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

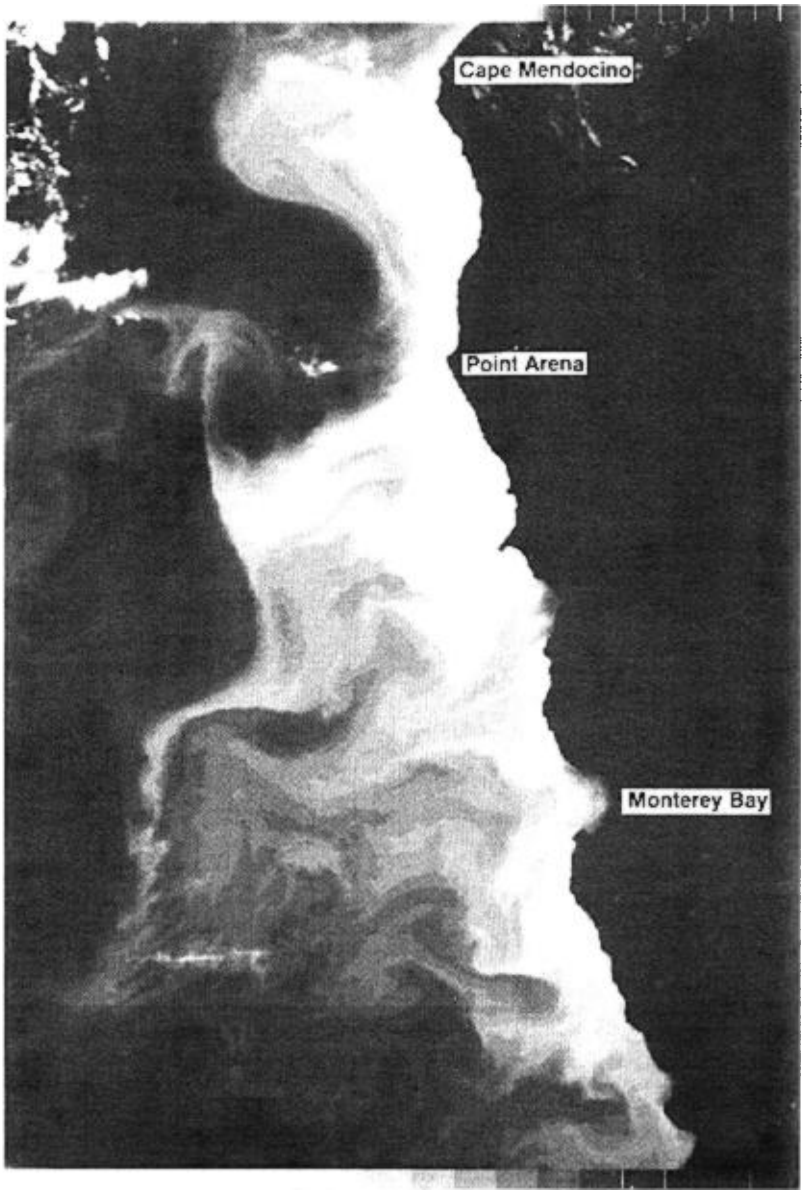


FIGURE 2. Satellite infrared image of sea surface temperature off California on 21 September 1981. The coolest waters, represented by light grey shades, are 9 to 11°C, whereas dark shades mark waters warmer than 16°C. Several filaments of upwelled (cool) water extend for 100s of km from major headlands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