

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 cen-

tered 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 $\pm 0.2^\circ\text{C}$. 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 $\pm 25\%$ 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 ($^{\circ}\text{C}$) 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 $\pm 0.3^\circ\text{C}$ 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).