodroma* spp.

The status of *Pterodroma* petrels in waters off the U.S. Pacific coast is very poorly known. Three species have been identified in recent years and a fourth may have occurred but could not be clearly separated from the others. Mottled Petrels (*P. inexpectata*) occasionally move into California waters from the west during late winter (Ainley and Manolis 1979). These are thought to be non-breeders or failed breeders migrating from nesting areas in the southwestern Pacific to the Gulf of Alaska. Solander's Petrel (*P. solandri*) is known from sightings of about twenty individuals 65 to 110 km off Cape Mendocino to Point Reyes in May 1981 (R. L. Pitman pers. comm.). Additionally, Cook's Petrel (*P. cookii*) has been seen a few times during warm-water periods in summer and autumn, mostly off the coast of San Luis Obispo County. A single specimen record for this species exists for the Pacific coast: a live individual was recovered from a beach in Santa Cruz in November 1983 (Tyler and Burton 1987).

On the basis of typical dorsal plumage patterns and soaring flight characteristic of this genus, we considered eleven birds seen off central and northern California to be *Pterodroma* petrels. Ten of these occurred in late winter or spring (March through June) and the other in November. All were seen well offshore of the shelfbreak in scattered locations. In June 1985, three *Pterodroma* were seen in 14°C waters within 75 km seaward of the Farallones (D. G. Ainley, R. Ferris, and K.T.B. unpubl. obs.). Thus, these petrels probably occur each year seaward of the coastal upwelling zone.

Pink-footed Shearwater, *Puffinus creatopus*

Pink-footed Shearwaters nest along the southwestern coast of South America and visit California during the northern summer. We found that Pink-footed Shearwaters and Sooty Shearwaters (*P. griseus*) often occurred in mixed species flocks off California, but the two species pursued somewhat different patterns of seasonal habitat occupancy. The Pink-footed was about 10% to 20% as abundant as the Sooty on a statewide, average basis, but within its favored habitat, it was often the more numerous species. In contrast to the Sooty, the Pink-footed Shearwater was distinctly more abundant off southern California than off central California (and was still less common north of Point Arena).

Extrapolations of density values indicate that maximum numbers were reached in May through August or September, with peak populations of around 130,000 off central California and 60,000 to more than 400,000 off southern California. Population curves for southern California were bimodal each year, with May or June peaks followed by midsummer lows and later peaks in August or September. In 1977 the September peak was higher than that in the preceding spring, while in 1975, the reverse was true. Off central California, density curves for Pink-footeds were essentially unimodal in two years, with gradual build-ups to September peaks followed by abrupt October declines (Fig. 7). In 1982, however, when ENSO conditions were becoming established in the eastern tropical Pacific, we recorded an early, low population peak in May and June, an abrupt decline in July, and a second, lower peak in August and September (the bimodal pattern usually seen to the south).

Off central and northern California, we observed Pink-footed Shearwaters from near the shore to about 150 km at sea; numbers were much higher over the continental shelf and upper continental slope than farther offshore. The shelf areas from Point Reyes to Monterey Bay and from Morro Bay to Point Arguello supported the largest and most consistently occurring concentrations. Off southern California, Pink-footed Shearwaters were most common in Santa Barbara Channel, near the southern coasts of the northern island chain, and along the Santa Rosa-Cortés Ridge. Like the Sooty, these shearwaters preferred the cooler, shallow regions of the Southern California Bight. Outside the seasons

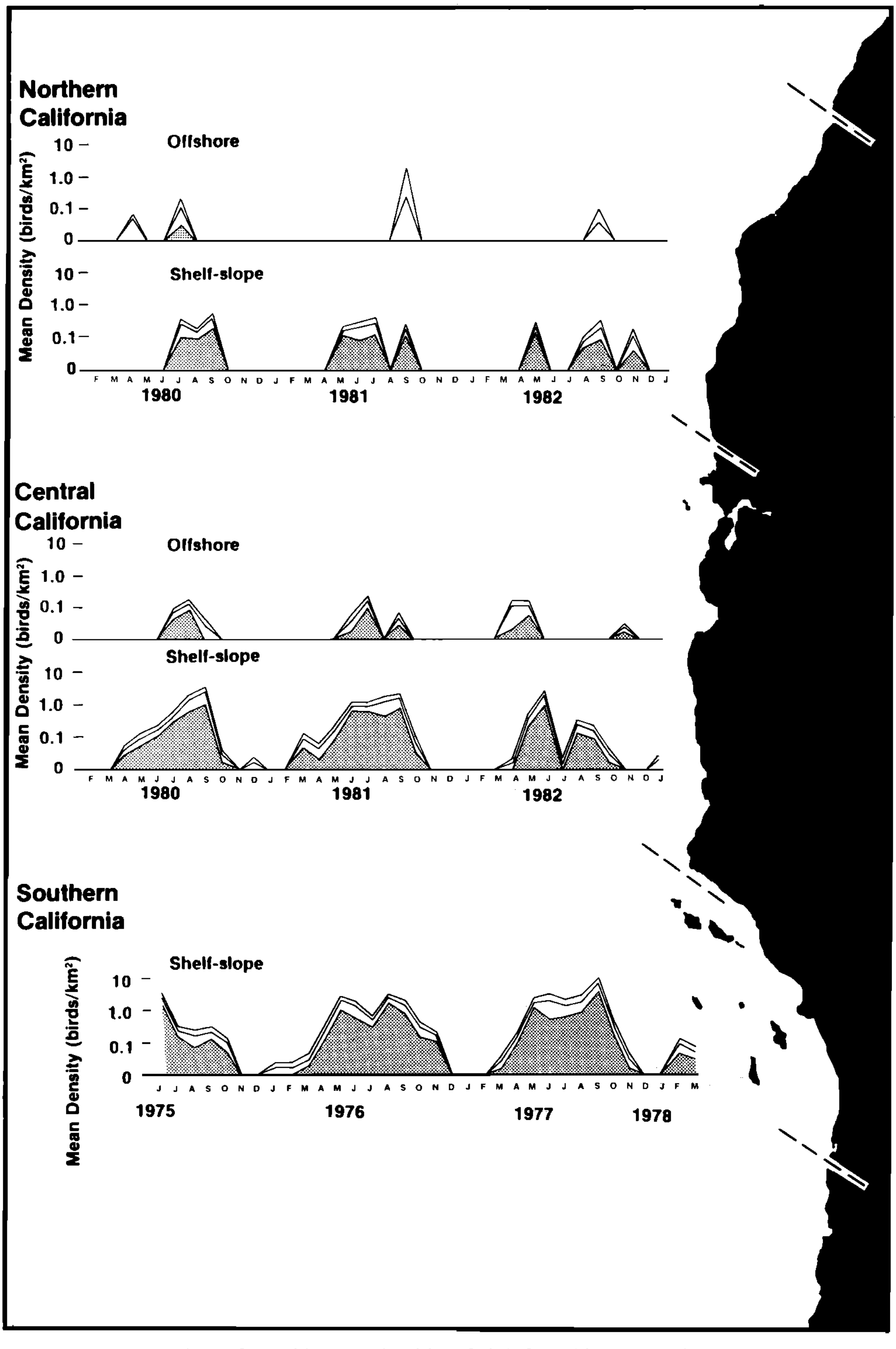

FIGURE 7. Comparison of monthly mean densities of Pink-footed Shearwater in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

of greatest abundance, Pink-footed Shearwaters were seen only in very low densities (usually less than 0.1 birds km^{-2}), primarily as solitary individuals. They occurred off southern California in almost every month but were absent from our central California counts in late fall through early spring.

The relationship between population size of Pink-footed Shearwaters off California and the stages of ENSO in the tropical Pacific is not clear. Ainley (1976) correlated higher bird numbers with warmer water temperatures at the Scripps Pier (La Jolla, San Diego County). However, a detailed examination of his Figure 4 reveals some conflicting patterns: Pink-footeds were abundant during the 1957–1958 ENSO, scarce during the weak event of 1963, scarce during the moderately strong event of 1964–1965, abundant in 1968 during the onset of the weak 1969 event, and abundant in all years 1970 through 1973, encompassing both ENSO and non-ENSO years in the tropics. We found Pink-footeds to be moderately numerous in the SCB during the coolest year (1975), moderately numerous in 1976 during the onset of an ENSO, and abundant in 1977, the second year of the two-year-long warming. In central California, Pink-footed Shearwaters were most numerous in the two years preceding onset of the very intense 1982–1983 ENSO. Although lacking direct counts for summer 1983, we believe that Pink-footed Shearwaters may be more abundant off California in the second year of prolonged warm events (1957–1958, 1972–1973), but that numbers are quite variable during warm-water periods of lesser intensity and duration.

Flesh-footed Shearwater, *Puffinus carneipes*

This species is very difficult to identify from an airplane; ship sightings included single birds in May, June, September, and October, with a total of eight individuals; locations included Cordell Bank, Guide Seamount, Monterey Bay, and the northwestern sectors of the Southern California Bight.

Buller's Shearwater, *Puffinus bulleri*

Buller's Shearwaters are migrants from the southwestern Pacific, appearing off California primarily during late summer and early autumn (Ainley 1976, Wahl 1985). We recorded them off central and northern California from April through December and off southern California in May, June, August, and September. They were present most consistently from Monterey Bay to Cape Mendocino. Peak numbers occurred in September in 1975 (the only sightings of that year), August in 1976 (when over 1300 Buller's joined a mixed-species shearwater flock near San Miguel Island), September 1977, and August in 1980, 1981, and 1982. Maximum mean densities were about 1.0 birds km^{-2}.

By far, the largest numbers of Buller's Shearwaters were seen seaward of the shelf break, usually on the warmer sides of temperature fronts. Affinity for these dynamic ocean features may in part account for the apparently irregular appearances of the species near the coast. For example, in July 1980 and 1981 we saw moderate numbers of Buller's well out to sea north of Point Reyes, but none near shore. However, in August through October, when upwelling slackened and disappeared for periods of several weeks, numbers increased nearer the coast. Presumably, Buller's moved closer to shore along with their preferred California Current habitat. Along these lines, DeSante and Ainley (1980) reported that Buller's were abundant near the Farallones primarily in early to mid-September. The same pattern is reflected in near-coast sightings in September and October reported by Ainley (1976) and Stallcup (1976).

From the limited data presently available, it appears that Buller's usually are least common in California coastal waters during years of warm temperatures (e.g., 1957–1958, 1972–1973, 1977, 1982).

Sooty Shearwater, *Puffinus griseus*

The status and seasonal distribution of this species off California were reviewed by Briggs and Chu (1986). Appearing throughout California in all months, Sooty Shearwaters reach greatest abundance in May, June, or July each year, when statewide totals reach an estimated "instantaneous" figure of 2.7 to 4.7 million. Since turnover rates during migration are unknown, it is possible that the numbers of birds occurring over the full course of the season may be as much as an order of magnitude higher. The breeding colony affinities of birds off California are debatable. Some authors suggest that most birds originate at South American colonies while others believe that most birds come from the southwestern Pacific (King 1970, Guzman and Myres 1982, D. G. Ainley in litt).

Sooty Shearwaters attained their highest regional densities at slightly later dates with increasing latitude: May in southern California, May through July off central California, and as late as September north of Cape Mendocino. Bi- or tri-modal seasonal curves of population density can be interpreted as showing more or less distinct northward and southward migrations. Off central California, a tendency toward a broad, unimodal curve of density probably results from mixtures of northward- and southward-migrating birds, together with a summering population of unknown size. During onset of ENSO conditions (1976 and 1982), populations were much lower after the late-spring peak than was the case in cooler years.

In all regions, Sooty Shearwaters were more abundant over the continental shelf than farther to seaward. Their numbers were relatively low where surface waters were warmer than 15°C or less than 10°C. Instead, they concentrated near, or downstream from stable upwelling centers especially where thermohaline fronts formed at the seaward edges of upwellings. Outer shelf waters off Point Conception, Point Montara, and Point Reyes were typically inhabited by the largest numbers of birds. In June 1981 an aggregation totalling about 630,000 birds was seen in a strong surface thermal gradient in northern Monterey Bay (Briggs and Chu 1986).

Short-tailed Shearwater, *Puffinus tenuirostris*

It was often impossible to be certain of the identification of dark shearwaters. In winter, shearwaters occurred as scattered individuals, and low light levels seldom afforded adequate views of underwing color patterns. This was especially problematic in aerial surveys. Extensive collections in Monterey Bay by Baltz and Morejohn (1977), Croll (unpubl.), and Chu (1984) and in southern California by ourselves (Briggs et al. 1981a) indicate, however, that Short-tailed Shearwaters are extremely rare off California during the months of high abundance of the Sooty Shearwater (April through September), but are probably the numerically predominant shearwater north of Point Conception in late fall and winter. South of there they are probably rare at all times.

Assuming that for waters north of Point Conception in winter, a large percentage of unidentified shearwaters were Short-taileds, we found them to be moderately numerous between Monterey Bay and Cape Mendocino, peaking in numbers in January and February. During December, sightings were scattered and infrequent. In January and February, however, we frequently saw unidentified, dark shearwaters near Cordell Bank, Monterey Bay, and Point Sur. Total estimated populations varied from about 5000 to 15,000. The largest number of sightings of this type came in February 1980, the coolest February of our central California studies. Only four birds were identified in southern California, all in January and February 1976 (also the coolest winter month of our southern California studies).

Black-vented Shearwater, *Puffinus opisthomelas*

North of Point Conception we saw Black-vented Shearwaters primarily near Monterey Bay and Morro Bay in October, November, and December. Sightings were rare north of Point Reyes; one record of three probable Black-vented Shearwaters near Eureka in December 1981 was quite unusual. Off southern California, we recorded this species in all months except April; peak numbers occurred in September through December. The waters occupied most consistently by Black-venteds were those nearshore from San Diego northward for 75 km.

Ainley (1976) noted that Black-vented Shearwaters penetrated northward off California in greater numbers during years of high fall temperatures at San Diego (which usually occur when the Davidson Current is strongly developed over the shelf). In support of this idea we found Black-venteds to be much more numerous and widespread off southern California in 1977–1978 than in the preceding two years. This was the end of a two-year period of environmental warming; sightings ranged from September through March. During September 1977, Black-vented Shearwaters occurred throughout the Southern California Bight east of the Santa Rosa-Cortés Ridge, with a large concentration in eastern Santa Barbara Channel and numerous flocks near Oceanside (where densities reached as high as 80 birds km^{-2}). Extrapolations from density estimates in fall 1977 indicate that peak populations were on the order of 20,000 to 30,000 birds.

Fork-tailed Storm-Petrel, *Oceanodroma furcata*

In the north, we found that Fork-tailed Storm-Petrel numbers reached annual peaks in March, April, and August 1980, March and July 1981, but had no definable peak in 1982, when total numbers were very low. In central California, most sightings came from June and November through March. Only twelve birds were seen in three years off southern California; these occurred irregularly from May through January, all in the sector north and west of Santa Barbara Island (seaward to Rodriguez Dome and San Juan Seamount).

Only near the colonies north of Trinidad Head did Fork-tailed Storm-Petrels routinely occur over neritic waters. Elsewhere they favored areas 20 km or more seaward of the shelfbreak. Although in California they nest only in the far north and occurred farther south in the cooler months of the year, these petrels were not necessarily restricted to cool water. In fact, in July and August, when these birds fledged their young, the waters off Eureka often were in the 13° to 16°C range and supported albacore tuna (*Thunnus alalunga*) fisheries. Our sightings suggest that Fork-tailed Storm-Petrels occur here in the upwelling frontal zone, seaward of the coolest coastal waters, but shoreward of Leach's Storm-Petrels (*O. leucorhoa*) foraging nearby. In this respect they resemble the summer distribution of the Ashy Storm-Petrel (*O. homochroa*), which predominates in the somewhat warmer waters of central California.

Leach's Storm-Petrel, *Oceanodroma leucorhoa*

Leach's Storm-Petrels were sighted off California in all months. In southern California, average densities were highest from June through October and lowest December through May (Fig. 8). We encountered the highest densities in 1977, when late August surveys produced an estimate of 2.6 birds km^{-2}, extrapolating to about 150,000 birds. Peak numbers off central California also occurred in early summer (1980 to 1982) whereas to the north, Leach's Storm-Petrels were most abundant at sea from March through August.

The observed large densities and seasonal shifts in areas of concentration apparently related to the interplay between a relatively small California nesting population and a much larger population of nonbreeders from both the California colonies and elsewhere. During spring, Leach's Storm-Petrels were most abundant (a) 25 to 40 km offshore of the colonies near Point St. George, (b) well offshore in central California, and (c) in southern California in an arc from San Miguel Island to Cortés Bank and eastward to just south of San Clemente Island. By midsummer, large influxes of presumed nonbreeders occurred over almost all waters more than 75 km from the mainland; densities were consistently high north of Cape Mendocino, from Monterey south to Point Conception, and in the waters from Cortés Bank to San Diego. Since estimated total populations at sea exceeded the California nesting total by up to a factor of 10, we assume that most birds present after June were nonbreeders. In late summer the southern California populations shifted to the northwest and were concentrated in California Current waters seaward of the outermost islands. Densities declined rapidly south of Monterey after September and north of there after August. Densities of this species in late fall and winter were in the range 0.05 to 0.15 birds km^{-2} seaward of the continental slope and negligible closer to shore. As reported by Crossin (1974), low numbers of Leach's persisted throughout winter in warmer waters more than 100 km seaward of Point Conception.

Leach's Storm-Petrels were always more abundant seaward of the central continental slope than over the shelf. Although occasionally occurring in aggregations with Black or Ashy storm-petrels (*O. melania* or *O. homochroa*), Leach's typically inhabited the relatively clear, blue waters of the California Current not favored by the other species. Thermal and optical fronts marking the outer edges of coastal upwellings coincided with the shoreward limit of distribution of this storm-petrel.

Ashy Storm-Petrel, *Oceanodroma homochroa*

We found Ashy Storm-Petrels at sea near their colonies in most months, with peak abundance in central California during September through January and near San Miguel Island in April through June. The waters within about 25 km of the shelfbreak from Monterey Bay to Bodega and Point Buchon to San Miguel Island most consistently harbored significant numbers of birds. Total estimated numbers south of Point Buchon occasionally rose to about 1400 whereas numbers to the north were 4 to 8 times that high. During the nesting season (roughly May through September; Sowls et al. 1980), Ashy Storm-Petrels primarily foraged along the shelfbreak and for 25 km to seaward. Birds presumably associated with the San Miguel colony were frequently encountered along the Santa Rosa Ridge to about 50 km south of San Miguel Island, and in western Santa Barbara Channel. Birds presumably associated with the Farallones colony appeared in highest numbers from Guide Seamount to west of Cordell Bank.

After the fledging of young in August to October, the population spread out from both major centers. Birds occurred in mixed-species storm-petrel flocks near Santa Catalina and San Clemente islands, throughout the waters overlying the Santa Rosa-Cortes Ridge, in the western half of Santa Barbara Channel and northward to Point Buchon, in Monterey Bay (where in fall 1981 we found one flock of over a thousand Ashys), and in scattered locations as far north as Eureka. Throughout spring, summer, and fall, Ashy Storm-Petrels occurred most consistently on the warm sides of thermal fronts bordering upwellings. Increasing frequency of sightings seaward of the continental slope after December suggests that many birds wintered well offshore in the California Current.

Black Storm-Petrel, *Oceanodroma melania*

Black Storm-Petrels occur off California in all months, primarily south of Point Conception, and reach peak abundance in late summer and fall. Our observations indicate that the favored habitat of the Black Storm-Petrel includes the warm coastal waters of the eastern half of the Southern California Bight and neritic waters of central California; visitation is greatest during the months when surface temperatures are highest.

We found Black Storm-Petrels at sea in southern California from May through November 1975

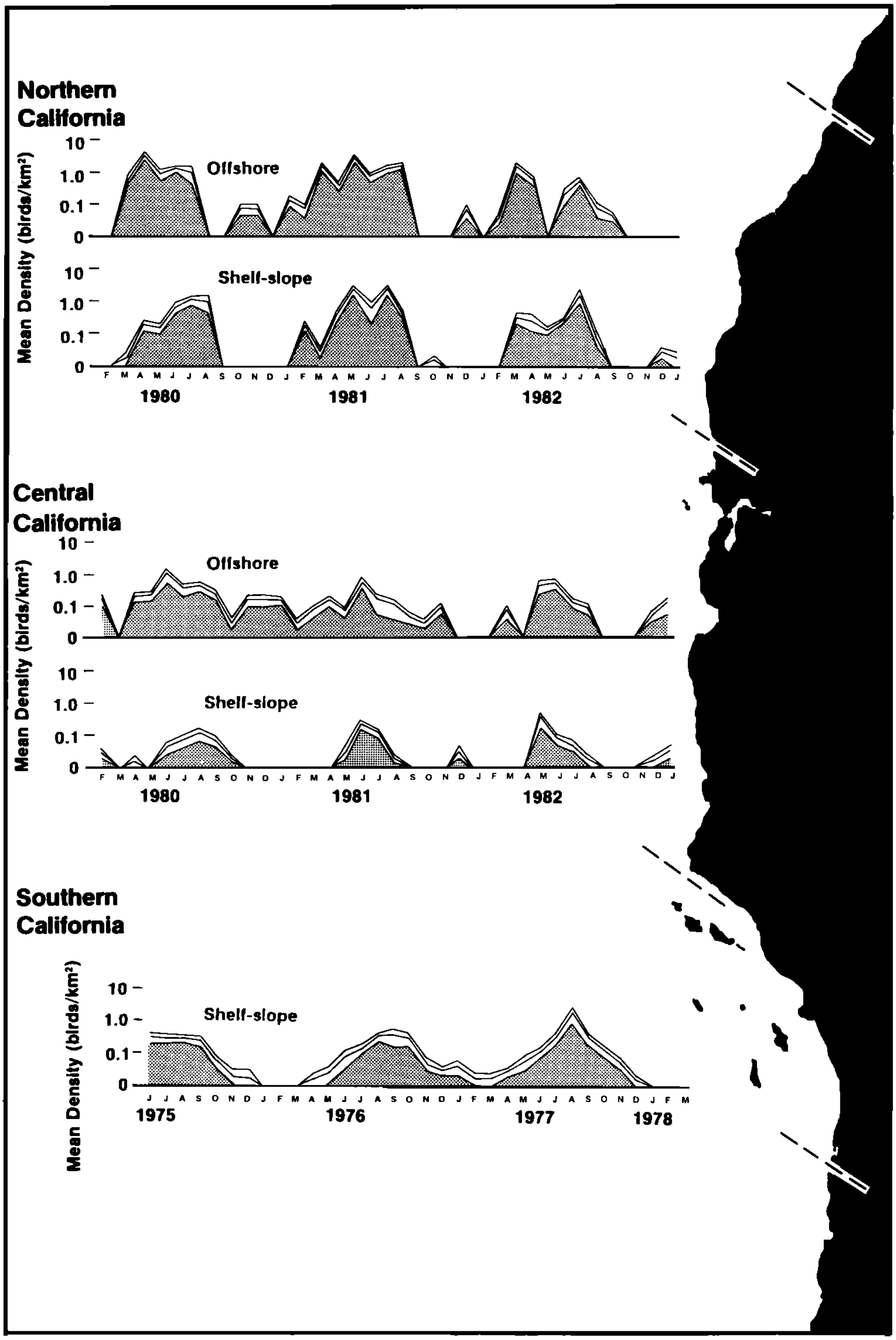

FIGURE 8. Comparison of monthly mean densities of Leach's Storm-Petrel in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

and 1977 and May 1976 through January 1977. Density peaks occurred in August and September, occasionally attaining an average of 2.0 birds km^{-2} which extrapolates to populations exceeding 100,000 birds; in most other months average density in the waters of southern California was less than 0.1 birds km^{-2}. Highest densities were seen within 50 km of the southern California mainland, though substantial numbers also were seen at times at FortyMile Bank (30 km southeast of San Clemente Island), near Santa Barbara Island, and along the Santa Rosa Ridge. Only a few birds were identified with certainty in winter.

North of Point Conception, we recorded this species during May through November, primarily south of the Farallones; none were identified north of Bodega, though some of the unidentified dark storm-petrels seen at higher latitudes in fall may have been of this species. Flocks containing up to several thousand of these storm-petrels have been encountered on Monterey Bay at times in August through October (Stallcup 1976); we saw one flock totalling 270 birds in August 1981.

Least Storm-Petrel, *Halocyptena microsoma*

This species is two to three times more abundant than the Black Storm-Petrel on waters of the Gulf of California (D. W. Anderson pers. comm.), but it is much less numerous off California, where it occurs primarily as a fall visitor. We recorded Least Storm-Petrels in southern California only once in 1975 (a single bird in August), but in 1976 and 1977 sightings were much more frequent, spanning the months August through October. Sightings in 1976 probably were related to the vigorous hurricane "Kathleen" that also brought Least Storm-Petrels to the Salton Sea in inland California (McCaskie 1976). Sightings in 1976 and 1977 occurred during the months of warmest water temperatures, a pattern recognized by Ainley (1976) from the longer-term AFN/AB data set. Our sightings of this species mostly were restricted to the sector from Cortés Bank to San Diego. Maximum estimated fall populations were on the order of 20,000 birds (1977).

We logged only one sighting of "tiny, all-dark petrels" in our studies off central California; several birds fitting this description were seen in Monterey Bay during January 1983 at the height of the winter expression of the ENSO episode.

Red-billed Tropicbird, *Phaethon aetherus*

Historical records of Red-billed Tropicbirds primarily have come from the eastern half of the Southern California Bight during late summer or fall. However, based on our 39 sightings, these birds apparently occur regularly, if not in large numbers, in the waters of the California Current, west of the southern California islands. Our sightings spanned the months April through January but most were logged in July, August, and September. Records in spring and December/January were from waters at the western edge of the Southern California Bight. An apparent shift in distribution occurred in late summer, when most records came from near the easternmost islands (where they usually have been reported by bird-watchers from southern California ports). We found them most consistently near Tanner-Cortés Banks, midway between there and San Juan Seamount, and along the Santa Rosa Ridge (Fig. 9). These are areas supporting important albacore tuna fisheries, and it may well be that tropicbirds here depend on tuna and perhaps small cetaceans to drive flying fish (which are quite numerous off southern California during summer) to the surface (c.f. Ainley 1976, Au and Pitman 1986).

We saw single unidentified tropicbirds, which may have been of this species, near Monterey Bay in July 1980 and June 1982.

Brown Pelican, *Pelecanus occidentalis*

With nesting populations in southern California varying annually from a few hundred to more than 6000 pairs, pelicans have substantially recovered from population declines noted in the 1960s and early 1970s. These relatively small numbers of breeding birds are augmented from about May through December by tens of thousands of pelicans that come to the California Current region from Mexican colonies. Briggs et al. (1983) noted that throughout the year populations south of Point Conception include a larger percentage of immature-plumaged individuals than is the case in central and northern California.

At the time of maximum numbers of pelicans (September or October), 70% to 80% of the statewide population occurred south of Point Conception. Numbers on land ranged as high as 20,000+ in central and northern California and 10,000+ in the south. Adding these figures to extrapolations from density estimates for open-water areas yields estimated total populations as high as 70,000 to 110,000 (Briggs et al. 1983).

Pelicans do not normally remain at sea overnight but instead return to specific coastal roosts (usually by late afternoon, but sometimes not until several hours after sunset). There are relatively few major nocturnal roosts (a myriad of smaller sites are used for daytime rests) and these harbor large numbers of birds. For example, we counted more than 6000 birds on Santa Barbara Island (September 1977), and the salt evaporation ponds at Elkhorn Slough (Monterey Bay) have served as a roost for more than 5000 birds

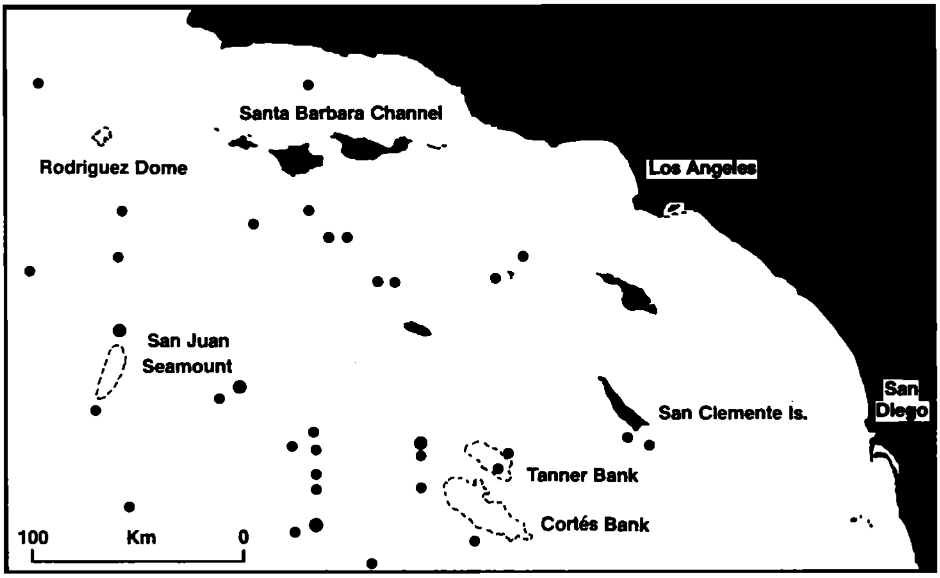

FIGURE 9. Distribution of sightings of Red-billed Tropicbirds in southern California, 1975–1982. Small dots represent single individuals while larger dots are pairs.

at once (October 1981). At six other sites in central California and three other sites to the south, we recorded daytime counts exceeding 1000 birds. Large daytime counts are significant because the population is most widely dispersed at sea and along the coast during daylight hours. Use of coastal roosts and countless smaller ones varies considerably between seasons and between years (thus annual variation at any single site may not reflect statewide trends). Although small numbers of birds were recorded along most of the coast, the islands off southern California and the mainland shore from Point Conception to Morro Bay and Monterey Bay to Bodega consistently harbored the largest numbers of roosting pelicans each summer and fall.

Distributions at sea generally mirrored numbers on land: in summer and fall, major concentrations were seen over the shelf from Cordell Bank to Monterey Bay, off Morro Bay, in Santa Barbara Channel, from Anacapa to Santa Barbara Island, and from San Clemente Island to San Diego (Briggs et al. 1981b).

Pelican numbers were lowest December through March. Fewer than 500 birds remained north of Point Conception at this time, and only about 5000 to 6000 pelicans, half of which were breeders, were present in southern California. In this period, sightings at sea were mostly restricted to the immediate vicinity of roosts and colonies.

By far the largest portion of the population foraged within the first 20 km of the coast; however, individual pelicans were recorded over waters deeper than 3000 m and at distances of 88 km off central California and 190 km off San Diego (where the presence of offshore islands extends the range of foraging pelicans farther from the mainland).

Pelican densities at sea were highest during or just after the period of maximum surface temperatures (August to October), but the birds did not necessarily occur in the warmest waters present along a given stretch of coast. They tended to occur in fronts with sharp thermal gradients. In fact, they sometimes flew over warm coastal waters to get to these frontal areas farther offshore (Briggs et al. 1983).

Double-crested Cormorant, *Phalacrocorax auritus*

This species was identified at sea only a few times, usually within 2 or 3 km of a known colony. Because thousands of cormorants were not identified as to species and this is by far the least numerous cormorant on California marine waters (Sowls et al. 1980), we refrain from analyzing our few records. Almost any unidentified cormorant seen at sea could have been a Double-crested, but on the basis of nesting populations, no more than 5% actually were of this species.

Brandt's Cormorant, *Phalacrocorax penicillatus*

Confined mostly to waters within about 25 km of island or mainland roosts and colonies, Brandt's Cormorants are conspicuous members of the neritic fauna. Sowls et al. (1980) indicate that the state's nesting population is on the order of 59,000 birds. The world's largest colonies are located on the Farallones, and important colonies also exist on the Santa Barbara Channel Islands, Bird Rock at Point Lobos (30 km south of Monterey Bay), and Castle Rock near Crescent City.

We found Brandt's Cormorants in almost all neritic waters within 20 km of a colony during May through November each year. In late fall and winter, they were seen primarily from Bodega to Point Sur and Morro Bay to Santa Barbara Island. Because of variation in patterns of occupancy of roost sites, density at sea was quite variable between months, but Brandt's Cormorants were rarely seen more than 10 km from shore. Density was highest from June through October in central California and from late summer through late spring in southern California (Fig. 10). This pattern is consistent with southward movement of some central California birds after the nesting season.

By adding shoreline counts to extrapolations from densities along transects at sea, we estimate that the total Brandt's Cormorant population in central and northern California reached 65,000 to 80,000 in mid- to late summer and fell as low as 30,000 in winter. We surmise that in fall half of the central and northern California population moved northward, out of the state, or southward, into southern California. Numbers of Brandt's Cormorants in southern California (about 5500 nesting birds; Hunt et al. 1981) increased about fourfold by late September. Due to large monthly variations in numbers of birds on shore and at sea, it is not clear how much the population varies from year to year. There is a suggestion, however, that during periods of ocean warming in southern California in 1977 and central California in 1982, total populations were relatively low after summer. It may be that in these years, more birds moved northward or into estuarine areas such as San Francisco Bay (that were not included in our studies).

Despite their affinity for relatively shallow waters, we did find Brandt's Cormorants over deep waters as well. This occurred particularly frequently near the southern California islands, where waters over 1000 m deep can be found within about 10 km of some roosts and colonies. Waters east of San Clemente Island frequently harbored large feeding flocks of these birds.

Pelagic Cormorant, *Phalacrocorax pelagicus*

Pelagic Cormorants reside on the state's shoreline throughout the year. The 16,000-bird nesting population is spread along almost the entire coast of California; hundreds of sites are occupied by small numbers of breeders, and colonies over 100 birds are rare (Sowls et al. 1980). About half nest at mainland sites while half nest on islands. The largest numbers of birds occur on the Farallones and between Point Reyes and Cape Mendocino; colonies become progressively smaller and less numerous south of Point Sur.

It was difficult for aerial observers to identify Pelagic Cormorants at sea, except during the nesting season when the distinctive white flank patches could be seen. All offshore records were from waters within 20 km of land, mostly within 10 km. Reflecting the distribution of colonies, largest numbers of Pelagic Cormorants were recorded from Point Sur to Bodega. Few were seen south of Point Conception, where the bulk of the nesting population (which comprises only about 450 birds) is concentrated in the northern island chain. There does not seem to be any seasonal movement as occurs among Brandt's Cormorants.

Brant, *Branta bernicla*

We saw Brant as far as 90 km offshore in flocks of up to 100 birds; locations were scattered and dates included March, April, October, and November. Brant were observed in flight over ocean waters and frequently fed along beaches and swam just offshore. The preferred locations during migrations appeared to be Santa Barbara Channel (rarely), Morro Bay, Point Año Nuevo, Bolinas Lagoon, Drakes Estero, and Humboldt Bay.

Surf/White-winged Scoter, *Melanitta perspicillata/fusca*

These two species often were indistinguishable to aerial observers. Both were found primarily in shallow, nearshore areas of the open coast, and in bays and estuaries. The Surf Scoter may have a North American population only one-quarter the size of the White-winged (Bellrose 1976), but it is the more numerous species everywhere along the Pacific coast south of Alaska (Phillips 1926, Johnsgard 1975, Vermeer 1981, Wahl et al. 1981, Gould et al. 1982). The White-winged Scoter becomes progressively less common southward along the coast of California; it accounts for only about 5% to 10% of the scoters identified with certainty south of the Santa Barbara Channel Islands.

Scoters occurred in waters north of Monterey Bay during all months of our study and were absent south of there only during summer. North of Cape Mendocino, populations began to rise in August or September each year (1980–1982); yearly maxima in October or November were followed by gradual declines except during winter 1980–1981, when numbers increased through

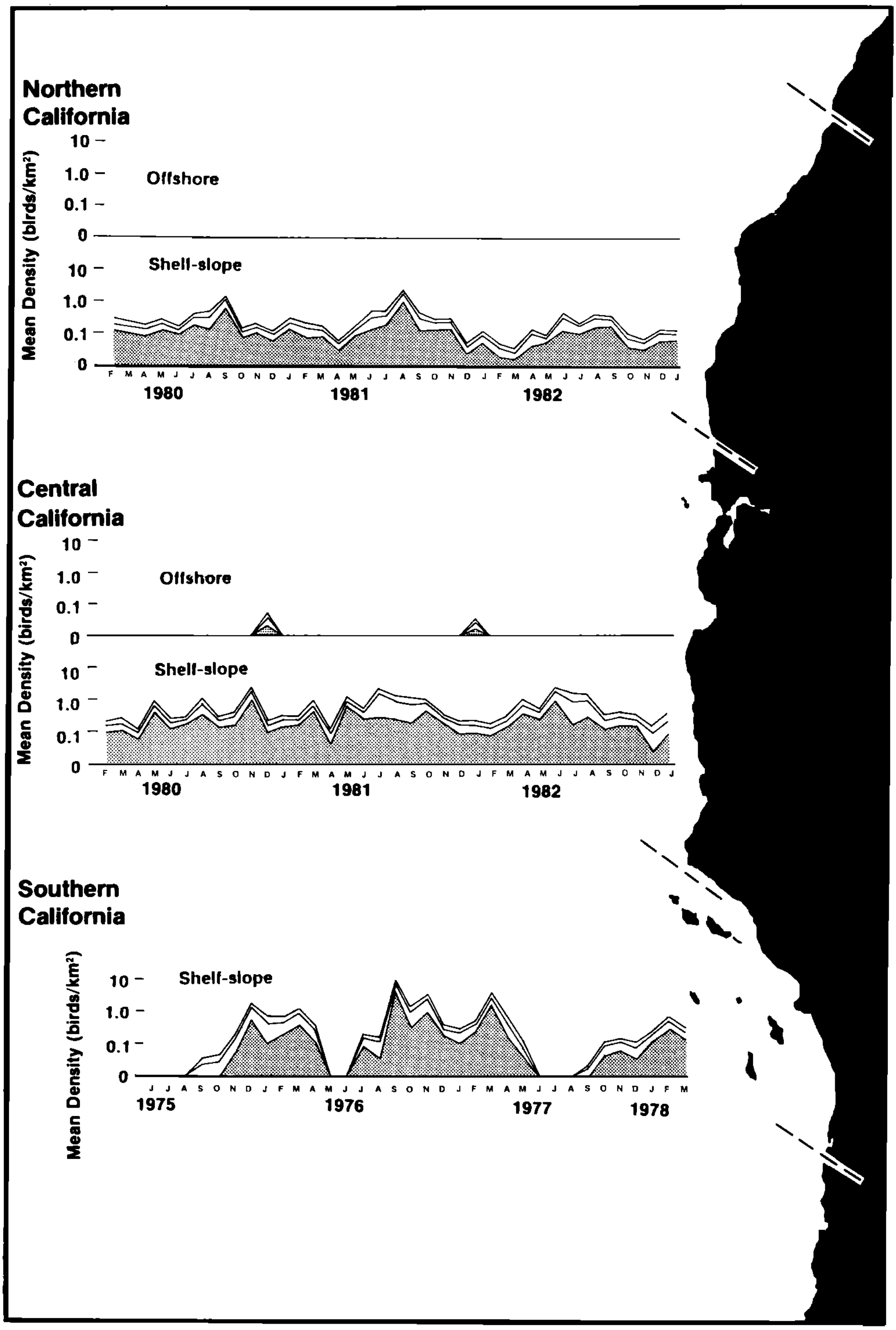

FIGURE 10. Comparison of monthly mean densities of Brandt's Cormorant in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

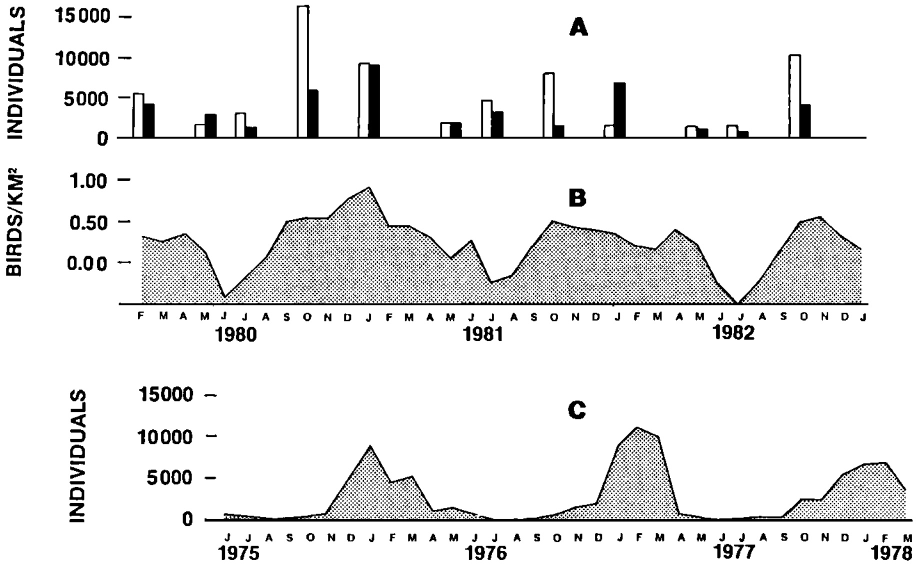

FIGURE 11. Shoreline counts and open-water densities of Surf/White-winged scoters. (A) Shoreline counts in northern California (open bars) and central California (solid bars) during 1980–1982. (B) Mean density of scoters in shelf waters of central and northern California (combined). (C) Total scoter population in southern California open coastal waters extrapolated from counts on island and mainland beaches. Additional tens of thousands of scoters occur on bay and estuarine waters not included in our counts.

January. Among birds referred to *M. perspicillata* there was an especially distinct spring migration peak in April 1982, but this feature was less clear in other years (Fig. 11). Some of this variation probably related to the degree of coincidence between the seasonal peak of migration and our monthly survey, and to the periodic movement of birds to (uncensused) estuarine and bay waters.

The massing of several thousand scoters in northern waters early in fall each year was correlated with surface temperatures. While more than 10,000 scoters were found on 10° to 13°C waters north of Eureka during September and October each year, only a few hundred occurred in the 14.5+°C waters south of there.

Scoters pushed into central and southern California during November and December, reaching a peak in numbers south of Point Conception in December through March. The majority of scoters migrated within a few kilometers of shore; sightings farther out to sea were most frequent south of Point Reyes and in the Southern California Bight. These are areas where the coast veers to the east, and suitable nearshore habitat can be found near offshore islands.

Peak populations in fall were about 30,000 birds, arrayed from Morro Bay northward. In January and February, when presumably only wintering birds remained and the migrants passed south of Point Conception, numbers in central and northern California dropped to 7000 to 18,000. In midwinter, southern California coastal populations reached an estimated 9900 birds, while an additional 2000 wintered around the islands. The size of the scoter population along the open coast is variable due to the periodic use of adjacent bays and estuaries.

Areas most heavily used by scoters in winter included the nearshore waters from near Eureka, Bodega and Tomales bays, the Gulf of the Farallones, Monterey Bay, Morro Bay, Santa Barbara Channel (especially the shallow eastern end and the northern shores of the island chain), Santa Monica Bay (west of Los Angeles), and the coast for 75 km north of San Diego. In general, waters over sandy substrate and lying in the lee of a promontory were favored.

During spring migrations, habitat usage patterns were similar to those seen in fall with the following exceptions: (1) the passages between the Santa Barbara Channel Islands served as staging areas or funnels for migrating scoters and often harbored hundreds or thousands of resting birds; (2) hundreds of scoters occurred on waters within 40 km south of Point Sur in spring, but not fall; (3) scoters occasionally numbered into the thousands in Tomales Bay, presumably partaking of the eggs of late-spawning Pacific Herring (*Clupea herangus*); (4) numbers of scoters north of Cape Mendocino were an order of magnitude smaller in spring than in fall. The last

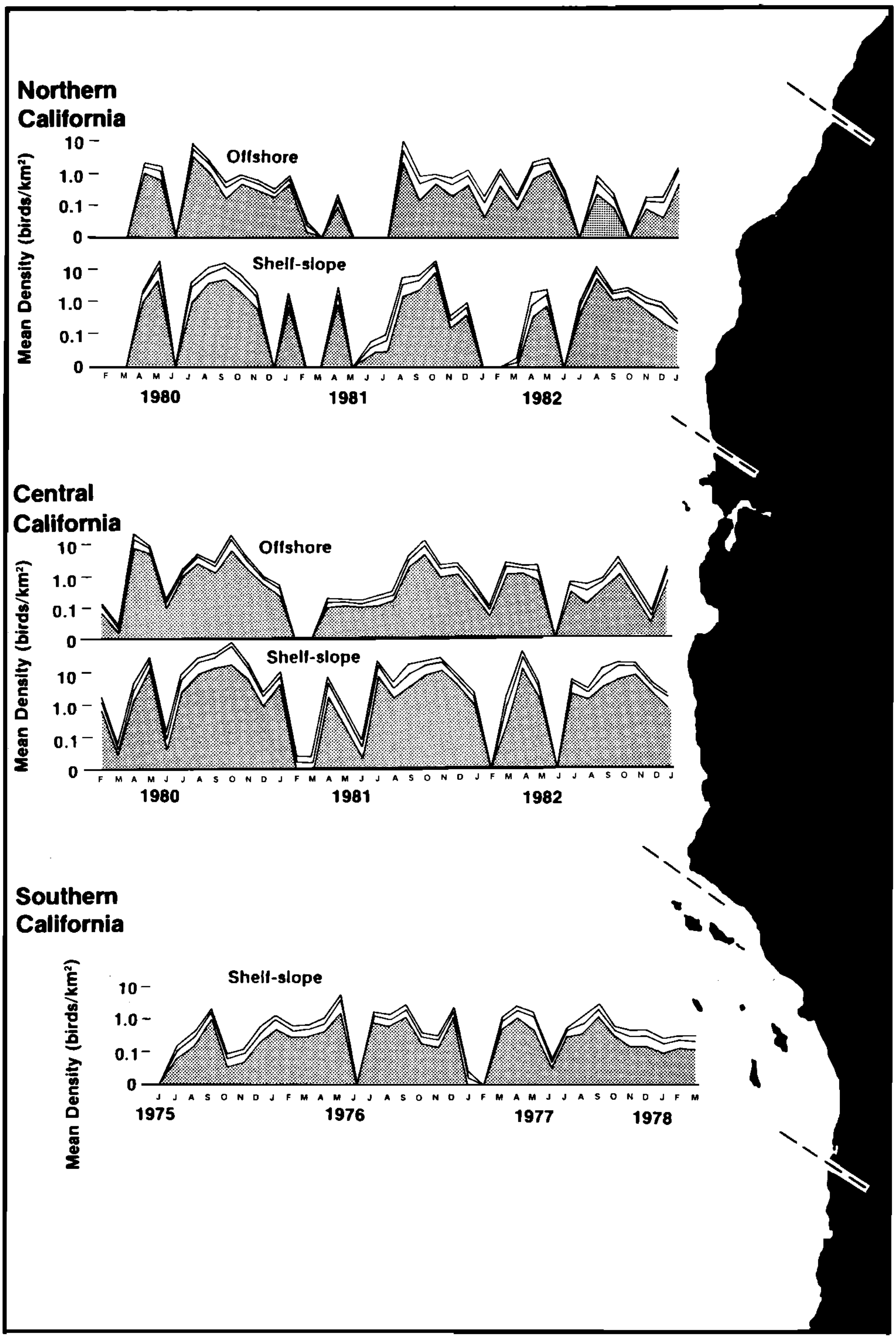

FIGURE 12. Comparison of monthly mean densities of combined Red and Red-necked phalaropes in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

pattern may simply indicate that birds did not linger on coastal waters north of Cape Mendocino but instead moved rapidly toward northern nesting areas. Statewide populations fell to about 3000 in midsummer, with most birds in waters from the Klamath River to the California/Oregon border.

Black Scoter, *Melanitta nigra*

Small numbers of this scoter undoubtedly were present among thousands of unidentified scoters we recorded in central and northern California. Thirty birds were recorded in ship counts from southern California, of which seven were from near the mainland, and 23 from the shores of the northern islands.

Red/Red-necked Phalarope, *Phalaropus fulicarius/lobatus*

Our ship data indicated that only the Red Phalarope was likely to be found more than 50 km from the mainland and that it migrated about one month later in spring and fall than did the Red-necked Phalarope (roughly March–April and July–September for the Red-necked versus April–May and August–November for the Red). Otherwise, the two phalaropes often occurred together at sea and ate much the same prey (Briggs et al. 1984).

Although these birds were easily identified by observers on ships, aerial observers seldom could distinguish between them. Because our data for central and northern California derive primarily from aerial observations, the two species will be considered together.

Migration was much more rapid in spring than in fall. Combined phalarope densities in central and northern California reached 15 birds km^{-2} in May 1980 and April 1982 but were only about 15% as high in spring 1981 (Fig. 12). This may have resulted from very rapid migration in 1981 (that is, peak migration occurred between our regular monthly surveys) or from the use of migration pathways lying inland or far at sea. In southern California, phalarope density reached about 7 birds km^{-2} in May 1976 but was two-thirds lower the following year. Few birds lingered through June, but some southbound Red-necked Phalaropes reappeared as early as the second week in July.

Phalarope density curves for the more protracted fall migration were unimodal: peaks occurred in July through October in the north and October or November in central California. In fall 1980, densities averaged almost 18 birds km^{-2}, making phalaropes the most numerous seabirds off California at the time. Densities in fall 1982 were almost four times lower, which we attribute to the influence of the incipient ENSO. In southern California, migration occurred in two pulses in 1976 (July and September) reflecting differences in timing of passage of the two species, but there was greater overlap in fall 1975 and 1977. Fall densities were highest (about 4.5 birds km^{-2}) in 1976. Extrapolation of densities encountered off the various sectors of California leads to an estimated peak population of at least 3.7 million in October, with about 25% south of Point Conception and the remainder evenly distributed farther north.

Winter populations were small relative to those during migrations, and data taken from ships in southern California indicated that Red Phalaropes made up the bulk (75% to 95%) of wintering populations.

We found phalaropes everywhere off California, from the shoreline to hundreds of kilometers at sea. However, three general patterns of habitat occupancy emerged: (1) during spring migration, numbers were highest in neritic waters, especially near the coast and islands (sightings of over 35,000 phalaropes within the kelp beds surrounding the Santa Barbara Channel Islands in May 1976 made these the most numerous of all nearshore birds at the time); (2) spring and fall migrants concentrated over the outermost shelf and upper continental slope; (3) in winter, densities were much higher in waters seaward of the shelf than closer to shore.

South Polar Skua, *Catharacta mccormicki*

We recorded skuas on twelve occasions in central and northern California. These all occurred in May and August through October. An additional 59 records were logged during ship surveys of southern California in mid-June through late October (the discrepancy in sighting numbers was due to frequent use of ships in the south). Most of our sightings came from near the shelfbreak from Monterey to Point Reyes and from Point Conception to Cortês Bank; one area overlying the Santa Rosa Ridge (40 to 60 km south of Santa Rosa Island) yielded fourteen records in three years.

Pomarine Jaeger, *Stercorarius pomarinus*

Occurring singly or in small flocks, this large jaeger was a consistent member of the seabird fauna seaward of the shelf in all seasons except summer. This was the most numerous jaeger off California except near the mainland, where the Parasitic Jaeger (*S. parasiticus*) predominated. Some individuals were present in all seasons, with largest numbers during migrations.

After leaving their arctic nesting grounds, Pomarine Jaegers increased in number in northern California as early as mid-August and reached peak abundance there and off central California

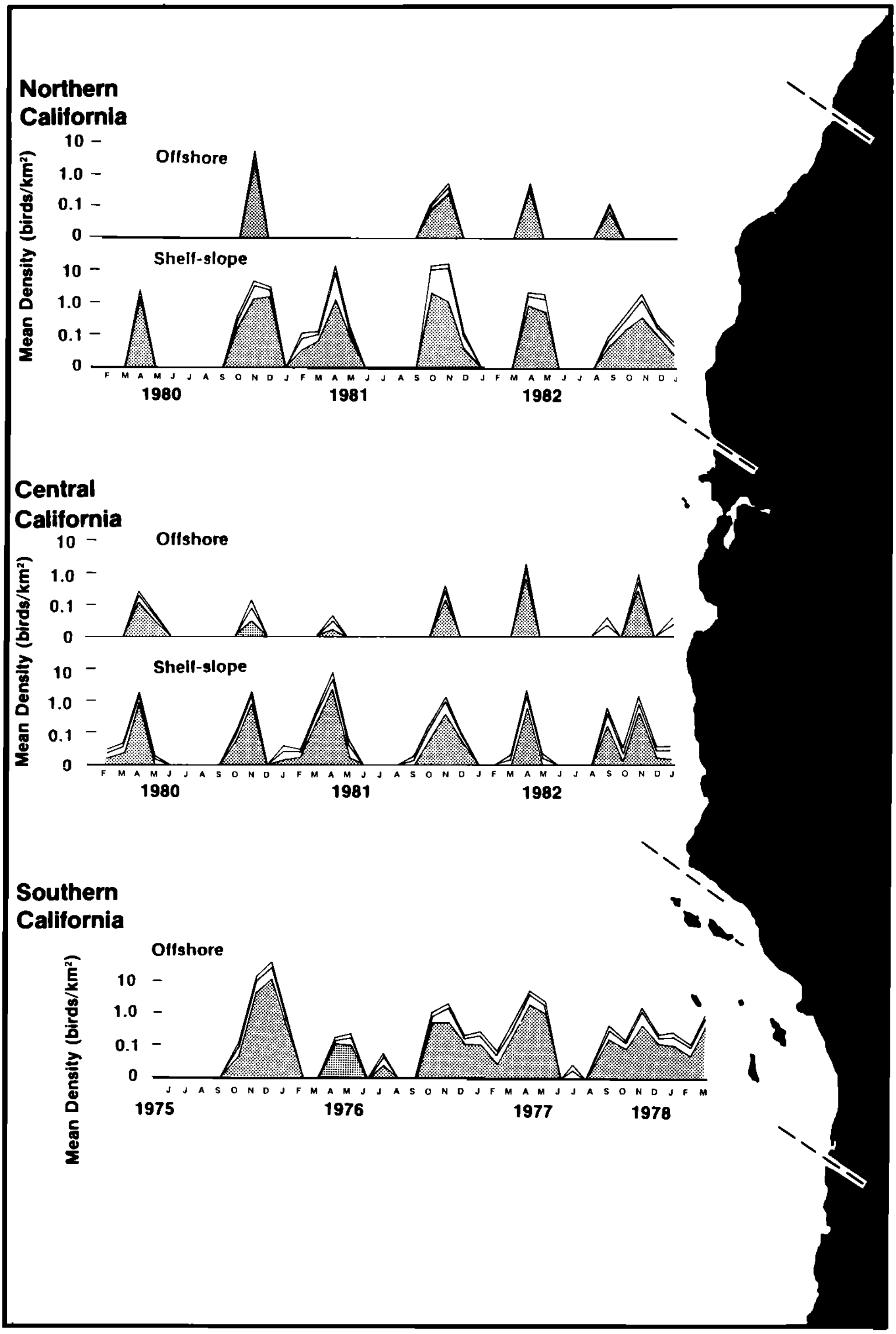

FIGURE 13. Comparison of monthly mean densities of Bonaparte's Gull in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

in late September and October; they were estimated to number 32,000 to 66,000 at peak. Migrants were concentrated in waters seaward of the shelf, and it was not until after October, when overall numbers began to diminish, that densities over the shelf were larger than those farther offshore. A few Pomarines also reached southern California in August; these concentrated near Santa Barbara Channel before pushing southward into the remainder of the Southern California Bight after mid-September. During the peak of fall migration in southern California, numbers of Pomarine Jaegers were highest in the cool waters within about 40 km of the Santa Rosa-Cortés Ridge; estimated total numbers in October 1975 were 60,000. The central axis of the California Current was not heavily used by Pomarine Jaegers: aerial transects to 460 km off Monterey Bay in August and September 1982 and a cruise to 425 km off San Diego in October 1976 produced few sightings. A similar pattern was noted by Pyle and DeLong (1968) for the area 100 to 950 km south and west of Point Conception.

Winter populations were much smaller, with estimates of 7000 to 18,000 birds in central and northern California in November 1980 through March 1981, and as few as 1000 birds in southern California during winter 1976–1977. We noted a fairly even distribution with distance from shore during winter and almost all sightings were of single birds.

Migration was less distinct in spring than in fall, and densities at sea were lower. As in the southward migration, waters seaward of the shelf were favored.

Parasitic Jaeger, *Stercorarius parasiticus*

Parasitic Jaegers were a significant part of the fauna only within 15 km of mainland and island shores. Often they were not distinguishable by aerial observers from the other jaeger species but, clearly, were at least an order of magnitude less numerous overall than were Pomarines. Our 47 sightings were concentrated in March–April and August through November, with annual peaks occurring during fall. Off central California, Parasitic Jaegers were recorded at all latitudes over the shelf and continental slope out to about 75 km. They were seen only within 45 km of the coast in southern California.

Long-tailed Jaeger, *Stercorarius longicaudus*

We obtained eight records of Long-tailed Jaegers in central and northern California during September, October, and May, while sixteen records from southern California occurred from September through February and in May. Most southern California sightings came from offshore waters from Cortés Bank to Rodriguez Dome, and those north of Point Conception were scattered seaward of the shelfbreak. An adult and an immature were collected in September at Cortés Bank; undoubtedly other Long-taileds occurred among the several hundred unidentified jaegers seen throughout the study.

Bonaparte's Gull, *Larus philadelphia*

Bonaparte's Gulls occur abundantly off California during migration in spring and fall and in lower numbers in winter. They arrived off California in large numbers during September and October, and were surprisingly abundant at sea, occasionally eclipsing numbers of any other gull (Fig. 13); peak fall numbers were attained in late October through November. Following migration, a few birds remained to winter along mainland and island beaches. All waters of the shelf and slope were visited by Bonaparte's Gulls, though the largest numbers always occurred within 40 km of the mainland or Channel Islands. Relatively low numbers wintered along the open coast north of San Francisco, and the population appeared to be centered in southern California; about 15,000 birds inhabited southern California mainland beaches from December through March.

The spring migration was rapid, beginning in March and ending in May. We estimated maximum "instantaneous" populations in April and May to be about 300,000 birds in southern California (1976) and 530,000 in the larger area north of Point Conception (1981). During 1977 and 1982, these gulls were only about half as numerous as in the preceding years; whether they wintered farther north or inland is unknown.

Heerman's Gull, *Larus heermanni*

In southern California Heermann's Gulls arrived as early as late April or May, but an influx in late June was more typical. Large numbers were present as far north as the Oregon border by late July (1981). Southern California beach counts in July indicated a mainland population of 8000 to 10,000, about the same as July average figures for central and northern California. Maximum fall populations were estimated to be about 13,000 in central California in 1982 and 15,000 in southern California in 1975 (Fig. 2 of Briggs et al. 1983). In all seasons, Heermann's Gulls were most numerous at beaches of Monterey Bay, Morro Bay through Santa Barbara Channel, and San Diego County. Though Heermann's Gulls were not abundant near the Channel Islands or over open waters between the islands and the coast, we estimated populations at sea in southern California to be several thousand birds during August and September. We never identified

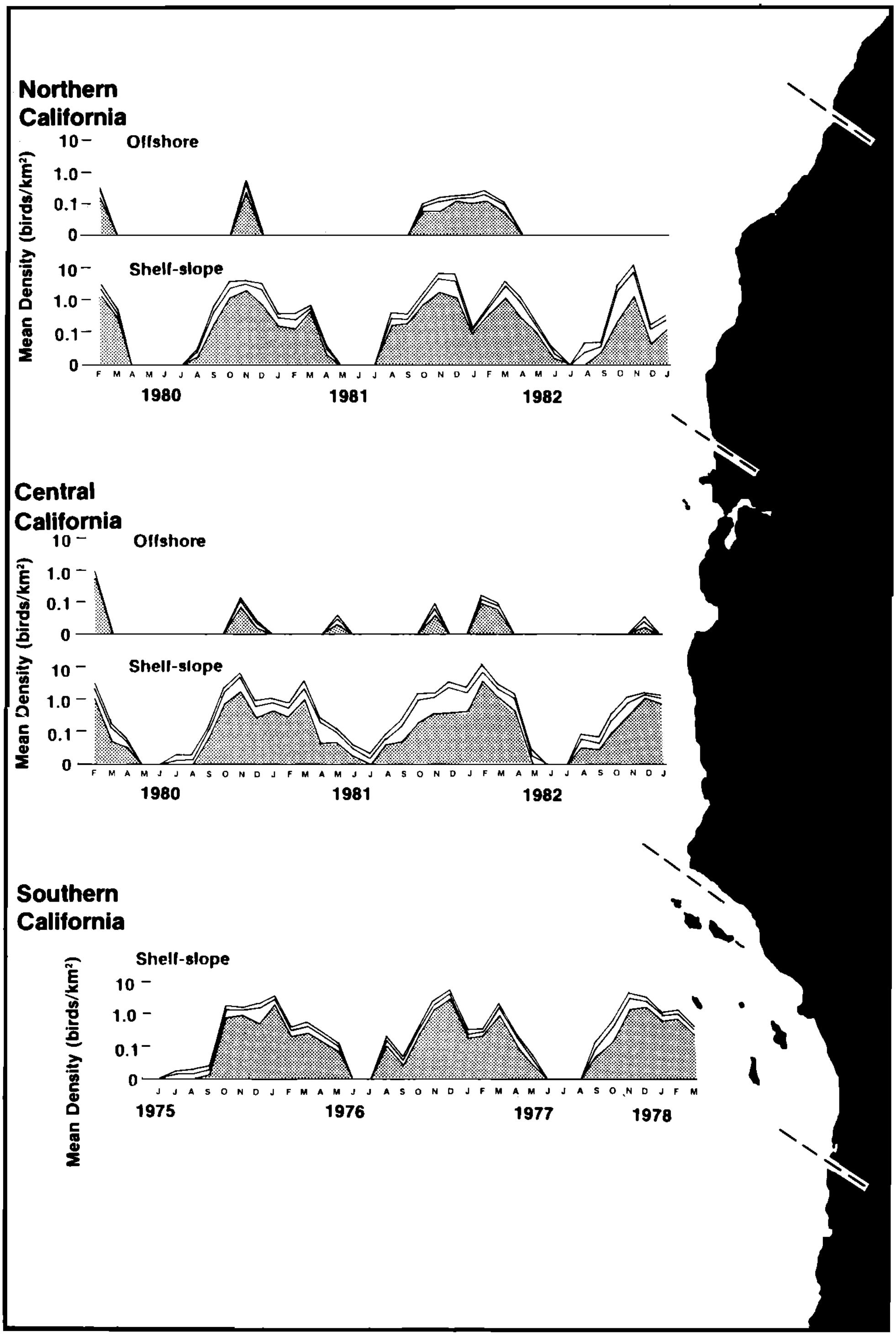

FIGURE 14. Comparison of monthly mean densities of California Gull in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

Heermann's Gulls more than a few hundred meters from shore in central or northern California, though they undoubtedly foraged to a few km offshore. After the late-summer peaks in numbers, Heermann's Gulls departed southward toward their Mexican nesting areas.

Mew Gull, *Larus canus*

We saw small numbers of these gulls along the entire coast and around islands during November through March; numbers identified with any certainty were always small, but thousands of gulls went unidentified in winter aerial surveys. Mew Gulls often associated with windrows or tidal "rips" close to the shoreline. Counts along southern California beaches and islands indicated a total population of around 1500 in midwinter, concentrated around the shores of Santa Barbara Channel (including the northern island chain) and Santa Monica Bay. We never identified Mew Gulls far at sea.

Ring-billed Gull, *Larus delawarensis*

This was a locally abundant inhabitant of mainland beaches the length of the state, but was seldom seen along exposed coast or more than one kilometer from shore. Southern California beach counts indicated a population of up to 10,000 birds; they were undoubtedly also present among thousands of unidentified gulls on central and northern California beaches, but typically Ring-billed Gulls were numerous only on protected bays and estuaries.

California Gull, *Larus californicus*

California Gulls were among the most abundant gulls near the coast in fall and winter, especially over neritic waters. They usually arrived by late September or October, nearly simultaneously at a range of latitudes from Los Angeles northward. Numbers were somewhat concentrated north of Cape Mendocino in early autumn and south of Point Arena after November. Total coastal counts reached about 5000 in central and northern California in September 1981 (when an additional 40,000 gulls went unidentified as to species). Birds drifted south to southern California through November and December; counts from southern California beaches and islands were around 5000 birds, but peaked in January through March.

California Gulls were sighted at sea in almost all months, with high numbers during October through March (Fig. 14). We think this reflects generally larger numbers of birds in the study area rather than increased tendency to forage far from the coast. At the peak of migration we estimated population levels of around 150,000 birds both north and south of Point Conception, but these were in different periods and so are not additive. Conover and Conover (1981) estimated that total nesting populations for interior North America were on the order of 10^5 birds. We identified these gulls as far seaward as the central continental slope off Point Reyes and 75 km west of San Nicolas Island (about 160 km off the southern California mainland), but densities were always highest within 50 km of the mainland. Only a few thousand birds remained along the coast during summer.

Herring Gull, *Larus argentatus*

We found Herring Gulls at coastal sites in central and northern California throughout the year; numbers were small from May through September. Early fall arrivals were seen in October and November, and peak counts occurred in December through February in 1980–1981 and 1981–1982. The timing of annual events in southern California was similar, and departure from all areas occurred after March. During onset of the 1982–1983 ENSO episode, Herring Gulls arrived in northern California in larger numbers than in the previous two winters, reached a peak in November, but declined to low numbers by January.

We counted over 7100 Herring Gulls during coastal aerial censuses of central and northern California in December 1980, at which time there were 33,000 additional gulls unidentified as to species. Peak mainland and island counts in southern California occurred in January through March 1977, when combined totals were on the order of 2500 birds. Devillers et al. (1971) reported that hundreds or thousands of additional Herring Gulls winter at refuse dumps in the San Diego area. Shoreline areas harboring the greatest numbers of birds included dozens of river and stream mouths north of Point Arena, the beaches of the Gulf of the Farallones, and Monterey Bay. In southern California, the beaches of eastern Santa Barbara Channel and the San Diego area had the highest counts.

At sea, Herring Gulls were sighted north of Monterey Bay in all months except the summer of 1980 and June 1982. From Point Conception to Monterey Bay, Herring Gulls were common during winter but were rarely and irregularly seen from May through October. Peak densities were attained in November, December, or January (Fig. 15). At this time Herring Gulls concentrated over neritic waters, though appreciable numbers also occurred over slope and offshore waters. In their winter of greatest abundance (1980–1981), an estimated 100,000 Herring Gulls occurred at once in central and northern California.

Herring Gulls also inhabited waters throughout southern California during winter, but in

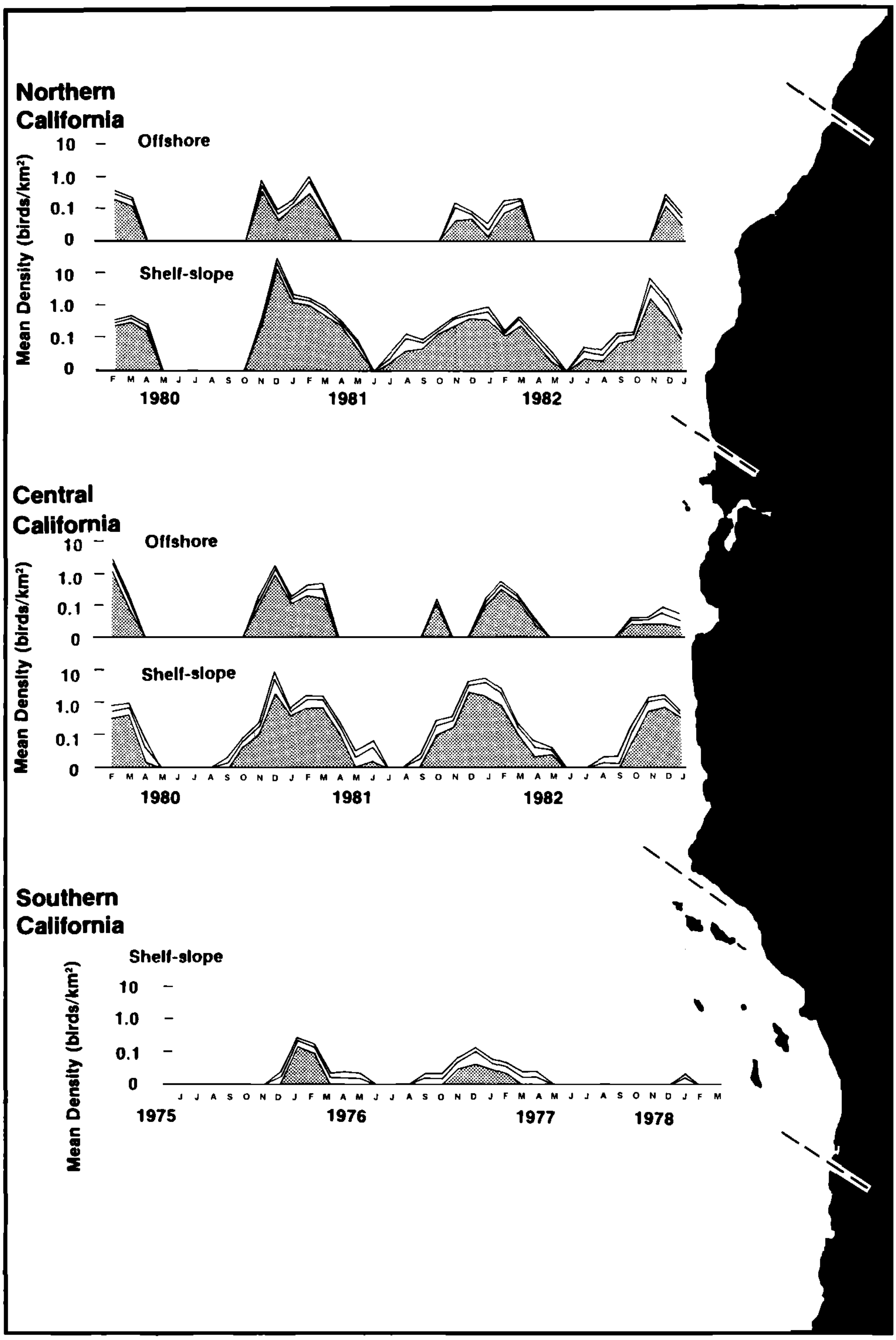

FIGURE 15. Comparison of monthly mean densities of Herring Gull in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

much smaller numbers than to the north. They were numerous west of the Santa Rosa-Cortés Ridge and less so to the east. Total populations in southern California reached about 30,000 (January 1976).

Thayer's Gull, *Larus thayeri*

We recorded Thayer's Gulls on eight occasions in winter, throughout the islands of southern California. They were very uncommon but regularly seen among Herring Gulls in central California, especially at seal rookeries and refuse dumps. At Año Nuevo Island Thayer's make up about 5 to 8% of Herring/Thayer's Gulls in mid-winter (where, in 1972–1975 daily numbers of Herring/Thayer's gulls peaked at about 2000; K.T.B. unpubl. obs.).

Western Gull, *Larus occidentalis*

We found Western Gulls on neritic waters throughout the state during all months. They were most restricted to the vicinity of colonies during April through August and most evenly distributed in November through January or February. Like previous authors, we seldom found Western Gulls more than 25 km seaward of the shelf-break, though scattered individuals were seen up to 95 km west of Monterey Bay. In all seasons, numbers were highest at sea from Cape Mendocino to the Oregon border, from Point Sur to Bodega, and from Morro Bay through an arc to about San Nicolas and Santa Barbara Islands (including Santa Barbara Channel). Probably due to above-average winds and winter storminess, we seldom saw Western Gulls more than 25 km at sea north of Point Arena. Numbers in the south grew from an estimated 5000 to 10,000 birds in the nesting season, to five times that number in January–February 1976. Seasonal increase of populations in southern California after the nesting season is consistent with banding data for central and northern California colonies, but birds from southern California colonies appear to move north (Hunt and Hunt 1974).

During fall 1982, estimated populations in central and northern California were one-third to one-half below figures for the same season in other years (roughly 18,000 versus 35,000 birds). Similarly, in southern California during fall and winter 1977–1978, numbers of Western Gulls were about one-half lower than in the preceding two years (e.g., maximum counts of about 10,000 on the Channel Islands in fall 1977 versus counts over 25,000 in 1976). These declines occurred during periods of environmental warming (and storminess in 1982), a situation that may lead to low food availability and consequent redistribution of gull populations northward or perhaps to bay and coastal sites (refuse dumps) not included in our samples. However, gull foods may also be exceptionally abundant in restricted areas during ENSO episodes. Stewert et al. (1984) describe mass strandings of pelagic red crab (*Pleuroncodes planipes,* a sub-tropical form carried northward by strong ENSO-related currents) at San Nicolas Islands in 1983, concluding that Western Gulls nesting on San Nicolas were able to avoid the reproductive failures seen elsewhere by taking advantage of the unusual masses of stranded crabs.

Glaucous-winged Gull, *Larus glaucescens*

We found Glaucous-winged Gulls in California throughout the year; numbers were decidedly largest from November through February. Southward migration began in September or October each year, and numbers dwindled after March. These birds occurred primarily along mainland and island shores and waters overlying the continental shelf, but small numbers were scattered offshore in winter (see also Sanger 1973). Peak densities at sea in central and northern California never attained 0.3 birds km^{-2}, though tens or hundreds of Glaucous-winged Gulls occasionally were noted in feeding groups including other gulls. We observed them as far at sea as 150 km and they are known to go much farther (Sanger 1973, Harrington 1975). Except on a very localized scale, immature birds outnumbered adults at all times.

Glaucous-winged Gulls were present in much larger numbers north of Monterey Bay than to the south: central and northern California totals were estimated to be 35,000 and 50,000 birds in December 1980 and February 1982, respectively, while maximum numbers south of Point Conception were only about 250 to 500 birds in January and March 1976.

Black-legged Kittiwake, *Rissa tridactyla*

Although we found at least a few kittiwakes in every month, numbers generally were very low from May through October. Arrival of wintering birds occurred in November through January, peak populations were reached in January through March, and kittiwakes left California in April and May (Fig. 16). In several cases, midwinter dips in density curves probably separated north and south migrations and occurred when birds that wintered off Mexico had pushed through California.

Kittiwakes were most numerous north of the Russian River (39°N); densities in northern California often exceeded those farther south by 125% or more. Kittiwake density in central California exceeded that in the north on only one-fifth of the winter surveys and never by more than 32%. During fall 1982–winter 1983 (when

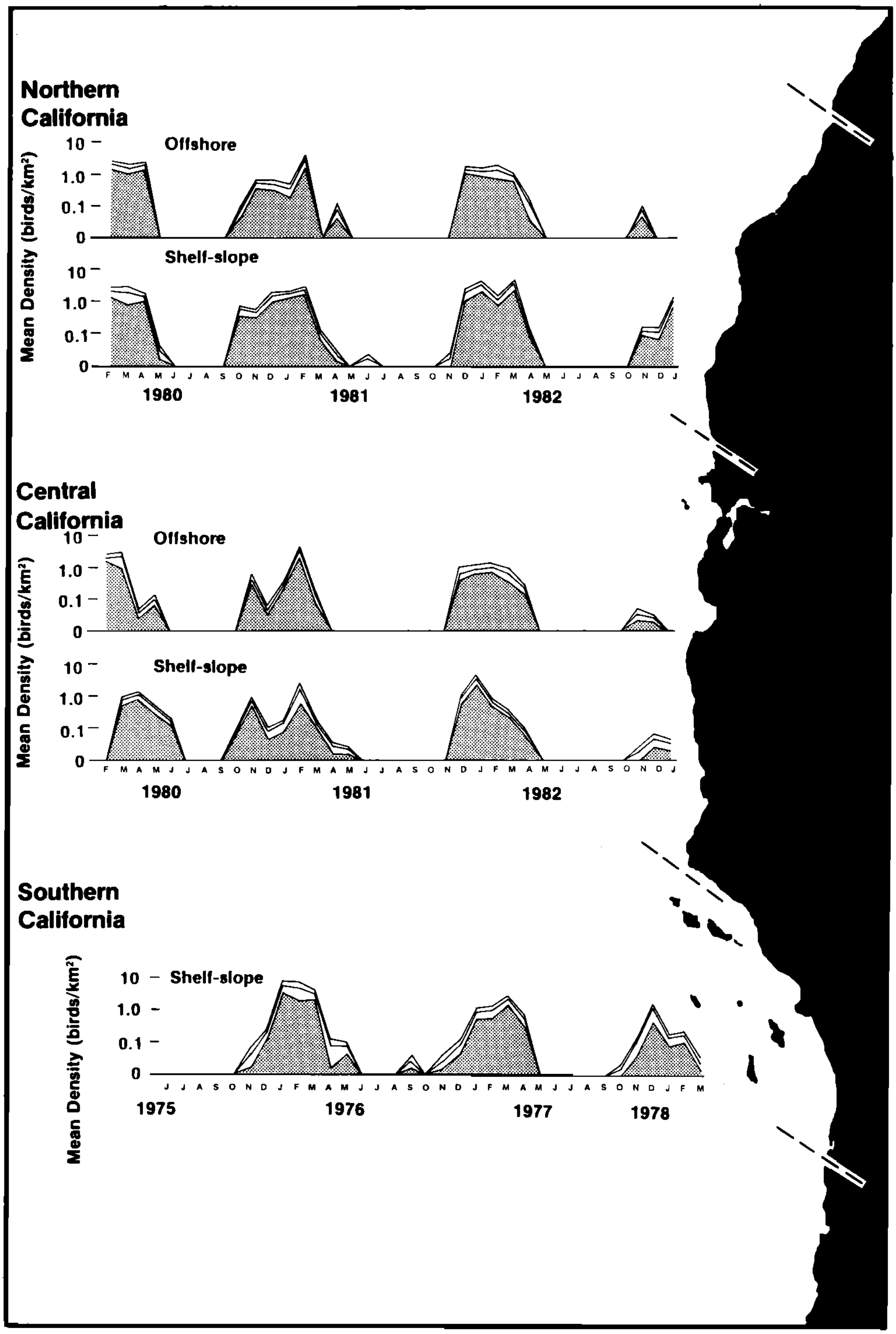

FIGURE 16. Comparison of monthly mean densities of Black-legged Kittiwake in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

ENSO effects were most pronounced in this region), kittiwakes were essentially confined to waters north of Point Montara.

During 1975–1976, kittiwakes were very abundant in southern California (we do not know what the numbers were farther north), but in 1977 and 1978, densities in the south were well below the average (1980–1982) for northern California. Extrapolations of peak winter densities indicate that 50,000 to 300,000 kittiwakes occurred off southern California in 1976, 1977, and 1978, while about 350,000 birds occurred off central and northern California in 1980, 1981, and 1982. Numbers present during the ENSO episode in winter 1983 were only about 10% as large as those in the preceding winters.

Kittiwakes occurred from the shoreline as far offshore as we surveyed. Densities over the shelf and slope often were matched by those in the larger, offshore regions of central and northern California, occasionally peaking at 2 to 3 birds km^{-2}. Like Harrington (1975), who analyzed POBSP data taken south and west of Point Conception, we saw little diminution of kittiwake numbers with distance from the coast.

Sabine's Gull, *Xema sabini*

Sabine's Gulls occurred statewide from the shoreline to at least 200 km offshore, and typically were most numerous beyond the shelfbreak, seaward of the most intense coastal upwellings. For the most part, they occurred off California only during migrations between their Alaskan nesting grounds and the wintering areas off northern South America.

Spring migrations were rapid, beginning in April and ending in late May, and, in southern California at least, were more concentrated spatially than in fall. Spring records for southern California occurred in a zone from about 35 to 85 km offshore of the mainland; the passages between the four northern islands concentrated many flocks of 10 to 100 birds. The peak of spring migration in the south fell during the middle third of May, though a few birds were seen as late as 23 June. Off central California sightings were very rare over the shelf, numerous over the slope, and uncommon farther out to sea; birds were noted as far out as about 180 km off Monterey Bay. Early migrants were seen in March and April, and numbers were much higher in May; scattered individuals were seen throughout summer. Although northern California sightings followed much the same time course, most birds occurred nearer the coast, particularly near Point Arena and for 75 km north of Cape Mendocino. Individual gulls were seen as far offshore as 169 km off Cape Mendocino.

The southward migration occurred in August through October, with peak numbers in September or October. Compared with spring, Sabine's Gulls were more widespread in autumn and were present in lower densities. As was seen among jaegers and phalaropes, the southward migration was more "leisurely" than that in spring. We estimate that fall populations off central and northern California contained about 15,000 to 20,000 birds at once, while during the May peak, numbers were as high as 50,000. In southern California, many records came from seaward of the Santa Rosa-Cortés Ridge; peak numbers during fall amounted to only about 5000 to 10,000 at one time.

Royal Tern, *Sterna maxima*

Royal Terns were present in very low numbers along the southern California mainland, with up to 435 birds around the shores of the islands, particularly San Miguel, Santa Rosa, and San Clemente. Records of this species spanned all months, peaking in September. Royal Terns were very rare more than one km at sea, and were rare along beaches of central California as far north as Point Reyes.

Elegant Tern, *Sterna elegans*

We regularly found Elegant Terns in numbers up to several thousand along the mainland beaches of southern California. During late summer and autumn each year, Elegant Terns moved north into central California, concentrating at Morro Bay and Monterey Bay, where we counted as many as 800 birds in September and October. Offshore foraging was rare; only 8 birds were recorded more than 4 km from the coast.

Common/Arctic Tern, *Sterna hirundo/paradisaea*

These two terns are not separable by aerial observers, but our sighting records and modest collections from ships in Monterey Bay and southern California indicate that the Common Tern is most numerous within 25 km of the mainland and occurs by the hundreds along coastal beaches and in protected bays and estuaries. On the other hand, the Arctic Tern predominates everywhere seaward of about 25 km from shore and certainly occurs to at least the central portion of the California Current, 450 km off Monterey.

Migrations in spring were very rapid, with exceptional dates in March and June and peak numbers in late April and May (Fig. 17). Densities recorded in spring were five to ten times lower than those in autumn. Few of these terns were seen during July, and southward migration

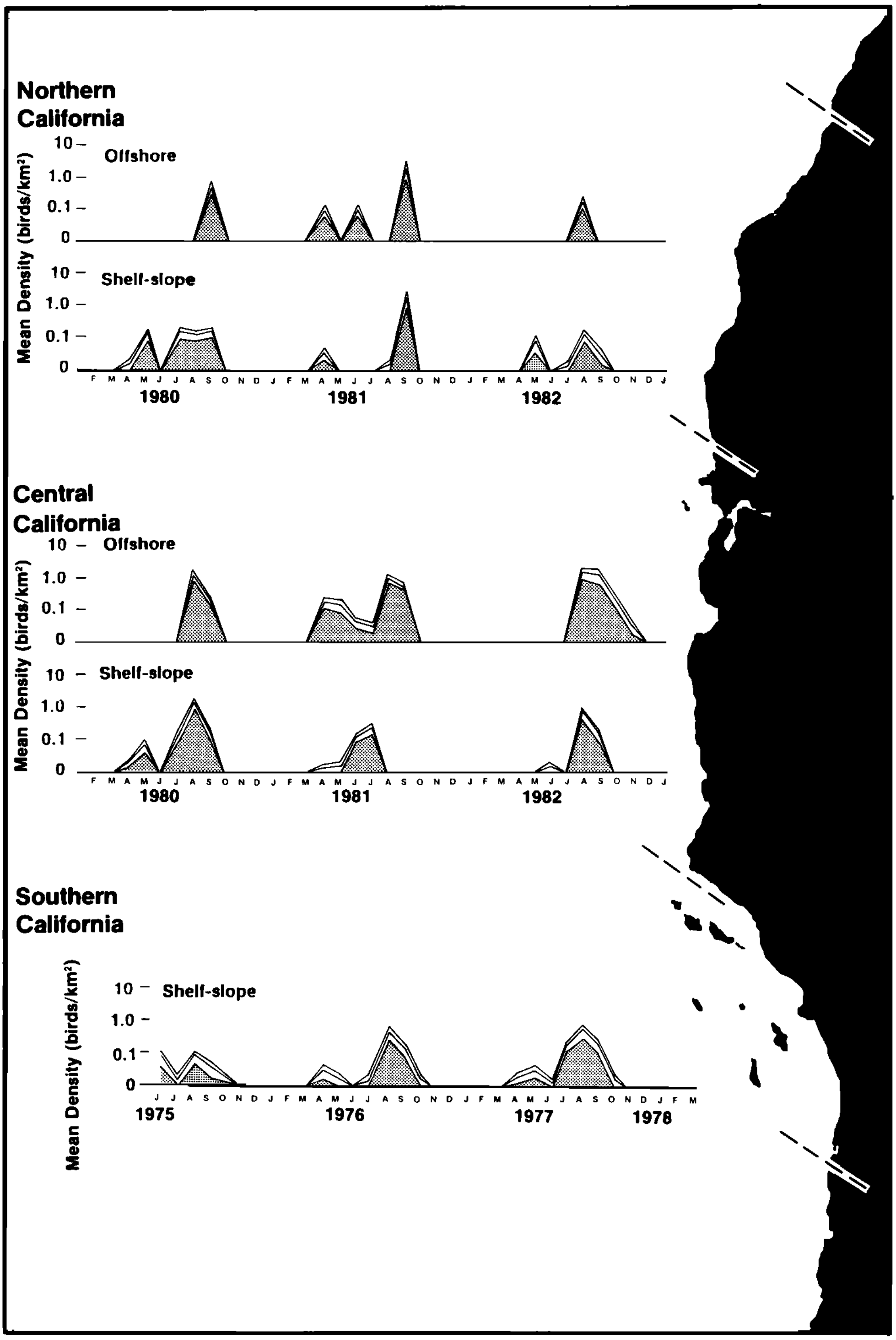

FIGURE 17. Comparison of monthly mean densities of Common and Arctic Terns (combined) in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

occurred in August through October, with a peak in late August or early September. Densities in southern California were only 30 to 50% of those in areas to the north, so we surmise that substantial numbers of (probably Arctic) terns passed seaward of the Southern California Bight. At the fall peak in numbers, perhaps 200,000 birds occurred at once off central and northern California, compared with 30,000 to 50,000 off the southern coast.

These birds were present at all latitudes and concentrated over the continental slope, primarily in clear waters outside the upwelling zone. Where warm-core eddies of the California Current approached shore in late summer, as off Point Arena, we occasionally saw substantial numbers of terns within about 15 km of the mainland. The highest observed densities occurred from Point Arena to Point Sur. Migration through southern California was concentrated from western Santa Barbara Channel to Cortés Bank.

Forster's Tern, *Sterna forsteri*

This tern is an abundant nesting resident and was seen regularly along mainland beaches, coastal bays, and estuaries. As they attained their widest distribution in July, we encountered Forster's Terns the length of the state and offshore for about 15 km from central California nesting areas (especially Monterey Bay and off Point Montara, where terns probably went after nesting along San Francisco Bay). In both southern and central California we counted up to about 500 birds in late summer, and essentially none in winter. A flock of 6 possible Forster's Terns recorded at Crescent City in January 1982 would be the northernmost winter record for the state.

Common Murre, *Uria aalge*

The Common Murre, with a population exceeding 150,000 pairs in 1982, is California's most numerous nesting seabird (Sowls et al. 1980). The largest colonies are located north of Trinidad Head and in the Gulf of the Farallones. Murres now nest no farther south than Hurricane Point, near Point Sur. Details of habitat occupancy are discussed in a later section.

The annual cycle of murre abundance is a function of year-round presence of locally nesting birds, combined with substantial immigration in fall and winter of birds from colonies north of the state. These immigrants seem to concentrate north of Point Arena, but beached-bird data taken at the time of the 1971 oil tanker collision at San Francisco suggested that many immature birds near the coast were from the northern populations (Smail et al. 1972).

Statewide numbers reached an annual peak in about January each year and declined toward summer lows after March (Fig. 18). In large measure we think this winter-to-spring decline reflects departure of wintering birds. Winter populations at sea during 1981 and 1982 were on the order of 700,000 to 800,000 birds, whereas in summer, numbers at sea dropped to about 150,000 (i.e., the foraging portion of the adult population). Aggregations near colonies at Crescent City (approximately 140,000 murres occupied Castle Rock during July 1982) and the Gulf of the Farallones (where we estimated a combined nesting total of almost 200,000 birds at four major sites) often resulted in densities exceeding 100 birds km^{-2} extending for about 10 km from the colonies during the nesting season. Elsewhere, densities of this magnitude were seen only in winter. Locations supporting large numbers of murres in fall or winter, but not other seasons, included Santa Barbara Channel (20,000 to 30,000 birds), Morro Bay to Point Arguello (to 30,000 birds), and Monterey Bay (to 30,000 birds). At all times, murres were commonest in waters less than 150 m in depth. However, we also recorded murres in densities up to 0.5 birds km^{-2} to 100 km off northern California.

During nesting season (from April through July), more than 75% of all murres were found within 40 km of a colony (Sowls et al. [1980] list 17 sites with more than 1000 pairs in 1980). Even in winter, the season of widest distribution, when they occurred throughout California, murres still were most abundant near (<50 km) their colonies. Largest numbers were always encountered from Trinidad Head to the California-Oregon border and from Point Reyes to Monterey Bay. Murres were present south of Point Sur only outside the nesting season.

We estimated the aggregate nesting population to be 520,000 birds in July 1982. Since that time, populations in central California have declined. This decline is almost certainly attributable to the combination of deaths of several tens of thousands of birds due to entanglement in gill nets (H. Carter and J. Takekawa pers. comm.), mortalities in two fall–winter oil spills, and nesting failure during the 1982-1983 ENSO. On the Farallon Islands, numbers dropped by about 55% between 1982 and 1986 (H. Carter pers. comm.). Specific effects we noted during the 1982–1983 ENSO were: (1) overall reduction by two-thirds in the densities recorded at sea in midwinter, (2) failure to occupy waters north of Cape Mendocino and south of Point Sur in large numbers, and (3) unusually distant foraging by murres from central California colonies during synoptic ob-

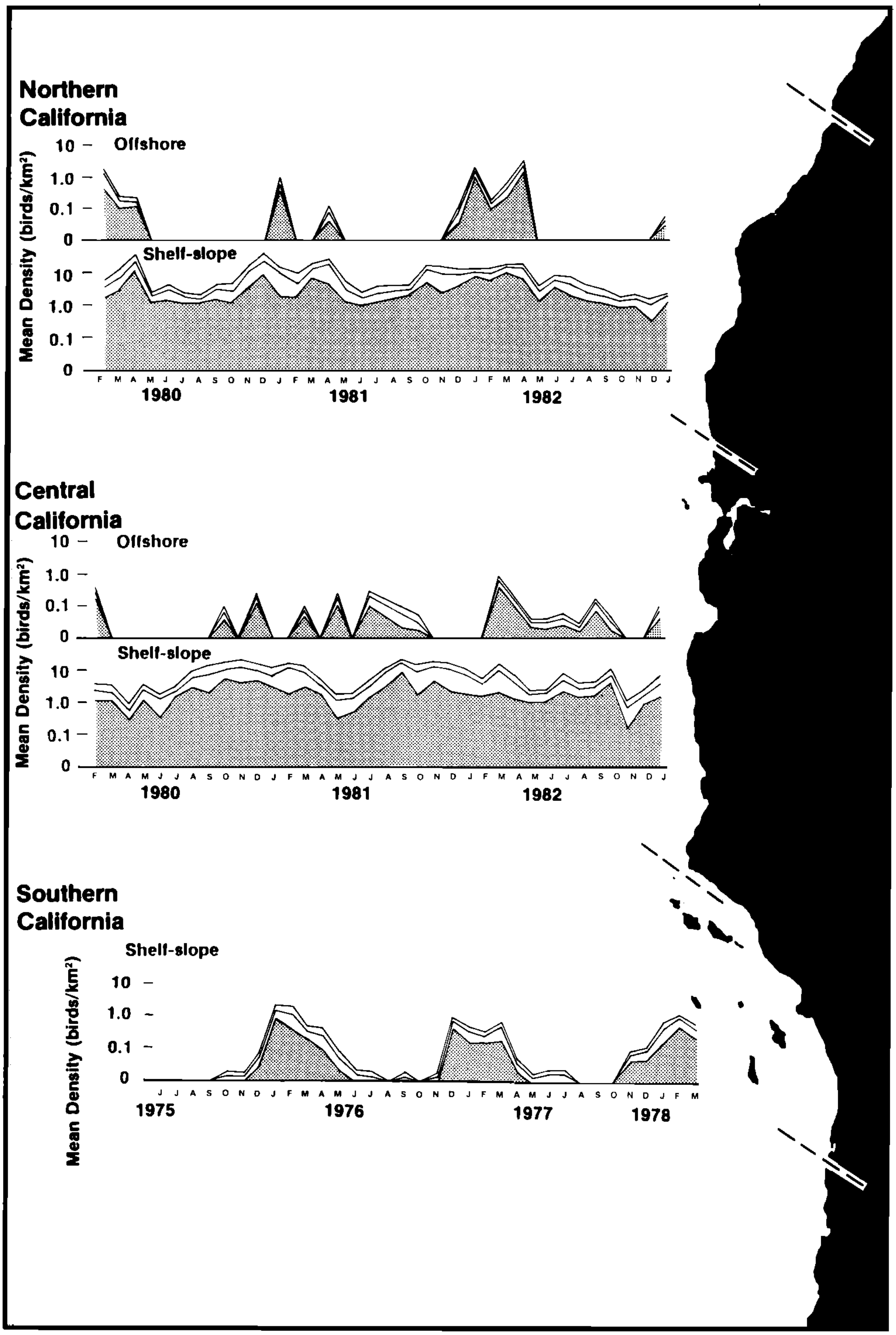

FIGURE 18. Comparison of monthly mean densities of Common Murre in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

servations in summer 1983 (to 75 km off Point Sur).

Pigeon Guillemot *Cepphus columba*

In California, guillemots are seen almost exclusively within about 5 km of the mainland and island shores where they nest. The state's nesting total includes about 14,700 birds scattered at hundreds of sites from Santa Barbara Island to the Oregon border (Sowls et al. 1980). Most birds leave California from August through February and probably winter in Washington and British Columbia.

These birds nest in rocky crevices, so their total numbers cannot properly be assessed from an airplane. Nevertheless, aerial observations can indicate relative distribution of adults on the water near nesting cliffs. We saw Pigeon Guillemots near mainland and island coasts from Santa Barbara Channel north, few more than 1 or 2 km at sea. By far, the largest numbers (100 to 300 birds) were seen from Santa Cruz to Point Reyes, including the Farallon Islands (usually 25 to 40% of survey totals). Elsewhere, they were evenly distributed in low numbers along rocky shorelines. Peak populations (to 1100 individuals) were noted on the water in June and July, when foraging adults were joined by recently fledged young. Three birds seen along the central California coast in January 1981 and a single bird far at sea off Monterey Bay in January 1983 were our only midwinter records. Early visits to nesting sites in the northern Channel Islands were noted by shipboard observers in late February 1976.

Marbled Murrelet, *Brachyramphus marmoratus*

These murrelets were seen in low numbers (to several dozen per coastal survey) beyond the surf zone off central and northern California, especially adjacent to inland nesting areas. Sightings were most frequent from northern Monterey Bay to Año Nuevo Point and from Trinidad Head to Crescent City. With maximum counts (up to 77 birds) in fall and winter, numbers always were concentrated north of Point Arena.

Xantus' Murrelet, *Synthliboramphus hypoleucus*

Xantus' Murrelets nest in Mexico and southern California and are found in fall and winter as far north as Washington (Jehl and Bond 1975). The California nesting population of roughly 5000 birds is centered on Santa Barbara Island (Sowls et al. 1980, Hunt et al. 1981).

We found that the population was densely concentrated in the vicinity of Santa Barbara Island during the breeding months of March through May, with scattered sightings from just southeast of San Clemente Island to about San Miguel Island. As adult murrelets escorted their dependent young to sea in May, we saw scattered groups throughout the SCB from near San Diego to near Rodriguez Dome. Some of these birds undoubtedly were dispersing from Mexican nesting colonies.

From August through October, annual population lows occurred within the SCB (with average densities falling below 0.02 birds km^{-2}), while murrelet numbers rose to annual highs in the area from Point Conception to Monterey Bay. The population was widely scattered in fall, with a few birds as far north as Bodega. We estimated numbers as high as 3000 birds from Point Año Nuevo to San Miguel Island, but few southeast of there. Interestingly, substantial numbers (perhaps several hundred) of these murrelets occurred in warm waters west of the Farallones during June 1985, perhaps a result of unusually rapid northward post-nesting dispersal (K.T.B., D. G. Ainley, and L. B. Spear unpubl. obs.). Previous records from the Farallones included single occurrences in May, July and August (DeSante and Ainley 1980), whereas according to Evans et al. (1983), sightings have occurred only occasionally off Monterey Bay in May and June. North of Point Conception these murrelets typically occurred from 20–100 km offshore.

Retreat from waters north of Point Conception occurred after November, though there are a number of recent winter records south and offshore of Monterey Bay (A. Baldridge, pers. comm.). We encountered unidentified murrelets off the Monterey and San Luis Obispo coastlines regularly, but in very low numbers, from February through April. These and other central and northern California sightings occurred at the time of year when upwelling was least prevalent; often, sightings were from clear, blue waters, well offshore.

Craveri's Murrelet, *Synthliboramphus craveri*

Craveri's Murrelets move into southern California waters each year after nesting in Mexico. We occasionally encountered them south and east of Santa Barbara Island; monthly totals were no higher than 10 birds. Sightings usually included single birds or pairs. We noted none north of Point Conception, although a few records exist in the literature.

Ancient Murrelet, *Synthliboramphus antiquus*

This species occurred occasionally and in relatively low numbers in winter, primarily seaward of the shelfbreak. Most records came from south of Point Arena in February through April. We saw as many as 15 birds in a given month but

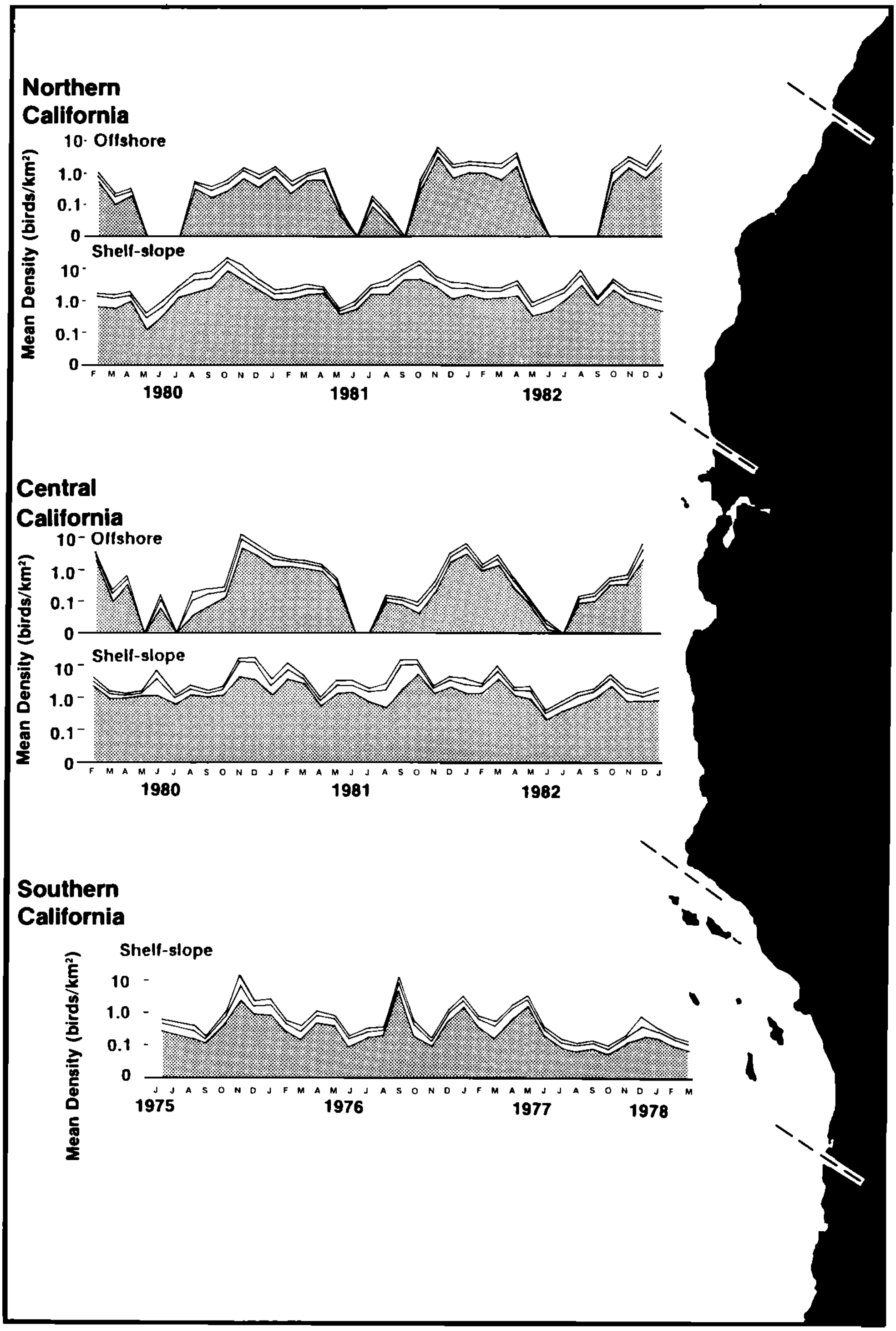

FIGURE 19. Comparison of monthly mean densities of Cassin's Auklet in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

other birds could easily have been overlooked in winter. We saw four Ancient Murrelets near Santa Barbara Channel in January and March 1976 and 1977.

Cassin's Auklet, *Ptychoramphus aleuticus*

With nesting numbers totalling around 130,000, Cassin's Auklets are the second most abundant of California's breeding seabirds (Sowls et al. 1980). Numbers are concentrated at two sites: the Farallones (100,000+) and San Miguel Island (20,000). This is one of the half-dozen most numerous inhabitants of waters from the mid-shelf to about 150 km offshore.

Cassin's Auklets occurred throughout the year off all sectors of the state (Fig. 19), but were very concentrated in late spring and summer in the vicinity of the major colonies. Densities exceeding 100 birds km^{-2} were often encountered within 25 km of the Farallones and San Miguel Island, and similar elevated densities occasionally occurred along the shelf break from Point Año Nuevo to Bodega and for 40 km north and south of Point St. George.

Post-nesting dispersal (August through October) from the colonies led to scattered sightings of Cassin's Auklets throughout the Southern California Bight west of San Clemente Island, over the shelf and slope from San Miguel Island to Point Buchon, and all along the shelfbreak and continental slope north of Monterey Bay. In this season and earlier in summer, Cassin's Auklets often occurred in bands a few kilometers in width parallel to shore, with few birds on either side.

Large numbers of Cassin's Auklets entered California from the north in September and October, swelling statewide populations by at least 100%. The estimated magnitude of the increase (250,000 to 500,000 birds) alone argues that most of these auklets came from large colonies north of the state, but some immigrants might also have come from the smaller colonies in Mexico. Arrival of immigrants was delayed until December in 1982, probably as a result of the unusual environmental conditions prevailing at the time. Peak annual densities, corresponding to estimated populations of around 500,000 to 1,000,000 birds, were recorded each year in January or February. The population was distributed most broadly in this season with relatively few birds over the shelf and large numbers over the continental slope (to about 90 km off central California).

Cassin's Auklets were less numerous south of Point Buchon than to the north, though estimated numbers in southern California reached about 50,000 to 100,000 birds. Most sightings were recorded in the central and western portions of the Southern California Bight. A few birds, perhaps those associated with Mexican colonies, were seen 50 km south of Cortés Bank. Large numbers of auklets persisted in these southern latitudes through late March in 1976, and late January in 1977 and 1978.

Cassin's Auklets exhibited a seasonal shift in depth preferences. Half or more of the auklets present in May through October were found over the outer shelf, whereas half or more of the auklets were in deep (>2000 m) waters seaward of the slope in the months of November through April. Near the Farallones in March–April 1985, we noted a shift from offshore waters toward the shelfbreak at the onset of upwelling (and egg-laying; Briggs et al. in press). Proportions of the population over the continental slope were relatively constant. Affinity of Cassin's Auklets for the coastal upwelling zone in spring and summer is analyzed below.

Rhinoceros Auklet, *Cerorhinca monocerata*

Rhinoceros Auklets maintain small nesting colonies at eight sites in California; prior to 1980 the total nesting population was approximately 360 birds (Sowls et al. 1980), but numbers appear to be growing rapidly and at least one small colony (Año Nuevo Island) has been formed in recent years (D. G. Ainley, D.B.L. unpubl. obs.). Due to seasonal influxes from northern colonies, Rhinoceros Auklets are abundant on offshore waters the length of the state in winter and constitute one of the most important elements of the wintering fauna south of Monterey. Throughout the year, they are commonest in waters seaward of the shelfbreak.

During the nesting months of May through August we found very few Rhinoceros Auklets off California, mostly within about 50 km of the small Farallones, Castle Rock, and (suspected) Point Arguello colonies. By late October, immigrants appeared in the waters north of Cape Mendocino, raising densities over the continental slope and offshore waters to 0.75 to 2.35 birds km^{-2} (Fig. 20). Density of these birds dropped appreciably in this northern area in November or December, while numbers rose abruptly from Bodega to Point Conception. For most of the winter, 50% to 95% of Rhinoceros Auklets in central and northern California were located south of Bodega.

The central California density peak in late autumn was followed by a January or February decline of about 30%. Our 1975 to 1978 studies indicated that Rhinoceros Auklet numbers in the south increased abruptly from extremely low levels in summer and fall to a sharp winter peak in January, February, or March. Extrapolations of densities obtained in these months yield

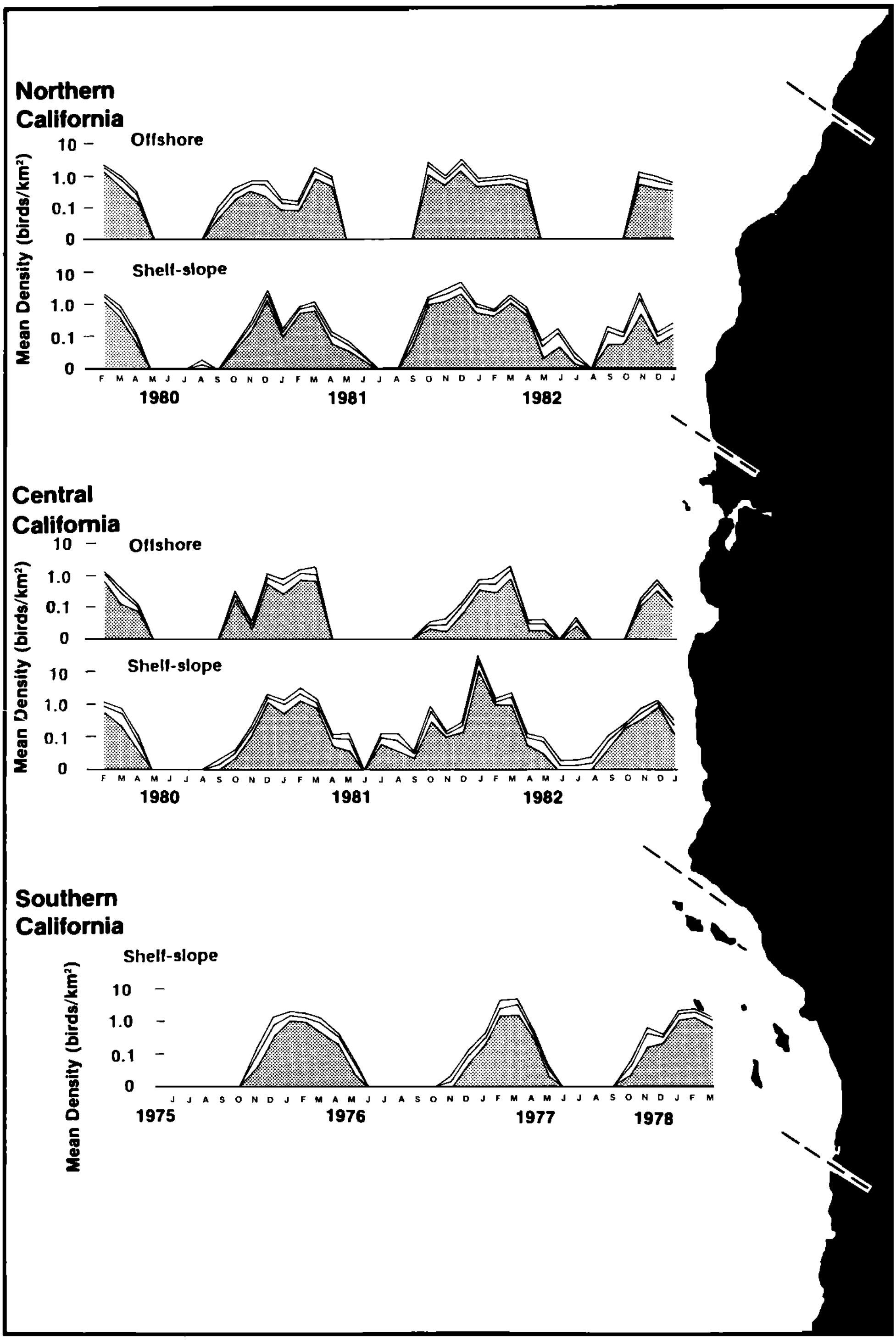

FIGURE 20. Comparison of monthly mean densities of Rhinoceros Auklet in three regions off California. In each panel, three curves represent mean density ± one SE. Shaded values lie more than one SE below the mean.

southern California population estimates of 100,000 to 300,000 birds; at this time, they may have been more numerous south of Monterey than north of there. Rhinoceros Auklets were ubiquitous except near the mainland shore and accounted for up to 30% of all seabirds off southern California in winter. With estimated totals of 200,000 to 300,000 birds, it appears that the bulk of the eastern Pacific nesting population is located off California in February and March.

Departure from southern California was rapid after the winter peak, and our density curves for central California in 1981 and 1982 show a peak in February or March, which may reflect northward passage of these birds. This contrasts with the data reported in Ainley (1976) for waters 15 to 80 km from the coast. Ainley found that numbers of Rhinoceros Auklets reported in AFN/AB peaked in December and January; most sightings came from north of Morro Bay.

Few birds remained each year after April. In spring we encountered Rhinoceros Auklets along the western margin of the Southern California Bight, in the passages between the Santa Barbara Channel Islands, and all along the shelfbreak from Point Arguello to Oregon. These birds occupied waters slightly to seaward of the main concentrations of Cassin's Auklets, but much overlap occurred. These small, piscivorous puffins did not form the large aggregations seen in the more numerous, planktivorous, Cassin's Auklet.

Tufted Puffin, *Fratercula cirrhata*

With small numbers of California nesting birds in central and northern California (250 birds; Sowls et al. 1980), Tufted Puffins are only now becoming re-established after many decades of severe population decline (Ainley and Lewis 1974). They formerly nested as far south as the Channel Islands, but now nest only from Hurricane Point (near Point Sur) northward. Many more puffins are seen in winter than during the nesting season, although there are records in every month.

We observed Tufted Puffins near the Castle Rock and the Farallones colonies (about 100 birds each) throughout the year. Peak numbers of sightings here and elsewhere north of Point Sur occurred in March and April. In southern California, largest numbers were recorded in January, April, and May. After May, when visitors from the north presumably had left for their nesting areas, sightings became infrequent and were mostly noted seaward of the colonies.

Throughout the year sightings of Tufted Puffins were commonest seaward of the central continental slope, a few birds were noted as far offshore as 180 km (near the limit of our routine sampling). Sightings were very rare from Monterey Bay to Point Conception but were more numerous south of there. In the coolest waters 50 to 300 km off the southern California mainland, we encountered these birds in densities up to about 0.1 birds km^{-2}. At the time of the winter and spring population peaks, the total "instantaneous" numbers of Tufted Puffins in California were on the order of 10,000 to 20,000, with perhaps 1000 to 5000 birds off southern California and the remainder distributed evenly north of Monterey.

Horned Puffin, *Fratercula corniculata*

We encountered low numbers of Horned Puffins from January through May off central California, and January through August north of Point Arena. Never very common, this species was nevertheless a regular component of the fauna seaward of the shelf. During April, May, and June 1975 and 1976, Horned Puffins were surprisingly abundant near San Miguel Island (the coolest waters off southern California), where local numbers were on the order of several thousand birds. Lesser numbers were seen in spring 1977; a cruise in April of that year encountered Horned Puffins in low density (<0.1 birds km^{-2}) from Rodriguez Dome to San Juan Seamount. They were also surprisingly common off the Farallones during a cruise in June 1985 (K.T.B., D. G. Ainley, and L. B. Spear unpubl. obs.).

Our sightings of Horned Puffins corroborate the interpretation of Hoffman et al. (1975) that this species returns northward (to Alaska) through California waters each spring. In fact, Horned Puffins clearly outnumbered Tufted Puffins during April and May, when total numbers reached 5000 to 10,000 birds at once, statewide. Sightings were concentrated near San Miguel Island, from Point Sur to the Farallones, and Cape Mendocino to the Oregon border. These apparent concentrations may partly reflect the overall paucity of data; in reality Horned Puffins may occur evenly throughout the offshore regions.

SEABIRD DENSITY AND BIOMASS

In central and northern California, seabird density and biomass were much higher in neritic waters than in deeper waters farther out to sea (Fig. 21). In central California, for example, density averaged 111.3 ± 19.8 SE, 27.5 ± 2.8, and 7.8 ± 0.9 birds km^{-2} for shelf, slope, and offshore waters, respectively, during the 36 months of study. For biomass density, the comparable averages are 68.2 ± 5.93 SE, 13.3 ± 1.9, and 3.3 ± 0.6 kg km^{-2} (these, and differences in density, are all significant at the $P < 0.025$ level; n = 36, Z statistics). There was no month during which density or biomass in the two deep-water strata exceeded those for the shelf. The disparity

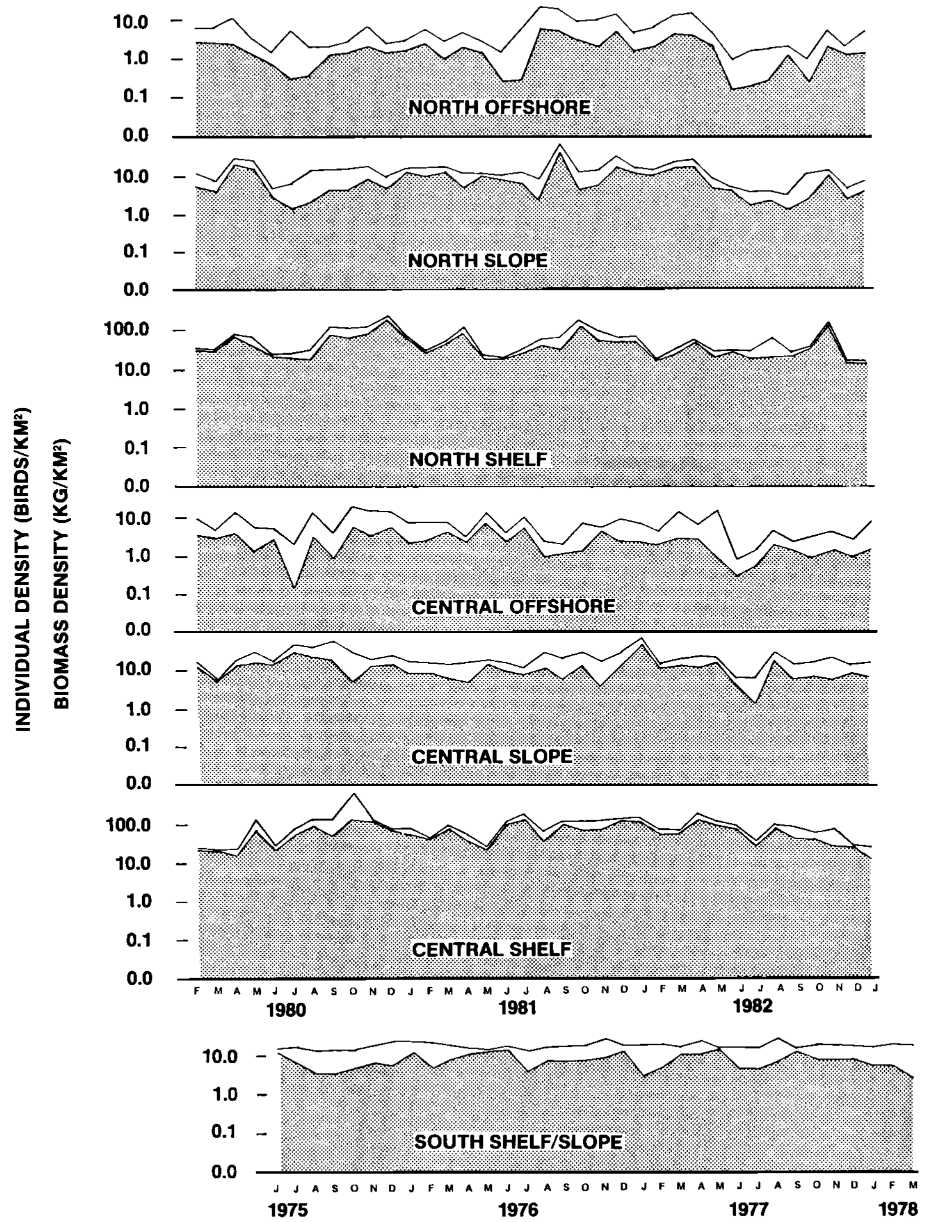

FIGURE 21. Comparison of average monthly biomass density (lower curves) and individual density (upper curves) for different depths and latitudes off California.

was greatest during spring and fall, when shelf averages were seven or eight times higher than those for the slope and offshore areas, and least in midwinter, when the difference between shelf and slope was as low as 40 to 50%.

Additionally, average density and biomass were significantly higher in central California than to the south. For shelf waters, three-year average biomass was 55.2 ± 8.7 SE kg km^{-2} in northern California, 68.3 ± 5.9 kg km^{-2} in central California, and 8.38 ± 0.9 kg km^{-2} in the south (where samples included some waters of the continental slope). Biomass over the slope in northern California averaged 10.87 ± 1.8 kg km^{-2}, while over the slope in central California the average was 13.34 ± 1.9 kg km^{-2}. Similar trends are seen with average bird density.

Despite the asynchronous sampling of southern California versus other areas (potentially aliasing regional comparisons due to secular trends in populations or major environmental variations), the data can be matched up with reference to timing of ENSO episodes. Within our field studies, ENSO episodes occurred in fall 1976 to winter 1976–1977 and fall 1982 to winter 1982–1983. Using these as endpoints, 20-month periods can be matched as follows: for southern California, June 1975 through January 1977; for central and northern California, June 1981 through January 1983. From these data, pairwise comparisons of density and biomass in the various depth/latitude regions indicate that highest density and biomass occurred on the central California shelf, followed by the northern shelf and the southern shelf/slope. Biomass, but not density, was significantly higher on the central California slope than in southern California, while the northern slope and southern shelf/slope did not differ significantly in these measures. Density and biomass in the deeper offshore regions (central and northern) were much lower than those seen over the shelf and slope.

For neritic waters, there generally were two or three peaks in biomass and density each year. In northern California, density peaks were observed in spring and in late summer to late autumn: May, September, and December 1980; April and October 1981; and August and November 1982. Similarly, in central California, the peaks were in May, August, and October 1980; July and December 1981; and April and November 1982. Southern California density peaks were seen in June and December 1975, May 1976, June and October 1977, and February 1978. When matched by month in the 20-month subsample, peaks in density or biomass in the various regions occurred asynchronously; simple pair-wise correlations were not statistically significant. This is not unexpected, given the potential movements of populations between regions (especially migrants in spring and fall) and known annual and seasonal variations in environmental conditions that might influence bird abundance.

In central and northern California, seabirds were present in much lower densities during fall 1982 than earlier in the study, largely as a function of substantial declines over the shelf and slope. This reflected low numbers of diving birds and species that visited in fall and winter from breeding stations in the North Pacific and Bering Sea (especially Northern Fulmar, Black-legged Kittiwake, several *Larus* gulls, and alcids).

Seabirds were most concentrated in neritic waters of five areas: 1) from Crescent City to Trinidad, 2) from Point Reyes to Monterey, 3) from Morro Bay to Point Arguello, 4) Santa Barbara Channel, and 5) the Santa Rosa-Cortés Ridge. Average aggregate bird density in these regions exceeded 50 birds km^{-2}, corresponding to biomass values of 34 to 46 kg km^{-2}. These shelf areas occasionally harbored birds in densities exceeding 1000 birds km^{-2} for periods of a month or more.

DIVERSITY AND SPECIES COMPOSITION

The seabird fauna off California is dominated by approximately thirty species. These species fall into four main groups based on their seasonal status and breeding affinities. Numerically predominant *breeding residents* include Leach's Storm-Petrel, Brandt's and Pelagic cormorants, Brown Pelican, Western Gull, Pigeon Guillemot, Common Murre, and Cassin's Auklet (for some of these, the numbers of nonbreeders greatly eclipse those of locally nesting birds). Abundant *winter residents* include Western/Clark's Grebes, Northern Fulmars, Surf/White-winged scoters, Herring Gulls, California Gulls, Black-legged Kittiwakes, and Rhinoceros Auklets. These species all nest in interior North America, the maritime Pacific Northwest or Alaska. The dominant *summer visitors* are the Sooty, Pink-footed, and Buller's shearwaters from the South Pacific, Black-footed Albatross from the Hawaiian Islands, and Black Storm-Petrel and Heermann's Gull from the Gulf of California. The most abundant *spring and fall migrants* include the Pacific Loon, Red and Red-necked phalaropes (which also winter off California in much smaller numbers), Pomarine Jaeger, Arctic and Common terns. The four species or groups that reach estimated "instantaneous" population levels above one million (Sooty Shearwater, the two phalaropes taken together, Common Murres, and Cassin's Auklets) are decidedly most abundant in the cooler waters of the state, primarily near upwellings, but reach peak numbers at different times of the year. The shearwaters are most abundant during May through July, the phalaropes in May and September through November, and the two alcids in winter.

Species composition varied by region and season, reflecting the presence of migrants and seasonal visitors and the breeding cycles of residents (species composition by habitat is discussed later). As noted by Ainley (1976), the contrasts between the fauna of southern California and other regions are more striking than are those between central California and northern California. In fact, the most striking contrasts in species composition occur when one travels from the warm waters near San Diego to the vicinity of Point Conception, where upwelling exerts an important influence on ocean conditions. Moving toward the cooler northwest waters, the importance of subtropical species diminishes rapidly in favor of

TABLE 1
COMPARISON OF DIVERSITY INDICES (SHANNON'S H') AND SPECIES RICHNESS IN GEOGRAPHICAL UNITS OF DIFFERING SIZE[1]

Unit	Area sampled within unit (km^2)	H'				Number of species
		Mean	Max.	Min.	SD	
1) All central and northern California	245.37	2.50	—	—	—	37
2) Central California, shelf/slope	117.25	2.26	—	—	—	34
3) Central California						
Shelf	38.76	2.01	—	—	—	26
Slope	78.49	2.10	—	—	—	22
4) Central shelf, individual transects	1.01 to 4.93	1.12	2.37	0.1	0.67	1 to 16
5) Central shelf 5' × 5' grid cells	0.83	0.60	1.83	0.1	0.60	1 to 13

[1] Data from February 1980.

the species found in abundance in central and northern California. Species such as Least and Black storm-petrels, Pink-footed Shearwaters, Elegant and Royal terns, and Xantus' Murrelet give way to Ashy Storm-Petrel, Black-footed Albatross, Sooty Shearwater, Cassin's Auklet, and in winter, Common Murre. Ainley (1976) and Hunt et al. (1981) note that present-day or historical limits to the nesting ranges of several species occur within the Southern California Bight: Ashy Storm-Petrel, Black Storm-Petrel, Brown Pelican, Pelagic Cormorant, Elegant Tern, Common Murre, Pigeon Guillemot, and Xantus' Murrelet. Additionally, uncommon tropical and subtropical species are more often seen in the eastern half of the Southern California Bight than elsewhere; examples include Black-vented Shearwaters, boobies (*Sula* spp.), frigatebirds (*Fregata magnificens*), tropicbirds, and Craveri's Murrelet (Jehl and Bond 1975, Ainley 1976, this paper).

Despite geographic differences in composition, there is a broad similarity in the size and diversity of the fauna at all latitudes, and most species are shared by all regions. Considering the three areas encompassing continental shelf waters, monthly diversity indices (Shannon's H') averaged 1.91 (SD = 0.27, range 1.31 to 2.41) for northern California, 1.81 (SD = 0.38, range 0.95 to 2.38) for central California, and 1.90 (SD = 0.57, range 0.64 to 2.50) for southern California. Values for areas of continental slope off central and northern California were fairly similar to those for the shelf (northern California average = 1.87, SD = 0.34, range 1.13 to 2.59; central California average = 1.60, SD = 0.43, range 0.78 to 2.37), while diversity in offshore waters was slightly less (northern California average = 1.57, SD = 0.46, range 0.64 to 2.36; central California average = 1.56, SD = 0.50, range 0.64 to 2.35).

Diversity indices varied with size of the geographic unit considered. Our closest approach to point diversity, the 5' × 5' latitude-longitude grid cell, had diversity indices averaging half that of a transect comprising several cells, and one-fourth that of the total area sampled (Table 1). High variability in the index for 5' × 5' grid-cells implies that samples taken at this scale relate to substructure of the community; that is, many such samples are required to adequately characterize the fauna as a whole. Since diversity values did not stabilize near the maximal values (H' = 2.0 to 2.5) until we considered diversity at the level of regions, it appears that faunal composition varies most importantly over geographic distances of at 100 to 300 km (the scale of 'regions' considered here).

The timing of peaks in diversity was similar in all regions: within the 20-month subsample matched on the basis of ENSO episodes, species diversity in southern California correlated significantly with that in every other latitude/depth region (Pearson's $r = 0.48$ to 0.65, all $P < 0.05$, $n = 20$). The general pattern was one of lowest diversity in May through August, increasing diversity in fall, and high values in late fall through early spring (Fig. 22). It is important to note that high values of both species diversity and bird numbers in fall and winter result from visitation and winter residency of species that nest elsewhere. In fact, in all seasons except late spring through early summer, the California nesting fauna is substantially overshadowed by nonresidents. Since the young of California nesting species may not fledge until mid- to late summer (or even October in some storm-petrels) the greatest potential for interspecific competition for food may in fact come from species that come to California after having already raised and fledged their own young (see also Ainley 1976).

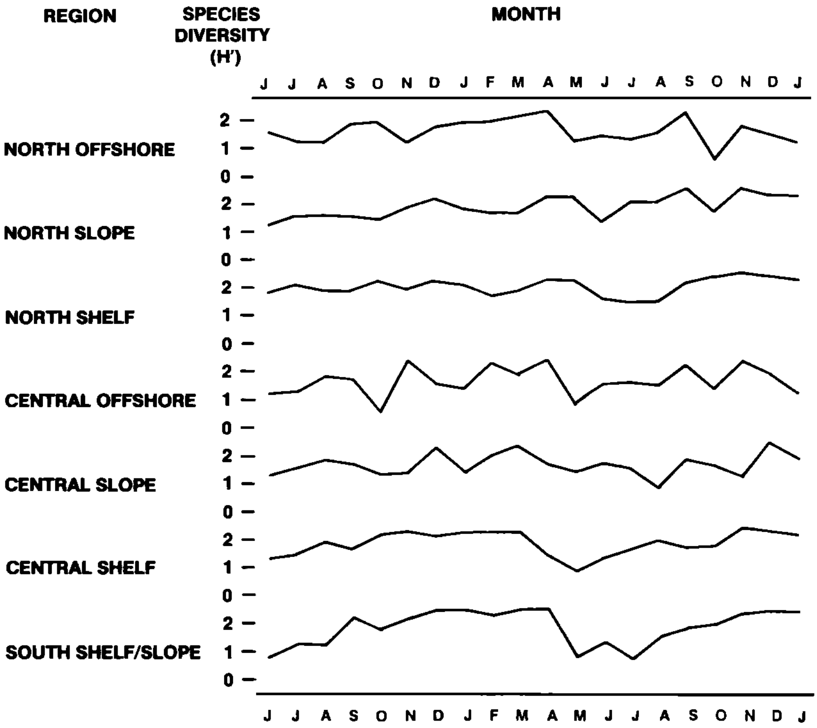

FIGURE 22. Comparison of species diversity indicies among latitude and depth regions off California. Values are from 20-month periods encompassing onset of ENSO events in fall 1976 (south) and fall 1982 (central and north).

This certainly is true of the gulls (one species breeding on the California coast is joined by 5 to 8 abundant species each winter). The same can be said for resident populations of storm-petrels, pelicans, cormorants, murres and auklets, all of which are augmented, sometimes greatly, by seasonal immigrants from other nesting populations.

Numbers of species recorded each month varied from averages of 9.5 and 13.5 for the northern and central offshore regions, to 18.0 to 25.7 for shelf areas in the north and south. The highest numbers of species generally were seen during spring and fall migrations, while low numbers generally occurred in June or July, when the fauna mainly comprised locally breeding species. For each of the three depth divisions (shelf, slope and offshore), peaks in species numbers occurred at about the same time throughout central and northern California. With peaks occurring in winter 1976 (36 species seen in two months), April 1977 (34 species), and September 1977 (39 species), the seasonal pattern of species richness (contrasted with diversity) in southern California was asynchronous with those in the 20-month sample for central and northern California. This may be due to the fact that the proportion of the southern California fauna attributable to nesting residents is quite small; the fauna is mostly a composite of species that nest elsewhere. This is especially true of the many species of sub-tropical birds that visit southern California but do not reach farther north in large numbers. North of Point Conception the proportion of nesting residents increases and a few species (murres, auklets, gulls, and cormorants) are numerically important in all regions (in general leading to synchronous changes in regional diversity).

The annual declines in species diversity in late spring and early summer reflected dominance of the entire fauna by two species groups: the shearwaters and the phalaropes. At times of maximal abundance (early summer for the shearwaters and fall for the phalaropes), these species accounted for half or more of the individuals in the entire fauna, regionally and state-wide. For both species, peak numbers probably exceeded three million, with possible turnover of 100% or more during migration. In general, numbers of species recorded each survey increased with average bird

TABLE 2
NUMBERS OF BIRDS SEEN IN MONOSPECIFIC AND MIXED-SPECIES FLOCKS IN CENTRAL AND NORTHERN CALIFORNIA DURING 1980–1983[1]

Species	Number of birds in monospecific flocks	Number of birds in mixed-species flocks	Number of birds of other species joining mixed flocks
Pacific Loon	2224	1085	4118
Western Grebe[2]	16,041	5288	6040
Black-footed Albatross	971	122	2560
Northern Fulmar	3245	1536	3088
Pink-footed Shearwater	681	965	9348
Sooty Shearwater	134,818	76,281	22,339
Short-tailed Shearwater	834	367	2950
Buller's Shearwater	1167	299	6333
Leach's Storm-Petrel	1243	37	88
Brown Pelican	4211	455	2618
Brandt's Cormorant	6206	1112	3305
Surf Scoter[3]	14,281	1118	943
Phalaropes	64,855	12,210	13,925
Black-legged Kittiwake	7721	2486	3080
Bonaparte's Gull	4766	2527	13,298
Heerman's Gull	1169	905	1347
California Gull	10,318	8772	6214
Western Gull	9710	6072	53,328
Herring Gull	4991	2086	5285
Common Murre	54,885	11,031	22,214
Rhinoceros Auklet	5910	222	1037
Cassin's Auklet	19,942	1057	3593

[1] Excluded are several very large flocks of shearwaters ($>10^4$ birds) recorded away from regular transect lines. Because of presence in mixed flocks of other species not listed here, the column totals do not balance.

[2] Includes Clark's Grebe.

[3] Includes White-winged Scoter.

density except in April through July, when the numerical dominance of shearwaters and phalaropes was most complete.

ASSOCIATIONS BETWEEN SPECIES

Species composition within an area is a function of the movements, nesting schedules and foraging habits of many individual species (Wiens 1985). There may also be behavioral interactions between seabirds such as feeding competition, interference (e.g., kleptoparasitism), and mutualism (prey herding) that lead to community structuring beyond the level of simple co-occurrence, but detailed observations are few (Sealy 1973, Porter and Sealy 1981, Hoffman et al. 1981, Duffy 1983). The extent to which species co-occur probably is always a function of scale: it is possible, for example, to find species that consistently co-occur in the same region but that avoid each other in feeding aggregations. We investigated consistency of species associations on different scales, looking first at associations within flocks, then examining the spatial scales over which birds aggregate. This is complemented by analyses of occurrence of abundant species along major habitat gradients, discussed in the following section.

Tables 2–5 present statistics concerning numbers of birds participating in mixed-species and monospecific flocks and values of Cole's Coefficient of Association for 22 species that were abundant off central and northern California in at least one of the three seasons: breeding, post-breeding and winter. These analyses include only those species that occurred in at least ten flocks containing at least one other species.

A total of 1214 Pacific Loons were seen in mixed-species flocks containing 4118 birds of other species; 2224 loons were seen in flocks containing no other species (Table 2). During spring migration Pacific Loons avoided flocks containing Sooty Shearwaters, Leach's Storm-Petrels and Western Gulls, while in winter they formed part of an inshore fauna comprising scoters, Western Grebes, pelicans, cormorants and Western Gulls (Tables 3, 4, and 5). Other members of this inshore fauna showed varying affinity for different gull species (e.g., Brandt's Cormorants and Brown Pelicans associated frequently with Heermann's and Western gulls while Western Grebes and scoters mostly avoided gulls).

The shearwaters, fulmar, albatross and Leach's Storm-Petrel as a group exhibited a range of tendencies to associate with other birds, from the gregarious Sooty Shearwater to the relatively solitary albatrosses and petrels. The shearwaters frequently associated with one another (depending on seasonal cycles of abundance of each species) but they were avoided by a variety of other species. This was especially evident with the phalaropes and alcids (Common Murre and the two auklets): only one significant positive association among these species was noted, that of phalaropes with Northern Fulmars in winter (Table 5). With both Leach's Storm-Petrel and the albatross, coefficients of association were almost all negative, though usually not significantly so. The small numbers of these two species participating in mixed flocks (122 albatrosses and only 37 petrels) on the one hand indicate that these birds avoided (or were avoided by) other species, and on the other hand rendered most of the negative association coefficients statistically insignificant.

Numbers of phalaropes in flocks, both monospecific and mixed, were quite large (Table 2), but almost all statistically significant association coefficients were negative. Only with the fulmar in winter did we see significant positive association by phalaropes. This was the season of least abundance of phalaropes, lowest flock size and

TABLE 3

ASSOCIATIONS BETWEEN SPECIES IN CENTRAL AND NORTHERN CALIFORNIAN FLOCKS SEEN IN THE MONTHS OF APRIL THROUGH JULY, 1980–1982)[1]

		Species (numbered as to the left)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
1	Pacific Loon (34)	—												
2	Black-footed Albatross (17)	−1.0	—											
3	Pink-footed Shearwater (33)	−1.0	−.05	—										
4	Sooty Shearwater (204)	−.47	−.06	.85	—									
5	Leach's Storm-Petrel (17)	−1.0	−.02	−.06	1.0	—								
6	Brown Pelican (10)	−1.0	−1.0	−1.0	.22	−1.0	—							
7	Brandt's Cormorant (13)	.01	−1.0	−1.0	−.40	−1.0	.08	—						
8	Phalaropes (58)	−.20	−.01	−1.0	−.46	.01	−1.0	−1.0	—					
9	Bonaparte's Gull (36)	.08	−1.0	−1.0	−.49	−1.0	−1.0	−1.0	.10	—				
10	California Gull (10)	.04	−1.0	−1.0	−.73	−1.0	−1.0	.06	−1.0	.03	—			
11	Western Gull (78)	−.80	−1.0	−.38	−.20	−1.0	.30	.37	−.18	−.62	.06	—		
12	Common Murre (56)	−.22	−1.0	−1.0	−.61	−1.0	−.62	.27	−.80	−.89	.62	.03	—	
13	Cassin's Auklet (46)	−.32	−.32	−1.0	−.49	−1.0	−1.0	−1.0	−.60	−1.0	−1.0	−.26	−.58	—

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[1] Cole's Coefficient of Association (Cole 1949) ranges from −1.0 (complete avoidance) to 1.0 (complete association). Values significant at $P < .05$ (Chi-square) are underlined. N = 528 flocks. In parentheses are numbers of flocks in which each species was seen.

TABLE 4
Associations Between Species in Central and Northern California Flocks Seen in the Months of August through November, 1980–1982[1]

		Species (numbered as to the left)														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Pacific Loon (53)	—														
2	Northern Fulmar (37)	−1.0	—													
3	Pink-footed Shearwater (25)	−1.0	−1.0	—												
4	Buller's Shearwater (25)	−1.0	−.41	.21	—											
5	Sooty Shearwater (98)	−1.0	−.10	.85	.41	—										
6	Brown Pelican (29)	.05	−.49	−.03	−.25	.07	—									
7	Brandt's Cormorant (20)	.08	−1.0	−.03	.01	−.17	.21	—								
8	Surf Scoter (11)	.25	−1.0	−1.0	−1.0	−1.0	.01	.23	—							
9	Phalaropes (103)	−.17	−.12	−.78	−.78	−.67	−.63	−1.0	−1.0	—						
10	Black-legged Kittiwake (11)	.09	.03	−1.0	−1.0	−.49	.01	−1.0	.10	−.02	—					
11	Bonaparte's Gull (34)	.01	.02	−1.0	−.36	−.67	.01	−.20	.01	−.37	.01	—				
12	Heermann's Gulls (22)	.06	−1.0	.04	−.55	.02	.31	.21	.24	−.75	.05	−.27	—			
13	California Gull (86)	.02	−.04	−1.0	−1.0	−.55	.10	.16	.01	−.75	.03	.13	.12	—		
14	Western Gull (86)	−.39	−.14	−.68	−.40	.00	.21	.46	.00	−.56	−.28	.01	.19	.19	—	
15	Common Murre (101)	−.59	−.85	−.57	−.78	−.44	−.26	.26	.00	−.57	−.51	−.68	.02	−.37	−.17	—
16	Cassin's Auklet (42)	.01	−.30	−1.0	.05	−.73	−.55	.01	−1.0	.36	.03	−.62	−1.0	−.40	−.71	−1.0

[1] N = 543 flocks. See footnote to Table 3 for for further explanation.

TABLE 5

ASSOCIATIONS BETWEEN SPECIES IN CENTRAL AND NORTHERN CALIFORNIA FLOCKS SEEN IN THE MONTHS OF DECEMBER THROUGH MARCH, 1980–1983[1]

		Species (numbered as to the left)														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Pacific Loon (11)	—														
2	Western Grebe (19)	.15	—													
3	Northern Fulmar (46)	−1.0	−1.0	—												
4	Short-tailed Shearwater (14)	−1.0	−1.0	.13	—											
5	Brown Pelican (13)	−1.0	.23	−1.0	−1.0	—										
6	Brandt's Cormorant (15)	.06	.24	−1.0	−1.0	.15	—									
7	Surf Scoter (22)	.23	.33	−1.0	−1.0	.04	.16	—								
8	Phalaropes (17)	−1.0	−1.0	.21	.11	−1.0	−1.0	−1.0	—							
9	Black-legged Kittiwake (88)	−.48	−1.0	−.24	.05	−1.0	−1.0	−1.0	−.66	—						
10	Bonaparte's Gull (24)	.05	.03	−1.0	−1.0	−.40	.00	−1.0	.04	.05	—					
11	California Gull (88)	.01	−.70	−.37	−.59	−.11	.00	−1.0	−.66	−.08	.01	—				
12	Western Gull (101)	−.56	−.74	−.68	−.66	.00	.03	−1.0	−.42	−.22	.01	.07	—			
13	Herring Gull (117)	.00	−.77	−.15	−.68	−.67	−.71	−1.0	−.74	−.07	.23	.22	.21	—		
14	Common Murre (87)	−.47	−.38	−.61	−.01	−.55	.05	−.73	−1.0	−.53	−.58	−.33	.06	−.45	—	
15	Rhinoceros Auklet (38)	.02	−1.0	−.41	.07	−1.0	−1.0	−1.0	−.21	.09	−.05	−.89	−.22	.00	.07	—
16	Cassin's Auklet (63)	−.27	−1.0	.01	.02	−1.0	−1.0	−1.0	.01	−.63	−1.0	−.72	−.30	−.72	−.63	.10

[1] N = 508 flocks. See footnote to Table 3 for further explanation.

frequency, and most even distribution among phalaropes. And, winter was the season of greatest numbers and geographic extent of the fulmar. Both species were numerous over the continental slope and the deep waters offshore, and we logged many records of small flocks (5 to 20 birds) containing phalaropes, a gull or two, and a few fulmars, particularly from Monterey Bay to Bodega.

As a group, gulls associated with one another in all habitats and seasons, but did not frequently associate with procellariiforms, phalaropes or alcids. Several species associated with pelicans, cormorants or other members of the nearshore, non-larid fauna. The association between Heermann's Gulls and Brown Pelicans is well known from historical observations and the synchrony of their post-breeding dispersals to California from Mexican nesting colonies has been noted (Briggs et al. 1983). It is thus not surprising to find pelicans and Heermann's Gulls associated in mixed flocks at sea, mirroring their associations on land.

Among the alcids we found a tendency toward significant avoidance of mixed-species flocks in all seasons. Significant, negative coefficients were found between murres and all procellariiforms, most gulls and Cassin's Auklet. Rhinoceros Auklets infrequently participated in mixed flocks (less than 4% of Rhinoceros Auklets in flocks were in the company of other species) and significantly avoided flocks containing California Gulls and Cassin's Auklets. Cassin's Auklets rivaled Leach's Storm-Petrels in number of negative associations but were much more abundant and more inclined to form monospecific flocks of 10 to several hundred birds.

SPATIAL SCALES OF AGGREGATION

The sizes of aggregations characteristically formed by seabirds may give an indication of the scales over which behavioral interactions take place, the dimensions of important patches of habitat, and identity of scale-dependent processes that shape community structure (reviewed by Hunt and Schneider 1987). Scales of aggregation of plankton inhabiting coastal waters and the North Pacific Central Gyre (Sverdrup, Johnson and Fleming 1946) have been studied by Haury (1976) whereas Schneider and Duffy (1985) have attempted to evaluate scale-dependent patchiness among seabirds of the Benguela upwelling area and eastern Bering Sea. However, assessments of seabird patchiness and aggregation are lacking for the eastern North Pacific. We evaluated patchiness in several dominant species for indications of overlap of habitat use within mixed-species flock associates.

The index used for determining degree of aggregation, I′, is sensitive to the magnitude of average bird abundance (simple number of birds) per sampling unit, or bin. That is, for a given species, the higher the average abundance, the higher will be the index of aggregation. Correlations of maximum I′ versus average bird numbers per bin (for 3-km bins) range from $r = 0.63$ to 0.89 for seven species in central California (Pearson's r, $n = 199$ to 517, $P < 0.01$). Between species, however, birds having the same mean abundance per bin may have quite different maximum values of I′. For example, during central California surveys conducted in September 1981, the mean densities of Common Murres and Cassin's Auklets were about the same (4.5 versus 4.8 birds km^{-2}), but maximum values of I′ differed by more than a factor of three ($I' = 441$ for the murre at a bin size of 16 km and $I' = 102$ for the auklet at a bin size of 12 km). According to this measure, then, murres were aggregated into larger groups than the auklet. Acknowledging problems that might be introduced by differences between habitats, we will proceed to compare values of I′ among abundant species.

Considering data collected on cross-shelf aerial transects, values of I′ typically increased to a maximum value at bin sizes of 12 to 50 km, following patterns that appear to be more or less typical for each species and season. Common Murres, Cassin's Auklets, and phalaropes usually showed maximum values of I′ at bin sizes of about 10 to 20 km, while for Western Gulls and Common/Arctic terns, I'_{max} was reached usually at bin sizes of 40+ km (Fig. 23). Schneider and Duffy (1985) term the kind of pattern seen among auklets and murres as "spaced aggregation," while those of the gull and tern are termed, respectively, "extended aggregations" and "uniform patches." In the last case, the indication is that the birds treated all of the transect as one uniform piece of habitat.

Several additional generalities can be drawn from these data. First, aggregation intensity was usually much stronger in the vicinity of colonies than away from them. For gulls, murres, and auklets, I′ values obtained near the Gulf of the Farallones, where large colonies exist, were typically at least an order of magnitude higher than in areas removed by more than 40 km (see for example data for Cassin's Auklet, Fig. 24). This effect was due to sensitivity of the index to average bird abundance per bin, which peaked near colonies. These near-colony aggregations showed maximum values at the same bin sizes as in the other regions, indicating that additional flocks or individuals were joining birds in already occupied habitat, rather than extending aggregations farther into adjacent habitats. Thus, these species were selecting habitat patches of similar scale near and away from colonies. Specific data on

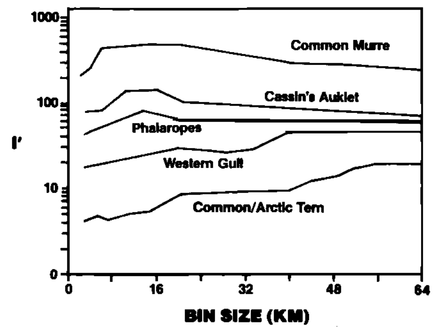

FIGURE 23. Comparison of scale-dependent intensity of aggregation among five seabird species during cross-shelf aerial counts in September, 1981. The bin size corresponding to maximal values of I′ is considered to be the scale of maximum intensity of aggregation.

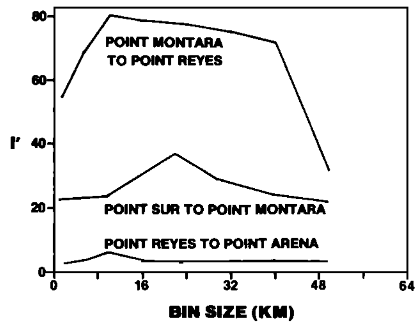

FIGURE 24. Intensity of aggregation among Cassin's Auklets in three areas off central California during June 1982. Large colonies exist near Point Reyes (upper curve); birds in the other areas likely were failed- or non-breeders.

prey patch sizes are not available for the areas and times included in this study. However, recent, preliminary work off central California indicates that Cassin's Auklet and euphausiid patches have similar spatial scales and orientations (narrow bands extending for many km along the outer shelf; Briggs et al. in press). We think that consistency of patch sizes at different locations in the 1980–1982 data indicates that birds were aggregating at scales corresponding to prey patches, which were themselves similar from place to place.

Second, irrespective of seasonal changes in the mean abundance of a given species, there were shifts between seasons in the bin sizes at which maximum aggregation occurs. For Cassin's Auklet, aggregation peaked at 30 km during December and April when large numbers of birds occupied waters seaward of the shelf and slope, but at 16 to 18 km during June and September. Among Western Gulls, aggregations were most intense on scales of 16 to 20 km in September but at 40 to 64+ km in other seasons. This shift from spaced aggregations in late summer to extended aggregation or uniform patches in other seasons probably was related to changes in the patterning of upwelling zone habitat. Alternating series of cool upwellings and warm eddies often appeared as one progressed along the shelf in late summer. Temperature was autocorrelated over shorter distances in late summer than at other times (see below). Habitat patches occupied by gulls may thus have been correspondingly foreshortened, alternating with patches of water relatively unoccupied by gulls.

Data gathered from ships indicates that maximum values of I′ are reached at smaller bin sizes in the cross-shelf direction than along the shelf (Briggs et al. in press, Schneider et al. in press). This parallels the findings of Schneider and Duffy (1985) and is reflected in spatial autocorrelations of temperature, where homogeneity is maintained over longer scales along the shelf than across it.

It is interesting to note that murres, Cassin's Auklets, and phalaropes all aggregated on relatively short cross-shelf scales (8 to about 16 km depending on season), and often appeared on the same transects, but did not frequently associate with each other in mixed-species flocks (Tables 3–5). These species feed on different prey and at different depths, so it may be that the best feeding opportunities for each species are found at slightly different locations. These three species also avoided flocks containing Sooty Shearwaters and Western Gulls. The gull and shearwater exhibited peak clumping (maximum I′) at scales of 16 to 64+ km and 8 to 32 km, respectively. In fact, when they occurred on the same transects, aggregations of the gull and shearwater tended to overlap several patches of murres, auklets, and phalaropes. Gulls are known to prey on auklets at the Farallones colonies and shearwaters are described as being disruptive of mixed-species feeding flocks in Alaska (Hoffman et al. 1981, Ainley and Boekelheide in press).

The offshore habitat occupied by terns and petrels was much more homogeneous over long distances than was the case in neritic waters (see below). Aggregations of these species occurred over correspondingly large scales. Based on limited analyses in seasons of maximum abundance, winter aggregations of kittiwakes, fulmars, and Rhinoceros Auklets were similar in scale to one another but reached peak values at larger scales than those of Cassin's Auklets or murres (i.e., I'_{max} at 24 to 32 km). For the Leach's Storm-Petrel we found that values of I′ rose progressively with increasing bin size. Along with the flock data presented above this indicates that Leach's occur solitarily and treat large areas of offshore habitat as uniform patches, at least to 64 km, the maximum scale resolved by our technique.

We found much overlap in characteristic scales of aggregation among the several gull species that inhabit shelf waters in fall and winter. California Gulls and Herring Gulls aggregated on scales similar to those of the Western Gull, and, as seen earlier, frequently associated in mixed-species flocks. Bonaparte's Gulls, which frequently eat large zooplankton, were unique among larids in forming patches over short scales, similar to those of the phalaropes.

As noted before, we made too few along-shelf aerial transects to support this type of analysis. And, we could not interpolate between our cross-shelf transects (in the along-shelf direction) because the average spacing between transects (19.8 km) was larger than the aggregation scales typical of several important species (e.g., auklets and phalaropes). For these reasons, we cannot as yet resolve the nature of variation in aggregations along the shelf.

SEABIRD HABITATS

Compared to areas north of Point Conception, the topography of the seafloor and, to some extent, the currents and thermal patterns of surface waters off southern California are relatively complex. One finds shallow banks or deep basins both near the mainland and far offshore. Similarly, upwellings lift cool water to the surface both along the far western margin of the Southern California Bight and along the southern California mainland. There is thus low correlation among several environmental variables (depth, temperature, distance from land) of potential importance to seabirds. This is not the case to the north, where depth and temperature are often correlated with distance from shore. Temperature also varies with latitude, and gradients in temperature are highest near the coast and at the shelfbreak. Because of this cross-correlation between environmental variables in central and northern California, we used Principal Components Analysis (PCA) to identify the most important aspects of coincident, or shared, environmental variation (communal variance). We did this both for each monthly data set from central and northern California and for that resulting from earlier studies off southern California. However, because it was sometimes impossible to obtain temperature data corresponding to the places and times of aerial sampling in the south, we emphasize results from the work north of Point Conception.

Evaluation of monthly data sets by PCA indicates that for the area north of Point Conception, three components account for much of the variance in the seven measured or calculated variables (water depth, distance from the mainland and from the shelfbreak, surface water temperature, gradients in temperature, latitude, bottom slope; Briggs and Chu 1986). The first component, generally explaining about 45% of communal variance, can be interpreted as the covariation between water depth and distance from the mainland. Water temperature (at the center of each 5′ by 5′ grid cell) varied positively with this component during most summer months (i.e., warmest waters occurred in the deepest waters farthest from shore; Fig. 25). Component II explained 19 to 38% of communal variance and generally reflected the inverse relationship between temperature and latitude. Gradients in temperature varied as the inverse of latitude in the winters of 1981 and 1982. Accounting for about 17 to 24% of variance and mostly comprising the unique variance in temperature gradients was Component III.

As explained by Briggs and Chu (1986), environmental variables from southern California studies grouped on only two significant axes or components. The first, comprising the inverse variation (seasonal) of temperature gradients on water depth and distance from the nearest land, explained about 39% of variance. Component II, which comprised mainly the inverse variation of temperature and longitude/latitude, accounted for about 24% of communal variance. This component reflected the presence of cool water at the northern and western borders of the southern California study area.

Analyses of individual surveys that represent the patterns typical of three stages of the annual cycle in central and northern California will be discussed in detail. In each case, after identifying the most important components within the environmental data, a separate analysis was made using the matrix of densities of all birds having mean densities exceeding 1 bird km^{-2}. Results of these analyses, showing bird density projected onto the three major environmental axes, appear in Figures 26–28. In these figures, mean scores of sites occupied by a bird along a PC gradient significantly differed from the expected when associated confidence intervals did not intersect the confidence interval of all sampled cells (depicted in the central panel of Figs. 26–28).

In the August 1981 analysis (Fig. 26), several of the most abundant species (Common Murre, Western Gull, and phalaropes, both species of which were undoubtedly present) occupied sites having high temperature gradients (confidence

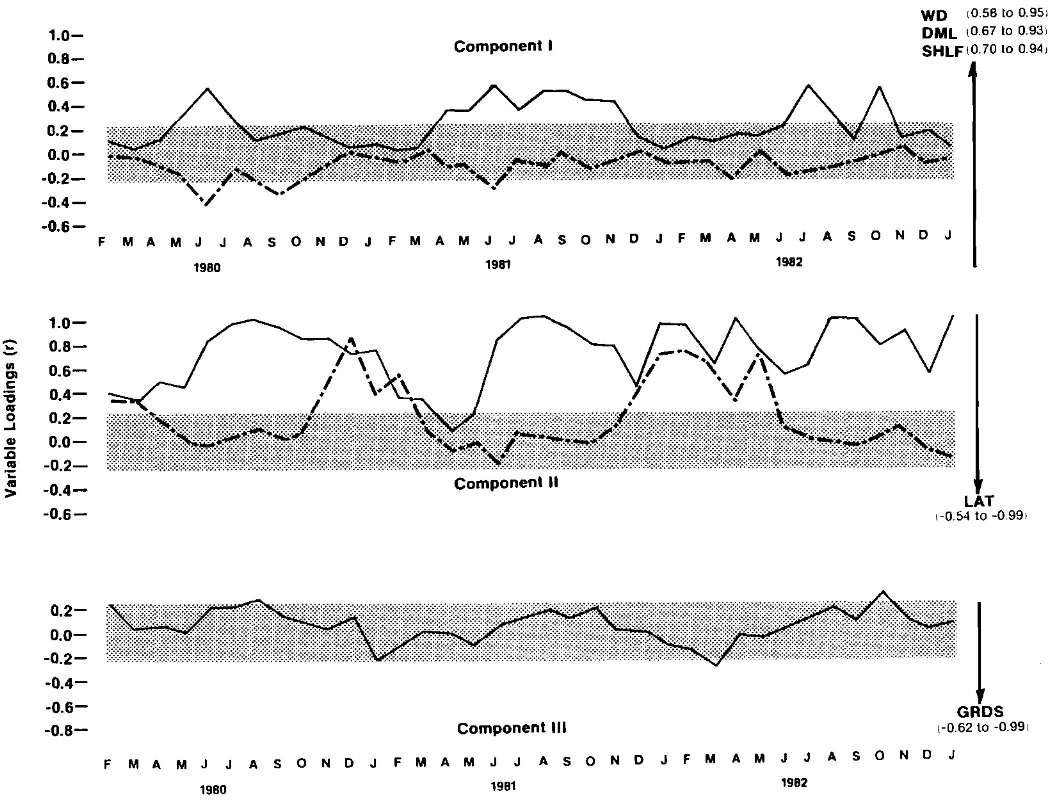

FIGURE 25. Seasonal loadings of water temperature (solid curve) and temperature gradients (broken) on the first three principal components for central and northern California environmental data. The shaded area indicates loadings that do not differ significantly from chance ($P > 0.001$). Abbreviations for variables: WD, water depth; DML, distance to the nearest point on the mainland; SHLF, distance to the nearest point on the continental shelf break; LAT, latitude; GRDS, gradients in surface temperature.

intervals on mean component scores lay outside the c.i. for all sampled cells). Buller's Shearwater, Sabine's Gull, Common/Arctic terns, and Leach's Storm-Petrels occupied sites well offshore (mean component scores exceeding 1.2 on Component I) but did not select strongly on other axes. Tufted Puffins occupied cool-water, high-latitude sites (PCII) having low temperature gradients (PCIII), while Western/Clark's Grebes occurred in inshore, shallow habitats (Component I). Mean scores (the small central spheres) for Sooty and Pink-footed Shearwaters, California Gulls, Black-footed Albatross, and Cassin's Auklets were displaced somewhat from the origin on one or more axes, but confidence intervals were large and intercepted those of the sample means.

In January 1982 (Fig. 27), there was less specificity among the birds for habitats with high or low thermal gradients (PCIII) and more separation along components I and II. In this analysis sites occupied by several species were not significantly different from the sample means: California, Bonaparte's and Herring Gulls and Black-legged Kittiwakes. The kittiwake in particular occupied a broad range of sites along the depth-distance gradient (PCI). Density of Rhinoceros and Cassin's auklets varied with latitude/temperature, while Western/Clark's Grebes, murres, and Surf/White-winged Scoters (not pictured) grouped closely together, sharing inshore distributions and weak positive loadings on component III.

Phalaropes (presumably almost all Red) and fulmars had similar patterns of regional occurrence, and they frequently mixed in flocks. This January analysis shows them to be quite distinct in selectivity for offshore waters (PCI), but similar in affinity for strong temperature gradients (PCIII). Analyses of other winter data show the two species to be more similar in inshore-offshore preferences (component I) than is seen here. This discrepancy resulted mainly from seasonal

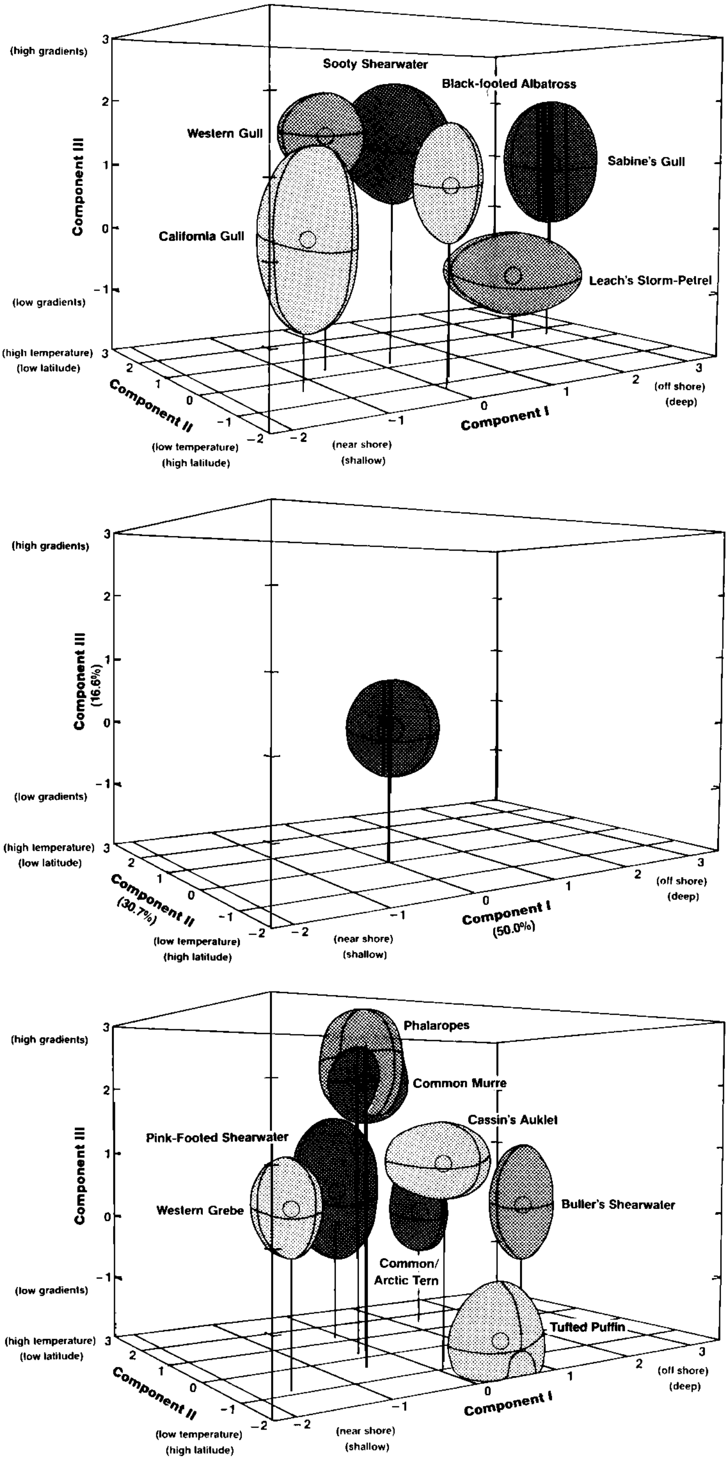

FIGURE 26. Comparison of distributions of seabirds along the first three principal components for central and northern California, August 1981. Mean scores and 95% confidence intervals for each species are represented respectively by central spheres and ellipses in three dimensions. The center panel depicts the mean score and confidence interval for all sampled cells while the top and bottom panels show positions of 14 relatively abundant species, grouped for clarity of presentation.

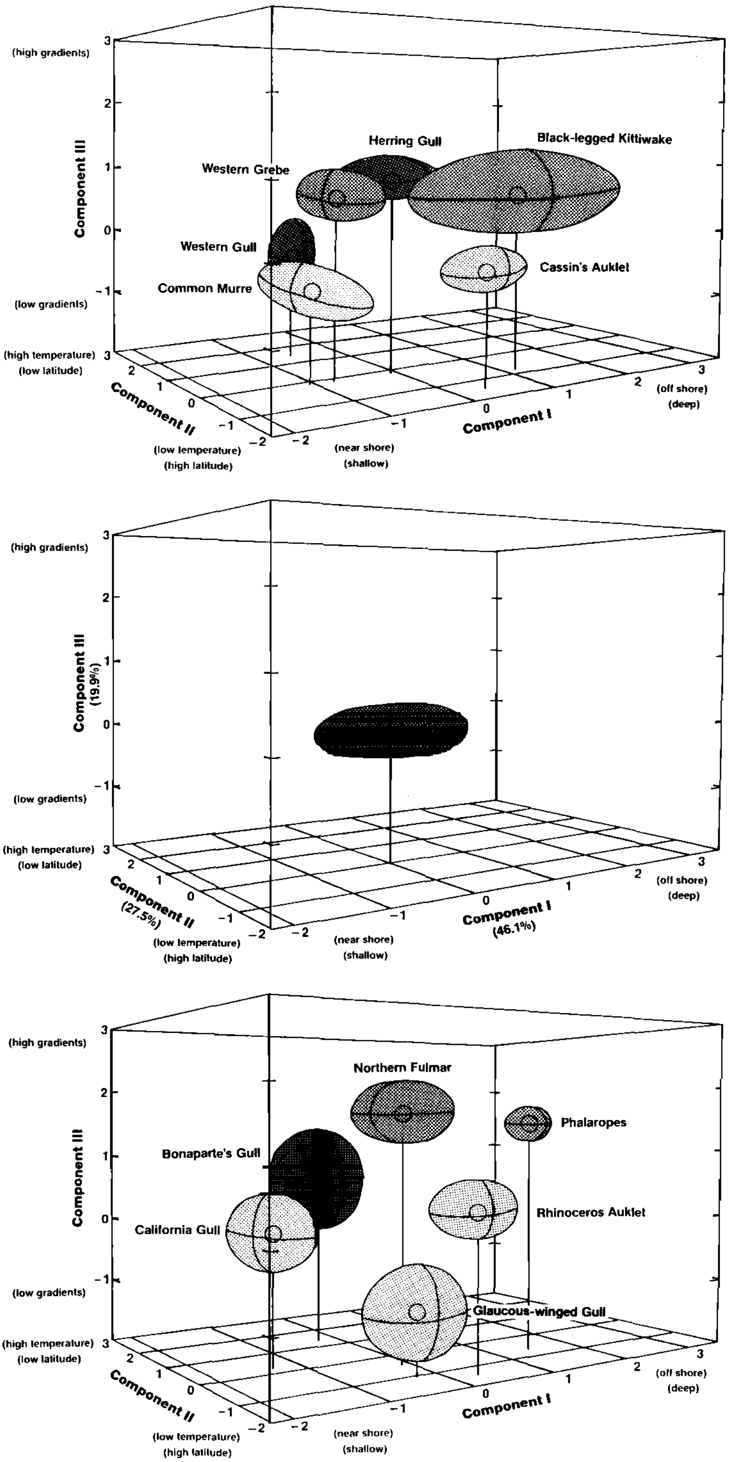

FIGURE 27. Comparison of distributions of 12 relatively abundant seabird species along the first three principal components for central and northern California, January, 1982. (For further explanation, see Fig. 26.)

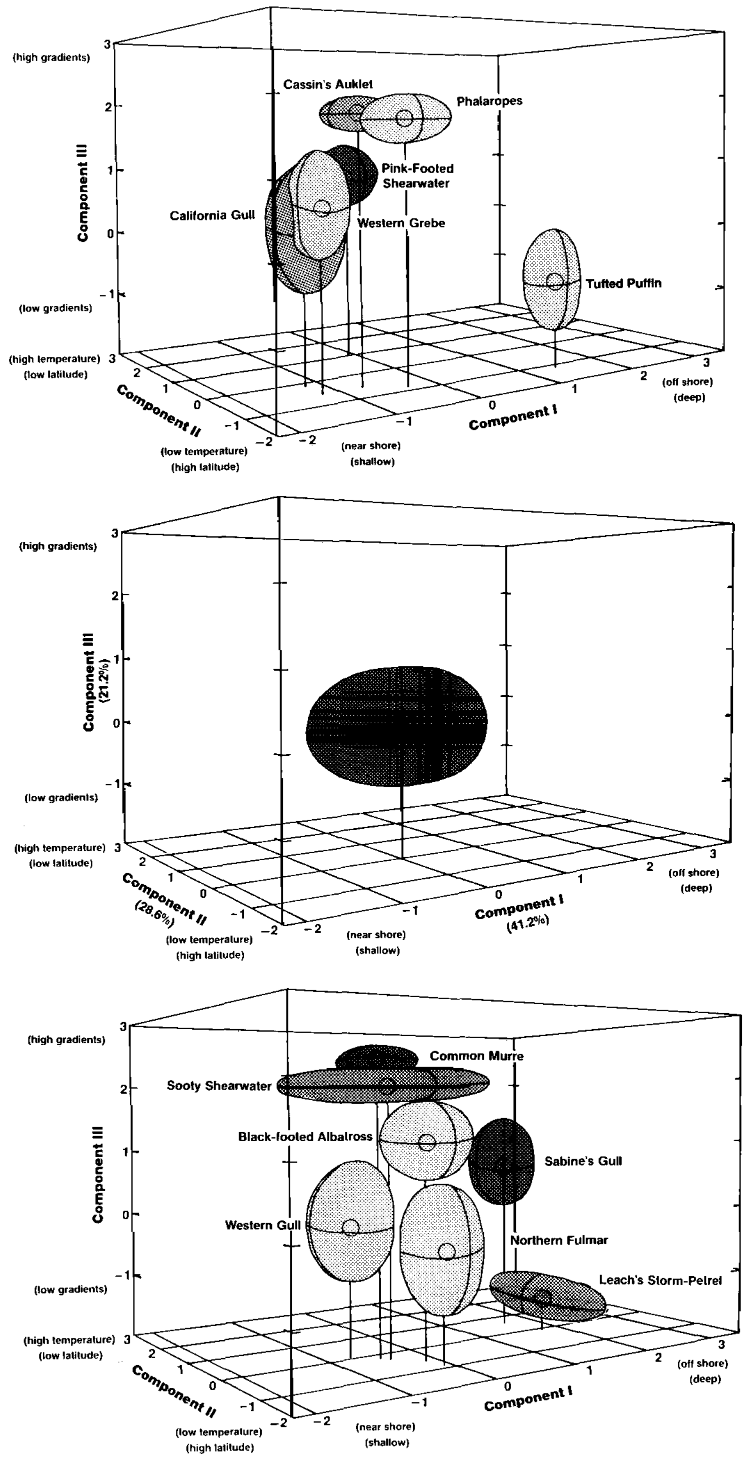

FIGURE 28. Comparison of distributions of 13 relatively abundant seabird species along the first three principal components for central and northern California, June, 1982. (For further explanation, see Fig. 26.)

aggregations of the two species at different latitudes. Where they did co-occur regionally, they shared habitat preferences and joined each other in mixed-species flocks.

In June 1982 (Fig. 28), a group of species shared affinity for waters of high temperature gradients, close to the coast. Of these, we previously showed that murres, Cassin's Auklets, phalaropes (probably mostly Reds), and Sooty Shearwaters each avoided flocks containing the others. In fact we typically saw closely adjacent, monospecific flocks. Whether these flocks interacted over time is a matter for further study. Distinct from these species on PC space, Leach's Storm-Petrels, Sabine's Gulls, and Tufted Puffins selected areas far offshore, while Western/Clark's Grebes did the opposite. Characteristics of sites occupied by California and Western gulls, Black-footed Albatross and Northern Fulmars did not differ from the sample means, indicating lack of specificity for habitats defined by these axes.

SCALES OF VARIATION IN SURFACE TEMPERATURE

If bird distribution and abundance were simple functions of temporally invariant habitat features like water depth or bottom topography, we would expect to find considerable stability in bird concentrations over time. Instead, almost all studies of bird distribution at sea show a high degree of temporal variability. Thus, there is probably much to be learned by assessing patterning in temporally varying habitat features such as temperature.

In this section we present information about the spatial variability in surface temperature through time. Among variables included in our PCA analysis only surface temperature and its derivative, temperature gradients, varied both in space and time (and have strong statistical relationships to bird abundance). A number of other environmental parameters, including topography of the thermocline, salinity and ocean color and transparency also share this temporal variability. Among these, ocean color was included in our measurements, but only sporadically, and will be the subject of a future analysis. Surface temperatures measured from the survey aircraft were used in the PCA analyses above and were collected simultaneously with bird data. However, to examine scaling phenomena our airborne SST data have the disadvantage of lacking resolution along the shelf at all scales less than the average separation between our east-west transect lines (about 20 km). We circumvented this problem by analyzing temperature patterns in coincident, digital satellite imagery. Correlations between SST's measured from satellites, airplanes and ships have been investigated several times: off Cape Mendocino Breaker et al. (1985) found correlations of r = 0.85 in SST's measured from satellite and airborne radiometers and 0.79 and 0.71, respectively, for SST's measured from satellite and ship (engine intake temperatures measured at 4 m depth) and aircraft and ship. For 150 grid cells visited during our September 1981 survey, we found a correlation of r = 0.89 between airborne and ship temperatures and 0.93 between satellite and airborne temperatures. Satellite observations covered all areas of our central and northern California study area repeatedly during each survey day, imaging the sea surface wherever the atmosphere was cloud-free.

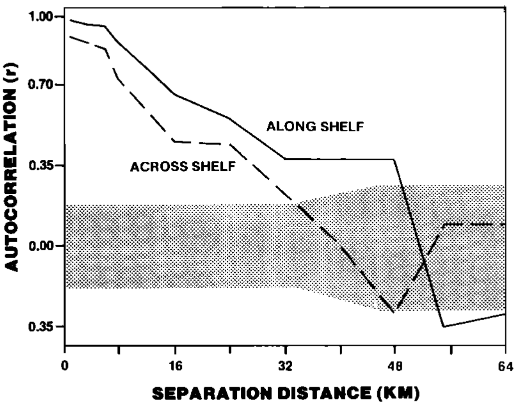

FIGURE 29. Autocorrelation of surface temperature at separations of 1 to 64 km; September, 1981. Values outside the shaded region indicate highly significant ($P < 0.001$) autocorrelation.

We selected satellite images for June, September, and December 1981 and March 1982 to examine variability in surface temperature in the area to 200 km seaward of Point Arena to Point Sur. After removing the mean latitude-longitude trends from each data set, residuals were plotted and prepared as a data matrix for autocorrelation analysis. In the September 1981 temperature data, the *residuals* appear as a series of relatively warm and cool patches alternating along the shelf and to seaward from the shore; autocorrelations are plotted as a function of separation distance (in km) in Figure 29. Temperatures were highly correlated at distances of 1 to 30 km in the cross-shelf direction and from 1 to 48 km along the shelf. At greater separations, temperatures either were uncorrelated or were negatively correlated. Thus, the "event scale," or predominant patch size of thermally homogeneous habitats in this image, was about 30 to 40 km. Thermal data for June 1981 showed an "event scale" of 40 to 45 km in both directions. December and March temperature data showed high correlation in both directions to at least 64 km, a sign of thermal homogeneity. Horizontally isothermal conditions in the surface layer probably derived from mixing due to storms and lack of upwelling (which otherwise would lend considerable cross-shelf structuring to surface temperature).

In an ongoing study of satellite image archives L. C. Breaker and J. C. Mueller (pers. comm.), found that thermal and color features having length scales of 30 to 60 km typically persist for many days (up to several weeks). Smaller features rotate, advect, or evolve into unrecognizable forms within shorter periods (for features of 5 to 15 km, the durations may be on the order of hours to a few days). Large features such as shelf-edge eddies and associated current "jets" (that are traced because they entrain cold water upwelled over the shelf) may persist for several weeks and frequently recur at known sites such as Point Reyes and Point Sur. Thus, with larger features at least, seabirds are exposed to patches of habitat that offer a degree of persistence and stability, and that recur seasonally at given locations.

DISCUSSION

These are the first data collected in such a way that the abundance, distribution, and selected habitat affinities of seabirds off California can be assessed synoptically. As a result of regular monthly sampling, quantitative aspects of seasonality have emerged, and we have described certain attributes of the fauna as a whole: species diversity, composition, biomass density, and relationships of these measures to certain physical habitat characteristics. We have also determined which species occur together over different spatial scales, how certain species respond to habitat gradients at different scales, and how the apparent scales of seabird aggregations compare to patch size of ocean surface thermal habitat. When this new information is added to information on seabird breeding biology at the Farallones and several of the Channel Islands (Ainley and Lewis 1974, Hunt et al. 1981, Ainley et al. ms), the result is a compendium that makes the seabird fauna of the California coast perhaps the best known in the world.

VARIATION IN BIOMASS AND ABUNDANCE

Concentrations of seabirds over shelf waters off California were quite dense, comparable to those reported for other upwelling regions in eastern boundary currents, and those seen in high latitudes. In offshore (California Current) waters, densities and biomass were similar to the much lower values reported for western boundary currents and central ocean basins. Off California we found densities averaging about 6 birds km^{-2} in water deeper than 2000 m and more than 110 birds km^{-2} over the shelf. Densities reported by Wiens and Scott (1975) for a small number of numerically dominant species off Oregon are in this range (in fact, the two states share much the same fauna), and reports of bird densities off Washington and British Columbia are also similar (Wahl et al. 1981, Vermeer and Rankin 1984). For the Gulf of Alaska, Gould et al. (1982) reported aggregate densities ranging from 3.5 to 13.7 birds km^{-2} offshore and 44 to 158 birds km^{-2} over the shelf, whereas in the Bering Sea during the nonwinter months, densities were 6 to 24 birds km^{-2} in the oceanic zone and 9 to 240 birds km^{-2} over the shelfbreak. In all these studies much local variation is subsumed within the grand averages; for some areas of 10s to 100s of km^2 density may be on the order of 10^3 to 10^4 birds km^{-2}.

Fewer estimates have been reported for polar or subtropical regions. Based on ship sampling and estimates of breeding numbers, Ainley et al. (1983) calculated that density of adult birds peaked at about 16 birds km^{-2} throughout the Ross Sea, Antarctica, whereas in the Atlantic Haney (1986) computed densities of 0.6 to 10.9 birds km^{-2} in Gulf Stream cold-core eddies and 7 to 15 times less in oligotrophic shelf and Gulf Stream waters unaffected by the eddies. In oceanic areas of the South Pacific, Ainley and Boekelheide (1983) found densities ranging from 3.4 to 9.5 birds km^{-2}.

Estimates of biomass density or seabird standing stock have been made for a few of these same regions, albeit with a variety of approaches. Biomass varied regionally off California from 2.2 kg km^{-2} to 67.6 kg km^{-2}; off central California it ranged as high as 283 kg km^{-2} and as low as 0.2 kg km^{-2} in shelf and offshore waters, respectively. Matching monthly estimates from different years in the south and north, we arrive at maximum "instantaneous" populations of 5.5 to 6.0 million birds in late fall or early winter, representing a biomass of about 4.8 million kg. Turnover rates were not determined for migrants so total numbers of birds passing through the area are not known. For 43,000 km^2 of shelf waters off British Columbia (one-sixth of the area upon which we report), Vermeer and Rankin (1984) estimated a peak of 6.4 million birds, mainly shearwaters and alcids. Schneider and Hunt (1982) estimated numbers ranging from a few million to 20 to 40 million birds in shelf/slope waters of the Bering Sea (10^6 km^2), most of these being Short-tailed Shearwaters visiting during summer. Bird numbers in the Benguela Current system off Africa are reported to be similar to those we found off California (Abrams and Griffiths 1981, Furness and Cooper 1982, Schneider and Duffy 1985), while numbers are lower in the upwelling region off Senegal (Brown 1979).

Bird biomass in the Peru Current has not been estimated from direct surveys at sea. The best estimates for the region are based on guano production figures, which do not include the fraction of total biomass attributable to species nesting outside the region (Duffy and Sigfried 1987). Idyll (1973) and Duffy (1980) have shown that collapse of the Peruvian anchovetta (*Engraulis ringens*) stock due to recurrent ENSO episodes and sustained overfishing led to a five-fold decline in the abundance of the Guanay Cormorant (*Phalacrocorax bougainvillii*) from the former level of around 20 million birds. At present, this and the Peruvian Booby (*Sula variegata*) remain the most numerous of birds within 20 or so km of the coast near Lima, followed by Sooty Shearwaters. It is reasonable to assume that seabird biomass density in the Peru Current is at least as high as that seen off California, perhaps a good deal higher. Interestingly, the bulk of seabirds off California are seasonal visitors, whereas off Peru breeding species make up a much larger proportion of the total fauna (at least historically). The pelagic wetfish fauna of the two current systems are very similar in structure and species composition (R. H. Parrish, pers. comm.). In the interest of understanding why only one region supports a large component of breeding species, it would, therefore, be very instructive to make a quantitative comparison of the community structure and feeding preferences of the two bird faunas.

Ainley et al. (1983) calculated that approximately 12 million birds inhabiting the Ross Sea in late summer represented a biomass of about 44 kg km^{-2}. In contrast to these high figures for cold water and upwelling areas, Haney (1986) estimated that in cold-core eddies of the Gulf Stream, bird biomass ranged from 0.1 to 7.9 kg km^{-2}, while in less fertile adjoining areas, biomass was 7 to 15 times lower. In the oceanic South Pacific, biomass averages 0.9 to 10.2 kg km^{-2} (Ainley and Boekelheide 1983).

How do these figures compare with those from terrestrial systems? Estimates of bird biomass have ranged from 2 to 78 kg km^{-2} for a variety of terrestrial ecosystems (Szaro and Balda 1979), roughly the same range seen in seabird communities studied to date. Because metabolic rate varies inversely with bird size, smaller, terrestrial birds have a higher mass-specific rate of energy consumption, placing seabirds at the lower end of estimates of energy flow per unit area. Model estimation of seabird trophic requirements remains a controversial and active area of research. At one end of the spectrum of estimates, Furness and Cooper (1982) note that several models of energy use agree that seabirds may consume 17 to 29% of the small, schooling fish produced annually in four different temperate (cool-water) areas (Schaefer 1970, Wiens and Scott 1975, Furness 1978, Furness and Cooper 1982). At the other end of the spectrum, Schneider and Hunt (1982) estimated that seabirds took only 0.03 to 0.05% of summer primary production in the Bering Sea (3 to 5% of tertiary production if we assume 10% efficiency in transfer of energy between trophic levels). Similarly, Briggs and Chu (1987) calculated that seabirds consumed about 500 to 600 metric tons of fish, squid, and plankton per day off California, representing 4 to 7% of estimated tertiary production. Sport and commercial fisheries in the same area represented landings 200% to 400% higher than the figures for seabird predation in general (albeit with several substitutions of age classes and species exploited by fisheries).

California seabirds probably consume no more than 10% of annual production of small schooling fish (Briggs and Chu 1987). However, several seabird populations nesting in California are well below historical sizes, whereas others may be somewhat larger (Ainley and Lewis 1974, Hunt et al. 1981). For example, Common Murres are probably an order of magnitude less abundant now at the Farallones than in the past century. Given the large proportion of total nesting birds represented by the murres, impact on California Current fish stocks (by nesting seabirds at least) may have been greater in the past than at present.

As a group, seabirds often have figured in conceptual debates about the role of food limitation of populations. The upper limits of bird biomass density consistently appear to be 50–100 kg km^{-2} in the most densely inhabited upwelling and polar regions, worldwide. This suggests that a practical limit to sustainable bird concentrations is reached at about 10% of tertiary production (perhaps representing 30% of biomass available at the level of schooling fish and squid; e.g., Wiens and Scott 1975, Furness 1978, Briggs and Chu 1987). Beyond this, Brown (1980) has argued that if mixed uniformly, background concentrations of bird prey in the ocean typically would be insufficient for the needs of these metabolically active predators; seabirds are thus selected to recognize and exploit physical and biological processes that concentrate prey above ambient levels. Brown (1980), Schneider and Hunt (1982), Ainley and Jacobs (1981), Haney (1985), and others have described situations in which birds concentrate at sites where physical processes truncate the usual diffusion of oceanic production (by trapping of plankton). From the perspective of the California Current, total food biomass probably does limit the size of the fauna: It is known that nesting species exhibit interannual variations in numbers of breeding attempts and various measures of reproductive output related in general to food abundance and specifically to food availability (Hunt and Butler 1980, Hunt et al. 1981, Anderson et al. 1983, Anderson and Gress 1984, Hodder and Graybill 1985, Ainley et al. ms), and some migrant and seasonal resident populations change dramatically in years of low prey abundance (Ainley 1976; this study). In certain, well-documented cases, many of the links between food abundance, predation rates, feeding of the young, and overall reproductive success of California seabirds are known. And, even for feeding generalists like Western Gulls, reproductive success and breeding numbers track the yearly and seasonal changes in prey abundance (e.g., Hunt and Butler 1980, Ainley and Boekelheide in press). These are exclusively colony data, however, and the details of foraging behavior at sea during times of food abundance and shortage are poorly known.

Interestingly, in early to mid-summer, when energy requirements of nesting species are maximal (due to provisioning of the young), waters off California harbor the largest numbers of shearwaters (10^5 to 10^6 birds)—the species described by Hoffman et al. (1981) as the primary "suppressors" of mixed-species feeding flocks in Alaska. Although there is known to be broad overlap in diets between shearwaters and several of the breeding species, our data show that flocks containing many shearwaters seldom contained many gulls, murres or auklets. It would be informative to observe bird behavior in flocks of breeders in the presence and absence of shearwaters. This might increase our understanding of whether the presence of shearwaters in years of food shortage poses additional problems to species attempting to raise young at nearby colonies.

COMMUNITY COMPOSITION AND DIVERSITY

The California seabird fauna is dominated in numbers and biomass by species that reach greatest abundance in cool waters of the upwelling zone. Many of these nest at high latitudes. Further, in warm waters seaward of the upwelling zone and in the eastern half of the Southern California Bight (east of the main influence of the Point Conception upwelling system and cool California Current), bird numbers are greatest in winter when visitors from arctic and subarctic regions predominate.

The fauna is quite similar in composition to that off Oregon, Washington, and British Columbia (Wahl 1975, Wiens and Scott 1975, Sanger 1973, Vermeer and Rankin 1984). Ainley (1976) pointed out the gradual decline in abundance of subtropical species as one passes northward along the Pacific Coast. At the latitude of Washington, a number of species common in warm waters off California are relatively rare (e.g., Brown Pelicans, Black-vented Shearwaters, Heermann's Gulls, Elegant Terns, Ashy Storm-Petrels, and Xantus' Murrelets). Several more species characteristic of cool waters in central California do not reach as far as Alaska (Western/Clark's Grebe, Western Gull, California Gull).

For the Common Murre, Cassin's Auklet, Sooty Shearwater, and the two phalaropes, abundance peaks where water clarity is relatively low. Ainley (1977) noted the predominance of diving species (in this case, alcids) in regions where upwelling and other processes maintain high standing stocks of phytoplankton, and thus relatively turbid waters. Sooty Shearwaters also obtain some prey by underwater pursuit (Brown et al. 1978), although surface-seizing certainly is the method of prey capture emphasized off California. Additional diving species are numerous: Pacific Loons, Western/Clark's Grebes, Brandt's Cormorants, scoters, and Rhinoceros Auklets. Gulls, which obtain most prey at sea by seizing organisms at the surface (Ashmole 1971, Ainley 1977), also reach high abundance in turbid waters of the upwelling zone. Only the phalaropes among the extremely abundant species feed exclusively at the surface and these birds occur primarily at the seaward edges of upwellings (Briggs et al. 1984).

Leach's Storm-Petrel is the only species reaching anything approaching high abundance in the clear, blue waters offshore, a habitat type exploited by this species throughout the Pacific Basin (Gould 1971, Crossin 1974, Ainley 1977).

At a finer scale avifaunal composition in shelf waters of central and northern California is somewhat distinct from that in southern California. In fact, the southern California fauna is similar to the offshore fauna of central and northern California. The disparity between shelf faunas is due largely to differences in abundance of birds that concentrate in the coastal upwelling zone (Common Murres, Cassin's Auklets, Sooty Shearwaters) versus those inhabiting thermally stratified, translucent waters of the California Current (especially storm-petrels). In essence, there seems to be a fauna of the coastal upwelling zone that disperses offshore into the California Current during winter, versus a fauna found everywhere else. Among the latter are included many gulls, storm-petrels, pelicans, cormorants, and migrant terns.

A similar disparity exists within the Southern California Bight. A changeover from cool-temperate to warm temperate and subtropical species occurs in the vicinity of Point Conception (Hubbs 1963, Ainley 1976). This change corresponds to diminution in the influence of sub-Arctic waters carried in the California Current (Bernal and McGowan 1981). As traced by the subsurface 32.4‰ isohaline, the tongue of sub-Arctic water penetrates about as far south as the latitude of San Diego (mean position), but only at distances of 200 to 300 km from shore (Chelton 1980). Warmer, saltier water of the Southern California Countercurrent lies closer to the coast. Our general impression from winter data is that high latitude breeders such as kittiwakes and fulmars mostly remain in the waters of the California Current, moving in large numbers eastward, toward the southern California coast, only when the warmer countercurrent is less well developed, or storminess thoroughly mixes the upper ocean (especially winter 1976).

Species diversity is much higher over the shelf and slope off California than in oceanic regions of the South Pacific, where Ainley and Boekelheide (1983) reported values of H′ from 0.54 to 0.88. Compared to species diversity of terrestrial bird faunas, the fauna of the California continental shelf is similar to that found in physiographically diverse forests (Noon et al. 1980), whereas oceanic faunas have low species numbers and diversity, comparable to those seen in grassland (Willson 1974, Szaro and Balda 1979). Almost certainly this difference in species diversity between ocean habitats is related to greater horizontal and vertical variability of shelf habitats. Particularly important are topographic (seabed) influences on currents, shallow thermocline structures (within diving range from the surface), and access to the bottom itself. Indeed, we found species diversity to be much higher where habitat heterogeneity was highest: over the shelf and slope.

SPECIES ASSOCIATIONS

Association between species and between a species and a type of habitat is a function of the scale at which a pattern is analyzed; i.e., species sharing similar patterns of seasonal occurrence over large regions (10^4 km^2) may or may not associate over smaller spatial scales. Obviously, it is among birds that co-occur at all scales that we should look for interactions that might shape communities in terms of mutualism, interference, competition, predation, parasitism, etc. Along these lines we found several groups wherein the species co-varied in density through space and time, generally occupied similar positions relative to the simplified gradients in PC space, and frequently associated in flocks. The most prominent of these were: (1) a nearshore fauna including Pacific Loons, Western/Clark's Grebes and Surf/White-winged Scoters in winter together with Brown Pelicans and Brandt's Cormorants (and other cormorant species) at other times of the year; (2) Common Murres and Brandt's Cormorants, the most numerous piscivores among the nesting species; to which also might be added Western Gulls, which frequently formed mixed-species flocks with the cormorants and which are neither avoided nor actively attracted to murres; (3) the four species of shearwaters and Northern Fulmar, which associated with each other but appeared to be avoided by almost all other birds; (4) a gull fauna that intermingled freely at sea but was avoided by alcids, several of the inshore species, and the phalaropes [Gulls frequently associated with pelicans and cormorants; this was especially true of Heermann's Gulls. This group does not include the kittiwake, probably because of limited overlap between offshore range of the kittiwake and the neritic ranges of most other species.]; (5) (Red) phalaropes and Northern Fulmar, species that co-occurred spatially and associated frequently in flocks over the outer shelf during winter. As a group, the alcids avoided flocks containing gulls, shearwaters and all the inshore species. Leach's Storm-Petrel associated consistently with no other species and was quite distinct in regional distribution and occurrence in PC space.

Our flock data corroborate some of the finding of Hoffman et al. (1981), Porter and Sealy (1981) and Grover and Olla (1983). These authors show that one or more seabird species such as kittiwakes and murres act to locate concentrations of fish, squid or plankton. These are joined by diving species, gulls and shearwaters that appear to recognize which individuals of the 'nuclear' or 'catalyst' species have discovered aggregations of prey. The behavior of the 'joiners' may serve to further concentrate the prey (e.g., murres, auklets and puffins promoting tight schooling behavior in fish by approaching from below or the sides of a school) or, if joiners are numerous (especially shearwaters), may disrupt cohesive schooling behaviors of the prey, contributing to termination of feeding opportunities for all but the deepest divers.

Off California the most numerous catalysts are murres, Brandt's Cormorants, Western Gulls, kittiwakes and Brown Pelicans; porpoises, sea lions and large predatory fish also frequently serve to concentrate seabird food fishes near the surface. Bird species that might be classified as 'joiners' include all above-mentioned catalysts, as well as other cormorants, jaegers, Rhinoceros Auklets and shearwaters. As is seen elsewhere, the primary suppressors are the shearwaters, whose aggressiveness and splashing, shallow dives were described by Hoffman et al. (1981). The plunging behavior of feeding pelicans is of the sort reported to disrupt dense schools of fish (Hoffman et al. 1981), so the importance of pelicans as catalysts probably lies in the fact that fish must already be concentrated and visible to pelicans before feeding begins for these large and visible birds.

Because they do not penetrate below about one meter when feeding, gulls probably do not disrupt concentrated schools of prey like shearwaters do, but they certainly steal the foods brought to the surface by other species. This aggressiveness may be at the root of the many significant negative flock association indices between gulls and other species (Tables 3–5).

The basis for co-occurrence among the nearshore species may be shared food (e.g., loons, grebes, gulls, and cormorants feeding on fish schools in shallow waters) but in other cases is probably simple partitioning of shared habitat according to food specialization (e.g., cormorants feeding on fish while nearby scoters take benthic invertebrates).

Among congeners that might potentially compete for foods we noted much mixed-species flocking among shearwaters and fulmars and much overlap among the two phalaropes (within ship counts where species could be distinguished). The shearwater species are sufficiently distinct in geographic/temporal abundance that competition for food may not be important: Buller's Shearwaters concentrate over the continental slope in central and northern California in late summer; the Sooty is most numerous over the shelf in late spring; the Pink-footed reaches greatest abundance in the south in late summer. Shearwater diets and foraging techniques may also be somewhat dissimilar (Baltz and Morejohn 1977, Briggs et al. 1981, Chu 1984).

In contrast, gulls, especially the larger species, are aggressive towards each other when they occur in interspecific flocks (Briggs 1977). We saw Western and Glaucous-winged gulls (the largest-bodied and socially dominant species) inhabiting seal rookeries in winter (where competition for defensible food sources is intense), while Herring and California gulls mainly frequented refuse dumps, estuaries and shelf waters. Kittiwakes, Bonaparte's Gulls, Sabine's Gulls, and Heermann's Gulls do not compete with the larger gulls on seal rookeries and specialize instead in fishing nearshore (Bonaparte's), far offshore (Kittiwake, Sabine's), or with pelicans (Heermann's).

Large, mixed-species flocks of storm-petrels are quite exceptional (notwithstanding the repeated occurrence of these flocks in Monterey Bay; Stallcup 1976). Mostly, these birds occur in different habitats and reach peak abundance at different times.

SEABIRD HABITATS AND HABITAT CHOICE

Several studies of the last decade have quantified habitat characteristics of birds at sea. As in terrestrial studies, variations in bird occurrence and density "fit" best to environmental conditions when evaluated over large scales. The finer the scale, the less evidence there is for close tracking of habitat characteristics: i.e., birds appear not to "fine-tune" their preferences to local habitat conditions (Rotenberry and Wiens 1980).

Unfortunately, we cannot ignore the problem of scale, or we are met with one or the other of two pitfalls noted by Wiens (1985): ignorance of mechanisms whereby individuals choose among habitats and thus produce discernable patterns at large scale; or, ignorance of environmental events outside the scope of a study but that nevertheless affect the results. Wiens (1985) advocates approaching studies of habitat selection through a hierarchy of scales.

For seabirds, virtually all the detail and process of ocean habitat choice remains to be discovered. Thus, we have chosen to use broad-scale studies to allow the birds themselves to indicate responses to habitat variation. We can then proceed toward studies of habitat selection, focusing on times, areas, and conditions where such choices produce readily discernible patterns.

A growing body of evidence now shows that seabirds are distributed in ways implying the importance of subdivisions of the ocean environment. Murphy (1936) and Ashmole (1971) documented affinity of some seabirds for specific current systems, gyres, and coastal regions. Later workers have explored relations of bird numbers to surface thermal and salinity conditions (e.g., Ainley 1976, Pocklington 1979, Ainley and Boekelheide 1983), nutrients, chlorophyll, and plankton stocks (Ainley 1977, Bradstreet 1979, Brown 1980, Ainley and Jacobs 1981, Briggs et al. 1984). For our studies off California we examined habitat primarily on the basis of various distance and depth functions and surface temperature. Three important axes of shared variation emerged from principal components analyses: PCI was a distance-depth gradient often correlated with temperature; PCII (which, of the three main components, included coarse-scale environmental variation; i.e., that occurring over of hundreds of km) reflected the latitudinal variation in temperature (and surely also included general trends in chemical properties in the California Current); PCIII comprised mainly the variation in thermal gradients. We did not directly measure salinity, but ignored this variable for two reasons: First, surface thermal conditions vary much more widely than does salinity (about 14°C versus about 2‰); birds thus may select along a broader thermal gradient. Second, temperature is the most important factor driving surface density variations (reviewed in Hickey 1979, Huyer 1983). Since surface circulation, and thus potential convergence/divergence mechanisms affecting surface concentrations of seabird prey, depends mostly on winds and density gradients, the importance of temperature probably overshadows that of salinity to California seabirds.

We recognized four main groupings of species in PC space. Density within the group including Common Murres, Cassin's Auklets, Western Gulls, and Sooty Shearwaters varied inversely with Component I (depth, distance from shore, and often temperature), and usually varied positively with gradients in temperature (Component III). The group including Rhinoceros Auklets, Black-legged Kittiwakes, and sometimes Northern Fulmars and Black-footed Albatross loaded strongly on the latitude-temperature component (II) and usually on Component III as well. Leach's Storm-Petrel, phalaropes, and in some cases Common/Arctic terns and Buller's Shearwaters varied in density as distance from shore and depth increased (Component I). Finally, density of Pink-footed Shearwaters, sometimes pelicans, and sometimes California Gulls varied as the inverse of Component II, indicating affinity for warmer, southern waters. The data presented above are representative of recurrent patterns; bird occupancy of these PC gradients was conservative through time and was usually similar between years.

In California, upwelling fronts (represented in PC space by short distances to the shelfbreak [PC I] and high temperature gradients [PC III]) appear to be the most important factor segregating different elements of the seabird fauna. There is good reason to believe that concentration of birds at upwelling fronts is biologically meaningful. At upwelling boundaries, circulation is very complex and may be convergent or have much vertical shear (Flament et al. 1985). Convergent fronts are thought to concentrate mobile zooplankton to levels above those found in surrounding waters, thus enhancing feeding opportunities for fish and birds (Brown 1980, Bourne 1981, Briggs et al. 1984, Haney 1985).

Timing is one aspect of scale-dependent variation; the other is patchiness in space. Our analyses of aggregation indicated that much important variation in abundance of murres, auklets, and phalaropes takes place over cross-shelf (spatial) scales of 8 to 16 km. On average, temperature was autocorrelated over broader scales than these (roughly 30 to 50 km in the analyses we presented). A variety of processes affecting temperature could lead to variation over 30- to 50-km scales. Among them are the eddies and current jets studied by Mooers and Robinson (1984) and Flament et al. (1985), which are prominent features of the California Current offshore environment. Processes that might generate the 8- to 16-km patterns seen in the bird data include behavioral aggregation (i.e., feeding flocks attracting birds from distances of 4 to 8 km), formation and maintenance of thermohaline or color fronts bordering upwellings; estuarine outflow from the Golden Gate; shear instabilities along surface density fronts; Langmuir circulation (three-dimensional wind-driven circulation in the upper few meters under low turbulence conditions); and internal wave propagation. We have seen phalaropes and auklets, as well as a variety of other species, aggregating on one side or the other of each of these kinds of features (e.g., Briggs et al. 1984), and these features are often embedded within larger structures, such as discrete upwellings. Haney (1985, 1987) and his co-workers have looked at seabird numbers as functions of each of these processes in the Gulf Stream/shelf/Sargasso Sea region off the southeastern United States. In that generally oligotrophic environment, each process appears to dramatically affect the distribution of one or more species, but not the whole fauna. Compared to the area studied by Haney, California Current waters typically are much more productive and support higher bird numbers, and the environment is cooler and windier. Nevertheless, physical features correlate with important structure of the bird communities in both areas. Ultimately, it is most important to discover how these processes affect prey abundance and availability and how well seabirds are able to detect and associate these features with enhanced feeding opportunities.

Consideration of scales of habitat features and of bird aggregations leads us toward certain questions about habitat choice. Habitat choice by individuals is the primary process leading to observed patterns of bird distribution and must also have important consequences in the life histories of the individuals themselves. In this regard it is interesting that among coastal plankton communities, species composition tends to be coherent over much larger scales than does abundance (Haury and Wiebe 1982, Mackas 1984). The practical implication is that seabirds or other predators can employ a strategy of first finding a habitat patch having suitable prey composition, then hunting within the patch for prey abundance maxima (*sensu* Haury and Wiebe

1982). Three aspects of this process for which we have no current information are (a) the role of individual experience and behavioral interaction (e.g., following) in truncating search time, (b) the relative sensory capabilities of different species, and (c) the role of "patience" in finding prey abundance maxima. In contrast to protocols (such as ours) of sampling a parcel of water "instantaneously," then moving on, a seabird can choose to wait at a spot for prey to aggregate. This process, coupled with monitoring of success of near neighbors is probably employed by gulls and other birds when they prey on ephemeral surface swarms of euphausiids (S. E. Smith pers. comm., D. G. Ainley and K.T.B. unpubl. data).

Obviously, very different strategies might be employed by storm-petrels, whose "patchiness" extends over scales greater than 64 km, and who might spend much time commuting between ephemeral abundance peaks of their prey (in fact, it seems certain that many records of solitary petrels reflect the protracted 'search' phase), versus Cassin's Auklets, whose aggregations are fairly similar in duration (days to weeks) and extent (~15 km across the shelf and 30+ km along the shelf) to patches of euphausiid prey (Briggs et al. in press). The alcids' morphological trade-off of excellent flight in water versus poor flight in air is related to exploitation of dense, predictable patches of prey (Ainley 1977). However, we do not yet have a clear understanding of the degree of correspondence of bird patches and those of their prey. Woodby (1984) found poor correspondence between patches of murres and their prey in the Bering Sea, whereas Obst (1985) and Schneider and Piatt (in press) found close juxtaposition of predators and their prey. Much work remains to be done in this area.

How do seabirds locate prey patches? Considering the nature of birds' sensory apparatus and the supporting media (air and water), we believe that for most birds the primary cues must be optical. Hutchinson and Wenzel (1980) and Hutchinson et al. (1984) have demonstrated use by procellariiforms of olfactory cues for food-finding, but most seabirds seem to lack this ability. In all cases, however, the amount of phytoplankton and other suspended particles in surface waters must directly influence the ability of seabirds to locate prey and the ability of prey to avoid being eaten (Ainley 1977). Optical properties, including sharp boundaries between waters of different color or clarity, may present seabirds with visual cues for locating current shears or frontal zones that support prey in elevated concentrations (abundance maxima within larger compositional patches). Preliminary results from a study of satellite-measured ocean optical properties and some of these seabird data suggest that Cassin's Auklets preferentially occupy recently upwelled waters of intermediate clarity (5–8 m optical depths) while murres select murky water (1–3 m optical depths) without regard to temperature and salinity characteristics (Briggs et al. in press). For murres, murky water may influence the effectiveness of predation on (relatively) mobile fish, while for auklets, water clarity may influence prey capture or may only be a "tracer" for habitat having the largest stocks of euphausiid prey.

The number of variables included in our analyses is but a fraction of those that might affect bird distribution. Data do not yet exist to investigate some possible habitat characteristics, but it is tempting to wonder about the importance to (particularly) diving seabirds of the depth of the thermocline. The scales of variation in thermocline topography have not been resolved for much of the coastal zone. However, this is an important aspect of the environment of diving species. For instance, Haury (1976) points out that off California, as much variation in environmental conditions is encountered in 50 to 100 meters in the vertical dimension as in 50 to 100 km in the horizontal dimension at the surface. Off California, the mixed layer (that above the thermocline) generally is thinnest near the coast and deepens progressively offshore (Hickey 1979). Many authors have shown that a variety of mobile zooplankton and micronekton (e.g., euphausiids and copepods) remain at or below the thermocline by day and migrate toward the surface at night. Thus, we would expect birds such as auklets to forage near the thermocline during the day. This proposition is simple and testable in the field, and we wonder if patterns of horizontal distribution of these birds reflect something of the thermal (or density) structure at depth. Do diving seabirds base their habitat selections in part on variations in vertical structure of the coastal ocean in a manner analogous to the ways in which terrestrial birds react to vertical structure of vegetation (reviewed in Cody 1985)? Do variations in thermocline topography have surface correlates (optical?) that could be sensed by foraging seabirds? Supposing a relatively high energetic cost of underwater feeding (and other factors being equal), birds would harvest more net energy per dive where the thermocline is shallow than where it is deep. Are Cassin's Auklets, for instance, limited in their offshore distribution by the deepening thermocline? Do murres, cormorants, and shearwaters obtain schooling fish and squid by feeding at shallow thermoclines where the prey are themselves feeding on abundant plankton?

As might be expected, a major result of work such as ours is the generation of many new questions. With the appreciation that to find prey, seabirds probably depend on a suite of environmental cues, past experience, and behavioral interactions, we should now focus on determining how physical processes affect concentrations of prey, how well seabirds are able to recognize habitats having enhanced feeding opportunities and how such choices might affect bird life history parameters. This should involve not only behavioral and physiologic studies of foraging individuals but also simultaneous, integrated measurement of the foraging environment. We need to know much more about factors that make prey available to birds, and we need to determine the consequences of different habitat choices (mortality, reproductive output, etc.). These challenges will be technologically difficult, but the answers will provide a striking counterpoint to studies now proceeding in terrestrial environments.

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