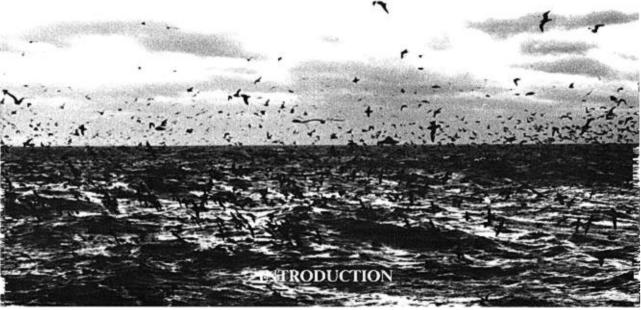


FIGURE 1. Map of the coast of California showing significant place names and undersea topography. The 200 and 2000 m isobaths delimit shelf and slope habitat divisions, respectively.



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

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.